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## 2

### Wolf Behavior: Reproductive, Social, and Intelligent

*Jane M. Packard*

A LARGE WHITE WOLF appeared on the bank of a drainage flanking a meadow on Ellesmere Island in Canada's High Arctic. Through binoculars, I identified him as the breeding male "Left Shoulder" (Mech 1988a; Mech 1995d). Several hours earlier, he had left four pups playing in this meadow of gently rolling heather and willow tundra. Later, however, they had followed their mother out of view and toward their den. What would Left Shoulder do when he did not find the pups there?

Raising his chin, he released a long, low howl. We both waited. I was expecting to hear a chorus of high-pitched puppy howls in response, but heard none. Apparently the wolf didn't either. Looking toward where he had last seen the pups, Left Shoulder made his way down the slope, crossing their trail. Would he pick up the scent that was 15 minutes stale? Nose to the ground, he ambled up the drainage. However, the pups had gone the other way. Left Shoulder back-tracked the pups for about 3 meters, paused, reversed direction, and headed after the pups! I wondered if he would track the pups and his mate directly to the den.

Trotting briskly, Left Shoulder kept his nose to the ground for about 30 meters. Then, he raised his head, veered away from the scent, and headed directly toward the den, where he often met his mate and two yearlings, who also tended the pups. He seemed to have expected the behavior of the pups to be predictable.

Intelligence is demonstrated when a canid anticipates the behavior of a social companion (e.g., the pups) or solves a novel problem in obtaining food. Left Shoulder used several senses in solving the problem of how to find the pups: he scanned the landscape visually, he listened

for replies to his howl, and he sniffed the ground. He appeared to combine this sensory information with expectations based on what he had learned about the behavior of family members. Such integration of information will be emphasized by Harrington and Asa with regard to wolf communication in chapter 3 in this volume.

This chapter focuses on interactions between nature (genotype) and nurture (phenotype). Each wolf inherits genetic propensities (instinct; also called "neuroendocrine programming") that lead it into situations in which it learns from its environment (Fentress 1983). Its genotype enables it to solve ancient problems predictably encountered in the history of the species. Communication during social interactions helps fine-tune these responses, enabling individuals to solve new problems and respond to the unpredictable nature of their environment. (For a different perspective, see Mech and Boitani, chap. 1 in this volume.)

Wolves live in diverse and changing environments (see Boitani, chap. 13 in this volume). Variation in the environment is probably one of the keys to understanding why several species have evolved flexible problem-solving behavior (Byrne 1995). Not only does the wolf's physical environment pose challenges, but its social environment also provides both a challenge and a support to individuals learning to maneuver within the dynamic complexity of their physical environment.

This chapter will examine the three-way interaction among wolves, their social environment, and their physical environment (fig. 2.1). First, I will look at problem solving in courtship and reproduction: how are pups produced and cared for until they can start their own

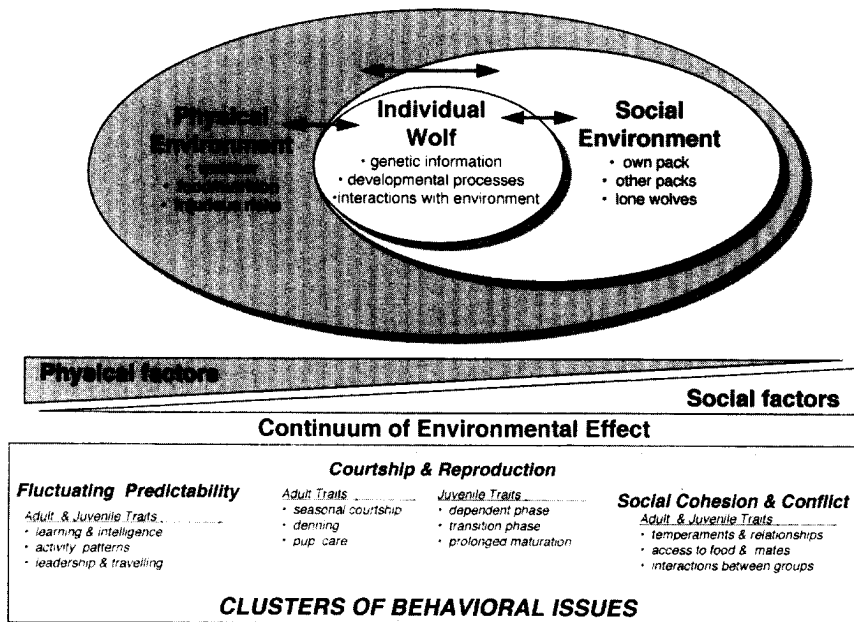


FIGURE 2.1. A conceptual map of this chapter, illustrating how cross-cutting themes (interactions among individual behavioral traits, social environment, and physical environment) overlap in the three sections addressing the categories of reproductive problem solving, physical problem solving, and social problem solving.

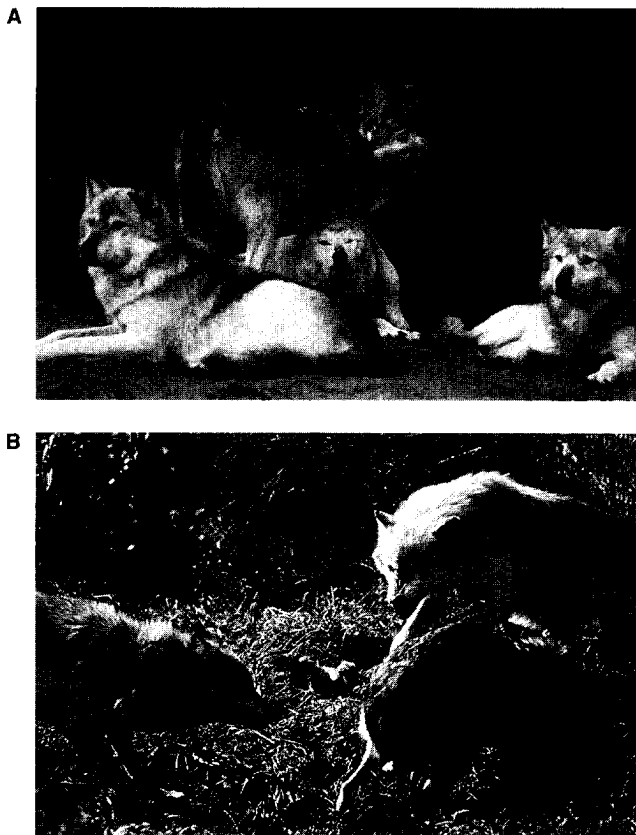


FIGURE 2.2. Behavior in a family group of wolves includes both (A) peaceful coexistence and (B) conflict over access to resources, such as food.

families? Second, I will explore the additional social problems of wolves living in families and extended families, sometimes sharing resources peacefully (fig. 2.2A) and sometimes competing for them (fig. 2.2B). Third, I will focus on how wolves survive in the midst of fluctuating predictability (e.g., obtaining and conserving energy while avoiding risks of death).

However, before addressing reproductive, social, and physical problem solving by wolves, I must (1) review the basics of what is known about wolf sociality, (2) examine what is meant by social and physical environments as they affect wolf sociality, and (3) explain the ethological approach I will use.

### Wolf Sociality

Left Shoulder's pack can help us understand several key aspects of wolf sociality (fig. 2.3). Wolf packs are usually family groups that move within exclusive home ranges and are hostile to strangers from neighboring packs, although there are exceptions to this generalization due to the dynamics of social and physical environments (see Mech and Boitani, chap. 1 in this volume). Left Shoulder's pack, known as the Ellesmere pack, was a family whose breeding members remained together for over 10 years (Mech 1995d). As a group and alone, the wolves defended food resources from other wolves (Mech 1993a). In some years, the breeding female produced

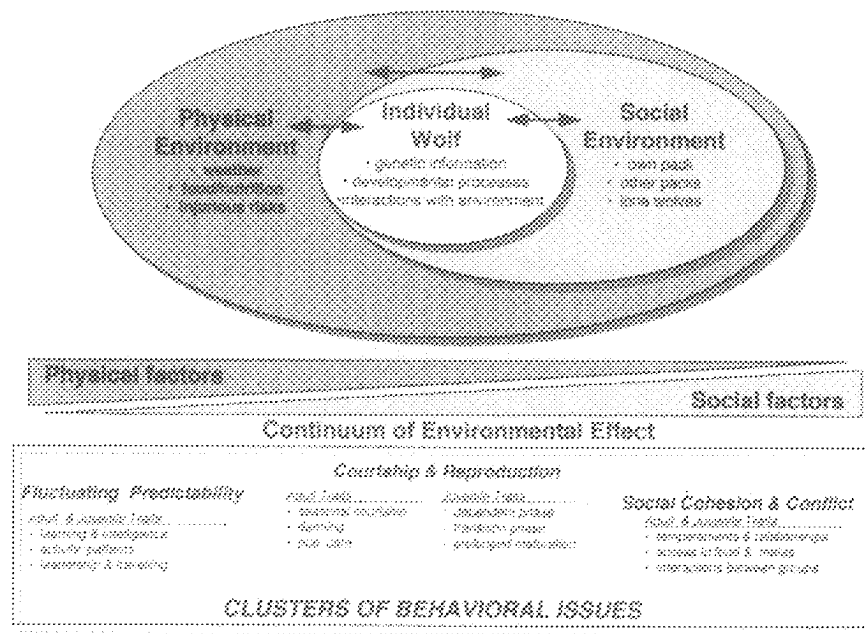


FIGURE 2.3. A conceptual map of this chapter, illustrating how cross-cutting themes (interactions among individual behavioral traits, social environment, and physical environment) overlap in the three sections addressing the categories of reproductive problem solving, physical problem solving, and social problem solving.

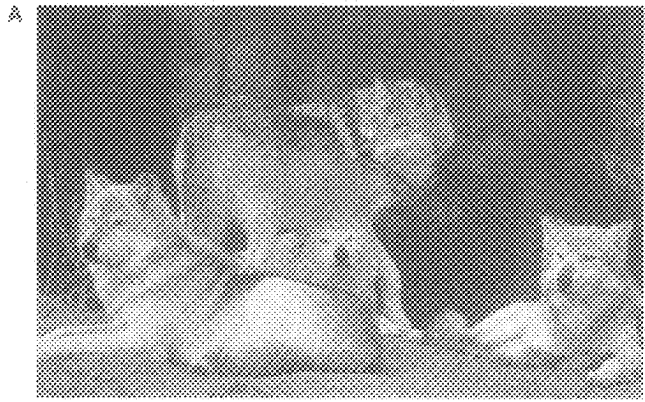


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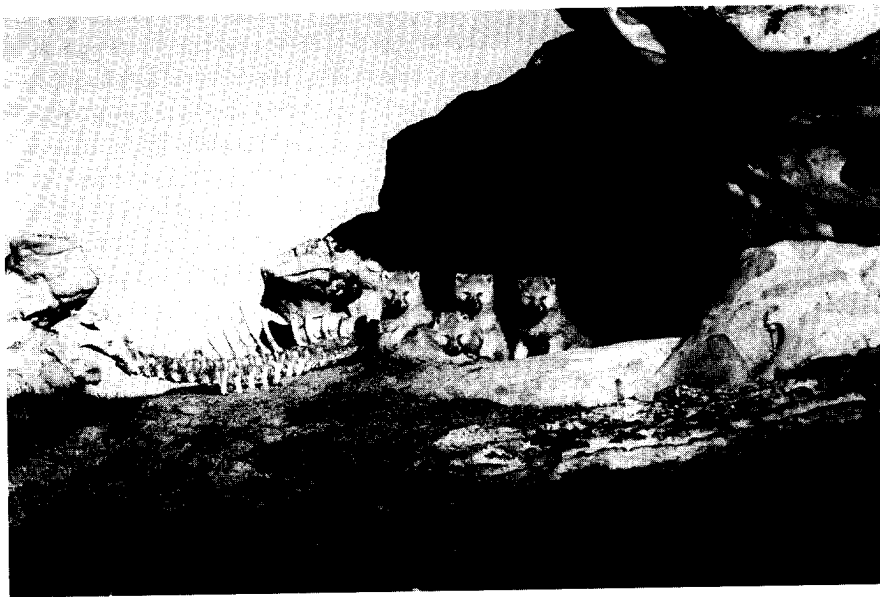
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**FIGURE 2.4.** A litter of four pups born in a cave den on Ellesmere Island, which had probably been used by a series of family groups for centuries. (From Mech 1991b.)

pups in a cave den that had probably been used intermittently for centuries (Mech and Packard 1990) (fig. 2.4). In other years, pups were born in a pit scraped into the ground (Mech 1993b). When no pups were produced, the adults fed offspring from the previous year (Mech 1995e). Family membership and reproductive status changed over the years due to deaths, dispersal, and births (Mech 1995d). For example, when Left Shoulder's first mate, Mom, stopped producing pups, she

switched to caring for pups produced by Left Shoulder and her daughter, Whitey (Mech 1995d).

How did Left Shoulder's pack compare with wolf packs in other environments? The following description of the structure of wolf populations provides a general overview. This basic framework will aid in understanding variation in the spacing, group size, and movements of wolves in different populations, topics detailed by Mech and Boitani in chap. 1 in this volume.

In low-density populations such as that of Ellesmere Island, wolves are generally monogamous, although there are exceptions. Wolf packs usually are founded by an unrelated male and female (D. Smith et al. 1997). After dispersing from the families where each was born, the members of a new pair travel together in an area not defended by other hostile packs (Rothman and Mech 1979; Fritts and Mech 1981). The chance of a new pair starting a family is relatively low in high-density populations where all suitable areas are already defended (i.e., "saturated populations") (Packard and Mech 1980). Occasionally, new packs consist of other combinations of members (Mech and Nelson 1990b), but groups without a breeding pair rarely persist for more than a few months (see Mech and Boitani, chap. 1 in this volume).

Each pack expands as it produces litters, averaging 5–6 pups, and shrinks as offspring disperse at 10–36 months of age (see Mech and Boitani, chap. 1 in this volume). For example, the Ellesmere pack's four 1988 pups were attended by a yearling female, "Whitey," and male, "Gray Back," in addition to Mom and Left Shoulder (Packard et al. 1992; Mech 1995d). Although Mom remained with the family when Whitey replaced her in 1990 as the breeding female, no other offspring remained with the pack for more than three winters (Mech 1995d).

As in most other packs, Left Shoulder, his mate, and the two yearlings delivered food to the pups, interacted congenially with them, rested near them, chased intruders, and were highly attentive to the pups as the family moved together during the summer (Packard et al. 1992; Mech et al. 1999). In a variety of ways, the social environment of the family buffered the pups from threats in the physical surroundings. However, there are variations on this theme; for example, even lone females have successfully raised pups (Boyd and Jimenez 1994).

### Variation in Pack Structure

The tenure of breeders in wolf packs varies from 1 to 8 years, typically lasting only 3 to 4 years (Mech et al. 1998). For example, Left Shoulder was not the breeding male in the Ellesmere pack when it was first studied (Mech 1995d). We do not know whether Left Shoulder was born into the family or whether he joined it, as has been observed elsewhere (Van Ballenberghe 1983a; Mech et al. 1998). Outsiders are most likely to be accepted into a family by a widowed breeder seeking a new mate (Rothman and Mech 1979; Fritts and Mech 1981; Mech and

Hertel 1983), although that is not always a requirement (Meier et al. 1995).

In a small percentage of wolf packs, more than one female may reproduce in a given year (see Mech and Boitani, chap. 1 in this volume). Breeding by two or more closely related females in the same pack has been noted after loss of one or both members of the original breeding pair (Packard et al. 1983; D. W. Smith, unpublished data), although whether such a loss is necessary for multiple breeding in a pack is unknown. In unsaturated populations, it is unlikely that two or more sisters will remain reproductively active in the same pack for more than 1–2 years (Packard 1980; D. W. Smith, unpublished data). In contrast to sisters, the relationships between aging mothers (over 7 years old) and their daughters appear more tolerant (Packard 1980; Mech 1999).

Although the Ellesmere pack has averaged four to five members over 10 years, the individual members have changed over the years (Mech 1995d; Mech 1999). At 3 years of age, Whitey replaced her mother as breeding female. Why didn't Whitey produce her own pups as a yearling? Wild female wolves usually don't ovulate until their second, third, or fourth winters (see Mech and Boitani, chap. 1 in this volume), and first deliver pups at 2–5 years of age (Rausch 1967; Mech et al. 1998). Physiological maturation may be delayed a year or two by nutritional or other stress (Packard et al. 1985; Mech and Seal 1987; Packard 1989). Under extremely good nutritional conditions, physiological maturation may also be accelerated a year, both in captivity (Zimen 1976; Medjo and Mech 1976; Packard et al. 1983) and in the wild (D. W. Smith, unpublished data).

Thus, reproductive characteristics vary within and between wolf populations, as well as within the lifetimes of individuals. For example, Left Shoulder and Whitey produced pups in only 5 of the 7 years when they were the breeders in the Ellesmere pack (Mech 1995d; L. D. Mech, unpublished data). In the Denali wolf population, packs failed to produce pups in 15% of 91 pack-years (Mech et al. 1998). Successful reproduction was lower in younger wolves (and in those breeding for the first time), as has also been reported for captive wolves (Packard et al. 1983).

Although no analyses of the variation in reproductive success among wolves in various packs and populations have been done, the Ellesmere pack helps illustrate general patterns. Left Shoulder produced seventeen pups over 9 years, and Whitey produced nine pups in 7 years.

Of these pups, seven (41%) of Left Shoulder's and three (33%) of Whitey's survived for at least 14 months (possibly longer); at least one survived for at least 8 years (Mech 1995d; L. D. Mech, unpublished data). Such information is difficult to obtain for free-ranging carnivores (Mech 1987a; Packer et al. 1988), which places a major constraint on the testing of hypotheses about the ecological and evolutionary functions of the variation observed in wolf reproduction. Therefore, this chapter focuses primarily on reviewing the literature on proximate mechanisms of wolf behavior, with only brief reference to hypotheses about its ultimate function and evolution.

### Factors Affecting Wolf Sociality

Wolves are affected by both social and physical factors in their environment (see fig. 2.1). "Social environment" refers to the conspecifics with which a wolf interacts, including the members of its own pack, other territorial packs, and lone wolves not associated with a pack. "Physical environment" refers to abiotic factors (e.g., weather and landscape) as well as biotic factors other than wolves in the wolf's environment (e.g., prey species and animals that threaten wolves; see Mech and Peterson, chap. 5, and Ballard et al., chap. 10 in this volume).

Why distinguish between the effects of physical and social environmental variation on the behavior of wolves? To understand variation among wolves, we must understand the variation in both aspects of their environment (Packard and Mech 1980). Most packs within a local population usually experience similar environmental variation due to ecological cycles involving climate and the dynamics of predator and prey populations (see Mech and Peterson, chap. 5, and Fuller et al., chap. 6 in this volume). However, the wolves in any one pack share social experiences that differ from those of neighboring packs. For example, social relationships in packs may vary as diagrammed below in figure 2.7.

From the northern tundra to the southern desert mountains, the physical environment of wolf populations varies greatly (see Fritts et al., chap. 12 in this volume). Furthermore, changes in prey abundance affect each wolf population over the lifetime of family groups (Mech 1970; Packard and Mech 1983; Peterson, Woolington, and Bailey 1984). Thus, social and physical factors are both distinct and overlapping influences on individuals and on their reproductive fitness relative to the pop-

ulations in which they live and reproduce (see fig. 2.1). The additive effects of social and physical factors contribute to the variation observed between populations and across years within each population.

To understand wolf sociality in general, we must understand how it varies within and between populations in different physical environments. In part, the variation *within* each population results from the different histories of the packs that form the reproductive units in that population (i.e., social environment). Wolf families appear and disappear for reasons not directly linked to ecological cycles (Mech et al. 1998), although there are, of course, indirect linkages because nutritional condition can affect social interactions within and between packs (Packard and Mech 1983).

To the extent that wolves share genetic propensities for certain kinds of social behavior (Fentress 1983, 1992), the basic social reasons for pack dynamics are likely to be similar across wolf populations. To understand this neuroendocrine programming, we look for similarities in behavior across wolf populations that differ in latitude, prey species, and the phase synchrony of wolf-prey population dynamics (i.e., their physical environment). From an ethological perspective (Bekoff 1981), we seek to understand how much of that similarity results from shared information in the genome and how much from similar experiences that all wolves encounter growing up within families (i.e., their social environment).

Researchers are just beginning to develop and test hypotheses about the similarities and differences among wolf populations. One of the major problems has been the degree to which behavior observed in captive populations might differ from that in non-captive populations; for practical reasons, many more studies of wolf social behavior have been done in captivity than in the field (table 2.1).

Some field researchers discount certain aspects of captivity-based studies as being analogous to studying human behavior in refugee camps (Mech 1999). Other researchers point out that specific factors can be held relatively constant in captivity to tease out the independent effects of social, physical, and genotypic variation. For example, Bekoff (1972) compared play among wolves, dogs, and coyotes while holding the social grouping and physical conditions constant. In free-ranging populations, both the social and physical environments fluctuate simultaneously in an interactive and uncontrolled manner (Packard and Mech 1983). Thus, our under-



TABLE 2.1. Variation in structure of captive wolf families whose behavior has been studied

Structure	Description	Number of packs (pack-years) <sup>a</sup>
Nuclear family	Parents and their offspring, as in a newly formed pack in which unfamiliar breeders pair and produce a litter. The offspring may be of several ages.	6 (23) <sup>b</sup>
Extended family	Parents plus one or more of their siblings, and their direct offspring.	3 (6) <sup>c</sup>
Disrupted family	A family in which one or both of the original parents is missing. (Variations include disrupted nuclear family, disrupted extended family, disrupted foster family.)	11 (29) <sup>d</sup>
Step-family	A disrupted family that has accepted immigration of an outside breeder.	1 (6) <sup>e</sup>
Foster family	A family that has accepted immigration of nonbreeding individual(s) not born into the pack. (Foster pups are more likely in captivity than in the wild.)	5 (10) <sup>f</sup>
Complex family	A group of wolves with a history that does not fit into the categories defined above; e.g., a group of hand-raised siblings to which additional hand-raised pups have been fostered.	1 (5) <sup>g</sup>

<sup>a</sup>Abbreviations in notes: BeP = Berlin pack (Altmann 1987); SoP = South pack and NP = North pack (Packard 1980); CP = Connecticut pack (Jenks and Ginsburg 1987; Schotté and Ginsburg 1987); BuP = Burgers Zoo pack (Derix 1994; van Hooff and Wensing 1987); BrP = Brookfield Zoo pack (Rabb et al. 1967), WP = Washington Zoo pack (Paquet et al. 1982); OP = Oregon pack and ShP = Shubenacadie pack (Fentress and Ryon 1982; Fentress et al. 1987); RP = Rickling pack, KP = Kiel pack, and BaP = Bavarian pack (Zimen 1981); PI = pack I, PII = pack II, and PIII = pack III (Fox 1973).

<sup>b</sup>BeP (1959–66, 1974–78, 1978–81), NP (1977), CP (1975–80), BuP (1969–73).

<sup>c</sup>BrP (1960–63), WP (1968–70, 1973–74), BuP (1978–79).

<sup>d</sup>BeP (1959–66), BrP (1959, 1964–66), NP (1978), SoP (1977), CP (1981–82), ShP (1975–79, 1980–81), KP (1970), WP (1967, 1971–72), PI, PII, PIII.

<sup>e</sup>BuP (1981–85).

<sup>f</sup>SoP (1978), WP (1975–76), OP (1973–74), RP (1968–69), BaP (1970–72).

<sup>g</sup>BaP (1973–77).

standing of wolf social behavior will advance more rapidly when we integrate the information from both captive and field populations, so long as we take great care to recognize the limitations of each perspective and to understand the whole as the sum of the parts.

### An Ethological Perspective

An ethogram is a catalogue of behaviors that functions like a dictionary of the meanings of all the actions of a particular species. However, rarely is it possible to document all possible behavioral acts, so such catalogues prepared for the purpose of specific studies are necessarily incomplete (Bekoff 1979a). A catalogue of the basic be-

havioral traits of wolves, as defined by diverse researchers, is compiled in table 2.2.

Many more hypotheses have been developed to explain wolf behavior than have been systematically tested. Students of wolf behavior have come from a wide range of disciplinary backgrounds (e.g., physiology, psychology, behavioral genetics, behavioral ecology, ethology, sociobiology, wildlife management). They have defined terms and questions in ways that are not always coherent, yet these workers provide a rich diversity of perspectives. Haber (1996), for example, described wolves as “eusocial,” a term reserved by evolutionary biologists for species that live in colonies (e.g., social insects) in which some phenotypes cannot reproduce due to the

TABLE 2.2. Abbreviated ethogram of wolf behavior; conceptual model of internal states associated with behavioral assays (see also table 3.9)

Category	Subcategory code	Typical action patterns (behavioral assay of state)
Activity <sup>a</sup>	A1	Inactivity: lying sitting, or standing; without changes in angle of neck
	A2	Moderate activity: walking, interacting, exploring, feeding, grooming; neck angle changes
	A3	Strenuous activity: directional rapid movement (e.g., trotting, galloping, running)
Care <sup>b</sup>	C1	Care-solicit: suckle, whimper, lick-up, paw, roll-on-back, solo-howl
	C2	Care-ritual: grovel, over-the-muzzle-bite, roll (passive submission), curl (active submission)
	C3	Care-give: nurse, carry-pup, carry-food, regurgitate, lick-other, watch, follow, lead
Flight/Fight <sup>c</sup>	F1	Flight: avert-gaze, avoid, crawl, head-down, low-posture-retreat, ignore, leave, run, slink, refuge
	F2	Defensive (mixed fight/flight): bark, crouch, gape, growl, hackles, snap, snarl, whirl
	F3	Fight: chase, face-off, holding-bite, lunge, jaw-spar, nip, pin, sidle, stand-high, wrestle-fight
Humbleness <sup>d</sup>	H1	Humble-low: pricked-ears, high-posture, high-tail, flexed- and raised-leg-urination, scrape-back
	H2	Humble-neutral: ears-side, hanging-tail, squat- and stand-urinate, wait
	H3	Humble-high: brows-together, ears-back, low-posture, tuck-tail, long-mouth-line, hunchback
Ingest <sup>e</sup>	I1	Hunt: directional trot, chase, zigzag, sniff-ground, give-eye, dig
	I2	Handle: sprint, grab, hold, lunge, knock-down, pounce, neck-shake, nose-stab, cache, pluck
	I3	Consume: chew, swallow, rip, drink, lick
Maintenance <sup>f</sup>	M1	Maintenance-low: apathetic, foot-drag, disgust-mouth, head-hang, glazed-eyes, disheveled
	M2	Maintenance-normal: lick-self, scratch-self, head-shake, rub-body, urinate, defecate
	M3	Maintenance-high: repetitively-lick-injury, vomit, scoot-rear, limp, diarrhea
Proximity <sup>g</sup>	P1	Proximity-brief: approach, touch-nose, lick, lie-near, pass
	P2	Proximity-moderate: chorus-howl, carry-object, rally, stand-near, look-over-shoulder, wag-tail
	P3	Proximity-prolonged: bow, bounce-follow, gallop, play-wrestle, circle-wag, play-jaw-spar, roll
Sexual <sup>h</sup>	S1	Bonding: follow, mark-over (double-mark), nuzzle, parallel-walk
	S2	Courtship: chin-rest, prance, dart, ears-together, head-flick, hug, sniff-rear, T-formation, wrestle
	S3	Copulatory: escort, tail-avert, mount, thrust, ejaculatory-contraction, dismount, tie, tooth-clack

Note: This behavioral catalogue was compiled for observer reliability training at the Houston Zoo. A more complete ethogram compiled from several sources (Bekoff 1972; 1979a; Derix 1994; Fox 1971e; Goodmann and Klinghammer 1990; Zimen 1971, 1982) is available from the author. Categories are not mutually exclusive; subcategories are mutually exclusive within categories. See also Harrington and Asa, chap. 3, table 9 in this volume.

<sup>a</sup>Model A: Indicator of low (A1) to high (A3) cardiovascular activity; measured in field by variation in radiotelemetry pulses.

<sup>b</sup>Model C: C1 indicative of generalized state of need in juveniles (hunger, cold, full bladder); C2 indicative of low serotonin and moderate adrenal activity in juveniles, subadults, and adults; C3 indicative of high prolactin.

<sup>c</sup>Model F: indicative of adrenal activation above the individual's set-point range: F1 more effect of adrenaline than noradrenaline (Sapolsky 2002; Watkins 1997, 11); F3 more effect of noradrenaline than adrenaline (probably associated with high androgens); F2 indicative of both noradrenaline and adrenaline activity.

<sup>d</sup>Model H: continuum of serotonin above the group norm (H1) to serotonin below the group norm (H3).

<sup>e</sup>Model I: I1 indicative of low blood glucose, low fatty acids, empty gut in context of no food; I2 indicative of burst of epinephrine and endorphin activity; I3 indicative of low blood glucose, low fatty acids in context of available food, caching when stomach is full.

<sup>f</sup>Model M: M1 indicative of one or more diagnostic blood parameters outside the normal range; M2 indicative of diagnostic blood parameters within normal range; M3 may be indicative of active healing processes (e.g., cortisol, histamines).

<sup>g</sup>Model P: indicative of serotonin activity at or above the individual's set-point range and a continuum of endorphin activity below (P1) to above (P3) the individual's set-point range.

<sup>h</sup>Model S: S1 indicative of low steroid hormones (Seal et al. 1987); S2 indicative of estrogen above 2.5 pg/ml in females, baseline testosterone above 240 mg/dl in males; S3 indicative of declining estrogen, rising progesterone above 10 ng/ml and LH above 3 mg/ml in females, peak response to LRH above 600 mg/dl in males.

type of nutrition received at specific developmental stages (Lacey and Sherman 1997). In contrast, all wolves retain the readiness to breed when the social environment permits, and most disperse by 3 years of age (see Mech and Boitani, chap. 1 in this volume).

In part, the diversity of perspectives voiced by wolf biologists is related to the schools of thought encountered in their academic backgrounds. Botkin (1990) traced the roots of two schools of thought, the deterministic and the stochastic perspectives, back to the

Greek philosophers. According to the deterministic perspective, events in the natural world unfold according to certain predictable or predetermined rules and return to steady states. In contrast, from the stochastic perspective, order is apparent only at a specific time as a reflection of chance events. The dynamic changes between relatively steady states are characterized in terms of probabilities.

Although they are contrasting viewpoints, the deterministic and stochastic perspectives are not mutually exclusive. The basic research questions may be rephrased in terms of "those aspects that are relatively unchanging" (deterministic) and "those aspects that do change" (stochastic). Both perspectives should be integrated in predicting the responses of wolves to their ever-changing environment.

These contrasting viewpoints (stochastic and deterministic) are both reflected in the ethological approach of this chapter. Such a balanced perspective on canid behavior is reflected in the ethological writings of Fentress (1982, 1983, 1992) and Bekoff (1981, 1989). Other wolf researchers have tended to emphasize one perspective over the other, as may be apparent in other chapters.

According to the deterministic perspective, sociality evolved in wolves as an adaptation to their habit of hunting and feeding on large prey (see Peterson and Ciucci, chap. 4, and Mech and Peterson, chap. 5 in this volume). In contrast, the stochastic model examines the sources of variation within and between individuals, social groups, and populations (Botkin 1990; Creel and Waser 1997; Lucas et al. 1997); it allows for the hypothesis that behavioral traits of social mammals may not be currently adaptive (Solomon and French 1997), or may be neutral by-products of other traits that were adaptive in the species' history (Pusey and Packer 1994).

In this chapter, my approach to examining wolf sociality will be to (1) identify behavioral mechanisms from captive and field studies, (2) place these mechanisms in the context of limited information about the variation observed in field studies, and (3) clarify hypotheses that might be tested in the future. In short, I intend to explain the biological basis of wolf social behavior by relying on the four basic ethological concepts, two at the proximate level of individuals (causation, ontogeny) and two at the ultimate level of populations (function, phylogeny) (Solomon and French 1997), with an emphasis on the former. Causation addresses the relatively static aspects of behavioral traits, whereas on-

togeny addresses the dynamics of behavioral variation with age.

## Courtship and Reproduction

The behavior of adult wolves and juvenile wolves may be viewed as having coevolved over millions of years. For example, one can view care-giving behavior (in adults) as having coevolved with care-soliciting traits (in juveniles, subadults, and some nonreproductive adults). A deterministic perspective would posit that the benefits of group foraging shaped both juvenile and adult wolf traits in an optimally beneficial manner. According to a stochastic perspective, however, the factors affecting production of offspring (i.e., mating and care-giving traits) may be distinct from the factors affecting the survival of juveniles to reproductive age (i.e., survival and care-soliciting traits) (Caro 1994; Packard et al. 1992; Pusey and Packer 1994).

A coherent model of wolf reproductive behavior must explain the variation in both adult and juvenile traits. I will attempt this by addressing the following subjects: (1) seasonal courtship, (2) phases of the reproductive cycle, (3) behavior at dens and homesites (indirect care), (4) pup birth and stages of development, (5) direct biparental care of pups, and (6) the familial hunting school.

### Seasonal Courtship

Domestic dogs (*Canis lupus familiaris*) can breed year-round (Haase 2000); why not wolves, from which dogs were derived (see Wayne and Vilà, chap. 8, and Nowak, chap. 9 in this volume)? In most of the Northern Hemisphere, wolf pups are born early enough in spring (Mech 1970; Fuller 1989a; Servín-Martínez 1997) that their nutritional needs coincide with a birth pulse of herbivores (May and June), providing relatively easy prey for wolf parents to catch. By autumn, the pups are large enough to follow adults on hunts for larger prey, which are more difficult to kill. Pups are born after the worst of the winter weather and grow to almost adult size before it returns (Van Ballenberghe and Mech 1975). Thus, wolves copulate in winter (Mech 1970), gestation being 61–64 days. However, new pairs form at all times of the year (L. D. Mech, unpublished data), and existing pairs remain together year-round, their tandem urination conveying essentially the same information a wedding ring

does (Rothman and Mech 1979; Mertl-Millhollen et al. 1986).

Most of our knowledge of canid courtship behavior (see table 2.2) has been provided by captive studies (Schenkel 1947; Rabb et al. 1967; Packard 1980; Zimen 1981, 1982; Packard et al. 1983; Jenks and Ginsburg 1987; Schotté 1988; Derix et al. 1993; Asa 1995; Servín-Martínez 1991, 1997). Wolf researchers use these detailed studies to interpret the glimpses of reproductive behavior reported from the wild (Mech 1966b; Haber 1968, 1977; Peterson 1977; Mech and Knick 1978).

### Phases of the Reproductive Cycle

Seasonal peaks in wolf reproductive behavior are correlated with seasonal changes in reproductive hormones (Seal et al. 1979; Zimen 1982; Asa and Valdespino 1998). In autumn, testosterone in males and estrogen in females begin to rise, priming the reproductive organs for a predictable sequence of behavioral and physiological phases: proestrus, estrus ("heat"), metestrus (pregnancy or pseudopregnancy), pup care, and anestrus (Packard et al. 1983). However, the duration of each phase and the magnitude of hormonal changes within each phase vary among individuals, possibly depending on interactions among such factors as genotype, age, experience, body condition, latitude, and the social environment (Packard et al. 1983, 1985).

The phases of the canid reproductive cycle can be recognized in the field. For example, during the 2 months prior to estrus, paired wolves sleep within 1 meter of each other, significantly closer than after mating (Mech and Knick 1978; Knick and Mech 1980). Usually, the breeding female in each pack is followed more closely by her mate than by other pack members (Mech 1966b; Peterson 1977). Each courting pair engages in reciprocal nuzzling, prancing, genital investigation, and scent marking (Schenkel 1947; Rabb et al. 1967). By back-tracking known radio-collared wolves during winter, Rothman and Mech (1979) learned that established pairs scent-mark more frequently than lone wolves and that newly formed pairs scent-mark more frequently than established pairs.

Observations of captive wolves help detail how the courtship behavior of a pair becomes synchronized when male and female are sexually naive. Wolves hand-raised by Erik Zimen (1981, 133) bred successfully although they had no opportunity to learn from experi-

enced breeders. For example, one sexually naive male, Näschen, "took a great interest in the places in the snow where Finsterau urinated. . . . Näschen kept almost perpetual skin contact with Finsterau. At the end of February, Finsterau for the first time stopped, though only briefly, when Näschen tried to mount her. A few days later things progressed to a point at which she presented herself by approaching Näschen sideways and then in front of him, with her tail turned to one side. Näschen mounted her and, after a number of vigorous thrusts of the pelvis the two 'locked' in the fashion typical of canids."

Each mated pair of wolves progresses through the same fixed sequence of behavioral phases. The duration of each phase is determined by the rate at which ovarian follicles develop and mature within each female each season (Seal et al. 1979, 1987; Packard et al. 1983, 1985). The basic endocrinological patterns of wolves are described in more detail by Kreeger in chapter 7 in this volume; the physiological correlates of wolf reproductive behavior are outlined below.

#### *Pre-proestrus*

Pre-proestrus occurs in late autumn or early winter, before adult females show a bloody vaginal discharge (Seal et al. 1979). During pre-proestrus, it is not unusual for either a male or a female wolf to express unreciprocated interest in a potential mate. For example, in Zimen's (1981, 132) captive Bavarian pack, "Finsterau kept pressing against Wölfchen and whimpering, rolling on her back in front of him, and pulling his coat . . . but the more importunate she became the more he withdrew."

One theory is that flirtatious female behavior during pre-proestrus is affected by the hormonal changes associated with rising gonadotropin levels and waves of incomplete follicular development (Packard 1989). At this time, plasma estradiol rises above the 10 pg/ml typical of anestrus (Packard 1980, 75). More frequent scent-marking by males during this period may be correlated with elevated testosterone levels prior to proestrus in females (Hart and Haugen 1971; Packard et al. 1985; Packard 1989). In captive wolves, fights between males appear more likely in autumn and early winter prior to proestrus in females (Zimen 1975; Packard 1989). For adult male wolves, average baseline values for plasma testosterone ranged from 106 to 408 ng/ml, and average testosterone response to injection of LHRH ranged from

384 to 716 ng/ml, during this period prior to February 1 (Packard 1980, 91).

### Proestrus

The proestrous phase begins when a bloody vaginal discharge appears, associated with squamous cells shed during rapid growth of the uterine lining. Plasma estrogen rises during proestrus, and adult males usually become very attentive to odors in the urine and vulva of their mates (see Kreeger, chap. 7 in this volume). Most likely, this olfactory communication functions primarily in behavioral synchronization of sexually naive, newly formed pairs. Experienced males copulate even if they cannot smell their mates (Hart and Haugen 1971; Asa et al. 1990; Asa 1995).

Typically, a proestrous female will prance, body-rub, paw, nuzzle, place her chin on her mate's back, or present her rear near his nose (Schenkel 1947). Such courtship behaviors (see table 2.2) are referred to as "active solicitation" or "proceptivity" (Beach 1976). However, the frequency of active solicitation varies greatly among individuals (Bernal and Packard 1997), as does female attractiveness to males (Packard et al. 1985). The most proceptive (solicitous) females are not necessarily the most attractive (Zimen 1981; Packard et al. 1985).

### Estrus

In *Canis*, behavioral estrus is the phase in which a female is receptive to copulating (Concannon et al. 1975, 1977). Two diagnostic behavioral changes occur in a receptive estrous female: (1) she averts her tail to the side of her vulva (flagging), and (2) she stands still when a male mounts her. If a male is inattentive, an estrous female may paw at him, rub against him, straddle him, or even mount him (J. M. Packard, unpublished data). Cornified cells in vaginal smears and a soft or swollen vulva also define this phase (Concannon et al. 1975; Packard 1980, 83).

Due to their phylogenetic similarities, neurophysiological studies of estrous behavior in dogs provide an appropriate model for wolves (Seal et al. 1979, 1987; Asa and Valdespino 1998). The hormonal determinants of estrous behavior are complex (Hart 1970; Concannon et al. 1975; Thun et al. 1977). Receptivity appears to be correlated with rising plasma progesterone after priming by estrogen during proestrus.

The courtship behaviors of wolves described above are similar in form to those of dogs. Actions associated with play and conflict may also occur during courtship

interactions. For example, a courting pair of wolves I watched in the Houston Zoo rose up on their hind legs with forelegs entwined in brief wrestling matches.

The male may respond to the female's visual and olfactory stimuli by licking her genitals, then mounting her. Inexperienced males may direct mounting behavior to the head or side of the female before learning to mount at the rear. An unreceptive female may snap, growl, pull away, lie down, roll over, or shove the male away. When receptive, females avert the base of the tail to one side, exposing the swollen vulva. Experienced females may spread the rear legs slightly, enhancing their stability as the male mounts and the penis is inserted into the vulva. In a successful copulatory sequence, rapid pelvic thrusts follow, while the male's forelegs clasp the female behind the ribcage.

When a wolf ejaculates, his final thrust is prolonged a bit and his chin and/or rear legs may be raised slightly. During pelvic thrusting, the bulbous gland at the base of his penis engorges with blood and locks the pair in a copulatory tie (Fuller and DuBuis 1962; Rabb 1968, cited in Mech 1970). Usually, the male dismounts, and the two stand or lie rear-to-rear until the swelling declines in 5–36 minutes (Mech 1970; J. M. Packard, unpublished data). The tie is shorter if the female struggles and tries to pull away, or if other wolves interact with the tied pair.

Ejaculation followed by expansion of the penile bulb to form the copulatory tie in *Canis* are spinally mediated reflexes facilitated by androgens (Hart 1968, 1974b). Female canids respond to stimulation by the penile bulb with rhythmic contraction of the smooth muscle of the uterus, such that sperm are squeezed toward the ovaries (Evans 1933), presumably in response to a short-term pulse of oxytocin. The copulatory tie may function in postcopulatory sperm competition (Dewsbury 1972) or in reinforcement of the pair bond (Mech 1970).

The total number of copulations per estrus varies among individuals, ranging from one to eleven and averaging six for five captive females observed continuously during estrus (Packard 1980). Although estrus usually lasts less than a week in experienced captive pairs (J. M. Packard, unpublished data), estrous periods of up to 15 days (Zimen 1976), and even multiple peaks of estrous activity, have been reported in captive wolves (Bernal and Packard 1997; Zimen 1981).

### Metestrus

During metestrus in *Canis*, high levels of progesterone (10 to 19 ng/ml; Packard 1980, 75) are maintained

whether pregnancy occurs or not (Asa and Valdespino 1998). Because these species are spontaneous ovulators, polyestrus does not occur in *Canis* (Asa 1995, 1997). Metestrous females that are not pregnant are said to be "pseudopregnant" (Johnston 1986), since some individuals show physical (slight growth of mammary tissue, loss of belly hair) and behavioral changes (den construction, pup care) usually associated with pregnancy (Packard et al. 1983; Mech, Phillips et al. 1996).

Despite much speculation (Moehlman 1986, 1987; McIntyre 1995; Lewis and Pusey 1997; Moehlman and Hofer 1997), there is no published evidence that pseudo-pregnant female wolves have nursed pups. Although milk can be expressed from the nipples of some pseudo-pregnant females during metestrus (Mech and Seal 1987), the secretion is probably nonfunctional. Reported cases of cooperative nursing in wolves (Packard 1980; Paquet et al. 1982; Fentress and Ryon 1982), have all involved females that were both pregnant.

Because estrus in a wolf population probably lasts only about a month (see Kreeger, chap. 7 in this volume), male wolves have less incentive than male dogs do to abandon their pregnant mates in search of other estrous females. Without much opportunity to inseminate other females, theoretically there is little ultimate cost to males that stay with their mates and help care for pups. Male care of infants is associated with obligate monogamy in other mammals in which males have few opportunities to inseminate other females and females are unlikely to succeed in raising young alone (Kleiman 1977).

Male care of pups may be indirect (den preparation, pup defense, food delivery to the breeding female) or direct (food delivery to the pups). This distinction is important, because all pups in a litter may share equally in the benefits of indirect care, while direct care may be unequally distributed (Malcolm and Marten 1982).

#### Dens and Homesites: Indirect Care

Preparations for pup care by family members may start before wolf pups are born. Dens may even be dug in autumn (Thiel et al. 1997). Adults and yearlings of both sexes participate in den digging (Ryon 1977; Mech, Phillips et al. 1996) and provisioning the pregnant female (Fentress and Ryon 1982).

Experience may influence choice of a den site (Fuller 1989a); however, experience is not a prerequisite for successful denning in wolves. For example, during her first

pregnancy, a hand-raised female in Zimen's (1981, 134) captive Bavarian pack "dug small holes at several places in the enclosure, preferably in the sandy soil immediately under a tree stump. . . . The sand was easy to dig in, and the roof of the den was protected by the wide-spreading roots of an old pine tree which assured it against collapse."

Pregnant females may "localize" near a den for up to a month before parturition (Harrington and Mech 1982c; Fuller 1989a; Boyd, Ream et al. 1993), although they do not always do so (L. D. Mech, unpublished data). Usually, other pack members accompany the pregnant female near the den, but family members vary highly in their degree of association with the breeding female (Murie 1944; Clark 1971; Haber 1977; Harrington and Mech 1982c; Mech 1988a; Ballard, Ayres, Gardner, and Foster 1991). Reported dates of den localization correspond to the range of parturition dates recorded in captivity (Servín-Martínez 1997). As expected, the same latitudinal difference is seen in denning dates as is apparent in breeding dates (Mech 1970, 2002).

Wolf dens usually are located away from peripheral zones of the territory, where hostile encounters with neighboring packs are most likely (Ballard and Dau 1983; Fuller 1989a; Ciucci and Mech 1992). In the Superior National Forest of Minnesota, only 11% of twenty-nine dens were located within 1 km (0.6 mi) of territory boundaries (Ciucci and Mech 1992), a zone where 56% of the wolves killed by other wolves died (Mech 1994a). Dens in larger homogeneous territories tended to be more central (Ciucci and Mech 1992) unless there were attractive geographic features in the territory, such as a river or road (Mech et al. 1998, 104).

Distances between the active dens of neighboring packs vary with territory size; for example, in a south-central Alaska population, inter-den distances averaged 45 km (Ballard and Dau 1983). Several dens within each home range may be used (Joslin 1967; Chapman 1977; Mech et al. 1998), and females vary in the probability that they will reuse a previous den (Ballard and Dau 1983; Fuller 1989a; Ciucci and Mech 1992; Mech 1995d).

The characteristics of dens vary across diverse locations (Mech 1970; Mech et al. 1998), depending on what is available to the wolves, although most natal dens are located near water (Joslin 1967; Mech 1970). In the frozen tundra above the Arctic Circle, one pack used crevices on a rocky ridge, a shallow scrape, and a rock cave (Mech 1988a, 1993b). North of the tree line in the Alaskan Arctic, many dens are located on sandy bluffs (Stephenson

1974; Ballard and Dau 1983; Lawhead 1983; Williams 1990; Heard and Williams 1992). Where the thick root mat of vegetation on these sandy bluffs is intact, the roof of the burrow may be held fast; however, where the vegetation is sparse, the roof may cave in, resulting in multiple entrances to the burrow (Clark 1971; Murie 1944; Peace River Films 1975). In forested areas, dens may be dug under the roots of trees (Criddle 1947; Scott and Shackleton 1982). Mech et al. (1998) summarized the various kinds of dens that wolves use.

Hypotheses regarding the proximate mechanisms associated with pre-denning behavior include the following: (1) that rising prolactin is associated with den digging in males as well as both pregnant and nonpregnant females (Mech, Phillips et al. 1996; Asa and Valdespino 1998); (2) that the breeding female is often the focus of attention for her mate and offspring (Zimen 1976, 1981, 1982), who may be stimulated to dig where she digs; and (3) that den digging and homesite attendance by yearlings and subadults may be a by-product of a slow maturation rate and prolactin cycles in prereproductive wolves of both sexes. Insufficient data are available to test these hypotheses, but reports of den digging in autumn tend to refute the prolactin hypotheses (Thiel et al. 1997).

From a deterministic perspective, hypotheses about the ultimate reasons why nonreproductive pack members provide indirect pup care include the following: (1) to pursue the best option for promoting the genes they share with their kin while they are nonreproductive (kin selection), (2) to enhance pack social bonds, and (3) to gain experience for when they become breeders themselves (Macdonald and Moehlman 1983; Moehlman and Hofer 1997; Asa and Valdespino 1998). This "alloparental" care by nonbreeders allow breeding females to remain with the pups continually when prey are not readily available near the den (Harrington et al. 1983). These hypotheses are also untested, and the issues associated with such babysitting behaviors are complex (Clutton-Brock et al. 2001).

Wolf pups live in and around a den during their first 8 weeks (Mech 1970), but their mother might move them from one den to another during this period (Mech et al. 1998). From about 8 to 20 weeks of age, pups inhabit an area above ground that includes a "nest" or nests where they huddle together, a network of trails, and various play areas. Known as loafing sites (Young and Goldman 1944) or rendezvous sites (Murie 1944; Joslin 1967; Theberge and Pimlott 1969), these areas,

along with dens, are considered "homesites" (Harrington and Mech 1978a).

Wolf packs vary widely in the amount of time that pups remain at the natal den, in the number of activity centers within a homesite, and in the number of homesites used during the summer season of pup care. Variation in a pack's homesite use may be related to annual variation in the movements of prey between winter and summer feeding grounds (Scott and Shackleton 1982).

At homesites, pack members provide indirect care to pups in at least two ways: through general defense (Mech 2000a), and by provisioning lactating females (Mech et al. 1999). Aggressiveness toward intruders increases in both reproductive and nonreproductive males during denning (Mech 1970; Zimen 1981).

Prolonged bark-howling is a defensive response to unexpected movements of an intruder near a homesite. One day when I changed my 1988 observation site of the Ellesmere Island pack, Gray Back (a yearling male) bark-howled eighty-five times as the breeding female and her four pups calmly returned to the cave den from an open meadow. Sometimes the movement of pups to a new homesite is not associated with bark-howling, and the circumstances of disturbance are more ambiguous (Chapman 1977; L. M. Thurston, J. M. Packard, and D. W. Smith, unpublished data).

Indirect care is provided by all non-pup pack members, although not all participate equally. Harrington et al. (1983) suggested that larger packs may be more likely to successfully defend homesites from predators. In the reintroduced population of Yellowstone wolves (Phillips and Smith 1996), Thurston (2002) confirmed that gender, age, and pack affiliation influenced trends in homesite attendance. Furthermore, patterns of attendance changed over the pup-rearing season.

### Pup Birth and Stages of Development

Birth and development in wolves are similar to those processes in dogs (Scott 1967), so it is useful to adopt Scott's and Fuller's (1965) classifications of pup developmental periods for wolves (Mech 1970). These authors recognized four developmental periods: (1) the neonatal period, from birth to the age of eye opening (12–14 days); (2) the transition period, from the age of eye opening to 20 days; (3) the period of socialization, from 20 to about 77 days; and (4) the juvenile period, from 12 weeks to maturity.

Within the socialization period, Packard et al. (1992) referred to phases of (a) milk dependency, (b) transition to solid food, and (c) independence from milk. They hypothesized that the duration of these phases might be affected by food availability, the nursing female's condition, and pup demand (litter size).

I once peeked in on the birthing behavior of a hand-raised wolf named Sitka. As I cautiously lifted the lid of her den box, I saw a pup emerging. Curled around the other pups nestled against her belly, Sitka licked the new arrival and nibbled gently at the membrane surrounding it. When the membrane slipped off, she swallowed the tissue, breaking the placenta in the process. The pup sprawled on its back, and Sitka nudged it gently until it was near the other pups at her belly. When Sitka looked at me and growled, I was afraid she might redirect her maternal defensiveness and bite the pups, so I withdrew.

Compared with smaller canids, wolves bear relatively large pups in relatively small litters (Moehlman 1986). There has been much speculation about this correlation (Bekoff 1989; Moehlman 1989; Geffen et al. 1996; Moehlman and Hofer 1997). Larger pups may be more resistant to wet, cold weather (Mech 1993b). However, larger pups also need more nutrition from their mother.

#### *Neonatal Period*

With eyes closed, newborn wolf pups look much like German shepherd pups. They are dark, and some even have a white star on the chest. Their tiny drooping ears and pug faces add to the round appearance of their heads. Holding a tiny pup in my hands, I used to marvel that such a little creature would someday look like its mother. The pups' small, uncoordinated legs are good for little more than crawling and kneading their mother's belly while nursing. When cold, they crawl toward warm objects. It is amusing to watch wolf pups as some squirm and crawl on top of one another, while others fall and tumble off the pile. When sleeping in a pile, sometimes a leg will twitch as if the pup is dreaming.

Within hours of birth, canid pups suckle in a reflexive response to a nipple-like object touching their lips (Fox 1971b). When their mother crawls into the den and lies with them, young wolf pups struggle to reach her belly, and move their heads from side to side until they encounter a nipple and start suckling. Some pups may doze off, tipping the head, then wake up with a start and continue suckling. Their mother may lick at the rear or

inguinal area of the pups, stimulating them to urinate and defecate. She consumes eliminations, keeping the den clean, until the pups are large enough to walk to the entrance and eliminate outside.

At birth, wolf pup behavior is little more than a simple set of reflexes (e.g., heat seeking, nuzzling, suckling, elimination in response to maternal licking, crying when hurt, whimpering when cold, hungry, or isolated) (Scott and Fuller 1965; Fox 1971b). However, as the pups' senses and coordination develop, simple reflexes expand into interactive routines (Fentress 1983; Bekoff 1989; McLeod and Fentress 1997). For example, reflexive urination in response to maternal licking develops into the "belly-up" response, often referred to as "passive submission" in yearlings and adults (Schenkel 1967; Fox 1971e, 1972a).

#### *Transition Period*

Wolf pups' eyes open at about 12–14 days (Mech 1970), when the pups also become coordinated enough to stand and walk. At first the pups explore the natal chamber in the den, gradually moving farther each time before collapsing again in a puppy pile. Eventually they stumble out to the den entrance and stand looking at the outside world. It is not unusual for them to startle and duck back into the den after their first peek. Gradually, the growing pups explore farther, and soon they are playing, lying, nursing, and eliminating around the mouth of the den.

As indicated above, newborn wolf pups are relatively helpless, and their visual and auditory senses are poorly developed compared with their olfactory and tactile senses (see Harrington and Asa, chap. 3 in this volume). Their sensory systems, size, and muscular coordination develop rapidly during the transition period (Fox 1971b; Bakarich 1979; McLeod 1987, 1996; McLeod and Fentress 1997). The manner in which neuronal connections develop in the brain during the first few weeks of life may be determined by the pups' experience with their mother and siblings in the den (Klinghammer and Goodmann 1987). During this early window of development, pups learn to recognize familiar individuals, usually family members (Bekoff 1989). Rapid learning during the transition and socialization periods (Scott and Fuller 1965; Scott 1967; Fox 1971b) has important implications for the social context of learning later in life; for example, vocalizations become differentiated and associated with specific contexts.



### **Socialization Period**

About 20–24 days after birth, the pups become mobile enough to explore as far as the mouth of the den (Mech 1970; Ryon 1977; Ballard et al. 1987; Fuller 1989a). They begin to elicit care from other pack members (Murie 1944; Ryon 1977; Fentress and Ryon 1982), and they start ingesting solid food (Mech 1970). In another 2 weeks, they are spending a lot of time outside the den and interacting with the adults.

I recall a typical scene at this stage from around the Ellesmere pack's den in 1988. Left Shoulder was lying like a sentinel near the den entrance when we first approached. As the 5-week-old pups milled around the head of their reclining mother, she arose and escorted them out of sight into the cave den, followed by the yearling female. Later, when the pups saw us, they disappeared into the den on their own, a highly effective response to intruders. When the yearling male, Gray Back, entered the den briefly, a pup followed him out, then waddled back in to rejoin its siblings. The pups appear rather indiscriminate of which family members they approach during this sensitive period of socialization.

While the pups are still small and immobile, they suckle from a lying position within the den (Coscia et al. 1990; Lawrence 1990). At about 3–5 weeks, they are large enough to reach their mother's nipples in a standing position, and will approach her outside the den, often in response to soft squeaks (Crisler 1958; Fentress 1967; Coscia 1989; Goldman 1993). At this stage, suckling bouts average 3 minutes in duration and occur at an average of 5-hour intervals (Packard et al. 1992).

Up to 5 weeks of age, wolf pups are relatively uncoordinated, and their range of movement is usually less than 0.5 km (0.3 mi). When a small pup is away from the safety of a den, its mother may pick it up gently in her mouth and move it to a safer site (see table 2.2). Mother wolves also carry pups when they lag behind while following adults between sites, or when the adults move the entire litter from one den to another. Pup carrying has been reported for a non-nursing female (D. W. Smith, personal communication), but not for male wolves (Mech 2000a).

The pups are very likely to follow their mother if she interrupts a nursing bout and trots away in response to a disturbance (Packard et al. 1992). Their behavior is quickly shaped to follow a departing adult moving in an intent, directional manner. This following response is effective in moving 5-week-old pups between homesites

(Mech 1988a, 44). It could be a precursor to heeling, as in dog training.

At about 5 weeks of age, the pups are sufficiently coordinated to seek shelter from inclement weather and potential predators. They are still small enough to be carried by adult females and large enough to follow adults for short distances. Their sensory systems are fully developed, and their gastric system has developed to a stage at which solid food can be digested. Although their teeth have erupted, they do not have sufficient bite strength to chew large pieces of meat. The full capability of shifting to a meat diet develops later.

Between 5 and 10 weeks of age, wolf pups advance from dependent toddlers to active individuals engaged in learning from their physical and social environments (Mech 1970, 1988a; Havkin 1977; Havkin and Fentress 1985; Packard et al. 1992; Jensen 1993; McLeod 1996; McLeod and Fentress 1997). If there is a shortage of food during this period, the pups still have access to milk as a nutritional alternative, although their growth may be slowed. Under poor food conditions, individual variation in body size begins in the transition period and is likely to be accentuated by the end of summer (Van Ballenberghe and Mech 1975).

In the Ellesmere pack (in 1988), suckling bout duration declined to 1 minute, on average, at about week 9 (Packard et al. 1992). The intervals between bouts increased to an average of 10 hours, until the pups no longer solicited nursing during week 10. Weaning in the Ellesmere pack was not associated with agonistic interruptions (Packard et al. 1992), as reported for dogs (Scott and Fuller 1965). Theoretically, the degree of weaning conflict would be negatively correlated with food supply and positively correlated with litter size (Packard et al. 1992; Malm and Jensen 1996). We believe that food was abundant during our observations because pups received a daily average of one arctic hare and two regurgitations during their tenth week, when they stopped soliciting milk (Packard et al. 1992).

With increasing independence from milk, the following response of pups generalizes to whichever family member feeds them. When hungry pups spot an approaching pack member, they rush over and poke their muzzles around the adult's mouth, an action called "lick-up" (fig. 2.5). If the care-giver has a full stomach, this stimulus seems irresistible: the adult regurgitates food to the pups. In 76% of 115 regurgitation bouts we observed on Ellesmere, regurgitators delivered food



FIGURE 2.5. Pups solicit regurgitation by a behavior called licking-up, in which they poke their muzzles around the mouth and chin of an adult. This behavior persists into adulthood, when it serves an additional function of appeasement of conflict.

where they were met; in 11% of the bouts, pups followed the regurgitator 10–50 meters before it regurgitated; and in the rest, they followed up to 800 meters (Mech et al. 1999). Usually the pups were so excited and active that it was hard to see what food reached the ground in the midst of the confusion. By the age of weaning, pups are sufficiently mobile and have enough endurance to follow adults to carcasses (Gray 1993; L. D. Mech, unpublished data).

On days of food surplus, the pups cached food around the homesite, essentially filling “the pantry” with snacks that they later sought out or encountered haphazardly when the adults delivered little food and the pups were active. Caching routines initially are highly stereotyped in pups (Phillips et al. 1990), implying neuroendocrine programming. By measuring three cached regurgitations, Mech et al. (1999) estimated that an average of 1.25 kg (2.75 pounds) of meat was stored per cache.

The duration of activity bouts increases during the socialization period (Packard et al. 1992). Pups learn the contingencies of their interactions with other pups, and their combative routines increase in complexity during “play-fighting” (Moran 1978; Moran et al. 1981; Havkin and Fentress 1985; McLeod 1996; McLeod and Fentress 1997). Theoretically, cardiovascular conditioning increases with activity at this stage (Bekoff 1972, 1974b), and individual differences may become more pronounced (Folk et al. 1970; Fox and Andrews 1973; K. B. MacDonald 1983, 1987; Zimen 1978). During this stage, pups also become familiar with the identity of

family members, acquiring information that will influence how their social behavior is directed later in life (Bekoff 1981, 1989), particularly when they encounter hostile neighbors.

### *Play*

Based on his observations of the Ellesmere pack during the pup-rearing season, Mech (1988a, 61) emphasized the importance of play in the socialization of wild wolves. He reported very few dominance interactions outside the context of food contests. He saw less conflictive than cohesive behavior, with much of the latter occurring in the form of social play.

Not all researchers agree on definitions of play. Typical characteristics of play include (1) actions also observed in other contexts (e.g., stalking, pouncing, chasing, face pawing), (2) metacommunication signals (e.g., bowing, tail wagging, grinning, head tossing), (3) repeated and exaggerated movement indicating a pleasurable quality (e.g., approach/withdrawal, leaps, bouncy galloping) and (4) exchange of roles (e.g., the “chaser” becomes the “chasee”), maintaining mutual participation (Bekoff 1974a, 1984). Object play also may occur when pups encounter novel stimuli, such as water (Coscia 1993).

While watching wolf pups play in the Ellesmere and Yellowstone packs, I was eager to see whether certain pups learned to avoid others during play. We were entertained by hours of play, including interactions analogous to keep-away, tag, wrestling, and king-of-the-mountain. Repetitive routines were interspersed with novel events resulting in new combinations of actions. I saw only two episodes in which elements of conflictive behavior occurred during play. However, the same frequent “play-wrestling” interactions that I saw were interpreted by another observer as “fighting.” Clearly, interpretation depends on each observer’s experience and mind-set.

According to a deterministic model of wolf behavior, there must be some sort of “social glue” that allows wolves to cooperate in caring for the young (Fox 1980). Fox (1975) compared the play behavior of pups in asocial, semi-social, and social canids (e.g., foxes, coyotes, and wolves). He hypothesized that wolves would be the most playful and the least aggressive (Fox 1969, 1970). Bekoff (1974a,b) obtained evidence from single litters of each of these species that supported Fox’s hypothesis. He observed a stereotyped play bow in all species,

presumably a trait inherited from a shared ancestor (Bekoff 1977c).

Detailed studies of play routines in wolf pups (Havkin 1977) have opened researchers' minds to the importance of examining relative probabilities as well as absolute rules (Fentress et al. 1987). For example, in 3-week-old pups, a side approach is more likely to knock another pup down, due to simple mechanical advantage, in contrast to a frontal approach (Havkin and Fentress 1985). Via trial and error, pups learn the consequences of their actions. With experience, older pups develop effective counter-tactics, including somersaulting.

The ability to learn counter-tactics during play may provide a basis for the learning of complex social relations later in life (Bekoff 1984). Other hypotheses about the function of play in canids include (1) physical exercise related to aerobic conditioning, (2) development of muscular routines, (3) practice of instincts useful for hunting later in life, and (4) "animals that play together, tend to stay together" (Bekoff 1974a, 338).

#### Direct Biparental Care

During the first month after birth, mothers generally contribute directly to pup care in the form of milk and body warmth, as well as choosing and maintaining a dry, clean environment. Fathers contribute indirectly in the form of defense of homesites, hunting, and provisioning the lactating female.

For newborns, pup care by a lactating female is quite different from care by her mate, who only occasionally enters the natal den (Fentress and Ryon 1982; L. D. Mech, unpublished data). Father wolves contribute to the feeding of their newborn pups only indirectly by feeding the nursing mother. According to the "division of labor" model (Mech 1999), the male spends most of his active time hunting while the female attends the pups during their first 3–4 weeks (Harrington and Mech 1982c; Ballard, Ayres, Gardner, and Foster 1991). Unless a focal-follow technique is used, however, it is hard to tell whether a male is hunting or resting when away from the homesite (Thurston 2002).

In Yellowstone packs, the relative probability of homesite attendance differed more between the breeding male and female during the first month than during the second month of pup care (Thurston 2002). In 44% of nine pack-years, the difference in den attendance between mother and father declined to zero by 5 weeks of

pup age, on average. In a third of the cases, no difference could be detected between mother and father throughout the monitoring period 1–12 weeks after birth. In two unusual cases involving communal denning by two sisters, the breeding male initially spent more time at the den than the mothers, although this difference was negligible by the second month of pup care. In nine of twelve cases, alloparental care was less than or equal to parental care when cases were matched for sex, pack, and year.

#### Regurgitative Provisioning

When the father wolf obtains food, he returns to the den and presents food to his mate, either by carrying it in his mouth or by regurgitating it to her from his stomach (summarized by Mech et al. 1999 and Mech 1999, 2000a). When the pups are out of the den, the breeding male and any other adults regurgitate food to the pups. The mother wolf may try to usurp whatever portion of this food she can get, later delivering some of it to the pups. When the mother joins the family on hunts, she similarly brings food back to her pups.

In the Ellesmere pack, the ratio of regurgitations by the breeding male compared with the breeding female varied by year (Mech et al. 1999). Relative female effort was not related to pack size, although it was positively correlated with litter size (Mech et al. 1999).

How much does the food provided by male wolves help offset the lactational drain on a female? No quantitative information on this subject is available. Mech (1999) proposed that the mother wolf probably can usually maintain her nutritional condition throughout the summer because prey is usually abundant then; furthermore, she travels little during the month or so after parturition and is fed mostly by the male and other pack members.

For wolves, monogamy does not appear to be obligate in the sense defined by Kleiman (1977), meaning that care by the father (fig. 2.6) is not essential under all conditions. At least one female wolf raised pups, apparently from birth, without help from other pack members (Boyd and Jimenez 1994). Other examples include situations in which mothers, and in one case a father, raised pups after losing a mate (Boyd and Jimenez 1994; D. W. Smith, unpublished data).

In their second month, when the pups can ingest solid food, biparental care may be more symmetric; that is, the difference between the sexes in homesite atten-



FIGURE 2.6. Adult and subadult wolves of both sexes care for and show tolerance toward pups within the family, although they may attack pups from another pack. Here, a father babysits pups.

dance and provisioning is less, but still apparent (Ballard et al. 1981; Harrington and Mech 1982c; Mech et al. 1999; Mech 2000a). Both male and female parents hunt and bring food to the pups. The female, however, continues to nurse them and still spends much of her time near the homesite. In the Ellesmere pack, the breeding male, Left Shoulder, was occasionally absent for more than a day at a time. Homesite attendance may be an indirect measure of parental care, correlated with direct care (Thurston 2002).

When parents return to the homesite, they regurgitate to the pups one or more times. On Ellesmere, adult wolves, including parents and helpers, regurgitated only once during each of 61% of the food deliveries, although they occasionally regurgitated up to five times during a single delivery, within 5–35 minutes after arrival (Mech et al. 1999). The food delivered per regurgitation bout was tentatively estimated to range from 1.10 to 7.25 kg (2.4–16 pounds). Since the average number of regurgitations per bout was 1.5, the average amount of food delivered per bout would have been 1.9 kg (4.2 pounds). This estimate assumes, however, that the amount of meat regurgitated to pups was the same as that regurgitated into caches (since that was the only time it could be measured)—a tenuous assumption. Theoretically, the amount actually received by each pup would vary with litter size, size of meat chunks, and individual skill at competing for meat.

Pups successfully competed with their mother and older siblings for regurgitated meat, receiving 81% of 171 regurgitations recorded over 6 years in the Ellesmere pack (Mech et al. 1999). The nursing female received

14% of the regurgitations, mostly from her mate, and primarily during the neonatal and transition periods, before the pups could reach the den entrance or digest solid food. Family members other than the parents were half as likely as parents to regurgitate to the pups, and they themselves received only 6% of the regurgitations during this study. The overall pattern was similar in a captive pack (Fentress and Ryon 1982).

#### *Use of the Homesite*

The mother wolf remains with the pups for most of the time during their first 3–4 weeks of life (Ballard, Ayres, Gardner, and Foster 1991). After that, the amount of time pups are left alone varies (Chapman 1977; Harrington and Mech 1982c; Ballard, Ayres, Gardner, and Foster 1991). Chapman (1977) estimated that pups were unattended 40–73% of the time that he monitored three packs in Denali National Park. Under conditions of abundant food, pups were left alone 5–15% of the time that two packs were monitored in south-central Alaska (Ballard, Ayres, Gardner, and Foster 1991). It is difficult to interpret this variation among populations, since the presence of a carcass near the homesite influences den attendance (Harrington and Mech 1982c; Ballard, Ayres, Gardner, and Foster 1991; Jedrzejewski et al. 2001).

On the few occasions when Murie (1944, 29) watched a lactating female leave the den with pack members, she “ran as if she were in high spirits, seeming happy to be off on an expedition with the others.” However, she returned earlier than the other family members. Other researchers have reported a similar pattern (Harrington and Mech 1982c; Ballard, Ayres, Gardner, and Foster 1991; Vilà et al. 1995; Mech 1999, 2000a).

#### *The Familial “Hunting School”*

The association of pups with pack members between weaning and dispersal from the natal group is of particular importance to the pups’ opportunities to learn hunting techniques. We watched one of the first times that 3-month-old pups followed adults away from the natal homesite at Ellesmere in 1988. Left Shoulder disappeared behind the crest of a hill. Shortly thereafter, the screams of a dying arctic hare echoed across the barrens. I naively expected the pups to run over and receive one of their first lessons in killing prey. Instead, they turned tail and ran for the shelter of the closest rock pile! However, when Left Shoulder brought the hare carcass to the pups, they readily converged around him and consumed

the meal. Thus, the pups could have learned the association between food and the screams of the hare.

The propensity to chase and capture small moving animals appears to be genetically programmed in wolves, since it occurs without practice in hand-reared individuals (Sullivan 1979; Zimen 1981). I have watched 3-month-old wolf pups in Yellowstone repeatedly “mouse-pounce” in the stereotyped canid pattern (Fox 1971a, 1975). Such innate behavior gives young wolves a head start in practicing the skills that take learning, such as where to find prey, how to kill it, and how to avoid risks (Mech 1988a, 1991b; Fentress 1992).

At 3 months of age, wolf pups are full of energy, more likely to follow departing adults or to explore on their own, and less likely to remain at a homesite. Typically, they may move among sites where pack members are likely to return individually and in groups. For example, some tundra packs return to the site of a muskox kill, even after the carcass no longer provides food (Gray 1993). In Minnesota, where prey are not migratory, homesites may continue to function as activity centers in autumn and early winter (Harrington and Mech 1982b).

Between 4 and 10 months of age, juvenile wolves are sufficiently mobile to join adults on hunts, even though they have not attained full body size. Mech (1991b) has described the function of family groups at this stage as a “finishing school” for juveniles, implying that they have opportunities to hone their hunting while traveling with the family. I suggest that the name “hunting school” would be better than “finishing school,” since juveniles have already learned the “manners” of social interaction.

Most wolves disperse from their natal pack between the ages of 9 and 36 months (see Mech and Boitani, chap. 1 in this volume). In the Denali population, only 8% of dispersers were older than 3 years (Mech et al. 1998), although in northwestern Alaska, the average age of dispersal was about 3 years (Ballard et al. 1997). The complex and often subtle interactions within each family influence when offspring disperse. Conflictive behavior is tempered by gentle cohesive interactions in both captive and free-ranging families (see references in table 2.1).

### Cohesion and Conflict

In the popular literature (e.g., Fox 1980; Savage 1988; McIntyre 1993), wolf packs are often portrayed as a dom-

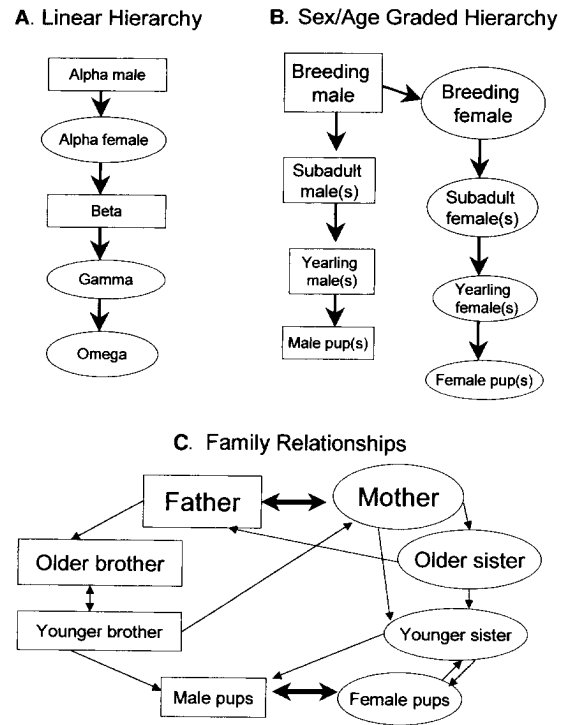


FIGURE 2.7. Three models that have been proposed for understanding wolf social structure.

inance hierarchy (fig. 2.7A), in which underlings are kept in line by dominant individuals. At first I was confused about how to describe social relations in the captive wolf packs I watched, because I did not see the amount of aggression I expected. Pups in the captive South pack spent endless hours in chase games, often joined by the yearling male and less often by their father. Adults in the North pack bedded near one another, tenderly licked one another’s wounds, rubbed shoulders in exuberant rallies after naps, and trotted off together to explore the woods.

After reading an intriguing discussion by Lockwood (1976, 1979), I reread the observations by Murie (1944) and Schenkel (1947). All of these authors perceived life in a wolf pack as a balance between cohesive and conflictive behaviors. They described “submissive” behavior as the persistence of care-soliciting by offspring who remained in the family as adults. Perhaps the relative importance of dominance varies with pack composition, food availability (and thus competition), and even the eyes of the observer.

What is meant by cohesive and conflictive behavior?

Cohesive behavior is whatever brings wolves closer together, and conflictive behavior is whatever drives them apart from sharing within a family (Fentress et al. 1987). In table 2.2, actions in the categories "Care," "Proximity," and "Sexual" often serve a cohesive function; actions in "Flight/Fight" and "Humbleness" categories are often associated with conflict. However, any one action may occur in several contexts. For example, a "stare" might function in both cohesion and conflict, depending on its context.

We have seen that since wolf packs are families, basic family ties promote cohesion. However, from a deterministic perspective, each individual must also ensure its own survival first, or it cannot assist relatives. Thus, during food scarcity, competition and conflict may be viewed as a way of ensuring family survival over the long term. In this respect, the following aspects of social cohesion and conflict in wolf populations bear discussion: (1) the dominance hierarchy concept, (2) variation in individual temperaments and relationships, (3) access to food and mates within packs, (4) leadership, and (5) interactions among packs.

#### Age-Graded Dominance Hierarchy

A linear dominance hierarchy is the simplest way of describing conflict behavior in a wolf pack (see fig. 2.7A). According to that concept, the most dominant wolf is the one that wins fights over all others, and is called the "alpha." The "beta" loses fights with the alpha, yet wins over all others, and so on down the line. The wolf least likely to win any fights is called the "omega."

These terms (alpha, beta, omega) have been used in describing interactions among orphaned siblings in captive groups (Rabb et al. 1967; Folk et al. 1970; Zimen 1975, 1981; Fox 1980) as well as free-ranging wolves (Murie 1944; Haber 1968, 1977; Mech 1970, 1977c, 1993a; Peterson 1977). The terms may be appropriate in ambiguous situations in which the relatedness among pack members is unknown or complex (e.g., more than a single pair of breeders). However, I agree with Mech (1999) that the terms are inappropriate for typical packs consisting of parents and offspring (Packard 1980). Simon Gadbois (2002) has reviewed the complex, often ambiguous terms used in the literature on dominance.

The linear dominance hierarchy concept has been adopted and perpetuated by popular educational materials about wolves (Savage 1988; Lawrence 1993; McIntyre

1993). Wolf enthusiasts can usually distinguish easily between an alpha and an omega wolf by noting which carries the tail higher, as described in by Harrington and Asa in chapter 3 in this volume. However, in most wolf packs, family dynamics are more complex. Thus it is important to review the development of scholarly thought about the dominance hierarchy in wolf packs.

The classic work on this subject was conducted by Rudolf Schenkel (1947) on a pack of up to ten wolves kept in a 200 m<sup>2</sup> pen. His article was published in German, but an English translation by Agnes Klasson has long circulated among wolf biologists in North America. In that work, Schenkel wrote of "two sex orders of precedence," a "status order," a "rank order," a "dominance status order," and a "clear-cut hierarchy."

In the first book summarizing wolf natural history published since Schenkel's article, R. J. Rutter and D. H. Pimlott (1968, 43) wrote the following:

Normally, a wolf population is divided into *packs*, and a pack is an organization within which every wolf knows its social standing with every other wolf. Each pack has its own territory and operates as a unit in its relations with neighboring packs.

Dr. Niko Tinbergen, an internationally known authority on animal behavior, described a similar social order among Eskimo dogs in Greenland: "Within each pack the individual dog lived in a kind of armed peace. This was the result of a very strict 'pack order': one dog was dominant and could intimidate every other dog with a mere look; the next one avoided this tyrant but lorded it over all the others; and so on down to the miserable 'under dog.'"

We believe this describes the fundamental organization of a wolf pack. . . .

Mech (1970, 69), citing Schenkel (1947), also implied that wolves showed a linear dominance order within each sex (fig. 2.7B). This conceptual model, largely structured according to age, was reinforced by Zimen's (1976, fig. 5) study of a captive wolf pack that he formed by assembling unrelated wolves from three sources. (It is important to note that this was not a natural wolf pack consisting of a pair of parents and their offspring [Mech 1999].) Zimen (1981, 128) later acknowledged that any model of rank order is an oversimplification.

Several researchers who have observed larger wolf packs over several years in a wider range of contexts (e.g., competition over food and mates) have rejected

the hypothesis that all wolf packs fit the model of a linear dominance hierarchy (Lockwood 1976, 1979; Packard 1980; Zimen 1981; Mech 1999). Furthermore, K. B. MacDonald (1983, 1987) found that consistent temperament differences measured in captive wolf pups were not correlated with the probability of breeding in a nuclear family (Jenks and Ginsburg 1987; Schotté and Ginsburg 1987; Jenks 1988; Schotté 1988).

Based on studies of a larger sample of packs over multiple years (see table 2.1), I tend to think of the alpha behavioral profile as an internal state (or mood). Moods are subject to change as the health and environment of an individual change. According to a model of human behavior, moods are influenced by both temperament (heritable propensities) and character (learned styles of coping) (Cloninger 1986). This hypothesis is consistent with the stochastic perspective developed by behaviorists to understand conflictive behavior in other species (Appleby 1993; Barrette 1993; Moore 1993). Zimen (1982) expressed a similar notion in terms of the "age-graded dominance hierarchy" model of conflict within wolf packs.

What is this age-graded model? In interactions with adults, juveniles typically are more humble; thus older wolves effectively intimidate younger wolves. Littermates may squabble over food or during rough play, and pups are disciplined by older family members. As juveniles mature, conflict is more likely between members of the same sex; that is, females fight females and males fight males. This model has been presented in two ways: first, simply as separate linear hierarchies within each sex, influenced but not absolutely determined by age (Schenkel 1947; Zimen 1982), and second, as male dominance over females within each age class (Rabb et al. 1967; Fox 1971a, 1980; Lockwood 1979; Zimen 1982; van Hooff and Wensing 1987; Savage 1988). I hypothesize that the former is more likely in young nuclear families and the latter in disrupted or complex families (see table 2.1).

Theoretically, a predictable linear hierarchy is more probable in a social group when (1) individuals are added to the group one by one, (2) additions occur after each dominant-subordinate relationship has stabilized, and (3) there is a clear difference in fighting ability between the two individuals in each relationship (Chase 1974). For example, in the captive North pack (Packard 1980), there was a clear linear hierarchy among the mother and her two daughters of different ages: the mother interrupted squabbles between her daughters, and the older sister was more likely to chase her younger

sister than vice versa. However, the relationships among the females in the North pack were not reinforced by constant fighting, fear, or control by the breeding female. She was the mother, and her daughters had deferred to her ever since she started muzzle-biting them when they licked-up to her chin too insistently. Logically, the conditions favoring stable relationships are more likely to be met in small, young nuclear families like the North pack (fig. 2.7C) than in larger, older disrupted families (Packard 1989).

Although the typical wolf pack is a nuclear or extended family (Murie 1944; Mech 1970), field studies point to much turnover in packs and populations. These studies show that wolf populations consist of dynamic packs that are continually forming and dissolving, with a high annual turnover of offspring (Mech 1977b, 1987a, 1995d; Fritts and Mech 1981; Peterson, Woolington, and Bailey 1984; Messier 1985b; Fuller 1989b; Mech et al. 1998). By 3 years of age, most wolves have dispersed from their natal packs (see Mech and Boitani, chap. 1 in this volume), and deaths from disease (Ballard et al. 1997), fights with neighboring packs (Mech 1977b, 1994a; Mech et al. 1998), and hunting by humans (see Fritts et al., chap. 12 in this volume) further disrupt the stability of wolf families.

To understand the dynamics of social relationships within natural wolf packs, it is useful to distinguish among families with different histories (see table 2.1). The social relationships of captive wolves have been studied in detail in groups at five research centers and five zoos, representing a variety of different types of social groupings. However, of thirty wolf groups studied (92 group-years), only 34% of the groups were nuclear or step-families, and 50% were extended or disrupted families. L. D. Mech (personal communication) considers packs in the categories of "nuclear family" and "step-family" to be closest to those most frequently observed in stable wolf populations. Under the dynamic conditions of a colonizing or declining wolf population, the incidence of other types of families (e.g., "extended family" and "disrupted family" categories) may increase.

Often, the results of initial studies are perpetuated in popular literature, creating impressions that are difficult to dislodge. For example, observations of two dominant males that apparently allowed beta males to breed in captive packs have been repeated in several popular books (Lawrence 1993; McIntyre 1993; Savage 1988). Breeding by a beta male occurred in two of the first studies of captive wolves. Both groups were in the category

of "complex family"—that is, siblings without parents (Rabb et al. 1967; Zimen 1975)—a situation rarely, if ever, found in wild populations (Mech 1970, 1999; Mech et al. 1998). Without the stabilizing influence of parents, the siblings fought, and their behavior was described in terms of competition for the social roles of "alpha," and "beta." However, there is no objective way of measuring a "social role" independently of the behavioral profile of its occupant, so this explanation is both circular and anthropomorphic.

### Variation in Individual Temperaments

Individual behavioral profiles are a way of describing variation in temperament, analogous to "personality" in humans. One of the most challenging aspects of studying wolf social behavior has been understanding this variation among individuals. For example, Zimen (1975) observed distinct changes in the personalities of two hand-raised wolves as the result of a fight. Before the fight, Wölfchen was confident and assertive, carrying his tail high, challenging dogs outside the fence, and escalating conflict when challenged by his brother, Näschen. After being injured during the fight, Wölfchen's tail hung low, he no longer challenged outsiders, and he avoided conflict with Näschen. Wölfchen assumed an intimidated profile (high humbleness in table 2.2). In contrast, his brother Näschen assumed the confident profile previously typical of Wölfchen (low humbleness). A similar switch in behavioral profiles in the Ellesmere pack preceded daughter Whitey's assumption of the pup-producing role from her mother (Mech 1999).

In a debate about the heritability of dominance in social species (Appleby 1993; Barrette 1993; Moore 1993), three basic issues were identified: (1) which animal is assertive (individual temperament), (2) which is assertive with which (relationships), and (3) in what context conflict occurs. From a stochastic perspective, the claim is that it is not dominance, but rather the predisposition of each individual to escalate or reduce conflict in specific social contexts, that is heritable (Appleby 1993; Barrette 1993).

From this perspective, what we call a humble mood is associated with a low probability of conflict escalation in a specific interaction, in contrast to a confident mood (low humbleness), which is associated with a high probability of escalation. In wolves, it has been proposed that each individual has the potential for self-assertion, and

that this potential is realized when a wolf becomes a breeder (Schenkel 1947; Zimen 1981; Mech 1970, 1999).

Prior to Zimen's (1975) work, researchers had hypothesized that there were "born alphas" in each litter of wolf pups; in other words, measurable physiological variation within litters of pups was thought to predict later variation in their individual temperaments as adults (Folk et al. 1970; Fox and Andrews 1973). According to this deterministic model, it was logical that there would be polymorphism in temperaments within each litter so that some individuals would become breeders (alpha temperament) and some would cooperate in the care of the breeders' offspring (Rabb et al. 1967; Woolpy 1968; Woolpy and Eckstrand 1979). However, the hypothesis of "born alphas" has been tested and rejected for both captive (Lockwood 1976, 1979; K. B. MacDonald 1983; Ginsburg 1987; Schotté and Ginsburg 1987; Jenks and Ginsburg 1987; Ginsburg and Hiestand 1992) and wild wolves (Mech 1999).

Why isn't a dominant individual destined to always act dominant? According to a stochastic model, individual temperaments may change due to each individual's social experience (e.g., the predictability of interactions within a family) and mood state (e.g., the activity of neuroendocrine systems) (Packard 1980; Fentress 1982; Packard and Mech 1983; Packard et al. 1983; Fentress et al. 1987; McLeod et al. 1991, 1996).

Although our understanding of the neuroendocrine basis of mood state is still incomplete (Cloninger 1986; Overall 2001), sufficient information is available to formulate theories about which behaviors are indicators of neuroendocrine activity in canids. According to the models outlined in table 2.2, I would hypothesize that high serotonin is associated with the action patterns interpreted as a confident profile (e.g., high posture, tail high, ears forward) and low serotonin is associated with an intimidated profile (e.g., low posture, tail low, ears back). The communication function of these postures will be described by Harrington and Asa in chapter 3 in this volume. However, their association with serotonin-related neural networks needs to be tested.

Neuroendocrine systems, which affect moods and motivation, interact in complex ways (Cloninger 1986). According to one idea, when serotonin is low, the adrenal system is more likely to be activated. Fight behaviors are more likely to appear when noradrenaline-related neural circuits are activated, and avoidance behaviors (e.g., flight) are more likely when adrenaline-related circuits are activated (Sapolsky 2002; Watkins 1997, 11). In a



finding consistent with this model, aggressiveness in dogs was reduced by treatment with fluoxetine, which inhibits the breakdown of serotonin (Dodman et al. 1996).

In captive wolves, assertiveness changes with age, reproductive state, nutritional condition, traumatic experience (fights), and resource context (pups, mates, or food) (Zimen 1975; Fentress 1982; Fentress et al. 1987). During the few field studies in which wolves have been observable interacting for any length of time, few fights have been seen among pack members (Murie 1944; Clark 1971; Haber 1977; Mech 1988a). Mech (1999) has been impressed with the peacefulness of interactions among pack members, at least in summer. Most serious aggression in wolves is directed at non-pack members (see Mech and Boitani, chap. 1 in this volume).

The issue of "which wolf fights" within a family is better phrased as "which wolf is more likely to be in an assertive versus avoidance state more often." The personality changes that occur with age and reproductive experience (Mech 1970; Packard et al. 1983) suggest that the patterns described as "temperament" are a function of the shifting internal state of an individual. Behavioral profiles may be predictable as long as internal states are relatively stable; however, fluctuations occur when external conditions or internal states change.

In his review of the literature on dominance and stress, Gadbois (2002) clarified that researchers in the field of human personality distinguish between temperament and character. "Temperament" refers to the aspects of personality that change little over a lifetime and many be highly heritable. "Character" refers to the aspects of personality that change as individuals mature and learn styles of coping with stressful situations. I agree that this is an important distinction that should be considered in future studies of the individual variation in wolves.

Several researchers have attempted to use multivariate statistical techniques to determine the basic dimensions of variation in personality among captive wolves (Bekoff et al. 1975; Colmenares Gil 1979; Lockwood 1979; Packard 1980; van Hooff and Wensing 1987; Derix 1994). Although the variables and results differed among these studies, all the researchers agreed on one conclusion: both cohesive and conflictive behaviors need to be considered in describing the variation in the personalities of individual wolves. This conclusion is consistent with the observations of wild wolves mentioned above, which

suggested that aggressive interactions are infrequent except during competition over food and mates.

To date, each research group studying wolves has used different terms to define and categorize wolf action patterns (Zimen 1971, 1982; Fox 1971b; Bekoff 1972, 1979a; Goodmann and Klinghammer 1990; Derix 1994). This diversity is appropriate, given the different questions studied (Bekoff 1979a). However, this variation also limits our ability to compare wolf temperament and its heritability across captive packs.

Behavioral indicators of social stress are the subject of one of the unsettled debates about conflictive and cohesive behaviors in wolves (Schenkel 1967; Packard 1980; Zimen 1982; Fentress et al. 1987; McLeod et al. 1996; Haber 1996; Moger et al. 1998; Gadbois 2002). Schenkel (1967) pointed out that inexperienced observers tend to interpret an "over-the-muzzle-bite" as adult aggression, stressful for the pup that receives it. However, he interpreted this behavior differently, because pups do not avoid an adult after muzzle-biting. They come back for more, indicating a cohesive function for the behavior. Indeed, the pups' behavior seems to solicit more interaction. Schenkel (1947, 1967) noted that such juvenile behavior persists into adulthood, when grown offspring continue solicitous behaviors that elicit muzzle-biting or pinning in such a manner that they acquire a new function of appeasement (i.e., conflict reduction). Based on his field observations, Mech (1999) agreed with Schenkel's interpretation of these behaviors as non-stressful conflict within the context of cohesive relationships within a social group. However, determination of stress without an independent physiological measure such as urinary metabolites is problematic (Creel 2001; Creel et al. 1997, 2002).

Thus, the social environment within a wolf pack may at first persist as a stable, predictable set of relationships. However, two main dynamic factors can eventually affect the relationships among relatives: competition for food and sexual tensions resulting from maturation of offspring. To better understand cohesion and conflict within wolf packs, it helps to look separately at each of these contexts in which conflict occurs.

### **Conflict within Packs**

Are subordinate wolves stressed? Although extreme cases of individuals with elevated aggressiveness and stress hormones (urinary cortisol) have been reported for cap-

tive packs (McLeod et al. 1991; Moger et al. 1998; Gadbois 2002), researchers are only beginning to explore this question in wild populations (Creel 2001; Creel et al. 2002). Clearly not all wolves in each pack have equal access to food and mates. Studies of conflict over food will be reviewed below, followed by a discussion of conflict over mates and the apparent "incest taboo."

#### *Access to Food within Packs*

As Mech (1988a) watched the Ellesmere pack feed from a newly killed muskox carcass, the yearlings approached their father with highly exaggerated movements, curling their bodies dramatically, lowering their ears, and pawing widely into the air in a "groveling" manner (National Geographic Explorer 1988). Although the carcass potentially provided enough food for all, the breeding pair intimidated their offspring. They limited access to the meat until they had gorged enough to feed their pups and had torn off enough chunks to cache and eat at a distance in relative peace.

Without the exaggerated groveling, I have seen similar behavior in captive wolves feeding on a deer carcass (see fig. 2.2B). In the North pack, two adult daughters approached their father in a low crouch, and he pinned each to the ground with an inhibited muzzle-bite typical of a care-giver interrupting begging pups. The grown daughters stayed away from the carcass until their father was finished. In this nuclear family, order of feeding at the carcass was correlated with appeasement, not conflict, behaviors (Packard 1980, 163). Appeasement gestures reduce the probability of escalation of conflict after it has started.

In the captive South pack (a disrupted family), I watched two 6-month-old juveniles approach their foster father while he was feeding from a deer carcass. When he snarled at them, they lay down and looked the other way until he returned to chewing on the carcass (fig. 2.8). Not completely intimidated, the juveniles crept closer while the male was feeding and eventually fed beside him without conflict. In this family, in contrast to the North pack, the order of feeding at the carcass was correlated with conflict interactions, not with appeasement (Packard 1980, 163). Apparently the juveniles had not yet learned to use ritualized appeasing gestures, as their small size conveyed little threat to their foster father. The most easily intimidated were two older sisters, who also had the lowest blood indicators of nutritional condition (blood urea nitrogen and hemoglobin).



FIGURE 2.8. Juveniles that behave solicitously, like pups, are more likely to gain access to food defended by adults, which may affect their nutritional condition and dispersal during times of food scarcity.

Thus, elements of both cohesion and conflict can be associated with interactions around a carcass large enough to be shared by family members. The individuals least likely to be intimidated (i.e., most likely to act like pups) are the ones most likely to gain access to the carcass. The "appeasement" gestures derived from juvenile care-soliciting behavior provide clear signals that a younger individual is unlikely to escalate conflict, and elicit care-giving tolerance from other family members. Those individuals most likely to be intimidated in the context of food are the older siblings in poorer nutritional condition, which show fewer cohesive interactions with parents and more conflict with siblings.

Appeasement gestures reduce conflict only within relationships in which interactions have been patterned by repeated food solicitation and delivery (Schenkel 1967). Individuals in such cohesive relationships have been able to learn the contingencies of one another's actions and to modify their own behavior accordingly. In contrast, fighting between a confident wolf and an intimidated individual (e.g., siblings or strangers) involves jockeying for position to bite without being bitten (Schenkel 1967; Golani and Moran 1983; Mech 1993a).

By 2 months of age, pups in the Ellesmere pack had learned complex tactics for defending and acquiring pieces of arctic hare carcasses (Packard et al. 1992). The hare carcasses were small enough (about 1–3 kg, or 2.2–6.6 pounds) that one pup could initially monopolize the meat, while siblings waited and watched for an opportunity to grab a piece beyond lunging distance of the

tive packs (McLeod et al. 1991; Moger et al. 1998; Gadsbois 2002), researchers are only beginning to explore this question in wild populations (Creel 2001; Creel et al. 2002). Clearly not all wolves in each pack have equal access to food and mates. Studies of conflict over food will be reviewed below, followed by a discussion of conflict over mates and the apparent "incest taboo."

#### *Access to Food within Packs*

As Mech (1988a) watched the Ellesmere pack feed from a newly killed muskox carcass, the yearlings approached their father with highly exaggerated movements, curling their bodies dramatically, lowering their ears, and pawing widely into the air in a "groveling" manner (National Geographic Explorer 1988). Although the carcass potentially provided enough food for all, the breeding pair intimidated their offspring. They limited access to the meat until they had gorged enough to feed their pups and had torn off enough chunks to cache and eat at a distance in relative peace.

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owner. Several researchers have noted that the wolf in possession of a food object is more likely to escalate conflict than an onlooker, even if the onlooker is bigger, older, or more assertive in other contexts (Mech 1970, 1999; Lockwood 1979; Zimen 1981; Townsend 1996). Likewise, it is very difficult to teach a hand-reared wolf to give up a bone or refrain from stealing steaks off the table!

According to a deterministic perspective, parents defend their right to monopolize food in order to continue producing pups, for which their immature older offspring will help care (Harrington and Mech 1982c, 1983). However, it is unclear whether alloparenting is a help or a hindrance to breeding wolves (Harrington and Mech 1982c; Harrington et al. 1983; Ballard, Ayres, Gardner, and Foster 1991). Indeed, its proximate costs and benefits are likely to vary with the wolf-prey dynamics of each population (Harrington et al. 1983; Mech et al. 1998).

A stochastic perspective would posit that if the physical environment is harsh, then strategies involving food sharing among relatives, high variation in rates of maturation, and a low probability of dispersal are likely to become fixed in mammalian populations (Honeycutt 1992; Lacey and Sherman 1997). Wolves certainly show a high degree of variation in rates of sexual maturation (see Kreeger, chap. 7 in this volume). Furthermore, food sharing in wolves appears to be conditional, varying with complex interactions among prey availability, maturation rates, and social conditions (Packard and Mech 1983; Ballard et al. 1997; Mech et al. 1998). Because of varying food conditions, the proportion of offspring dispersing also varies (see Mech and Boitani, chap. 1 in this volume), reflecting the dynamic competitive milieu.

When food is scarce, breeders may selfishly maintain their own nutritional condition at the expense of other family members, especially non-pups. Competition among siblings escalates in the context of food, until those that are more intimidated follow at a distance, dropping farther behind as they become more malnourished. Eventually they disperse (Mech et al. 1998).

#### *Access to Mates*

What about conflict in the context of mating? While offspring remain with their parents, there is no issue of sexual rivalry as long as the offspring are reproductively immature or defer to their parents (Packard et al. 1983, 1985). However, sexual rivalry can occur when offspring remain in the pack past the age of reproductive maturity

(Derix et al. 1993). In most packs, dispersal relieves this competition (see Mech and Boitani, chap. 1 in this volume). However, in larger packs enjoying a surfeit of food, as in the reintroduced Yellowstone population, sexual competition may occur among reproductively mature siblings (D. W. Smith, unpublished data).

Exclusive breeding by the dominant pair in a large nuclear family (e.g., having more than one mature member of each sex) apparently results from a delicate balance of asymmetric mate choice and same-sex rivalry (Packard et al. 1983, 1985; Schotté and Ginsburg 1987; Packard 1989). Monogamous relationships are likely in nuclear families only as long as (1) offspring are not reproductively mature, (2) the breeders are more attracted to each other than to their offspring, and (3) courtship between sibs is interrupted.

If these conditions are not met, plural breeding may occur (e.g., more than one female may reproduce within a pack in a given season). The term "plural breeding" is used by researchers studying cooperative breeding in other mammals (Solomon and French 1997) and is synonymous with the term "multiple breeding" used by Mech and Boitani in chapter 1 and elsewhere in this volume. A possible example of the apparent release of plural breeding was observed in the West pack on Isle Royale. Only one pair in the pack was reproductive until the breeding male disappeared prior to the breeding season in 1971 (Peterson 1977). When the breeding female accepted a mate from within the family, a second pair also successfully copulated (Peterson 1977, 80–84). In 1972, a subordinate female copulated with the West pack dominant male. Even though the subordinate was twice chased off the island by the dominant female and her companions, she returned each time (Peterson 1979). These observations illustrate the interaction of cohesion and conflict in determining the proportion of monogamous relationships in wolf populations.

Polygamous relationships have been reported in a few wolf step-families in which one of the breeding pair has died and a new breeder has immigrated into the pack (Haber 1977; Smith 1997, 2000), although polygamy was not reported in several other step-families (Rothman and Mech 1979; Fritts and Mech 1981; Mech and Hertel 1983). When a widowed breeder accepts an unrelated mate, the new step-parent may be less likely to interrupt rivals and more likely to be attracted to younger pack members in addition to the widowed breeder.

Occasionally, a cohesive relationship may persist be-

tween two adult males even though the less assertive individual appears to be more reproductively active (Murie 1944; Rabb et al. 1967; Haber 1977). In such cases, the assumption has been made that the more reproductively active wolf was the breeder, although the actual paternity of offspring is difficult to assess without genetic testing.

As indicated above, the proportion of monogamous packs (i.e., only one pair breeding per season) in the wild is high (Harrington et al. 1982). In captive packs in which more than one mature female was present and no dispersal was possible, plural breeding occurred in 30% of fifteen pack-years (Packard 1980). However, multiple litters were successfully raised in only 13% of these fifteen cases (Packard 1980); the losses were due to infanticide by females (Altmann 1974, 1987). Infanticide was also reported by McLeod (1990).

In captive wolves, mate choice may be influenced by sexual rivalry (Derix et al. 1993). For example, I was puzzled by the unsuccessful attempts of the North pack female, Chenequa (F60), to solicit sexual interest from an older brother, Negaunee (M64), after their father died. She stood near her brother, pranced coyly, rested her chin on his back, flagged her tail near him, and marked near his urine without eliciting a response. Why was Negaunee unresponsive to such a solicitous female? Often his older brother was looking over his shoulder (fig. 2.9)! Subsequently, Negaunee and Chenequa copulated during the night, when their older brother was sleeping. When the brother awoke and found his siblings in a copulatory tie, he rushed over and lunged at them. Big brother was too late, however. One tie was enough, and 9 weeks later, Chenequa produced pups in the same den as her mother.

#### *Incest Avoidance*

Is incest common in wolf packs? Incest is not common in wild wolves when they can choose mates other than close relatives (D. Smith et al. 1997). Packard (1980) hypothesized that close relatives in natural populations would be unlikely to form a pair bond that endured longer than a season or two. Genetic studies tend to confirm this hypothesis; in Denali National Park and the Superior National Forest of Minnesota, breeders are more distantly related to each other than neighboring packs are to one another (D. Smith et al. 1997). However, on Isle Royale, where there is no choice, wolves do breed with their close relatives (Wayne et al. 1991). During re-



FIGURE 2.9. Although a young male is being courted by his sister (on the left), he is unlikely to reciprocate as long as his older brother (on the right) is looking over his shoulder.

colonization of the Rocky Mountains, extensive dispersal should tend to reduce the probability of inbreeding (Boyd and Pletscher 1999; Forbes and Boyd 1996).

Does conflict in the context of courtship in wolves (Derix et al. 1993) serve a function analogous to that of parental manipulation in eusocial species (Lacey and Sherman 1997)? Currently, there is no evidence that nonbreeding adult wolves are physiologically suppressed, even under extreme conditions in which there is no option for dispersal (e.g., in captive packs) (Packard et al. 1985). In the captive North and South packs I studied, the nonreproductive adults all showed hormonal cycles typical of individuals that had reproduced. Thus, they retained the physiological readiness to breed (Packard et al. 1983, 1985), unlike African wild dogs (Creel et al. 1997). Although urinary indicators of stress may vary with aggressiveness (Gadbois 2002; McLeod et al. 1996), they may not be correlated with reproductive status.

Most nonbreeding adults within wild packs are merely in a transitory nonreproductive state (Mech et al. 1998). They may move into a breeding position within the natal pack if an opposite-sex parent dies and is replaced by a step-parent, they may disperse and start a new family, or they may enter a disrupted family as a step-parent (Rothman and Mech 1979; Fritts and Mech 1981; Mech and Hertel 1983; Packard and Mech 1983; Ballard et al. 1987; Mech et al. 1998). Similarly, senescent breeders that have lost a mate may continue to associate with the pack in a nonreproductive role (Mech 1995d; Thurston 2002). The probability of transition between these social roles will depend not only on the develop-

mental history of each individual (possibly slowed by poor nutrition), but also on the dynamics of prey availability (Mech et al. 1998).

In summary, parents are more likely to escalate, and offspring to reduce, conflict in the usual nuclear family pack. In disrupted families, step-families, and complex packs with multiple breeders, the outcome of conflict for food and mates is more difficult to predict, as it depends on a complicated interaction of intrinsic (nutritional condition, reproductive state, temperament, relationship, relative attractiveness of potential mates) and extrinsic factors (prey and mate availability).

### Leadership

Mech (1970, 73) defined leadership as "the behavior of one wolf that obviously controls, governs, or directs the behavior of several others." The first pack that he watched on Isle Royale contained a dynamic male who was consistently out in front of his family (Mech 1966b). Mech (1977c, 530) concluded that "the male leader guides the activities of the pack and initiates attacks against trespassers. Pack underlings can, however, sometimes effectively protest their leader's actions." Zimen (1981, 173) agreed that leadership in wolf packs is a "qualified democracy." This conclusion accords with a deterministic perspective.

The degree of authority the dominant male has over the pack has been disputed, however. Based on observations of a captive pack, Fox (1980, 128) asserted that there is "an alpha male who not only rules over the males but is the leader of the pack. He is the decision-maker. Other wolves, even older ones, respond to him submissively and affectionately as would cubs to their parents. Allegiance to the leader helps keep the pack together." Nevertheless, as Zimen (1981, 173) wrote, "no member decides alone when an activity is to begin or end, or which way or at what speed the pack is to move, or exercises sole power of command in any other activities that are vital to the cohesion of the pack. The autocratic leading wolf does not exist."

So, is the breeding male the leader of a wolf pack or not? Mech (2000a) has emphasized the concept of one-way, autocratic control by both parents in each family, consistent with the deterministic perspective. Taking a stochastic perspective, I like to emphasize the probability that parents influence offspring, but offspring also influence their parents. Wolf families can be so diverse

(see Mech and Boitani, chap. 1 in this volume) that both models probably have merit, depending on how the term "control" is defined and on the history of relationships within the pack.

Similar questions about leadership have been addressed by students of primates, and Rowell (1974) has suggested that researchers test the following hypotheses: (1) that one individual receives attention at each activity change, (2) that one individual is consistently in front of a line during directional movement, (3) that one individual defends the group, and (4) that the actions of others are policed by one individual.

Let us first examine the hypotheses that breeding male wolves are more likely to be the "attention center" and "at the front of the line." The notion that the breeding male is the center of the pack's attention may be traced back to Schenkel's (1947) description of behavioral expression in the two wolf packs he watched at the Zurich Zoo. He described the breeding pair as the center of attention for family members and the breeding male as the lead wolf. However, he was not able to document leadership during directional movement as it is observed in the field when wolves travel single file.

On a similar theme, Murie (1944, 28) enlivened his account of the East Fork pack in Denali National Park by describing a certain male as "lord and master of the group although he was not mated to any of the females." What he meant by "lord and master" is not clear, and he could not have known whose mate the male was. However, in his description of the interactions within the family, Murie gave the impression that the center of attention shifted among several individuals as they departed from and arrived at the den.

The "attention center" hypothesis has not been tested systematically for wolves in captive or field studies. Lockwood (1979) proposed that it might be a better model than a "dominance hierarchy" to describe the social interactions among wolves. However, the two measures of attention that he used (social proximity and looking across a barrier) did not account for the variation in social structure that he measured in seven captive packs over 3 years. Lockwood recommended that relations among wolves be analyzed in terms of dyads (e.g., which wolf looks at which more often?). In the few places where one can watch wolves in the field, it would be feasible to note the direction in which pack members look during a change in activity state (e.g., from resting to traveling). Although I know of no field studies in which

such data have been collected, future research should focus on testing the attention center hypothesis regarding leadership in wolves.

The object of an individual's attention is likely to change with its mood (i.e., its internal state). When an individual's prolactin level is high, for example, pups should be the center of its attention. When a female is in estrus, she is likely to receive the attention of males. Thus, without knowledge of internal state and external stimuli, researchers are unlikely to be able to test how the center of attention shifts in a wolf pack.

Offspring are clearly more likely to follow their parents than vice versa (Mech 2000a). This pattern is consistent with the following response that develops in 2-month-old pups (Packard et al. 1992) and is reinforced in juveniles that gain access to food by following adults during their first year (Mech 1966b; Haber 1977; Peterson 1977; Mech et al. 1998).

Are breeding males more likely to be at the head of the line during travel? Generally, yes (Mech 1966b; Mech 2000a), except during the courtship season, when the breeding female is usually followed by her mate (Mech 1966b; Peterson 1977). Even when younger pack members forge ahead of a breeder (Murie 1944; Haber 1977; Mech 2000a), they appear uncertain about direction and take their cues from the breeders (Mech 1966b; Peterson 1977).

The Ellesmere breeding female followed Left Shoulder on 76% of twenty-nine occasions when departing from the den and on 67% of seventy occasions when the wolves were already traveling (Mech 2000a). In 1993, when no pups were present, and three yearlings begged more often from Left Shoulder than from the breeding female, the female followed Left Shoulder significantly more often than vice versa. Apparently Left Shoulder was a good source of information about the location of food. In 1996, when no yearlings were present, there was no difference between Left Shoulder and his mate in their order of travel (Mech 2000a).

Leadership during travel was studied in three Yellowstone packs during early and late winter sampling periods from 1997 to 1999 (Peterson et al. 2002). The factors influencing leadership included the pack, the season, and the type of measure used (frequency or duration). In March, breeding males were significantly more likely than their pregnant mates to be in the lead in the Rose Creek and Druid packs, but not in the Leopold pack. In November/December, there was no significant differ-

ence between the breeding male and female in their frequency of being in front. The Rose Creek pack, however, came very close to showing a significant difference ( $P = .056$ ), with the male leading. Compared with non-breeders, the breeders were more likely to be in front in the two smaller packs (Leopold and Druid), but not in the larger Rose Creek pack. These data were collected during a period of social transition for breeding females in the Druid and Rose Creek packs.

In nuclear families, the breeders are the most likely to trot directly and confidently toward a goal, to be solicited by hungry juveniles, and to be followed by family members. However, variations on this theme would be predicted in step-families or extended families. Consider a pack that accepts an immigrant step-father who is less familiar than the rest of the pack with the activity and movements of prey within the home range. The stochastic model predicts that pack members would be likely to continue to follow the experienced breeding female more often than the inexperienced step-father (at least until he became a predictable source of food). This pattern was documented in the Druid pack when they accepted an immigrant male from the neighboring Rose Creek pack (Peterson et al. 2002). Likewise, if the movements of a brother became a better predictor of food than the movements of an aging father, then one would predict that the younger male would attract more followers than the older male.

### Conflict between Packs

As Rolf Peterson (1977) watched from an airplane over Isle Royale, the East pack encountered a scent post. First the breeders investigated the urine odor, then the younger pack members checked it. The breeding female reversed her direction and led the pack out of the edge of its territory and back toward the center. The scent was from the pack's neighbors, the West pack.

The West pack's range had covered the entire island until two changes occurred: (1) the pack's original breeding male died, and (2) their major prey (moose) became localized to the western end of the island (Wolfe and Allen 1973; Peterson 1977). A pair had then split from the West pack, found an eastern area where they could subsist on beavers during the summer, and produced pups of their own, becoming the East pack.

The reaction of the East pack breeders to the West pack's scent was predictable, given that direct encounters

during territorial trespasses escalate rapidly, resulting in chases, injury, and death (Murie 1944; Mech 1966b, 1993a, 1994a; Marhenke 1971). Fights probably escalate most rapidly between breeders of the same sex. Are male wolves more likely than females to lead the pack against hostile neighbors? Unfortunately, few territorial encounters have actually been witnessed (Mech 1993a), but breeders and immatures of both sexes have been killed during territorial trespasses (Mech et al. 1998).

The conflict between packs is probably related to competition for food and mates. In contrast to conflicts within packs, which are inhibited by cohesive family relationships, fights between packs are likely to be injurious. Mortality due to conflict with hostile neighbors varies among wolf populations (see Mech and Boitani, chap. 1 in this volume).

### Flexibility of Behavior: Physical Factors

Wolves can adjust to a wide range of physical factors in addition to the variation in social factors described in the previous section. This flexibility of behavior is illustrated in studies of activity patterns and intelligent problem solving.

#### Activity Patterns

How does one's dog know it is about 3:30 P.M. each day, such that he barks at his food bowl if he is not fed as usual by 4:00? The ability of wolves to learn predictable correlations among prey activity, temperature, and light intensity is not surprising to anyone who has watched a captive canid develop expectations of feeding time. When predictive cues fluctuate with season and weather, canids are flexible enough to learn new patterns and to adjust their activity accordingly. It takes my dog about a week to adjust to going off daylight savings time. The activity patterns of wolves can shift to adjust to changes in predictable patterns of temperature (Harrington and Mech 1982c; Fancy and Ballard 1995), prey activity (Oosenbrug and Carbyn 1982; Scott and Shackleton 1982; Fuller 1991; Theuerkauf et al. 2003), probability of encountering humans (Boitani 1986; Vilà et al. 1995), presence of a carcass (Harrington and Mech 1982c; Ballard, Ayres, Gardner, and Foster 1991; Mech and Merrill 1998), and reproductive season (Harrington and Mech 1982b,c; Ballard, Ayres, Gardner, and Foster 1991; Vilà et al. 1995).

Do wolves have an innate circadian rhythm? Mech and Merrill (1998) found that summer departures from the Ellesmere den occurred at predictable times (between 2200 and 0400). They proposed that this departure pattern was due to an internal rhythm because external triggers such as daybreak and nightfall were absent in summer at 80° N latitude. They cited supporting evidence from four denning studies in Alaska and Canada at latitudes ranging from 46° to 64° N (Kolenosky and Johnston 1967; Haber 1977; Scott and Shackleton 1982; Ballard, Ayres, Gardner, and Foster 1991). However, Mech and Merrill were not able to test alternative hypotheses related to several covariates (e.g., light intensity, temperature, food availability, and human activity). Variation in activity peaks has been reported from four other studies at latitudes also ranging from 42° to 64° N (Murie 1944; Harrington and Mech 1982c; Vilà et al. 1995; Theuerkauf et al. 2003).

In northwestern Alaska, the activity of twenty-three wolves (monitored continuously by satellite telemetry) was correlated with temperature in all seasons (Fancy and Ballard 1995). During summer, activity peaks occurred at 0600 and 2200. Activity was more likely in the morning than in the afternoon during summer, but occurred at a lower rate throughout the day in winter than in summer. On winter days in the Superior National Forest, wolves were more likely to be inactive (65% of the time) than traveling (28%) or engaged in activities such as feeding or socializing (Mech 1992). In summer, lower activity levels during midday may have been due to heat intolerance (Harrington and Mech 1982c). Whether such seasonal shifts in activity patterns are due to the wolves' own intolerance of heat or the activity patterns of their prey is hard to determine (Oosenbrug and Carbyn 1982; Scott and Shackleton 1982; Fuller 1991; Jędrzejewski et al. 2001).

In Spain, the time of day when two females were most active changed with the age of their pups (Vilà et al. 1995). During lactation, these females were most active during daylight, although their total activity was low (15%). When their pups were 2–5 months old, the females were more active at night, like their mates. During winter, the females' activity increased to 24% of the time and was relatively more evenly distributed across daylight (12%), dusk (18%), night (35%), and dawn (32%) (see also Theuerkauf et al. 2003).

Activity patterns also vary in captive packs. In one pack, daylight activity peaked in the morning and eve-



ning (MacDonald 1980). Morning activity associated with a cleaning routine was greater in a zoo enclosure than in a secluded naturalistic enclosure in Mexico (Bernal and Packard 1997). The overall amount of activity did not differ between wolves housed in outdoor chain-link kennels and in large (0.3–0.5 hectare) enclosures with natural vegetation in Minnesota (Kreger, Pereira et al. 1996).

The seasonality of courtship and reproduction may also influence wolf activity patterns. The frequency of overall interactions and of aggression peaked during winter in several captive packs (Zimen 1981; Fentress et al. 1987; Servín-Martínez 1991). The occurrence of such peaks during autumn in another captive pack may have been specific to the instability of the relationship between an aging father and a maturing son (Packard 1989).

Thus, wolves develop predictable activity patterns, which may vary across seasons, locations, and individuals. Insufficient evidence is available to tease apart the effects of correlated external variables such as light intensity, temperature, and prey activity. If wolves are like other carnivores, we would expect the variation in their activity patterns to be a complex function of (1) daily internal cycles, (2) seasonal shifts in external stimuli from the physical environment (e.g., temperature, light, prey activity, human activity), (3) variation in the internal states of individuals (e.g., nutritional condition, reproductive phase), and (4) expectations of the actions of companions.

### Learning and Intelligence

Why are wolves—or their domesticated descendants, dogs—so intelligent? Or are they? How do they learn to respond appropriately to changes in predictable patterns within their physical environment? To what extent does the social environment of the pack assist young wolves in learning what to expect from their physical environment?

Intelligence is the ability to apply knowledge gained from experience to novel problems (Byrne 1995). For example, a captive wolf learned to open his cage door by pulling a pulley rope that his caretakers had used predictably (Fox 1971d). From a human perspective, the “novel” problem for the wolf was how to open the cage door, obviously a challenge not encountered in the history of the species. By watching his caretakers, the wolf could have learned to associate the rope with the open-

ing of the cage door. Grabbing and pulling on the rope could be considered intelligent behavior because it opened the door. However, wolves also grab and pull on the noses, ears, and tails of exhausted prey (see Mech and Peterson, chap. 5 in this volume). To what extent was insight involved in this seemingly intelligent action, and to what extent was it motivated by reflex-like actions typical of all members of the species? Is learning any less intelligent if it is guided by programmed stimulus-response linkages shaped by problems solved in the history of generations of ancestors?

Questions related to wolf intelligence have been addressed in studies of (1) standardized problem-solving tasks in captivity (Cheney 1982; Frank and Frank 1984, 1985; Frank et al. 1989; Hiestand 1989; Hare et al. 2002), (2) the development of flexible hunting skills (Sullivan 1979; Crisler 1958; Mech 1988a, 1991b), (3) the modification of behavior contingent on the actions of social companions (Schenkel 1947; Moran and Fentress 1979; Moran et al. 1981; Lyons et al. 1982; Golani and Moran 1983; Havkin and Fentress 1985; Townsend 1996; McLeod and Fentress 1997), and (4) anecdotes in which wolves have solved unusual problems (Fox 1971d; Slade 1983; Fentress 1992; Ginsburg and Hiestand 1992; Mech 1999).

A standard approach to assessing wolf intelligence is to compare it with dog intelligence. Frank and Frank (1987) found that four juvenile wolves were better at standardized problem-solving tasks than were juvenile dogs raised in the same manner (cross-fostering to a wolf mother). As they had predicted based on models of canid domestication (Scott and Fuller 1965; Scott 1967; Frank and Frank 1987), the dogs were better at tasks that involved training by a human (Frank and Frank 1982; Frank et al. 1986, 1989). However, the wolves responded to the restraint of a leash or a box in an emotional way that seemed to interfere with their performance of the standardized tasks (Frank and Frank 1983). Was this really a fair test? Or did the physical restraint trigger an emotional response that has become neurally programmed in wolves? Does this neural programming exist because wolf ancestors that struggled against restraint (when grabbed by a bear or other predator, for example) were more likely to have survived than those that did not?

Addressing such questions about the interaction of emotional and learning systems in canid evolution, Hiestand (1989) tested spatial orientation in nine hand-reared wolves (Frank et al. 1986) and forty adult German

shepherds using ropes hanging from a ceiling. She did not use restraint; rather, she called out "good" when the individual pulled the correct rope. She opened a gate and/or petted the individual lavishly when it learned to pull two or three ropes in a pre-established order. She was gruff with or ignored individuals that did not behave correctly. Apparently, social interaction with a human caretaker was as effective a reward in training wolves as it is for dogs (Frank and Frank 1988; Hiestand 1989). The two adult wolves had little difficulty learning the three-rope task. The seven juveniles learned the two-rope task, but had more difficulty with the three-rope task. The adult dogs showed high individual variation: 12% learned the three-rope task, 35% learned the two-rope task, and 13% failed to learn to pull even one rope.

The wolves acted differently from the dogs when initially placed in the testing arena: they spontaneously oriented to physical objects in their environment and learned the one-rope task in significantly fewer trials than the dogs (Hiestand 1989). The wolves also irreparably shredded more ropes than the dogs! Hiestand hypothesized that wolves are more attentive to physical objects in their environment than are dogs, as noted anecdotally by others (Fentress 1967, 1992; MacDonald 1980; Zimen 1981).

The wolves behaved as if they had both the neuroendocrine programming that attracted them to situations in which they were likely to learn and the attentiveness to social companions that shaped their behavior in ways that were effective in attaining their immediate goals. However, wolves also show high individual variation in learning ability in captivity (Sullivan 1979; Cheney 1982; Lyons et al. 1982; Slade 1983; Hiestand 1989). Hypotheses about heritable differences in emotional and learning systems still need to be tested with sample sizes adequate to account for individual variation in different rearing environments.

Claims that dogs are more skillful than wolves at reading human gestures must be evaluated critically. Hare et al. (2002) documented differences between wolves and dogs in a series of object-choice tests. The seven adult wolves less often used human gestures (gazing, pointing, and tapping) correctly to choose between two overturned food bowls, one baited out of view of the subjects. The subjects were tested in locations familiar to each, a small pen for the wolves and rooms for the dogs.

The degree to which such findings can be generalized is questionable for several reasons. First, the dogs were

raised and housed continuously with humans in several households, whereas the wolves were raised with humans for 1.5 to 5 weeks, then housed outside with a wolf pack that had daily short-term contact with the experimenter (see supporting online material linked to Hare et al. 2002). No details were given about whether wolves and dogs had equal experience with humans delivering food in bowls. Second, the mean age of the wolves (6 years) was greater than that of the dogs (3.5 years), and age is important in the development of social cognition, at least in primates (Tomasello et al. 2001). Third, with such a small sample, a set of clever dogs or dull wolves may unintentionally have been used. Individual variation in how dogs and wolves respond to standard cognitive tests is high (Frank and Frank 1988; Hiestand 1989). Fourth, wolves respond to mechanical devices differently from dogs (Zimen 1981; Cheney 1982), as noted above. This fact accords with the observation (Hare et al. 2002) that wolf performance did not differ from that of dogs in a test involving food in a film canister in the experimenter's hands. Last, the use of standard cognitive tests across species can be problematic (Shumaker and Swartz 2002).

What are the indicators of learning and intelligence in wild wolves? Peters (1978, 1979) proposed that wolves learn to navigate in familiar landscapes by forming learned associations analogous to a cognitive map. However, because wolves are in no way unique in this ability (Tolman 1955; Hauser 2000; Santin et al. 2000), it is questionable whether the use of cognitive maps distinguishes wolf intelligence from that of any other mammal.

The wolf's diversity in hunting skills across a wide range of ecosystems (see Mech and Peterson, chap. 5 in this volume) could also be considered an indicator of flexible problem solving. Both spatial orientation and flexible hunting skills develop within the social environment of the pack, potentially providing a window of opportunity for individuals to learn about the specific physical environment in which they were born.

The social context of the pack has the potential to affect learning by pups in several ways. For example, in an episode of chasing play, I watched one pup "cut the corner" and grab a sibling that had evaded his chaser by making a sharp right turn. Later, such maneuvers were repeated, reminding me of a filmed hunting episode in which one wolf cut the corner and was able to grab a caribou that had evaded another wolf (Peace River Films 1975). The precursors to such combinations of actions in

the caribou hunt could have been learned during the play routines of pups.

Another question that often arises in studies of intelligent behavior is the degree to which individuals modify their own actions contingent on the actions of others (McLeod 1987, 1996; McLeod and Fentress 1997). For example, adults in one captive pack were less likely to cache food when another wolf was present, consistent with predictions based on a model of deceptive communication (i.e., individuals withheld information about a food source when the goal was to keep the food for themselves) (Townsend 1996). However, 71% of the caches made in the same study were recovered by wolves other than those that made them, and 43% of these recoveries occurred in the presence of the cacher without retaliation. Much more study needs to be done on this subject.

The ability of wolves to solve novel problems often appears to draw on both instinct and experience. Left Shoulder was presented with a novel problem one day in 1988 when a muskox wandered near his pack's den, which was at the base of a cliff. The nursing female initially rushed over to the intruder, then gradually lost interest and lay down out of sight. Alarmed by the wolves, the muskox backed up to the cliff in a typical defensive maneuver also observed by Mech (2000a). The muskox stood directly in front of the den entrance, while the pups were a hundred meters away from the security of the den!

First, Left Shoulder picked up an abandoned arctic hare carcass and delivered it to the pups, capturing their attention for a short period. However, the satiated pups rapidly lost interest and started wandering. Left Shoulder trotted directly across a stream to a sandy bluff, dug

out a cache (at least 8 days old), and delivered it to the pups. The cache held the interest of the pups, and they stayed away from the den. With no wolves nearby, the muskox relaxed and wandered away from the den entrance. Left Shoulder's "problem" was solved. To what extent was his action insightful?

In a similar episode in which another muskox assumed a defensive position in front of the Ellesmere den, Mech (2000a) believed that Whitey behaved in an insightful manner by bark-howling and directing yearlings to a position off to the side so that the muskox could escape. From a deterministic perspective, wolves need to be insightful in order to cooperate in capturing prey and in defending the pack against enemies (Fox 1975, 1980; Haber 1996). However, the extent to which groups of wolves actually do cooperate in hunting has been questioned (Schmidt and Mech 1997; see Mech and Boitani, chap. 1 in this volume).

From a stochastic perspective, the ability of wolves to solve problems under a wide set of circumstances may be explained by basic learning processes shared by all mammals (Frank et al. 1989; Fentress 1992): (1) innate, simple decision rules that govern general learning situations encountered in the evolutionary history of the species, (2) the ability to learn specific predictable consequences of their actions (operant conditioning), (3) the ability to associate diverse sets of cues (e.g., smell, sound, and taste of a prey item) with specific predictable situations (associative learning), and (4) emotional thresholds associated with the social context of learning and response to novelty (affective state). At issue is the degree to which intelligent behavior in wolves reflects ancestral knowledge stored in the genome and the degree to which individual experience results in novel insight.