

A PROPOSED ETHOGRAM OF LARGE-CARNIVORE PREDATORY BEHAVIOR, EXEMPLIFIED BY THE WOLF

DANIEL R. MACNULTY,* L. DAVID MECH, AND DOUGLAS W. SMITH

Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building,
1987 Upper Buford Circle, St. Paul, MN 55108, USA (DRM)

Biological Resources Division, United States Geological Survey, Northern Prairie Wildlife

Research Center, 8711 37th Street SE, Jamestown, ND 58401, USA (LDM)

Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190, USA (DWS)

Although predatory behavior is traditionally described by a basic ethogram composed of 3 phases (search, pursue, and capture), behavioral studies of large terrestrial carnivores generally use the concept of a “hunt” to classify and measure foraging. This approach is problematic because there is no consensus on what behaviors constitute a hunt. We therefore examined how the basic ethogram could be used as a common framework for classifying large-carnivore behavior. We used >2,150 h of observed wolf (*Canis lupus*) behavior in Yellowstone National Park, including 517 and 134 encounters with elk (*Cervus elaphus*) and American bison (*Bison bison*), respectively, to demonstrate the functional importance of several frequently described, but rarely quantified, patterns of large-carnivore behavior not explicitly described by the basic ethogram (approaching, watching, and attacking groups). To account for these additionally important behaviors we propose a modified form of the basic ethogram (search, approach, watch, attack-group, attack-individual, and capture). We tested the applicability of this ethogram by comparing it to 31 previous classifications and descriptions involving 7 other species and 5 other wolf populations. Close correspondence among studies suggests that this ethogram may provide a generally useful scheme for classifying large-carnivore predatory behavior that is behaviorally less ambiguous than the concept of a hunt.

Key words: behavioral classification, *Bison bison*, *Canis lupus*, carnivore, *Cervus elaphus*, ethogram, predator behavior, predator–prey interaction, wolf

The description and classification of behavior are fundamental to quantitative studies of animal behavior. Although sometimes neglected, this stage of a behavioral study is crucial because it determines the scope of analysis and often dictates the course of future research (Bekoff 1979; Hinde 1970; Hutt and Hutt 1970). However, classifying behavior is difficult because it occurs as a continuous stream of movement, and observer biases affect how units of behavior are separated and recombined from this stream (Fentress 1990). Nevertheless, regularities and discontinuities in patterns of movement do provide an empirical basis by which to subdivide behavioral streams into natural units (Altmann 1965; Lehner 1996; Martin and Bateson 1993). Investigators can therefore minimize bias in the classification of behavior by selecting behavior units that reflect these natural subdivisions.

Predatory behavior is traditionally subdivided into 3 natural units or phases: search, pursue, and capture (Holling 1965; MacArthur and Pianka 1966). This basic ethogram underlies decades of predation research and is the standard approach for classifying the behavior of nearly all predators with the exception of the large terrestrial carnivores. Behavioral studies of large carnivores generally classify predatory behavior in terms of a “hunt.” Authors have complained about this term since its 1st application to large carnivores because its definition is too subjective (Caro 1994; Creel and Creel 1995, 2002; Kruuk 1972; Mills 1990; Schaller 1972; Scheel and Packer 1991; Stander 1992; Stander and Albon 1993). Specifically, it is not obvious which behaviors should be scored as “hunting.” As a result, a hunt can refer to any 1 of several behaviors, individually or collectively (Table 1). Creel and Creel (1995, 2002) note that no single definition of a hunt can apply to all large carnivores because of variation in hunting techniques (stalking versus coursing). Nevertheless, the lack of a standard hunting definition has complicated taxonomic comparisons (Caro and FitzGibbon 1992; Gittleman 1989; Packer and Ruttan 1988).

* Correspondent: macn0007@umn.edu

TABLE 1.—Definitions used by studies of large carnivores to classify a hunt.^a

| Species | Definition | Reference |
|------------------|--|---|
| Cheetah | Stalking, attacking, or both | Eaton 1970b |
| Cheetah | Approaching prey undetected or running after prey | Schaller 1972 |
| Cheetah | Stalking or pursuing a prey group, or both | FitzGibbon and Fanshawe 1988 |
| Cheetah | Crouching at, stalking, or trotting toward prey | Caro 1986 |
| Cheetah | Crouching at, stalking, trotting toward, rushing, or chasing a group of prey animals | Caro 1987 |
| Cheetah | Crouching at, stalking, trotting toward, rushing at, or chasing prey | Caro 1994 |
| Coyote | Walking, running, or lunging | Lingle 2000 |
| Dingo | Pursuing or attacking prey | Thompson 1992 |
| Spotted hyena | Pursuing a selected individual from a prey group for at least 50 m | Gasaway et al. 1991; Holekamp et al. 1997; Kruuk 1972 |
| Spotted hyena | Stalking or pursuing a prey group, or both | Fitzgibbon and Fanshawe 1988 |
| Spotted hyena | Moving toward prey at an increased speed | Mills 1990 |
| Lion | Pursuing an individual or herd at a trot or run if the lion approached to within 60 m or closer | Schaller 1972 |
| Lion | Pursuing a prey animal at a run or trot, or approaching prey by assuming a stalking posture | Van Orsdol 1984 |
| Lion | Moving toward prey while exhibiting any one of the following behavior patterns: alert face (oriented toward prey) combined with waiting in ambush, alert walk, standing walk, crouching walk, crouch, trot, head-low trot, or rush | Scheel and Packer 1991 |
| Lion | Movement by at least 1 lion toward potential prey while using a typical stalking stance | Scheel 1993 |
| Lion | Stalking or running at prey, or both | Mills and Shenk 1992 |
| Lion | Staring at prey with an alert posture and alert facial expression, and stalking for more than 10 m | Stander 1992; Stander and Albon 1993 |
| Lion | Stalking or chasing prey, or both | Funston et al. 2001 |
| African wild dog | Stalking or chasing a prey group, or both | FitzGibbon and Fanshawe 1988 |
| African wild dog | Pursuing a prey group | Fanshawe and FitzGibbon 1993 |
| African wild dog | Pursuing prey; identified by the increased change in gait oriented toward prey | Fuller and Kat 1993 |
| African wild dog | Pursuing prey for at least 50 m at a full run, ending with the wild dog testing prey at bay, or ending in a kill | Creel and Creel 1995, 2002 |

^a Studies of wolves did not define hunt.

Defining a hunt also is problematic because it involves excluding predation phases, combining them into single measurement units, or both, and many aspects of predator and prey behavior are differentially affected by different phases. For example, predator diet preferences can be generated by differences among prey types in any of the phases, and interpretations of predator diet can be affected by the phase that is sampled (Creel and Creel 2002; Sih and Christensen 2001). This is especially relevant to optimal diet theory because it makes predictions about only 1 phase of predation, the probability of attack given an encounter with prey, and differences among prey types in other phases can produce diet patterns that do not fit the theory (Sih and Christensen 2001). Likewise, variation in the effectiveness of antipredator traits among phases can lead to incorrect conclusions about the value of an antipredator trait depending upon the phase in which it is sampled (Endler 1986; Lingle and Pellis 2002).

In addition to the 3 basic phases, large carnivores exhibit at least 3 others, including approaching (Fanshawe and FitzGibbon 1993; Kruuk and Turner 1967), watching (Carbyn and Trotter 1987; Eaton 1970a), and pursuing groups (FitzGibbon and Fanshawe 1988; Kruuk 1972). Approaching reduces predator-prey distance before pursuit, watching relates to prey assessment (FitzGibbon and Fanshawe 1988; Kruuk 1972), and pursuing groups involves the selection of a specific group member, which is indicated by an increase in velocity (Kruuk 1972; Lingle and Pellis 2002). When prey stand and defend themselves, however, harassing replaces pursuing in the sequence (Kruuk

1972; Mech 1970; Schaller 1972). Although much qualitative evidence suggests that these additional behaviors are functionally important, quantitative evidence is generally lacking.

The reintroduction of wolves to Yellowstone National Park provides a new opportunity to study the predatory behavior of large carnivores (Smith et al. 2004). However, the lack of a standard scheme to classify such behavior presents a methodological dilemma. To address this we developed a new approach to classifying large-carnivore predatory behavior based upon the basic ethogram. Not surprisingly, the basic ethogram is not a complete description of all the phases of predation that have been described for large carnivores. Modifying it to account for these phases is difficult because as phases are added that tailor the ethogram to 1 or a few species, its usefulness as a general description will diminish. Thus, the need to split the behavioral continuum into categories must be balanced against the need for generality. To achieve this we address 2 questions. First, is the function of any additional phase important enough to justify modifying the basic ethogram? Second, can functionally important phases be added to the basic ethogram without sacrificing its generality? We address the 1st question by examining the role of approaching, watching, harassing, and pursuing groups in interactions between wolves (*Canis lupus*) and elk (*Cervus elaphus*) and American bison (*Bison bison*) in Yellowstone National Park and consider the 2nd question by comparing our modified ethogram to 31 previous classifications and descriptions involving 7 other large carnivores and 5 other wolf populations.

MATERIALS AND METHODS

Study area.—Yellowstone National Park extends across 891,000 ha of a primarily forested plateau in northwestern Wyoming that ranges from 1,500 to 3,300 m in elevation. We observed wolves primarily in a 100,000-ha grassland in the northern quarter of Yellowstone National Park referred to as the Northern Range. This area is characterized by a series of open valleys, ridges, and minor plateaus. Low elevations (1,500–2,400 m) in the Northern Range provide important winter range for ungulates. During this study the Northern Range contained approximately 12,000 elk and 700 bison (D. W. Smith, National Park Service, in litt.) occurring singly or in groups of up to 800 and 75 animals, respectively. A road runs the length of the Northern Range and provides year-round access. In winter, we also observed wolves in Pelican Valley, a roadless area in the interior of Yellowstone National Park at approximately 2,500 m elevation, where the main prey for wolves was a small population of bison (≤ 150 individuals).

Study population.—Forty-one radiocollared wolves were reintroduced to Yellowstone National Park in 1995 and 1996 (Bangs and Fritts 1996). Each subsequent year Yellowstone National Park personnel radiocollared 30–50% of the pups born (Smith et al. 2000). Our wolf-handling procedures complied where applicable with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Wolves observed in this study were either members or descendants of the original reintroduced population. From 1995 to 2000, 14–110 wolves comprised 2–7 packs of 2–27 wolves per pack ($\bar{X} \pm SE = 9.9 \pm 1.0$ wolves/pack, $n = 37$ pack-years). In this study we focused mainly on 4 wolf packs: Rose Creek, Leopold, Druid Peak, and Mollie's. At least 2 individuals in each pack were radiocollared.

Foraging observations.—We systematically observed wolves during two 30-day periods (mid-November to mid-December and March) from 1995 to 2000 (Smith et al. 2004). Winter was the best time to view wolves because they were attracted to ungulates concentrating on open winter ranges. During each period, 2 observers monitored each focal wolf pack on the Northern Range daily from dawn to dusk, and observers in fixed-wing aircraft attempted to locate all Yellowstone National Park packs on a daily basis, weather permitting. Ground observers watched wolves for a total of 1,901 h and documented 296 encounters with elk and 40 with bison, whereas air observers recorded 6 encounters with elk and 3 with bison. Opportunistic observations outside study periods yielded an additional 214 elk and 24 bison encounters, respectively. These were mainly observed from the ground (95%) during nonwinter months (56%; 1 May to 31 October). Observations in Pelican Valley were recorded during a 2- to 4-week period in March from 1999 to 2003. The senior author and at least 1 additional observer monitored the single resident pack (Mollie's) from dawn to dusk each day. They watched wolves for an additional 249 h and documented 67 wolf encounters with bison and 1 with elk.

Ground observers located focal packs by using radio-telemetry from vantage points on or near the road (Northern

TABLE 2.—Proposed ethogram of the behavior of large carnivores hunting ungulate prey.

| Foraging state | Definition |
|-------------------|---|
| Search | Traveling without fixating on and moving toward prey |
| Approach | Fixating on and traveling toward prey |
| Watch | Fixating on prey while not traveling (e.g., standing, sitting, or crouching) |
| Attack-group | Running after a fleeing group or lunging at a standing group while glancing about at different group members (i.e., scanning) |
| Attack-individual | Running after or lunging at a solitary individual or a single member of a group while ignoring all other group members |
| Capture | Biting and restraining prey |

Range), or from a single vantage point 8 km from the nearest road (Pelican Valley), and observed packs at distances of 0.1–6.0 km with binoculars and spotting scopes (25–75 \times). Nighttime viewing of wolves with night-vision goggles was ineffective because of the long distances between wolves and observers. Most daylight predatory activity occurred in 2 periods, 0600–0900 h and 1600–1800 h.

From 1995 to 1997, observations of wolf predatory behavior were recorded ad libitum (Altmann 1974). Based on an examination of these initial observations we defined 6 exclusive foraging states (Table 2; see below for details). From 1997 to 2003, observers recorded each occurrence of each foraging state (all-occurrence sampling—Altmann 1974) together with information about the time of occurrence; number, age, and sex of wolves; prey species; number and age/sex class of prey (i.e., bull, cow, yearling, or calf); and prey flight response. The behavior of all pack members was not always synchronized, so in these situations we recorded the foraging state that was sequentially closest to resulting in a kill (the most escalated state). For example, if 4 of 5 wolves were “approaching” and the remaining one was “attacking,” we scored the foraging state as attacking. Thus, the behavior of a single wolf could determine the foraging state. Focal animal sampling was impractical because of the difficulty of continuously viewing the same individual at long distances (0.1–6.0 km) in variable terrain among the movements of other pack members (2–27 wolves) and prey (2–800 individuals). Scan sampling also was impractical because it was difficult to sight all wolves simultaneously. We recorded prey flight response at the beginning and end of each foraging state because it sometimes varied. Observations were dictated into voice recorders, noting times with digital stopwatches, or recorded with video cameras, and subsequently transcribed to data sheets. To standardize data collection, we trained observers to recognize and record foraging states before each study period.

Foraging states.—Our ethogram (Table 2) combined behavioral states from the basic ethogram with those from previous large-carnivore studies. We operationally defined (Lehner 1996) each foraging state as the simultaneous occurrence of 2 or more behavioral acts by at least 1 wolf, and we avoided using arbitrary distance thresholds (Mills 1990) because distances varied. We characterized each state by presence

of an action (walking or standing still), type of action (walking, running, or lunging), posture (standing, sitting, and crouching), orientation toward prey (attention fixed or unfixed on prey), and social status of the prey (solitary or group). We considered a group to be ≥ 2 prey individuals of the same species ≤ 10 m apart. States could occur in any order, and could repeat, and each ended with the start of another or of a nonpredatory behavior. States escalated if the subsequent state was sequentially closer to predation, for example, search to approach.

Because wolves are opportunistic predators that kill mainly vulnerable prey, which tend to occur at low densities (Mech and Peterson 2003), we considered searching to be synonymous with traveling (Fig. 1A). Thus, we could not distinguish searching for prey from searching for anything else. Nevertheless, we excluded incidental movements around dens, carcasses, and other fixed points. When searching, a wolf escalated the sequence by approaching, attacking, or capturing prey. Capturing directly followed searching or approaching if a wolf grabbed an immobile prey such as a neonate.

Approaching involved traveling toward prey (Fig. 1B). If prey fled and ≥ 1 wolf pursued, the foraging state was classified as an attack (see below). Co-occurrence of 2 behavioral acts distinguished approaching from searching: intent staring and travel toward prey. This conservative criterion was intended to maximize confidence in our determination of the onset of approach, especially from a distance. We did not distinguish between concealed and unconcealed approaches. A wolf escalated an approach by attacking or capturing prey.

Watching involved surveillance of prey, sometimes when close (< 10 m; Fig. 1C). We recorded watching only if it followed earlier orientation and movement toward prey. While watching, a wolf escalated the sequence by approaching or attacking.

When a wolf attacked a prey group, the attack involved 1 of 2 actions according to the group's response. Groups that fled were pursued (Fig. 1D), whereas groups that stood were harassed (Fig. 1E). We lumped pursuing and harassing into a single category because each had the same consequence (Bekoff 1979; Hinde 1970), that is, selecting a group member. When a wolf pursued a prey group it ran behind, alongside, or among the fleeing group, or subsets thereof, while turning its head from side to side to scan prey that crossed its field of view. When a wolf harassed a prey group, it lunged at 1 or more group members while glancing at others. A wolf escalated a group attack by focusing on a single member.

An attack on an individual involved either an individual selected from a group, or a solitary individual. Similar to attacks on groups, individuals that fled were pursued (Fig. 1F), whereas those that stood were harassed (Fig. 1G). Here again, we lumped pursuing and harassing because both had the same result, that is, prey capture. When a wolf pursued an individual, the wolf followed its flight path exclusively. Likewise, when a wolf harassed an individual, the wolf lunged only at it. A wolf escalated an attack on an individual by capturing it (Fig. 1H). During the capture, a prey escaped or was killed.

Data analysis.—We evaluated the functional significance of approaching, watching, harassing, and pursuing groups by

measuring the frequency and outcome of each behavior during wolf encounters with elk and bison. The sampling unit was a foraging state, and we pooled states across packs after checking that their frequencies and outcomes did not differ between packs. Pairwise comparisons were made with a chi-square test when all expected frequencies were > 5 , and a Fisher exact test was used when at least 1 expected frequency was < 5 . Results for all analyses were considered significant at $P \leq 0.05$.

We assessed the role of approaching, watching, and attacking groups by estimating the transition frequencies between foraging states (Haccou and Mellis 1992). A transition frequency is the probability that a following state will be entered once the preceding state has begun, and is calculated as the number of transitions from each state to each other state, divided by the total number of occurrences of the preceding state. This approach assumed that the probability of a foraging state occurring was dependent only on the immediately preceding foraging state. Transition frequencies included only foraging states for which the end was observed, and excluded transitions between foraging states and nonpredatory behavior. We compared transition frequencies between wolf encounters with elk (high vulnerability) and bison (low vulnerability—Smith et al. 2000) using a chi-square test that excluded transitions with 0 frequencies. As a result, degrees of freedom varied according to the number of different transitions compared.

To evaluate variation in wolf velocity during pursuits, we compared the stride frequency (Heglund and Taylor 1988; Taylor 1978) of 18 different wolves before and after each began following the flight path of a single elk in each of 18 filmed chases (Landis Wildlife Films, Gardiner, Montana). Stride frequency was measured by viewing film at slow speed and timing the interval of at least 5 cycles of 1 foot to the nearest second (strides/s). The number of cycles measured was typically much greater than 5 (pursue-group, 50.77 ± 9.99 SE cycles/individual; pursue-individual, 37.27 ± 7.76 cycles/individual). We tested pairwise differences in stride frequency using a sign test.

We tested if harassing was as effective as pursuing in escalating attacks to evaluate our claim that these 2 behaviors were functionally analogous. To account for differences in vulnerability between adult (> 1 year) and subadult prey (Mech et al. 2001; Smith et al. 2000), we limited this analysis to adult prey if the attack involved an individual selected from a group or a solitary individual. Attacks on groups included both adult and subadult prey because all-adult groups were rare. This analysis also was restricted to captures that led to kills and to attacks that were seen in their entirety. The latter allowed us to test how the outcome of harassment was influenced by its timing during the attack (beginning or end).

To assess whether approaching, watching, and attacking groups could be added to the basic ethogram without sacrificing its generality, we compared our modified ethogram (Table 2) to 13 previous classifications and 18 general descriptions involving 7 other large carnivores and 5 other wolf populations. We distinguished classifications from descriptions according to whether behaviors were explicitly categorized or illustratively narrated. We matched each 1 of

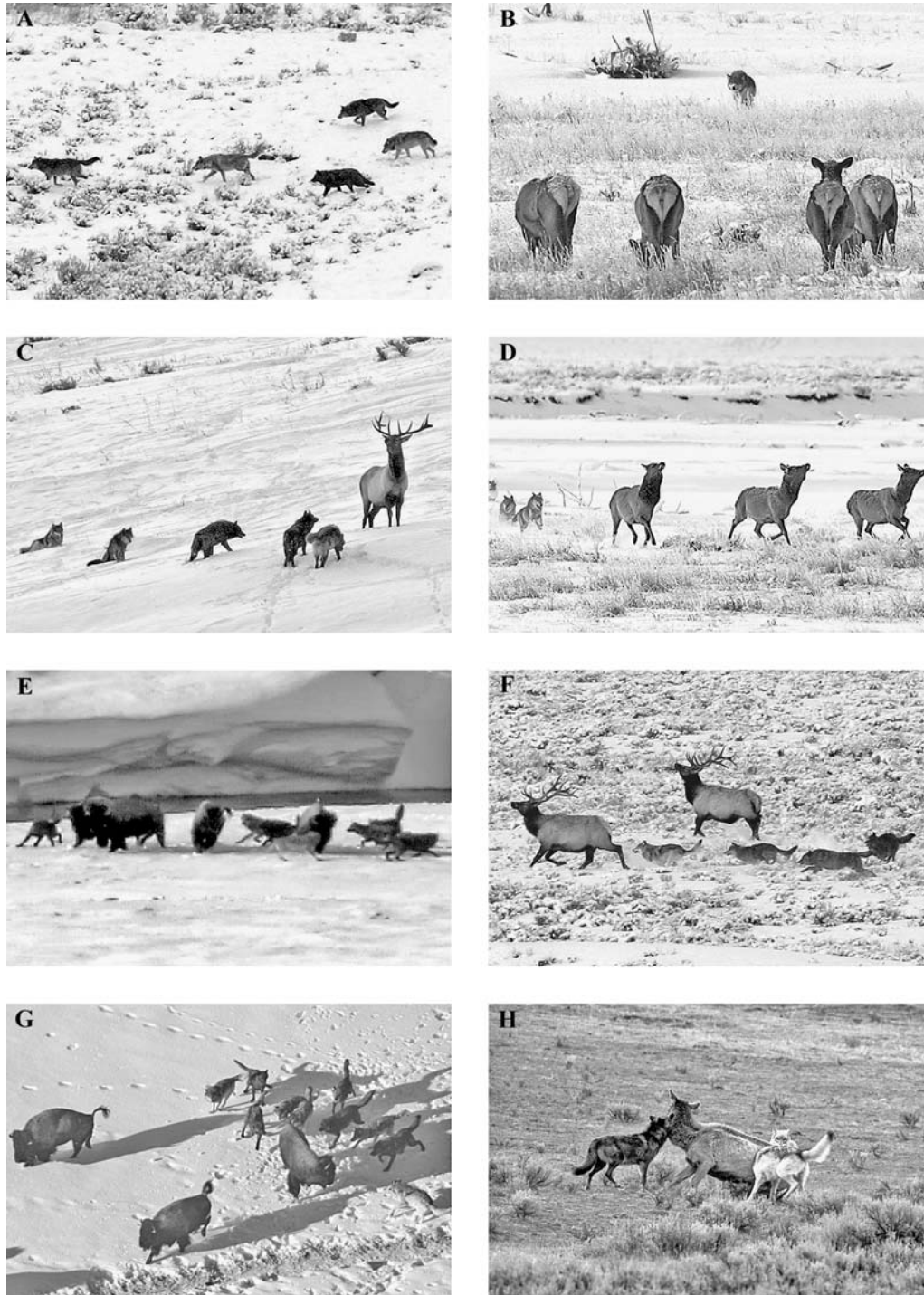


FIG. 1.—Behavioral subdivisions used in this study to classify the predatory behavior of wolves: A) search, B) approach, C) watch, D) attack-group (pursuit), E) attack-group (harass), F) attack-individual (pursuit), G) attack-individual (harass), and H) capture. Three characteristics indicate that the wolves in D have not fixated on the flight path of a single elk: the wolf on the left is looking away from all 3 elk; the elevated head and chest position of the wolf on the right suggests a slow gallop (compare with wolves in F), which is indicative of the attack-group phase (see text); and the wolf on the right is not obviously fixated on any 1 elk. (Photos courtesy of Douglas Dance and Daniel Stahler.)

our 6 foraging states to each category or term from a previous classification or description, respectively, according to whether they were defined by similar behavioral acts (running, walking, biting, etc.). Terminology varied across studies, with different authors sometimes describing the same

behavior with different terms and describing different behaviors with the same term. Where studies split or lumped behaviors relative to our 6 foraging states, multiple categories or terms were matched to 1 state or a single category or term was matched to ≥ 1 state. We measured correspondence

between the modified ethogram and previous studies by calculating the proportion of studies classifying or describing each foraging state.

RESULTS

Approaching.—Wolves typically approached elk and bison after discovering them (after search), sometimes after watching them, and occasionally after failing to select or capture an individual (Table 3). When wolves encountered elk, approaching mainly led to attack-group and only sometimes to watch. In contrast, when wolves approached bison, they were significantly more likely to stop and watch them before attacking. While approaching bison, wolves also were significantly more likely to skip attack-group and go right to attack-individual, and less likely to abandon the encounter and continue searching (Table 3). Encounters with bison generally involved more approaching than encounters with elk.

Watching.—Wolves watched elk and bison usually after approaching them, and sometimes after failing to select or capture an individual. The latter 2 transitions were more common with bison than with elk (Table 3). Watching usually led to approaching, but this transition was significantly more common in encounters with bison because wolves watching elk often continued searching or attacked. These latter 2 outcomes were significantly less likely when wolves watched bison. Watching rarely led directly to the selection of individual prey in encounters with elk or bison (Table 3). Overall, wolves watched bison more often than elk.

Attacking groups.—Wolves attacked elk groups more frequently than bison groups (Table 3) and did so in a somewhat different manner. Although wolves primarily attacked groups of either species after approaching, they also sometimes attacked elk groups immediately after discovering or watching the group. In contrast, wolves were significantly less likely to attack after discovering or watching bison groups. The results of attack-group also differed significantly between the 2 prey species. Attacks on elk groups primarily led to the selection of individuals, whereas attacks on bison groups mainly led to watching. Attacks on elk groups rarely led to watching. Moreover, if while attacking elk, wolves failed to select an individual, they typically abandoned the encounter and continued searching. This scenario was rare in wolf encounters with bison (Table 3). When wolves pursued elk, the transition from attack-group to attack-individual was marked by an increase in stride frequency (2.06 ± 0.08 SE strides/s versus 2.43 ± 0.06 strides/s; sign test, $P < 0.001$, $n = 18$).

Harassing.—Harassment was most effective at the end of attacks involving solitary elk or those that were selected from groups. In these cases the likelihood of a kill was as great or greater if wolves harassed elk instead of pursued them (attack-individual [group member], $\chi^2 = 0.05$, $d.f. = 1$, $P = 0.83$; attack-individual [solitary], Fisher exact test, $P = 1.00$; Fig. 2b). But if individual elk initially confronted wolves and the attack began with harassment rather than pursuit, a kill was less likely to occur, although this difference was significant only for elk selected from groups (attack-individual [group member],

TABLE 3.—Transition frequencies between foraging states when wolves encountered elk and bison groups in Yellowstone National Park.^a These data illustrate the general sequence of foraging states used by wolves in encounters with elk and bison, and should not be construed as estimates of encounter rate or hunting success because not all outcomes are reported, that is, transitions to nonforaging states are excluded.

| Prey species | Preceding state | Following state | | | | | <i>n</i> | |
|--------------|-------------------|-----------------|-------------|-------------|--------------|-------------------|-------------|-----|
| | | Search | Approach | Watch | Attack-group | Attack-individual | | |
| Elk | Search | 0.00 | 0.68 | 0.00 | 0.31 | 0.01 | 0.00 | 179 |
| | Approach | 0.09 | 0.00 | 0.12 | 0.69 | 0.09 | 0.01 | 231 |
| | Watch | 0.32 | 0.35 | 0.00 | 0.27 | 0.06 | 0.00 | 34 |
| | Attack-group | 0.24 | 0.09 | 0.03 | 0.13 | 0.51 | 0.00 | 275 |
| | Attack-individual | 0.16 | 0.06 | 0.02 | 0.16 | 0.08 | 0.52 | 134 |
| Bison | Search | 0.00 | 0.94 | 0.00 | 0.06 | 0.00 | 0.00 | 32 |
| | Approach | 0.04 | 0.00 | 0.49 | 0.31 | 0.16 | 0.00 | 164 |
| | Watch | 0.14 | 0.66 | 0.00 | 0.12 | 0.08 | 0.00 | 133 |
| | Attack-group | 0.09 | 0.15 | 0.38 | 0.13 | 0.25 | 0.00 | 86 |
| | Attack-individual | 0.03 | 0.16 | 0.41 | 0.10 | 0.05 | 0.25 | 61 |

^a The frequency is the probability that the following foraging state will be entered once the preceding foraging state has begun. This is calculated as the number of observed transitions from each state to each other state, divided by the total number of occurrences of the preceding state (*n*). The sums of the row frequencies are all equal to 1. Significant between-species differences are in boldface (search, $\chi^2 = 8.33$, $d.f. = 1$, $P < 0.01$; approach, $\chi^2 = 81.57$, $d.f. = 3$, $P < 0.001$; watch, $\chi^2 = 13.80$, $d.f. = 3$, $P < 0.01$; attack-group, $\chi^2 = 95.59$, $d.f. = 4$, $P < 0.001$; attack-individual, $\chi^2 = 63.34$, $d.f. = 5$, $P < 0.001$). Wolves killed elk and bison in 81% and 20% of captures, respectively.

$\chi^2 = 8.58$, $d.f. = 1$, $P = 0.003$; attack-individual [solitary], Fisher exact test, $P = 0.71$; Fig. 2a). Harassment never led to a kill when wolves selected bison from groups, regardless of its timing (Figs. 2a and 2b). All the attacks on solitary bison involved harassment and none was successful. Finally, harassment was generally less effective than pursuit for selecting individuals from groups no matter when it occurred, but this difference was statistically significant only for elk (elk, $\chi^2 = 10.73$, $d.f. = 1$, $P = 0.001$; bison, $\chi^2 = 3.61$, $d.f. = 1$, $P = 0.06$; Fig. 2a; elk, $\chi^2 = 16.54$, $d.f. = 1$, $P < 0.001$; bison, $\chi^2 = 2.29$, $d.f. = 1$, $P = 0.13$; Fig. 2b).

Applicability of the modified ethogram.—We found close conceptual correspondence between our modified version of the basic predatory ethogram and previous classifications and descriptions of large-carnivore behavior (Appendix I). In particular, approaching, watching, and attacking groups were classified or described in 94%, 71%, and 65% of 31 previous studies, respectively, with 42% of studies referencing all 3 behaviors. For species other than the wolf, approaching was specified in 100% of classifications and 94% of descriptions, and watching was included in 70% of classifications and 63% of descriptions. In addition, 40% of classifications and 69% of descriptions distinguished between attacking groups and attacking a specific group member. Among the wolf studies, our ethogram closely matched 1 classification (Gray 1987) and 2 descriptions (Clark 1971; Murie 1944). Among the nonwolf studies, our ethogram was most similar to classifications for

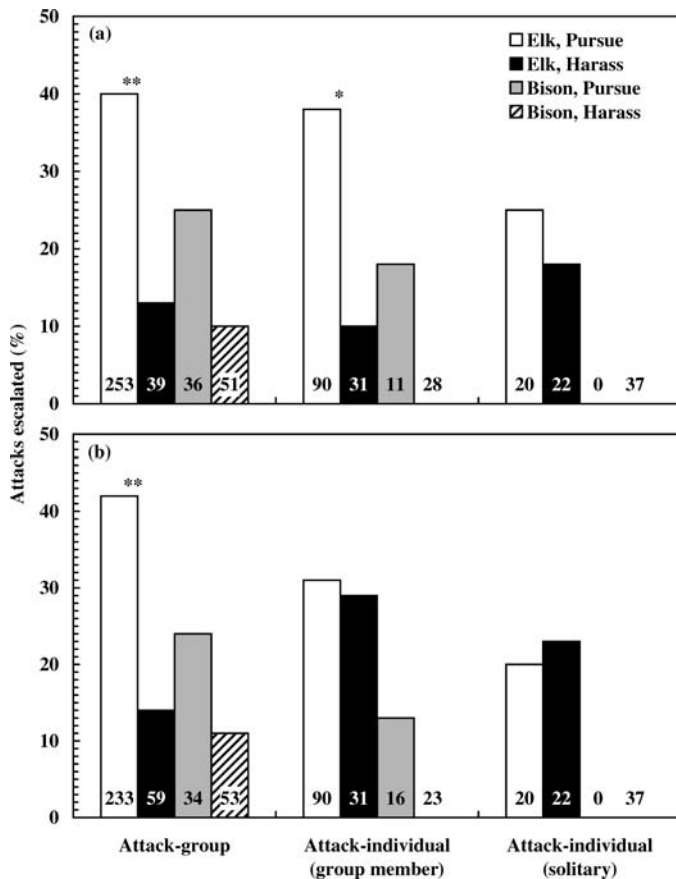


FIG. 2.—Percentage of attacks that escalated (attack-group to attack individual and attack-individual to capture) when wolves pursued or harassed elk and bison at the a) beginning or b) end of attacks. Only captures that led to kills are included. Data were collected in Yellowstone National Park, 1995–2003. Sample sizes given at the base of each bar and asterisks indicate significant within-species differences for each type of attack. * $P \leq 0.01$; ** $P \leq 0.001$.

coyotes (Lingle 2001; Lingle and Pellis 2002; Lingle and Wilson 2001) and spotted hyenas (Kruuk 1972) and descriptions for cheetahs (Schaller 1972), lions (Schaller 1972), spotted hyenas (Mills 1990), and African wild dogs (Reich 1981; Schaller 1972).

DISCUSSION

Our results demonstrate that approaching, watching, harassing, and pursuing groups are functionally important behaviors in the predatory repertoire of at least 1 large-carnivore population. Wolves in Yellowstone National Park used approaching to reduce distance and to decide whether to attack or continue searching. Which decision wolves followed probably resulted from assessing prey vulnerability. For example, elk were 3 times as vulnerable as bison (Smith et al. 2000) and wolves attacked elk twice as often (0.69 versus 0.31 attacks/approach). In contrast, wolves usually watched bison after approaching them, suggesting that watching also had a role in prey assessment (FitzGibbon and Fanshawe 1988; Kruuk 1972).

However, watching rarely led directly to attacking. Rather, wolves approached or continued searching after watching. Wolves may have decided to attack while watching but 1st approached to reduce distance. Because bison were more aggressive than elk, the tendency for wolves to watch them more often also suggests that watching may have reduced the risk of prey-caused injury. The risk of injury when watching was certainly less than when approaching or attacking, and may explain why wolves often watched bison after approaching them. In this case, watching may have provided a low-risk, but perhaps less informative (see below) technique for assessing prey. More wolves were killed by elk than by bison (5 versus 1—Yellowstone National Park Wolf Project, in litt.), but this was because wolves encountered elk more often (79% of wolf-prey encounters).

The function of attacking groups was to select an individual from a group. Although wolves occasionally selected individuals by approaching or watching, attacking groups was their primary method. Attack-group may have been the most efficient technique for selecting individuals because it provided the most reliable information on prey condition given that the threat of predation was imminent (FitzGibbon and Fanshawe 1988). In cases where wolves pursued elk groups, we found that their stride frequency increased as they transitioned from attack-group to attack-individual. Because velocity is in part a function of stride frequency (Heglund and Talyor 1988; Taylor 1978), this finding supports the claim that these 2 states can be distinguished by a change in velocity (Estes and Goddard 1967; Kruuk 1972; Kruuk and Turner 1967; Lingle and Pellis 2002; Malcolm and van Lawick 1975; Schaller 1972).

Harassing was a wolf response to prey that confronted them, and led to predation as often as pursuit, but only in encounters with elk and usually after an initial pursuit. Thus, elk that 1st confronted wolves and then fled were less likely to be killed than elk that fled 1st and confronted last. The latter were probably vulnerable individuals that had neither the strength to confront wolves nor the stamina to outdistance them. However, bison were too aggressive for harassment to be of much use at all. When wolves attacked groups, harassment did lead to the selection of individuals, but it was less efficient than pursuit, which appears to be case for most carnivores that use cursorial hunting techniques (Gray 1983; Malcolm and van Lawick 1975; Mills 1990; Schaller 1972). This may be because these carnivores rely on prey flight performance to make selection decisions (Estes and Goddard 1967; FitzGibbon and Fanshawe 1988; Kruuk 1972) or because it is safer to select individuals from groups that flee.

We probably underestimated the frequency of approaching, watching, and attacking groups for 2 reasons. First, we recorded most wolf-prey encounters in winter (80%) when prey were most vulnerable to wolf predation (Mech and Peterson 2003). Because the function of the aforementioned behaviors is related to finding vulnerable prey, they may occur less frequently in winter than at other times because of the relative abundance of vulnerable prey. Second, because of the characteristics of our study system we had to use a group-level

sampling approach and record the most escalated state when wolves behaved differently. Because approaching, watching, and attacking groups were among the least-escalated states we probably underestimated the frequency that an individual wolf exhibited them. An advantage of this sampling approach was that it minimized the chance we failed to document a kill, and this aided estimates of foraging success (Mech et al. 2001; Smith et al. 2000).

Our results also provide evidence that approaching, watching, and attacking groups can be added to the basic predatory ethogram without limiting its applicability to large carnivores. All 31 previous classifications and descriptions of large-carnivore behavior that we reviewed specified at least 1 of these behaviors and nearly half referenced all 3. These findings confirm previous reports that different large carnivores share similar phases of predatory behavior (Kleiman and Eisenberg 1973; Kruuk 1972; Kruuk and Turner 1967; Mech 1975). Because our modified ethogram reflects these common phases, it may provide a more unified scheme for classifying large-carnivore behavior than the concept of a hunt, which is defined differently for different species (Table 1). As a result, the modified ethogram may offer a general framework for comparing foraging characteristics within and across species.

The discrepancies between our modified ethogram and previous studies are important to note because they highlight the rationale underlying the ethogram. For example, in some cases our ethogram combines behaviors that other studies split, or splits behaviors that others lumped. These differences reflect what we believe is a compromise between the need to split behavior into meaningful categories and the need to maintain generality. The ethogram splits behavior according to broad functional criteria, such that behaviors with distinct outcomes are classified separately, whereas those with similar outcomes are combined. A consequence of combining some behaviors is that the ethogram does not explicitly describe every species-specific pattern of predatory behavior. But these patterns are not necessarily excluded because foraging states can be further subdivided to explicitly describe specific behaviors.

Discrepancies between our ethogram and previous studies also illustrate how the ethogram accounts for differences in hunting techniques and prey types. For example, attack-group was absent from most studies of felids (cf. Schaller 1972) and 1 study of wolves (Mech 1970). The former reflects a difference in hunting technique (stalking versus coursing), whereas the latter involves a difference in prey type (solitary versus social). Our ethogram accommodates these differences by treating them as variations in the motor pattern or occurrence of foraging states. Thus, the classification of stalking and coursing differs in only 2 respects: the motor pattern of the approach (crouching versus upright) and the occurrence of attack-group (stalking excludes, and coursing includes, attack-group, respectively). Likewise, the classification of a carnivore hunting social prey versus solitary prey differs according to whether attack-group is included or excluded, respectively. The capacity of our ethogram to describe different hunting techniques is a major advantage over traditional classifications of a hunt,

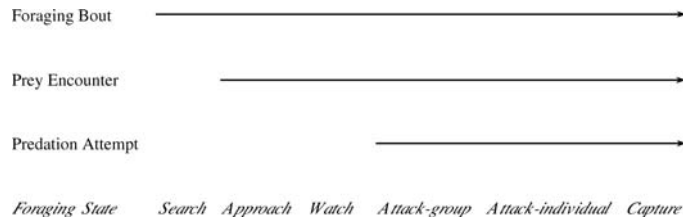


FIG. 3.—Conceptual model of how foraging states from the modified ethogram can be combined into higher-order categories of foraging behavior. Each arrow corresponds to 1 of 3 categories (foraging bout, prey encounter, and predation attempt) and states that fall beneath a particular arrow are assigned to the corresponding category. States can be assigned to more than 1 category.

because no one definition of a hunt describes all hunting techniques (Creel and Creel 1995, 2002).

Another useful feature of our ethogram is that it provides a framework for examining aspects of predator and prey behavior that are sensitive to different phases of the predation process, such as predator diet (Creel and Creel 2002; Sih and Christensen 2001), predator ontogeny (Fox 1969; Leyhausen 1965), and prey defense (Endler 1986; Lingle and Pellis 2002). This approach may be particularly useful in optimal diet studies because the subdivision between attack-group and attack-individual allows one to measure up to 3 decision variables: which group to attack, how long to spend searching the group for an individual (patch residence time—Stephens and Krebs 1986), and which individual to attack within the group. So far only the 1st decision variable has been analyzed in models of large-carnivore diet and the results have been mixed (Creel and Creel 2002; Scheel 1993). Conceivably, models that examined the 2nd and 3rd decisions, perhaps in conjunction with the 1st, might provide a better quantitative fit between predicted and observed diets.

We do note that hunting definitions have been useful precisely because they do combine multiple behaviors into single measurement units. These higher-order units have been used to quantify a number of important foraging characteristics such as foraging efficiency (kills per hunt) and encounter rate (encounters per hunt). In general, determining how behaviors combine into higher-order and rule-given configurations is an important step in understanding animal behavior (Fentress 1990), as well as for linking behavioral and ecological processes (Jeschke et al. 2002). Thus, we provide an example of how the foraging states from the modified ethogram can be combined to reflect up to 3 higher-order units of behavior (Fig. 3). In this conceptual model, a higher-order unit occurs whenever at least 1 of its assigned foraging states occurs. Thus, encounter rate and foraging success could be estimated as encounters per bout and kills per encounter, respectively.

Although there are certainly other ways that the predatory behavior of large carnivores could be categorized, we suspect that most classifications that, like ours, sought to balance specificity with generality would probably be similar. Moreover, considering that our modified ethogram corresponded reasonably well with previous classifications and descriptions, we

believe that it could be a generally useful alternative to the vague concept of a hunt.

ACKNOWLEDGMENTS

We thank the numerous volunteer field assistants from the Yellowstone National Park Wolf Project who dedicated a great deal of time to observing wolves; the many student volunteers from the University of Minnesota and Northland College who assisted with transcribing dictated observations; and C. Packer, L. G. Adams, and T. J. Meier for reviewing the manuscript. We also are grateful to R. Landis for contributing video, to D. Dance and D. Stahler for contributing photographs, and to the Yellowstone Center for Resources and the Biological Resources Division of the United States Geological Survey for administrative support. This research was supported by grants from the Yellowstone Park Foundation, National Geographic Society, Wolf Recovery Foundation, Dayton-Wilkie Natural History Fund, California Wolf Center, and by fellowships from the University of Minnesota Department of Ecology, Evolution, and Behavior.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sample methods. *Behaviour* 49:227–267.
- ALTMANN, S. A. 1965. Sociobiology of rhesus monkeys. II: Stochastics of social communication. *Journal of Theoretical Biology* 8:490–522.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BANGS, E. E., AND S. H. FRITTS. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24:402–413.
- BEKOFF, M. 1979. Behavioral acts: description, classification, ethogram analysis, and measurement. Pp. 67–80 in *The analysis of social interactions: methods, issues, and illustrations* (R. B. Cairns, ed.). Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- BOWYER, R. T. 1987. Coyote group size relative to predation on mule deer. *Mammalia* 51:515–526.
- CARBYN, L. N., AND T. TROTTIER. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Canadian Journal of Zoology* 65:2072–2078.
- CARO, T. M. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Animal Behaviour* 34:663–684.
- CARO, T. M. 1987. Indirect costs of prey: cheetah cubs reduce maternal hunting success. *Animal Behaviour* 35:295–297.
- CARO, T. M. 1994. *Cheetahs of the Serengeti Plains: group living in an asocial species*. University of Chicago Press, Chicago, Illinois.
- CARO, T. M., AND C. D. FITZGIBBON. 1992. Large carnivores and their prey: the quick and the dead. Pp. 117–142 in *Natural enemies: the population biology of predators, parasites and diseases* (M. J. Crawley, ed.). Blackwell Scientific Publications, Oxford, United Kingdom.
- CLARK, K. R. F. 1971. Food habitats and behavior of the tundra wolf on central Baffin island. Ph.D. dissertation, University of Toronto, Toronto, Ontario, Canada.
- COOPER, S. M. 1990. The hunting behavior of spotted hyenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *African Journal of Ecology* 28:131–141.
- CREEL, S., AND N. M. CREEL. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50:1325–1339.
- CREEL, S., AND N. M. CREEL. 2002. *The African wild dog: behavior, ecology, and conservation*. Princeton University Press, Princeton, New Jersey.
- EATON, R. L. 1970a. The predatory sequence, with emphasis on killing behavior and its ontogeny in the cheetah (*Acinonyx jubatus* Schreber). *Zeitschrift für Tierpsychologie* 27:492–504.
- EATON, R. L. 1970b. Hunting behavior of cheetah. *Journal of Wildlife Management* 34:56–67.
- ELIOT, J. P., I. M. COWAN, AND C. S. HOLLING. 1977. Prey capture by the African lion. *Canadian Journal of Zoology* 55:1811–1828.
- ENDLER, J. A. 1986. Defense against predators. Pp. 109–134 in *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates* (M. E. Feder and G. V. Lauder, eds.). University of Chicago Press, Chicago, Illinois.
- ESTES, R. D., AND J. GODDARD. 1967. Prey selection and hunting behavior of the African wild dog. *Journal of Wildlife Management* 31:52–70.
- FANSHAWE, J. H., AND C. D. FITZGIBBON. 1993. Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* 45:479–490.
- FENTRESS, J. C. 1990. The categorization of behavior. Pp. 7–34 in *Interpretation and explanation in the study of animal behavior*. Vol. I. Interpretation, intentionality, and communication (M. Bekoff and D. Jamieson, eds.). Westview Press, Boulder, Colorado.
- FITZGIBBON, C. D., AND J. H. FANSHAWE. 1988. Stotting in Thomson's gazelle: an honest signal of condition. *Behavioral Ecology and Sociobiology* 23:69–74.
- FOX, M. W. 1969. Ontogeny of prey-killing behavior in Canidae. *Behaviour* 35:259–272.
- FULLER, T. K., AND P. W. KAT. 1993. Hunting success of African wild dogs in southwestern Kenya. *Journal of Mammalogy* 74:464–467.
- FUNSTON, P. J., M. G. L. MILLS, AND H. C. BIGGS. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology (London)* 253:419–431.
- GASAWAY, W. C., K. T. MOSSESTAD, AND P. E. STANDER. 1991. Food acquisition by spotted hyenas in Etosha National Park, Namibia: predation versus scavenging. *African Journal of Ecology* 29:64–75.
- GESE, E. M., AND S. GROTHE. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133:36–43.
- GITTLEMAN, J. L. 1989. Carnivore group living: comparative trends. Pp. 183–207 in *Carnivore behavior, ecology, and evolution* (J. L. Gittleman, ed.). Cornell University Press, New York.
- GRAY, D. R. 1983. Interactions between wolves and muskoxen on Bathurst Island, Northwest Territories, Canada. *Acta Zoologica Fennica* 174:255–257.
- GRAY, D. R. 1987. *The muskoxen of Polar Bear Pass*. Fitzhenry and Whiteside, Markham, Ontario, Canada.
- HACCOU, P., AND E. MELLIS. 1992. *Statistical analysis of behavioral data: an approach based on time-structured models*. Oxford University Press, Oxford, United Kingdom.
- HEGLUND, N. C., AND C. R. TAYLOR. 1988. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *Journal of Experimental Biology* 138:301–318.
- HINDE, R. A. 1970. *Animal behavior: a synthesis of ethology and comparative psychology*. 2nd ed. McGraw-Hill, New York.
- HOLEKAMP, K. E., L. SMALE, AND S. M. COOPER. 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology (London)* 242:1–15.

- HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:1–62.
- HUTT, S. J., AND C. HUTT. 1970. Direct observation and measurement of behavior. Charles C. Thomas, Springfield, Illinois.
- JESCHKE, J. M., M. K. KOPP, AND R. TOLLRIAN. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72:95–112.
- KLEIMAN, D. G., AND J. F. EISENBERG. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour* 21:637–659.
- KRUUK, H. 1972. The spotted hyena. University of Chicago Press, Chicago, Illinois.
- KRUUK, H., AND M. TURNER. 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* 31:1–27.
- LEHNER, P. N. 1996. *Handbook of ethological methods*. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- LEYHAUSEN, P. 1965. Über die Funktion der Relativen Stimmungshierarchie. *Zeitschrift für Tierpsychologie* 22:412–494.
- LINGLE, S. 2000. Seasonal variation in coyote feeding behavior and mortality of white-tailed deer and mule deer. *Canadian Journal of Zoology* 78:85–99.
- LINGLE, S. 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. *Ethology* 107:295–314.
- LINGLE, S., AND S. M. PELLIS. 2002. Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. *Oecologia* 131:154–164.
- LINGLE, S., AND F. WILSON. 2001. Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). *Ethology* 107:125–147.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- MALCOLM, J. R., AND B. H. VAN LAWICK. 1975. Notes on wild dogs (*Lycaon pictus*) hunting zebras. *Mammalia* 39:231–240.
- MARTIN, P., AND P. BATESON. 1993. *Measuring behavior: an introductory guide*. Cambridge University Press, Cambridge, United Kingdom.
- MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday/Natural History Press, New York.
- MECH, L. D. 1975. Hunting behavior in two similar species of social canids. Pp. 363–368 in *The wild canids: their systematics, behavioral ecology and evolution* (M. W. Fox, ed.). Robert E. Krieger Publishing, Malabar, Florida.
- MECH, L. D., AND R. O. PETERSON. 2003. Wolf–prey relations. Pp. 131–157 in *Wolves: behavior, ecology, and conservation* (L. D. Mech and L. Boitani, ed.). University of Chicago Press, Chicago, Illinois.
- MECH, L. D., D. W. SMITH, K. M. MURPHY, AND D. R. MACNULTY. 2001. Winter severity and wolf predation on a formerly wolf-free elk group. *Journal of Wildlife Management* 65:998–1003.
- MILLS, M. G. L. 1990. Kalahari hyenas: comparative behavioral ecology of two species. Unwin Hyman, London, United Kingdom.
- MILLS, M. G. L., AND T. M. SHENK. 1992. Predator–prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* 61:693–702.
- MURIE, A. 1944. *The wolves of Mount McKinley*. United States Government Printing Office, Washington, D.C.
- PACKER, C., AND L. RUTTAN. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.
- REICH, A. 1981. The behavior and ecology of the African wild dog (*Lycaon pictus*) in the Kruger National Park. Ph.D. dissertation, Yale University, New Haven, Connecticut.
- SCHALLER, G. B. 1967. *The deer and the tiger*. University of Chicago Press, Chicago, Illinois.
- SCHALLER, G. B. 1972. *The Serengeti lion: a study of predator–prey relations*. University of Chicago Press, Chicago, Illinois.
- SHEEL, D. 1993. Profitability, encounter rates, and prey choice of African lions. *Behavioral Ecology* 4:90–97.
- SHEEL, D., AND C. PACKER. 1991. Group hunting behavior of lions: a search for cooperation. *Animal Behaviour* 41:697–709.
- SIH, A., AND B. CHRISTENSEN. 2001. Optimal diet theory: when does it work, and when does it fail? *Animal Behaviour* 61:379–390.
- SMITH, D. W., T. D. DRUMMER, K. M. MURPHY, D. S. GUERNSEY, AND S. B. EVANS. 2004. Winter prey selection and estimation of kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management* 68:153–166.
- SMITH, D. W., ET AL. 2000. Wolf–bison interactions in Yellowstone National Park. *Journal of Mammalogy* 81:1128–1135.
- STANDER, P. E. 1992. Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology* 70:8–21.
- STANDER, P. E., AND S. D. ALBON. 1993. Hunting success of lions in a semi-arid environment. *Symposia of the Zoological Society of London* 65:127–143.
- STEPHENS, D. W., AND J. R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey.
- TAYLOR, C. R. 1978. Why change gaits? Recruitment of muscles and muscle fibers as a function of speed and gait. *American Zoologist* 18:153–161.
- THOMPSON, P. C. 1992. The behavioral ecology dingoes in northwestern Australia. III. Hunting and feeding behavior, and diet. *Wildlife Research* 19:531–541.
- VAN ORSDOL, K. G. 1984. Foraging behavior and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 22:79–99.

Submitted 12 April 2006. Accepted 11 October 2006.

Associate Editor was John A. Yunker.

APPENDIX I

Comparison of the modified ethogram of predatory behavior to previous classifications (in boldface) and descriptions of large-carnivore behavior. Categories and terms listed under each foraging state were those used by authors cited and were matched to each foraging state according to the behavioral acts they depicted. If a study lacked a matching category or term it was marked accordingly (not applicable [NA]). Where studies split or lumped behaviors relative to our 6 foraging states, multiple categories or terms appear beneath 1 state or the same category or term may appear beneath multiple states, respectively. Percent correspondence is given in parentheses in the column heads and refers to the proportion of studies classifying or describing a particular foraging state in the modified ethogram.

| Species | Modified ethogram (this study) | | | | | | Reference |
|-------------------------|--------------------------------|-------------------------|----------------------|-------------------------|---------------------------|---------------------------|--|
| | Search (77%) | Approach (94%) | Watch (71%) | Attack-group (65%) | Attack-individual (100%) | Capture (90%) | |
| Cheetah | NA | Stalk | Watch, crouch | NA | Chase, knock over | Seize | Eaton 1970a |
| Cheetah | Travel | Approach | Watch | Chase herd | Select individual | Capture | Schaller 1972 |
| Cheetah | Move | Stalk, trot | Crouch | NA | Rush, chase | Chase | Caro 1994 |
| Cheetah | NA | Walk | NA | NA | Run | Grab | Kruuk and Turner 1967 |
| Coyote | NA | Approach | NA | Pursuit | Attack | Attack | Bowyer 1987 |
| Coyote | Travel | Approach | Watch | Chase | Chase | Grab | Gese and Grothe 1995 |
| Coyote | Search | Approach | Encounter | Pursuit | Attack | Attack | Lingle 2001; Lingle and Pellis 2002; Lingle and Wilson 2001 |
| Spotted hyena | Search | Approach | Watch | Random dash | Chase | Chase | Kruuk 1972 |
| Spotted hyena | Forage | Approach | Watch | Run at herd | Chase | Catch | Mills 1990 |
| Spotted hyena | NA | Approach | Observe herd | Rush herd | Chase | Catch | Cooper 1990 |
| Spotted hyena | NA | NA | Watch | Rush | Chase | Grab | Holekamp et al. 1997 |
| Leopard | Search | Stalk | NA | NA | Run | Grab | Kruuk and Turner 1967 |
| Lion | Search | Stalk | Stare | NA | Run | Grab | Kruuk and Turner 1967 |
| Lion | Search | Stalk | Watch | Pursue herd | Pursue individual | Grab | Schaller 1972 |
| Lion | Search | Stalk | NA | NA | Attack | Subdue | Eliot et al. 1977 |
| Lion | Search | Stalk | Ambush | NA | Charge | NA | Van Orsdol 1984 |
| Lion | NA | Stalk | Crouch | NA | Rush | NA | Scheel and Packer 1991 |
| Lion | Search | Stalk | Ambush | NA | Rush | Rush | Stander 1992 |
| Tiger | Search | Stalk | Crouch | NA | Rush | Attack | Schaller 1967 |
| African wild dog | Trot | Stalk | NA | Chase | Single-out | Grab | Estes and Goddard 1967 |
| African wild dog | Search | Slow walk | NA | Chase | Pursue individual | Grab | Kruuk and Turner 1967 |
| African wild dog | Travel | Approach | Watch | Chase herd | Pursue individual | Grab | Schaller 1972 |
| African wild dog | Travel | Approach | NA | Chase herd | Chase herd member | Capture | Malcolm and van Lawick 1975 |
| African wild dog | Forage | Approach | Watch | Chase herd | Single prey chase | Capture | Reich 1981 |
| African wild dog | NA | Approach | NA | Chase prey group | Pursue individual | NA | Fanshawe and FitzGibbon 1993; FitzGibbon and Fanshawe 1988 |
| African wild dog | Travel | NA | NA | Attack, chase | Chase—close on individual | Grab | Creel and Creel 1995, 2002 |
| Wolf | Travel | Approach | Watch | Chase group | Single-out | Seize | Murie 1944 |
| Wolf | Travel | Stalk | Encounter | NA | Rush, chase | Attack | Mech 1970 |
| Wolf | Travel | Stalk | Watch | Chase group | Pursue individual | Grab | Clark 1971 |
| Wolf | Travel | Trail, follow-up | Watch | Harass | Rush | Physical contact | Carbyn and Trotter 1987 |
| Wolf | Travel | Approach | Circle herd | Attack herd | Cut off individual | Contact individual | Gray 1987 |