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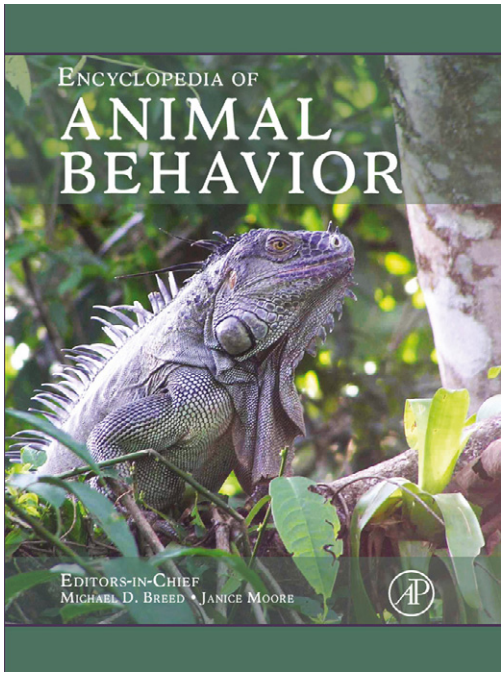

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Wolves

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Introduction

Among the large-bodied social carnivores, the foraging behavior of gray wolves is similar to that of lions, African wild dogs, dholes, hyenas, and killer whales, in that individuals hunt in groups as well as in singles and pairs. However, communicative and reproductive behaviors of gray wolves differ in distinctive ways from cat-like (Feliformia) and other dog-like (Caniformia) species in the taxonomic order Carnivora. Teasing apart which fixed aspects of wolf behavior are relatively more instinctive (associated with heritable genotypes), and which flexible aspects are relatively more variable due to individual experiential learning and behavioral plasticity has fascinated behavioral researchers for over half a century. Recent advances in technology have led to some unexpected answers and generated new questions about wolf behavior, at both the genomic and ecological levels of behavioral systems.

Both the foraging and communication behaviors of wolves illustrate how some actions may be categorized as more 'instinctive,' and others more 'learned' on the continuum that ethologists define as ranging from fixed reflex to flexible intelligence. For example, when a pup does a 'leap-pounce' the first time she hears a vole rustling in grass or sees a grasshopper moving, the action appears instinctive. Pups do not have to learn the reflex-like action, it just occurs; however, they do refine their capture skills with trial and error learning. The leap-pounce is common in coyotes and foxes, as well as in all subspecies of wolves. Applying the comparative method, an ethologist would infer that the genetic basis of 'leap-pounce' is highly heritable in canids.

Also on the fixed end of the continuum of instinct/learning, caching behavior appears in untutored wolf pups before they are weaned. A predictable sequence of caching motions (placing a food object on the ground, scraping debris over the object with the bridge of the nose, and tamping down with the muzzle) appear in several species of the dog-like (Canini) and fox-like (Vulpini) tribes in the subfamily Caninae. Likewise, the whines that newborn wolf pups emit when separated from the warmth of their mother and siblings appear to be a more instinctive reflex than a learned one. Therefore, the fixed actions (e.g., whine, cache and leap-pounce) that are similar across closely related canine species are hypothesized to have been retained in the ancestral part of the genome (phylogenetic inference).

In contrast, the hunting behavior of adult wolves is highly flexible, varying with the food web in the neighborhood where each individual grows up (**Figure 1**). Individuals fine-tune their innate hunting abilities directly by trial and error, as well as indirectly by joining group hunts. In the arctic, some wolf families follow migratory caribou that feed on sparse lichens, traveling across vast expanses of tundra. In wooded regions where more variety of food is available, caribou do not migrate and neither do wolves. Further south, in the boreal forest of Isle Royale National Park, some lone wolves and pairs supplement their moose diet with beaver and snowshoe hares; they learn to take the prey species that is most readily available. When food resources change, switching tactics appear to be an intelligent adaptive behavioral trait on the flexible end of the instinct–learning continuum (see below).

In regions where there are no longer large native prey species, and the food web offers less variety, wolves even scavenge from garbage dumps. Indeed, one hypothesis about the divergence of the ancestors of domestic dogs, which most taxonomists now recognize as a subspecies of the gray wolf, is related to appearance of a novel resource in the food web: refuse discarded by human hunters and early agriculturalists. An associated hypothesis states that the social cognition abilities of wolves were a preadaptation for domestication by humans worldwide.

This behavioral flexibility in hunting, which varies with the complexity of the food web, is not unique to wolves but rather, is one of many examples of social carnivores fine-tuning their actions through mechanisms of learning from individual experience, alone as well as in social contexts. Exactly how much learning in wolves occurs because of social transmission remains a question for future inquiry. In the sections that follow, I elaborate more on the research that has answered many questions about behavioral flexibility and intelligence in individual wolves: subtle communication, problem-solving, and learning in the social context of family groups. From the perspective of wolf populations, we will explore how behavioral flexibility is also linked with adaptive responses to environmental fluctuations: territoriality, deferred reproduction and dispersal mechanisms.

Before synthesizing recent studies and intriguing questions for future research about wolf behavior, we first need a historical perspective on how certain hypotheses have not stood the test of time. Unfortunately, many of these discarded hypotheses about wolves and myths in the

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Figure 1 Arctic wolf on Ellesmere Island.

popular literature persist, as remnants of earlier times. The subsequent review subsection is aimed at encouraging critical thinking about what evidence is needed to test hypotheses about wolf behavior and how difficult it has been to obtain.

Review: History of Canid Behavioral Research

Visual signals used by dogs in communication had been noted in the behavioral literature long before wolves were studied either in captivity or the field. Charles Darwin illustrated his hypothesis about the principle of antithesis by contrasting images of the upright posture of an alarmed dog in response to a person approaching in the distance, compared to the crouching posture that the dog switched to as soon as it recognized the person as its 'master.' In terms used in the nineteenth century, this expression of emotion signaled an unambiguous change in motivation, from dominance to submission. In modern terms, the change in visual signal conveyed the information that the dog was unlikely to escalate attack in response to a familiar care-giving companion. Unfortunately, the misperception that some individuals are always dominant and others are always subordinate has persisted despite the original context of the drawings that Darwin used; his drawings illustrate how one individual can rapidly change signals as it gathers more information about a stimulus (e.g., cues about familiarity).

In the popular literature, the anthropomorphic myth persists that a dominant male is needed to enforce order so that all wolves in a pack know their roles in a dominance hierarchy. For example, Douglas Pimlott quoted Niko Tinbergen's interpretation of a strict hierarchy in the sled dogs he observed in Greenland. At the time, it seemed reasonable to infer that those dogs that look more like wolves would behave like wolves. No published evidence about wolf behavior was available prior to the 1940s, so the hypothesis remained untested for decades. The popular notion of born losers and winners was reinforced by the insightful anecdotes about personal experiences with dogs and wolves published by Konrad Lorenz. However, Lorenz also noted both the persistent personality traits that varied across breeds of dogs, and the extreme changes in one individual deprived of his primary social companion.

Two seminal publications introduced a different interpretation of social interactions in wolf packs, both emphasizing the family structure. In Alaska, Adolph Murie observed a wolf family caring for pups near a den, now in Denali National Park. In a Swiss zoo, Rudolph Schenkel described in more detail how the food begging behaviors of pups developed into solicitous appeasement signals in juveniles interacting with both parents. He interpreted these interactions as the social glue that holds the wolf family together. Both studies emphasized the influence of age on the dynamics of dominance interactions, as both parents and older siblings cared for pups.

Is wolf pack structure more like a pecking order or like a caring family? Understanding the ancestral roots of dog behavior was a compelling justification for the multiple postwar studies that emerged in the 1950s and continued into the 1980s. An American team led by John P. Scott investigated the development and heritability of behavior in dogs, in the context of comparative studies of wolves. In Europe, Erik Zimen examined ontogeny of behavior in wolf/dog hybrids, inquiring in what ways arrested development in dogs might illustrate the principle of neoteny, the persistence of juvenile characteristics into adulthood. Benson Ginsburg's research group examined questions associated with the hypothesis that evolution of social cognition in wolves would have been accelerated if they had been isolated in groups that benefited from helpers caring for young. Among others, Mike Fox and Mark Bekoff studied behavioral development in litters raised without parents, comparing species considered to represent a continuum of solitary foxes, semisocial coyotes, and social wolves.

As evidence from more packs emerged, the variation in group structure became clear (**Figure 2**). Behavior in some groups fit the model of a pecking order and others were more like a caring family, as we will examine in more detail in a later section. Separate research teams examined ontogeny of behavior in long-term studies of hand-reared wolves assembled to form reproductive groups. These lines of inquiry were led by John Fentress, John Rabb, Erik Klinghammer,

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Figure 2 The direct stare of the father is enough to interrupt courtship by his adult son in a captive family group.

Erik Zimen, R. Derix, Dave Mech, and Ulysses Seal. Evidence was clear that not all adult-sized wolves reproduce in packs. However, integrated studies of behavior and physiology led to rejection of the hypothesis that nonbreeders were always physiologically stressed because of the behavior of dominants. This left open the question why packs contain adult-sized wolves that do not breed.

Do wolves need to cooperate to kill large prey? On a parallel track, the landmark study of wolves on Isle Royale by Dave Mech opened several lines of research about wolves as predators, including interaction with the dynamics of foodwebs. In the early 1960s, the ecosystem on Isle Royale was relatively stable, and the evidence supported the hypothesis that individual wolves needed to put aside their own interests in reproduction for the sake of group hunting and to avoid wiping out their food supply. The notion that wolves had to cooperate to be successful at hunting large dangerous prey like moose fit nicely with this model, but only for a few years. Over the subsequent decades, Rolf Peterson has monitored dynamic peaks and lows in wolf, moose, beaver, and other carnivore populations on Isle Royale. There have been years when the moose population crashed because of overbrowsing and years when wolves supplemented their diet with beaver and snowshoe hares, then crashed when availability of all prey species was very low. Winter severity and fire ecology have added to the complexity of these ecosystem dynamics.

As we will examine, evidence from additional field studies led to rejection of the hypothesis that wolves are obligated to cooperate in hunting. Under some foodweb conditions, wolves coordinate hunting and pup-rearing activities, but in other conditions they do not. Hunting large prey permits large group size, but does not require it.

Such diverse and dynamic conditions fit evolutionary models that predict that behavioral plasticity would be at a genetic premium for this large-bodied social carnivore that is widely distributed across all biomes of the northern hemisphere. In addition, the genetic diversity of wolves is illustrated by multiple subspecies isolated in fragmented habitats; one subspecies even lives in ambivalent symbiosis with humans, that is, domestic dogs.

Modern Synthesis: Nested Hierarchical Systems

The social structure of wolves has been analyzed in terms of three levels of selection, each nested within the other: family groups, subpopulations, and ecosystems. Viewed from a systems perspective, at the first level, individual decisions affect survival and reproduction of other wolves within the same family group (wolf pack). At the second level of analysis, the social environment, each family group is influenced by the actions of other family groups within the neighborhood. The groups of individuals that interact most frequently within a neighborhood are technically called a deme, or subpopulation, within a fragment of habitat relatively separated from other fragments. At the third level of analysis, the physical ecosystem, wolf populations are influenced by biotic (e.g., prey, competing species, diseases) and abiotic factors (e.g., winter severity, fire cycles, drought cycles). From a theoretical perspective, each of these systems is viewed as nested, because individuals fit within groups, subpopulations, and ecosystems.

This theoretical framework of nested biological systems becomes important when scientists apply sociobiological models to test hypotheses about wolf social behavior. For example, several general hypotheses about evolution of cooperative breeding have been proposed: (1) *eusocial*: obligate reproductive suppression under extremely harsh conditions in ecosystems where individuals do not survive outside a breeding colony; (2) *conditional suppression*: reproductive behavior is reversibly turned on and off in adults, depending on the social environment (groups and neighborhoods); and (3) *deferred reproduction*: the average onset of first reproduction is delayed by the interaction of social and ecosystem factors (e.g., body size, nutritional condition, olfactory signals, competition for mates). In the following sections, specific evidence from wolf behavior will be synthesized in a manner needed to test each of these three general models.

Individuals Within Family Groups

Food provisioning within a family group is key to understanding the social environment of canids. Although individual wolves may leave their natal group and spend varying amounts of time alone during the transition to another group, all wolves are born into and develop within a family group. Wolf litter size may vary from 1 to 10,

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usually 5–6 pups. Group size rarely exceeds 15 wolves, depending on whether a breeding pair is disrupted, how many females breed, and how long offspring of varying ages remain in the family group. Although the highest reported count was 42, the usual group size is 6–8 wolves, consisting of a breeding pair with 4–6 offspring (**Figure 3**). However, this varies with the history of each family group as well as environmental changes in the wolf population and ecosystem, for example, prey type.

Unlike most polygynous mammals, pup care by more than the mother matters in monogamous wolves. Pups are unlikely to survive to puberty without the care of parents and/or older siblings. In a study of 148 pooled cases of territorial breeding wolves, at least one pup survived the loss of a parent in 84% of the cases, presumably because pups were cared for by other members of the family group. Pups were more likely to survive the loss of a parent in large groups with auxiliary nonbreeders than in small groups. Older pups were more likely to survive the loss of a parent than younger pups.

Born in an earthen den or shallow scrape on the surface, altricial wolf pups are cared for exclusively by the mother for 2–3 weeks. Their eyes are closed until 12–14 days, and their first reflexive topo-taxic responses are to touch, warmth, smell, and taste. Hearing matures more slowly. Urination by pups in response to the mother licking the urogenital region is an example of a parent–offspring signal. As pups develop coordination to stand and walk, early learning begins to expand from the social context of littermates and soliciting care from the mother to include interactions with physical objects.

Between 3 and 5 weeks, pups explore the entrance of the den, retreating from unconditioned stimuli that elicit an alarm bark and approaching the soft squeaking vocalizations and multimodal stimuli they have learned to associate with the nursing female. In rare circumstances, more than one nursing female may share a den. However, currently there is no evidence that pseudopregnant female wolves initiate nursing without having previously given birth to a litter, despite speculation in the popular literature.

Figure 3 Sibling wolf pups in a family group on Ellesmere Island.

The social context of learning expands during weeks 5–8, as pups encounter family members that deliver food by regurgitation and carrying pieces of carcass. For example, in a pack on Ellesmere Island, regurgitations were directed to the pups (81%), the nursing female (14%), and other auxiliaries (6%). All adult wolves regurgitated food, including the breeding pair, yearlings, and a post-reproductive female. The breeding female and pups received most regurgitations from the breeding male. Regurgitations by the breeding female were directed exclusively to pups. Wolves respond by regurgitation to muzzle licking by another familiar wolf, a multimodal signal that changes meaning with age, social context, and the presence/absence of food.

During the transition stage from dependency on milk to solid food (6–10 weeks), not only do pups learn to recognize familiar kin, but they are also rewarded by food when they approach or follow adults. Detailed sequence analysis of interactions, in both pups and adults, have illustrated that individuals learn the physical and social consequences of their actions. At this transition stage, bouts of chase and wrestling play are typically 1–3 h between naps and feedings.

At 7–8 weeks, bite strength is sufficient for pups to feed from opened small carcasses, such as arctic hares in the Ellesmere Pack. In the weaning process for one litter, frequency of suckling bouts that occurred outside the den decreased gradually, as the nurser initiated bouts at longer intervals interrupted more bouts and pups persisted less when interrupted. Parent–offspring conflict was not obligate, although it may be conditional on food delivery and food storage by caching. On the average, by 11 weeks, pups no longer suckled and began to follow adults on foraging trips. Activity centers focused on dens and rendezvous sites may change several times, as a litter is carried to a new location by the breeding female or moves in response to disturbance.

Sound analysis indicates the vocal repertoire increases from four to nine call types as pups mature. Barks and howls are examples of vocal signals that have been studied in wolves. Pups bark in response to alarming stimuli and howl when separated from the group or in response to other howls. One hypothesis of the adaptive function of these signals is safety in numbers. Pups are vulnerable to predation by bears and unfamiliar wolves from neighboring packs.

The first agonistic signals used by wolf pups occur in the context of food. When conflict escalates over a large food item, such as a rabbit carcass, pups learn the consequences of uninhibited bites from a sibling. They learn the subtlety of signs (e.g., hard stare, snarl, ear posture, partial lunge) that predict likely escalation to uninhibited biting. Subtle signs of de-escalation include: look-away,

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lie-down, ears-back, lip-licking, crouch, roll-over, pawing, tuck-tail, and tail-wagging. To the extent that individuals vary in temperament at birth, each learns coping styles influenced by the contingencies of their interactions with siblings and the context of resources, although this complex process is not completely understood because it is so variable.

Current behavioral evidence does not support the hypothesis that the dominance hierarchy within a litter determines which individuals breed later in life. Behavioral profiles of individuals vary on several dimensions in addition to a shyness/boldness continuum. Multivariate quantitative studies determined that affiliate and play behaviors explain more variation in wolf behavior than agonistic actions within intact family groups. Disrupted families that have lost one or more parents are more variable and conflict is more likely to escalate as described in the next section.

Born in late spring, juvenile wolves are not quite adult-sized by their first winter. The synchronized birth season fits the functional hypothesis that the young are born at a time when food is readily available. Those that were born later would have been unlikely to survive the rigors of their first winter. Neonates born in winter would have risked exposure and malnutrition in times of scarce food. This genetic basis for seasonal reproduction has been modified in domestic dogs, which breed year-round. On average, birth dates occur weeks earlier in wolf populations at lower compared to higher latitudes, although the mechanism is still not entirely understood.

Group size expands seasonally, as pups are born, and declines as family members disperse or die. For example, on average in Denali, only half the pups of the year remained with the family through the first winter. Of those that remained, only half were still with the family through the second winter. Only a few wolves remained with their natal group past the third winter.

Despite the popular notion that young wolves are driven out of the pack by conflict with parents and siblings, the data suggest that dispersal mechanisms are a complex interaction of individual maturation, relationships within the group, food availability, and scent marks in the neighborhood. During their lifetimes, individuals may switch among the following categories of tactics: (1) 'biding' auxiliaries are nonreproductive members of a territorial group; (2) 'dispersing' floaters leave the group and wander alone or in transient groups that pass through or between group territories; and (3) 'breeding' parents defend the territory where they forage and reproduce, attacking outsiders of the same sex. Both sexes switch among these tactics.

This evidence of developmental plasticity has led to rejection of the hypothesis that the wolf social system fits the model of eusociality. Dispersing wolves do not cooperate in parental care and do successfully catch prey without the help of others. Transitions among behavioral tactics will be discussed in more detail in the next sections, because they are influenced by factors at both the population and foodweb levels of ecosystems.

Comparing canid species, large body size is correlated with later age of first reproduction. For example, on average, large-bodied wolves reach puberty in their second winter, 1 year later than smaller bodied coyotes. Puberty in wolves may be accelerated or delayed by a couple of years because of interactions of nutritional and social factors.

There is no evidence to support the hypothesis that social stress in wolves turns off the physiological readiness to breed after puberty. For example, fecal cortisol was higher for breeders than nonbreeders in samples from free-ranging wolves in Iberia. In one captive study, nonbreeding adults cycled normally; females ovulated and males produced sperm. In another captive pack, the positive correlation between stress hormones and aggression was skewed by one individual with abnormal adrenal hypertrophy. An early-winter peak in testosterone has been correlated with rates of scent marking and escalated conflict among males.

Deferred reproduction best explains the variation in reproductive tactics of wolves in family groups. In nuclear families, food provisioning shapes asymmetric relations between parents and offspring. During breeding season, parents are more attracted to mating signals from each other than from offspring (**Figure 4**). Adolescent wolves are less attracted to mating signals from siblings than parents, an attraction likely not reciprocated. Older wolves, both parents and siblings, are likely to interrupt sexual activity by younger wolves of the same sex. However, the subtle signs of asymmetric mate choice and same-sex rivalry are only a matter of probability and may shift within weeks when one or both breeders are removed.

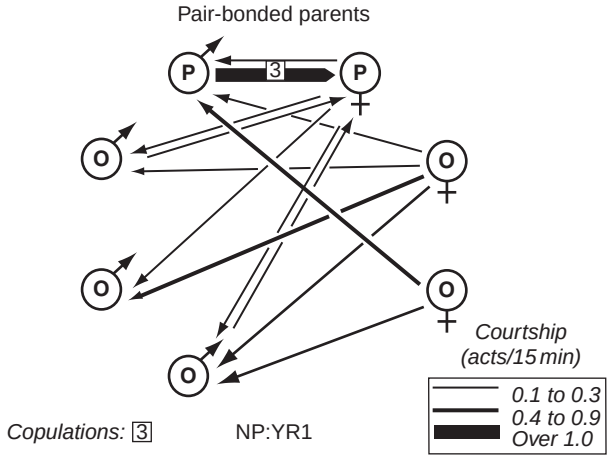

Figure 4 Relations among parents and their offspring during the breeding season in a captive pack.

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Wolf mating signals are multimodal, including pheromones and tactile, auditory, and visual cues. Sexual dimorphism is minor, on average males are 20% heavier; however, no visual signals distinguish the sexes. Howling is an auditory signal with the function of advertising presence of wolves; loners are more likely to howl when traveling in sparsely than densely populated regions. Pheromones deposited in urine and feces are the primary mode for advertising sexual identity in dispersers. Dispersers join up at all times of the year; males are more likely to find single females during proestrus vaginal bleeding, usually 2–8 weeks before ovulation. Plasma estrogen is elevated in females during proestrus and estrus, which occurs during January and February. Synchronized estrus usually peaks mid-February, although the exact timing varies with body condition, the social environment, and latitude.

Proximate mechanisms of reproduction have been well studied in both wolves and dogs. During 1–7 days of estrous, each breeding pair of wolves remains in close proximity (**Figure 5**), exchanging mutually stimulating olfactory, visual, and tactile signs of copulatory readiness, for example, sniffing, sequential-urinating, chinning, darting, ears-together, head-flick, and paws-to-shoulders. Within days of spontaneous ovulation, females signal readiness to stand by averting the tail to the side of the vulva, a reflex that is a fixed action. Ovulation is associated with a peak in plasma luteinizing hormone (LH), which coincides with a drop in elevated estrogen (**Figure 5**).

With experience, male wolves quickly learn to orient mounting to the rear. The ejaculatory reflex follows penetration and penile thrusting. Subsequently, tissues swell in the penile bulb, a reflex keeping the pair locked in a postcopulatory tie that usually lasts 20 min; the range in duration (3–30 min) is conditional on interruptions by familiar rivals. Hypotheses about the function of the postcopulatory tie include (1) oxytocin release that stimulates smooth muscle contraction increasing internal fertilization rate due to sperm and egg movement into the uterine horns and (2) reduced probability of extra-pair copulation during the male postejaculation refractory period.

Figure 5 A male stands near his resting mate, guarding her from rivals while she is in estrous.

The seasonal canid reproductive cycle is unusual among mammals because (1) there is only one estrus whether or not a female becomes pregnant, (2) the postovulatory growth of the corpus luteum is roughly the same duration for both pregnant and nonpregnant females, and (3) because of elevated prolactin in both males and females during the spring pup-rearing season. The cascade of hormonal changes following ovulation may stimulate growth of nipples, hair loss from the belly, abdominal swelling, denning behavior, and milk production, although these symptoms are highly variable among individuals and change with age. Seasonal peaks in prolactin are associated with den-digging and food-provisioning by both sexes (breeders and nonbreeders). Thus, it is difficult to diagnose pregnancy on the basis of external indicators; more accurate internal indicators may be obtained by sonography and measuring the hormone relaxin.

Although social monogamy is typical of smaller nuclear families of wolves, extended and disrupted families may include polygynous and polyandrous relationships. Since postpubertal wolves retain the physiological readiness to breed, loss of one or more breeding parents may destabilize dominance relationships. For example following deaths of the fathers in two Yellowstone packs, immigration of an unrelated breeding male was followed by multiple litters. A low frequency of plural breeding has been recorded in several field studies. Congenial relations among multiple breeding females are usually unstable and persist no more than a few years.

Agonistic interactions vary with both the immediate presence of resources and the social environment within each group of wolves. Resources include food, mates, and pups. Factors likely associated with escalated conflict are complex, including the quality of the resource, proximity to the resource, motivation (e.g., satiation, reproductive cycle, adrenal activity), personality (e.g., inherited temperament and learned coping styles), and relationships (e.g., learned contingencies of interactions among specific individuals). All these factors influence the complexity of dominance hierarchies (e.g., linear, triadic, age-graded, branched sex-specific, multinodal), which may change within a group over time as well as varying among groups depending on age/sex composition.

The variation in age/sex composition of wolf groups depends not only on internal factors, but also on the interactions among groups within populations and dynamic patterns of food availability within ecosystems. Interactions of internal and external factors are elaborated in the following section.

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Family Groups Within Fragmented Subpopulations

The social structure of wolf populations includes territorial reproductive groups and floaters that move between and through resident territories. In colonizing populations with low territory density, floaters are more likely to join up and start new breeding units in the gaps between territories. In established populations, the number of breeding groups is relatively constant despite turnover as groups break up and new groups are formed. Wolves that are slow to disperse from their natal family are 'biders' (nonbreeding auxiliaries) waiting for a chance to breed when the opportunity arises.

Within wolf populations ranging from those that are recolonizing an area (Yellowstone) to well-established (Denali, northern Minnesota), genetic relatedness is lower between breeders within a group than it is on the average between breeding groups. Wolf groups are semiclosed, usually accepting immigrants only upon loss of a breeder. Mate turnover ranges from 1 to 6 years, varying among populations. As elaborated in the following section, hypothesized mechanisms to explain this pattern of nonrandom genetic dispersal include the following ones: (1) individuals choose mates that are distantly related over those that are close relatives, (2) breeders defend their mates from same-sex rivals in neighboring groups, and (3) dispersal between groups is influenced by mate choice and same-sex rivalry. Given a choice of mates, wolves of both sexes are predicted to be more attracted to unrelated than to related individuals. Although it is unlikely that wolves have a mechanism for directly detecting genetic relatedness, familiarity is highly correlated. Given a choice, unfamiliar individuals are more attractive mates than family members. Contrary to prediction, inbreeding has occurred when a parent had no other choice than offspring and when siblings copulated in the absence of parents.

Same-sex combat may explain the intense, uninhibited conflict between wolf groups, resulting in documented death of breeders, biders, and floaters. Fights between groups have escalated during extra-territorial intrusions. Although breeders may be more likely to escalate conflict with same-sex rivals, in the excitement of a fight, all group members may mob a victim that displays defensive signals, for example, tucked-tail, ears-flat-back, and arched-back. While the sample size is not definitive, small groups are less likely to escalate than large groups. Social monogamy is reinforced and extra-pair copulations are reduced by same-sex combat between groups.

Several categories of dispersal between groups have been documented: (1) biders immigrate from an unrelated neighboring group to one that has lost a same-sex breeder, (2) one group divides into neighboring groups, (3) dispersers may travel distances as long as 1000 km, (4) dispersers meet up and establish a new breeding group within 100 km of their natal group, (5) dispersers return to a familiar group (siblings or offspring) after turnover in the breeding pair, and (6) dispersers immigrate into groups that have lost a same-sex breeder. Overall, genetic variation is likely to be lower between groups than between breeders within each group.

Auditory and olfactory communication influence distance between groups; in contrast to the momentary and ambiguous information conveyed in howls, scent marks may last for days. In response to playbacks of strange-group howls, groups that reply are more likely to remain in place compared to groups that do not reply and retreat. Response rate is positively correlated with group size, breeding condition, and presence of a resource. Single wolves are more likely to approach silently when the playback is a solo howl. The prevalence of scent marks, both urine and feces, on trails near junctions and at the edge of territories has been described as an 'olfactory bowl.' Breeders urine-mark on conspicuous objects at a higher rate than nonbreeders, and the urination rate is highest in newly formed pairs. Pairs deposit urine marks sequentially in the same location, a double-marking behavior that may function in intimidating rivals and stimulating mates.

Group howls occur when resting wolves arise and gather together prior to traveling, as well as when they come together after separation. During a group howl, individuals rub bodies, touch noses, and circle with wagging tails. Individuals that hold the tail high are more likely to respond with an over-the-muzzle bite to nose-licking by wolves with a lower tail posture. Similar to pups soliciting food provisioning, adults that receive an over-the-muzzle bite do not retreat from the group. Whichever individual departs with a confident gait is likely to be followed by those that are more solicitous. However, if a key food provider does not join the departing group, group cohesion may deteriorate.

Group decisions on movements vary between wolf packs, as well as seasonally within each group. Alone, adult wolves can easily travel 40 km in half a day. In general, movements revolve around pups in the spring/summer and the breeding female in the winter. In other seasons, the individual leading a traveling line of wolves is likely to be a breeder. Evidence supporting the hypothesis that the male is more likely to be a leader is ambiguous and depends on the definition of leading behavior. An alternative hypothesis is that variation in leading behavior may relate to which individual is most consistently associated with food acquisition, which likely changes with the age, experience, and personality of group members.

Within a given latitude, group home range size is positively correlated with group size in colonizing wolf populations but only marginally so under saturated conditions. For example, in northwestern Minnesota and Yellowstone, recolonizing groups initially were spaced far enough apart that there were no shared boundaries. As the open areas

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filled in, groups defended adjacent boundaries and potential for elastic expansion of home range was limited, presumably by encounters with sign left by neighboring packs.

Genetic variability between wolf populations is likely related to the connectedness of habitat patches. In some homogeneous stands of forest, wolves may travel hundreds of kilometers without encountering areas of low wolf density. In other landscapes, they travel hundreds of kilometers through areas without wolves before encountering the sign of wolf presence. From the same litter, some individuals have dispersed short distances and others long distances. Overall, both sexes are equally likely to disperse, although dispersal in some populations has been biased toward males and others were biased toward females.

In summary, an overall model includes neighborhoods of relatively low genetic variation which are nested within habitat fragments that vary in degree of connectivity. Sexual competition limits the openness of family groups to immigration of unrelated individuals; however, disruption of monogamous relationships facilitates movement of individuals between groups. Mate choice tends to favor outbreeding, although inbreeding occurs when choices are limited. Gene flow occurs via dispersal between fragmented habitats.

Populations Within Fluctuating Ecosystems

Sociobiological theory predicts that species adapted to fluctuations of their social and ecological environments will evolve behavioral traits with a high degree of plasticity. Variation in the distribution of resources is most likely to influence the distribution of reproductive females, including group size. In turn, the distribution of females likely influences male tactics for defending females and offspring from the risks of encounters with rival males. Secondarily, predation separately influences evolution of behavioral traits in males and females.

Ecosystems inhabited by wolves range from Arctic tundra (80 °N latitude) to desert mountains (less than 40 °N latitude). Foodwebs within these diverse ecosystems vary from simple to complex. Examples of simple foodwebs include (1) blackbuck (India), (2) arctic hares and musk oxen (Ellesmere Island), (3) migratory caribou supplemented by small mammals during denning (Alaskan Brooks Range), (4) white-tailed deer and snowshoe hare (Minnesota), (5) moose and white-tailed deer (eastern Canada), and (6) red deer and wild boar (Spain and Poland). More complex food webs include (1) moose, caribou, and Dall sheep (Denali National Park); (2) moose, snowshoe hare, and beaver (Isle Royale); (3) elk, mule deer, bison, mountain sheep, caribou, mountain goat, and small mammals (western Canada); and (4) red deer, wild boar, roe deer, fallow deer, and mouflon (Appenine mountains of Italy).

Where wild ungulate populations have died out in parts of Israel and Italy, wolves scavenge at garbage dumps in addition to hunting whatever small animals and livestock are vulnerable. Domestic animals (e.g., goats, sheep, pigs, cattle, and dogs) are primary prey in northwestern Spain, and the eastern Caucasus of Russia, wherever wild ungulates are scarce and livestock graze in or near forests. In northern Finland, wolves hunt semidomestic reindeer.

In seasonal environments, wolves may opportunistically feed lower on the food chain when fruits become available in the summer. Seeds of raspberries and blueberries have been found in scats (defecations), as have cultivated fruits (e.g., grapes, cherries, apples, pears, figs, plums, and melon). The frequency of grass in wolf scats ranges from 14% to 43%, based on studies from both continents.

The influences of foraging on wolf populations are evident in the variation of wolf territory size. The correlation between latitude and mean territory size is highly significant. The mean estimated territory size ranges from 137 km^2 in Wisconsin to over 2600 km^2 on Ellesmere Island. This variation is also correlated with (1) lower prey biomass at higher latitudes, (2) smaller ungulate body size at higher latitudes, and (3) lower productivity of the plants upon which herbivores feed at higher latitudes.

In a meta-analysis of 38 studies, about one-third of the variation in wolf territory size is positively correlated with prey biomass. Other factors contributing to the variation included (1) wolf density, (2) interaction between wolf density and rate of wolf population increase, and (3) interaction between the mean territory size and the rate of wolf population increase. For example, mean territory size in regions where wolves hunt deer (199 km^2) is one-quarter the size in moose regions (817 km^2), possibly because moose are harder to catch and wolves travel further between kills.

Do individual wolves benefit from cooperative hunting tactics? In contrast to lions, food acquisition per wolf decreases with hunting group size. Single adult wolves can kill a moose, bison, or musk-ox; however, calves and sick adults are more vulnerable to single wolves. Most hunting sequences described for wolves have been simple and straightforward. Field biologists differ in opinions about whether hunting tactics of wolves show evidence of cooperation, defined in terms of ambushing prey and relay running.

When group size increases, it is most likely due to recruitment of young inexperienced wolves, adding little advantage to capture success by the group. One hypothesis is that young wolves may benefit from group hunting in that they learn the consequences of their own

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interactions with prey as well as observing the consequences of actions by more experienced group members. However, in the Mexican wolf reintroduction, even inexperienced captive-reared wolves learned to kill elk within 3 weeks after release. Evidence to test this 'trade school' hypothesis about the function of group size would be very difficult to obtain because of welfare issues and limited visibility of wolf hunts in forested ecosystems and rugged terrain.

Alternatively, large groups wolves may have a competitive advantage in interactions with other predators (e.g., black bears) and scavengers at carcasses (e.g., ravens, eagles, foxes, coyotes, wolverines, and bobcats). In one study, the percentage of carcasses consumed by other scavengers was inversely correlated with wolf group size. Groups of wolves were more likely than singles to attack denning black bear or chase them off a carcass. However, grizzly bears usually displace wolves at carcasses independent of the number of wolves present. Single coyotes and foxes are vulnerable to being killed by wolves. Wolves rarely consume carcasses of competitors. Few interactions have been recorded between wolves and felids (e.g., bobcat, lynx, mountain lion, and Siberian tiger).

Do breeding wolves benefit from helpers at the den? One hypothesis is that auxiliaries may contribute more to provisioning under conditions of food abundance than when food is scarce. However, in good times, breeders are likely to be more successful at prey delivery, and auxiliaries are more likely to disperse. More auxiliaries in a group do not always increase the probability that pups will be attended around the clock. Some evidence points to auxiliaries returning to intercept provisioning at times when breeders are likely to return to pups. Older offspring may compete with younger siblings, under scarce food conditions. Further studies are needed to fully answer this question.

Do nonbreeding auxiliaries benefit by inheriting a territory when breeders are displaced? The current working hypothesis suggests that the answer depends again on the interaction of wolf density and prey availability. Under conditions of low wolf density and high food availability, dispersing floaters are more likely to start a new breeding unit than biders are likely to inherit a territory. However, when wolf density is high and prey density is low, mortality is higher in dispersers than biders. Extra-territorial forays and encounters with neighboring groups result in deaths of breeders under these conditions. Under conditions where breeders die, biders are more likely to inherit a territory.

This conditional model of switching tactics and variable pay-offs for wolves foraging in groups has emerged from studies of ecosystem fluctuations. On Isle Royale, the body condition of moose is correlated with browse forage quality. The forage for moose has changed over decades because of plant succession in patches disturbed by forest fire, as well the direct impacts of moose and other herbivores on the plants. When moose are unhealthy, they are more vulnerable to wolves, and wolf predation has more of an impact than when moose are relatively invulnerable. Vulnerability of prey to wolves is also increased by snow conditions and harsh winters.

Since Isle Royale is a closed system on an island, the fluctuations in plants, herbivores, and carnivores are more accentuated. However, similar dynamics exist in other fragments of forested habitat that are more open systems. The linkages among components of each system are harder to measure in regions where wolves and their prey disperse over larger distances. Large expanses of forest are not homogeneous; local conditions function as sources and sinks in terms of the dynamics of wolf populations on a broader scale of analysis.

Theoretical questions about the stability of predator and prey populations due to wolf foraging ecology are still actively debated. However, researchers agree on three generalizations: (1) wolf impact is highest on the juvenile age class of prey; (2) where wolf populations are increasing, the impact of predation is higher; and (3) the combined impact of predation by wolves and bears is more likely to tip prey populations into a declining trend.

Disease outbreaks also contribute to the instability of wolf populations. Over a 30-year study of canine parvovirus in northeastern Minnesota, pup mortality increased 70% in one region and varied from 40 to 60% over a larger scale. The rate of growth for the infected wolf population was 4% as against 16–58% in other wolf populations. Changes in dispersal potentially related to spread of disease included (1) fewer dispersing juveniles, (2) mortality of entire groups, and (3) a higher probability of adults dispersing following disruptions due to death of breeders.

In summary, variation in the canid genome has been shaped over geologic time scales by glacial cycles that repeatedly displaced northern populations and blocked or opened dispersal routes between continents. The behavioral plasticity that permitted wolves to invade ecosystems as diverse as deserts, forests, mountains, and tundra also permits individuals to adapt within lifetimes to ecological changes in prey availability resulting from shorter cycles (e.g., fire, precipitation, plant succession). Interactions of factors within dynamic ecosystems make it very difficult to test behavioral models on the basis of costs and benefits in terms of ultimate fitness. Given the behavioral plasticity in social carnivores, it is all too tempting to infer the adaptive significance of cooperative foraging despite the paucity of definitive evidence.

Some Current Questions

Recent expansion of research in social cognition and the canid genome have opened promising perspectives for

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reframing questions about behavioral mechanisms in wolves. For example, the behavioral traits currently interpreted as cooperative may also be viewed as by-products of directional selection favoring large body size. In the following section, alternative models that are emerging in diverse lines of research that view dogs as a subspecies of wolf are briefly outlined.

The genetics of domestic and wild canids are under investigation by the research team coordinated by Elaine Ostrander and Robert Wayne. Questions arise about how contrasts in body size as dramatic as a great Dane and Chihuahua illustrate the big variation that can result from small changes in the timing of action of 'controller genes.' Not only does the dog subspecies of wolves contain the genes of their ancestors, but substantial numbers of mutations have also accumulated during artificial selection over thousands of years of dog breeding.

New lines of research are opening in the study of which dog breeds conserve more of the genotypes typical of wild wolves from separate continents. This raises additional questions about how breed differences, associated with diversity of human culture, reflect variation in perceptual systems (e.g., sight hounds, scent hounds), cognitive abilities (e.g., shepherd breeds, guard/rescue breeds), emotional systems (e.g., retriever breeds, fighting breeds), and energetic systems (e.g., sled dogs, lap dogs).

Dogs are not just neotenous wolves. Breed differences may be productively viewed as experiments in differential reproduction, which has changed the timing by which behavioral and morphological systems develop. Behavioral studies of directional selection for tameness in silver foxes raised similar questions about how changes in the development of neurotransmitter systems, for example, serotonin, dopamine, epinephrine, may be linked in unexpected ways to timing of reproductive cycles and morphological traits such as a curled tail and white star on the chest.

Wolves are not just the ancestors of dogs. The genotype associated with black coat color in wolves appears to have originated in domestic canids and to have spread through wild populations of wolves. Questions arise about where mutations appeared and how they have persisted in canid lineages with histories of genetic bottlenecks, likely shaped by alternating phases of inbreeding and outbreeding. What are the implications for evolutionary models of behavioral processes in wolves and other wild canid species?

On parallel lines of investigation, more detailed questions about social cognition are progressing for canids. For example, questions about empathy and reconciliation after conflict have recently been examined for wolves. Intriguing differences between dogs and wolves have been documented in observational learning and the recruitment of social companions in problem-solving tasks. Questions arise about what are appropriate problem-solving tasks: contraptions humans devise to control extraneous variables or tasks that arise in foraging?

The challenges of teasing apart epigenetic influences during social learning raise questions about research design and sample size. Given the genetic and behavioral variation within and between breeds of dogs, which individuals should be chosen to compare with wolves? Given equivalent variation in wolves, which should be chosen to compare with dogs? To compare social cognition in dogs and wolves, should they both be raised in human families or in canine families? What are the implications of separating both dogs and wolves from social companions during development?

Answers to questions about how behavioral variation is related to the interaction of genetic variation and environmental variation are still elusive. However, the progress in understanding some of these linkages within the canid genome has accelerated in the past decade and holds promise for reframing future questions about the evolution of behaviors on both ends of the continuum between fixed actions and behavioral plasticity.

See also: Conservation and Behavior: Introduction; Domestic Dogs; Social Cognition and Theory of Mind; Spotted Hyenas.

Further Reading

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