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Abstract: This paper presents (1) a brief overview of several concepts important to predator-prey behaviors of coyotes, (2) results of an enclosure study of sheep-attack, -immobilization, and -ingestion responses involving 12 male coyotes (*Canis latrans*) that were paired with sheep after observing various sheep- predation events by conspecifics, and (3) an analysis of sheep predation based upon operant learning principles. Contrasts between comparative psychological and ethological approaches to the study of animal behavior are described. Results of the enclosure study (0.127-ha) showed that following matched-length trials of observing predation, non-predation, and lone sheep, 3, 2, and 1 coyote(s), respectively, made fatal attacks (FAs) of sheep. Although a transitive effect occurred for numbers of observer coyotes completing FAs in the 3 groups, the limited sample sizes precluded confirmation of the "observational-learning" hypothesis. Operant learning principles relevant to the predator-prey sequence are discussed.

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Key Words: predation, learning, coyotes, sheep

Comparative psychology and ethology offer dichotomous approaches to the study of animal behavior. Comparative psychology, with its grounding in American science, focuses upon experimental manipulations designed to highlight species differences in behavior and modes of adaptation, particularly learned adaptations of lower mammals, primates, and humans (Dethier and Stellar, 1961). Ethology, with its European and naturalistic traditions, invokes natural observation to describe behaviors of invertebrate, bird, and some mammalian dyads and social groups; fixed action patterns (FAPs), “releasing” stimuli, and instinctual bases of behavior are emphasized (Dethier and Stellar, 1961).

This report describes a study to assess certain learning effects involved in sheep predation by coyotes. I reasoned that coyotes which observe sheep predation by conspecifics should attack these prey more readily and more often relative to coyotes exposed to models of non-predation or lone sheep.

The influence of observational learning (enhanced acquisition or performance of behaviors via observation of conspecifics) on the predatory behavior of wild canids is well documented (e.g., Adler and Adler, 1977; Connolly et al., 1976; Curio, 1976; Fox, 1969, 1975; Kleiman and Eisenberg, 1973; Mech, 1970; van Lawick and van Lawick-Goodall, 1971; Vincent and Bekoff, 1978). For example, Connolly et al. (1976), in a study of coyote-sheep predation, mentioned that pairing

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coyotes with experienced predators seemed to increase the likelihood of attacks by inexperienced animals. These accounts suggest that the onset and efficiency of predatory behaviors in canids is facilitated by observations of conspecifics performing attacks on given prey.

MATERIALS AND METHODS

Animals

Sixteen, wild-caught, male coyotes weighing between 9.5 and 15.5 kg at the start of predation trials were used. Two coyotes each demonstrated predation (made Æ6 FAs upon sheep prior to this study) and non-predation (failed to attack a sheep during Æ30, 1-hr trials) (Sterner and Crane, In review)]. Twelve coyotes having unknown sheep-predation experience served as observer coyotes.

Test coyotes were caught using leg-hold traps and held between 5 and 14 months prior to the study. Upon arrival at the kennel, the coyotes were inoculated for rabies and quarantined for 60 days.

Domestic sheep (12.5-18.0 kg) of various breeds (n=26) were used as prey (i.e., 8 during demonstrations of sheep predation and 18 during later sheep-predation assessments of observer coyotes).

Facilities

The research was conducted in a 0.127 ha enclosure, with extensive kennel and sheep-holding areas nearby (see Sterner and Crane In review). Coyotes were housed in individual pens (3.0- x 1.5- x 1.8-m) with attached shelter boxes (1.0- x 0.8- x 0.7-m). Cages were situated such that coyotes could be moved to/from the enclosure in a fenced chute (14- x 1.2- x 2.0-m). Video-tape recordings (AKAI VC-150, Tokyo, Japan) of all coyote-sheep interactions were made from 2 brick observation buildings with 1-way glass windows.

Procedures

Test coyotes underwent a 3-phase procedure: (a) Acclimation, (b) Demonstration, and (c) Sheep-predation Assessment.

During Acclimation, test coyotes (n=12) received 6 daily, 1-hr trials to familiarize them with the test enclosure and handling. The procedure involved the release, exercise, and return of each coyote to and from the enclosure. Throughout acclimation, coyotes were provided Purina® Dog Chow® and water *ad libitum* in their holding cages.

The Demonstration Trials involved test coyotes being randomly assigned to 1 of 3 groups (n = 4/group), then placed in a 1.2-m^3, V-wire cage located near the center of the test enclosure. Group I observed 2 successive daily sheep neck attacks demonstrated by another coyote. Group II observed 2 successive days of matched-length pairings of a coyote and sheep in which no predation occurred. Group III observed 2 successive, matched-length trials of a lone sheep.

Trial-length matching was done by timing how long coyotes in Group I remained in the cage while observing demonstrator coyotes attack, immobilize, and feed on the sheep for 15 min. Test coyotes in Group II and III were confined in the cage for a length of time matching that of the paired Group I coyote. The 2 Group I demonstrator coyotes were deprived of food (Purina® Dog Chow®) for 72 hr prior to the first demonstration; Group II demonstrator coyotes and all test coyotes were provided food and water *ad libitum* during this phase.

During the Sheep-predation Assessment, 1-h per day trials took place in which a sheep was placed in the enclosure and a test coyote from Group I, II, or III was released. Trials for each coyote continued for 30 successive days or until it made 3 FAs. Trials in which FAs occurred lasted the time required for the coyote to attack and immobilize the sheep, and feed for 15 min on the carcass. If no FA occurred, trials lasted 1 h. During these assessments, coyotes were provided approximately 1.5 kg of Purina® Dog Chow® once every 5 days in their holding cages, with water available *ad libitum*.

Data analyses

Twelve predation (8 attack and 4 ingestion) and 2 weight variables (coyote and sheep) were used to quantify sheep-predation by test coyotes (Table 1). The predation variables were treated as ordinal measurements, but the weight variables were considered interval measurements. The 0.05 level of significance was used with all statistical tests.

Table 1. Attack, ingestion, and weight variables used to assess efficiency of coyote predation on sheep during fatal attacks (FAs); these were derived from Sterner and Crane (In review)

Attack	Ingestion
1. Number of 1-hr trials preceding FA	1. Site of initial feeding (portion of sheep's anatomy where coyote opened wound and fed during 15-min post-FA period
2. Latency to FA (time from release of coyote until start of FA)	2. Latency to feed (time from end of FA until start of feeding)
3. Number of attacks preceding or intervening FA; >30 seconds without pursuit/biting of sheep separated attacks	3. Number of feeding sites (anatomical sites on sheep where coyote opened wounds and fed during 15-min post-FA period
4. Site of FA (portion of sheep's anatomy subject to majority of bites)	4. Amount eaten (kg of sheep eaten during 15-min post-FA period)
5. Number of lost/regained footings during FA (frequency that sheep was downed)	
6. Duration of FA (time from initial bite until immobilization of sheep prior to onset of feeding by coyote)	Weight Variables 1. Coyote (kg) 2. Sheep (kg)
7. Proportion of total FA time that sheep remained standing	
8. Time-to-first downing (time from start of FA until sheep lost footing and was downed the first time)	

A point-biserial correlation (Roscoe, 1969) was computed between weights of coyotes and a dichotomous variable (0:1) of non-FA or FA in order to assess the propensity for heavier (larger) coyotes to make FAs.

Separate Kruskal-Wallis Analysis of Variance Tests (Siegel, 1956) were used to test the hypothesis that demonstrations of sheep predation affected onset of attack behaviors in test coyotes. These were computed for: (1) numbers of 1-hr trials preceding the criterion of 3 FA or 30 days without FA, (2) numbers of attacks and FAs preceding these criteria, and (3) cumulative durations (min:sec) of the 3 FAs.

Separate Friedman Two-Way Analysis of Variance Tests (Siegel, 1956) were computed for 10 of the 12 attack and ingestion variables (excluding Attack Variable 4 and Ingestion Variable 1) using pooled data for the coyotes that made FAs. These tests compared within-sample differences among FAs -- changes in efficiency. Significant Friedman results were separated using Multiple Comparisons Simultaneous Test Procedures (Sokal and Rohlf, 1969).

Sheep-ingestion behaviors were treated descriptively using a carcass-site illustration and narrative text.

RESULTS

Predation demonstrations

In the 8 demonstrations of predation witnessed by the test coyotes in Group I, demonstrators made FAs involving neck attacks characterized by prolonged, pressure bites to the trachea, with post-FA feeding on carcasses. Median latency to FA was 15:51 min:sec (range

0:38 to 19:08) and 1:00 min:sec (range 0:24 to 1:48) for the first and second demonstration trials, respectively (Table 2). Median duration of FA was 8:03 min:sec (range 3:52 to 16:09) and 8:01 min:sec (range 5:52 to 11:06) for these first and second trials, respectively (Table 2). Latencies to FAs were shorter during the second demonstrations; whereas, median lengths of FA were similar for both demonstrations, but had sizable ranges.

Effects of predation observations

A transitive effect occurred among numbers of coyotes that made FAs following demonstrations of predation, non-predation, and lone-sheep -- Group I, 3 > Group II, 2 > Group III, 1 (Table 3). Nevertheless, the Kruskal-Wallis Test showed no differences among Groups for predation variables: (1) number of 1-h trials preceding 3 FAs or 30 days (H = 2.49, NS), (2) cumulative attack durations for the 3 FAs of coyotes exposed to sheep-predation demonstrations (H = 1.23, NS), and (3) number of attacks preceding 3 FAs or 30 days without FA (H = 2.58, NS). Thus, coyotes observing sheep predation by conspecifics failed to reduce the number of trials and attack durations or increase the number of attacks relative to coyotes that observed no predation or lone sheep.

Table 2. Latency to fatal attack (FA) and durations of trials for demonstrator coyotes which determined trial lengths used for coyotes in Groups II and III

			Attack measurements		
Demonstration trial	Demonstrator coyote	Test coyote	Latency to FA (min:sec)	Duration of FA (min:sec)	Trial lengths (min)
1st	A	1	0:38	16:09	32
		2	19:08	3:52	38
	B	3	19:01	11:57	46
		4	12:42	4:49	33
2nd	A	1	1:03	7:35	24
		2	1:48	5:52	23
	B	3	1:00	9:08	25
		4	0:24	11:06	26

Table 3. Sheep-attack/fatal attack (FA) measurements for Group I, II, and III Coyotes during sheep-predation assessments

		Attack measures			
Group	Coyote	Number of coyotes making fatal attack (FA)[1]	1-h trials preceding criterion[2]	Number of attacks	Cumulative duration of 3 FAs (min:sec)
I	1		9	3	25:52
	2	3:4	22	3	20:43
	3		22	11	26:18
	4		30	1	NFA[3]
II	5[4]		21	7	22:53
	6	2:4	25	6	29:54
	7		30	1	NFA
	8		30	0	NFA
III	9		23	3	21:32
	10	1:4	30	1	NFA
	11		30	0	NFA
	12		30	0	NFA

[1]FA often involved a series of intermittent attacks; separation of attacks was defined as stopped pursuit and/or baiting of sheep for Æ30 sec.
[2]Number of 1-h daily trials preceding 3 FAs; shown as 30 days if no FA took place.
[3]NFA--No FA during the 30, 1-h/day sheep-predation assessments.
[4]Coyote 5 escaped after the 1st FA. Missing data were estimated using the median trials, attacks, and durations of FA for other predators (1 df was subtracted from respective Kruskal-Wallis Tests).

Coyote weights were not significantly correlated with occurrence or non-occurrence of FAs on sheep (r_{pbi} = -0.33, NS, critical value$_{0.05}$ =0.71), and heavier coyotes were not more likely to engage in predation than lighter coyotes (Table 4).

Neck attacks predominated (13 of 16 FAs; 81%) in FAs made by 6 test coyotes; however, 1 coyote always used body mauls (3 of 16 FAs; 19%). Characteristics of neck attacks and body mauls were described by Sterner and Crane (In review).

Table 4. Median (range) attack, ingestion, and weight measurements for 6 coyotes that fatally attacked sheep during sheep-predation assessments

Measure	Fatal attack (FA) 1st	2nd	3rd	Combined
<u>Attack</u>				
1. Number of l-hr trials preceding or intervening FA	14.5(1-21)	6.0(1-10)	l.0(l-4)	5.0(1-21)
2. Latency to FA (min:sec)	9:34(0:20-24:24)	2:44(0:20-9:15)	6:56(0:05-14:55)	(0:05-24:34)
3. Number of attacks	1.5(1-6)	2.0(1-7)	1.5(1-4)	2.0(1-7)
4. Anatomical site of FA	(Coyotes 1, 2, 3, 5 & 6 made Neck Attacks; #9 attacked Head and Flank--Fed on Sheep Alive)			
5. Number of 1ost/regained footings (downings)	l(l-3)	l(l-2)	l(l-3)	l(l-3)
6. Duration of FA (min:sec)	10:46(6:47-9:30)	7:51(7:08-13:44)	8:56(3:52-9:00)	7:38(3:52-13:44)
7. Proportion of FA that sheep remained standing	.10(.03-.34)	.13(.04-.17)	.24(.21-35)	.13(.03-.35)
8. Time to first sheep downing (min:sec)	1:10(0:05-2:32)	1:13(0:30-1:43)	1:55(0:51-2:11)	1:11(0:05-2:32)

Ingestion				
1. Anatomical site of feeding	(Hind-rib/hind-flank/fore-thigh junction = 10, neck = 5, fore-rib/fore flank = 4, hind-thigh = 3, head = 1)			
2. Latency to feed (min:sec)	3:30(0:12-6:15)	2:00(0:01-13:00)	1:00(0:0l-3:00)	2:00(0:01-13:00)
3. Number of feeding sites	l(l-2)	l(l-2)	1(1-3)	l(l-3)
4. Amount eaten (kg)	0.5(0.5-1.0)	1.0(0.5-l.5)	0.5(0.5-l.0)	0.5(0.5-1.5)
<u>Weights</u>				
1. Coyote (kg)	10.8(9.0-15.5)	10.0(8.5-15.5)	11.3(9.5-15.5)	10.0(8.5-15.5)
2. Sheep (kg)	14.5(12.5-17.0)	15.0(12.5-18.0)	16.5(14.0-17.5)	15.0(12.5-18.0)

Friedman Tests among FA variables yielded significance for 1-hr trials preceding successive FAs ($X_r^2 = 6.75$, $p < 0.05$) and proportion of FAs that sheep remained standing ($X_r^2 = 8.04$, $p < 0.05$) (Table 4). Nonparametric multiple comparisons revealed that the ranked number of 1-hr trials preceding the first FA was significantly greater than the trials intervening the second to third FA (i.e., median trials decreased from 14.5 to 6 to 1 for 1st, 2nd, and 3rd FA). Conversely, the rank of the proportion of FAs that sheep remained standing was greatest during the third FA (i.e., median proportions were .10, .13, and .24 for the 1st, 2nd, and 3rd FA). Latency to FA ($X_r^2 = 0.75$, NS), number of attacks ($X_r^2 = 0.25$, NS), number of lost/regained footings ($X_r^2 = 0.22$, NS), duration of FA ($X_r^2 = 0.33$, NS), and time to first downing ($X_r^2 = 2.22$, NS) were not different among FAs. In short, the number of sheep pairings intervening FAs decreased sharply following an initial FA, but coyote efficiency at downing sheep during FAs failed to improve from the first to third FA.

Sheep-ingestion measurements

All test coyotes that made FAs fed on the sheep. For these 6 coyotes and 18 FAs, feeding sites encompassed 23 singular or joint anatomical locations (Figure 1). The ordered occurrence of these sites were: hind-rib/hind-flank/fore-thigh junction (43%), neck (22%), fore-rib/fore-flank junction (18%), hind thigh (13%), and head (4%). Coyotes feeding at the junction of the hind-rib/hind-flank/fore-thigh typically opened a small wound and ingested mesentery fat and entrails.

No significant differences were detected among 3 FAs of the "killer" coyotes by Friedman Tests for latency to ingestion ($X_r^2 = 1.74$, NS), number of ingestion sites ($X_r^2 = 0.001$, NS), and amount ingested ($X_r^2 = 2.30$, NS). Latencies to ingestion varied greatly post FAs (range 0:01 to 13:00 min:sec), but median latencies were similar (range 1:00 to 3:30 min:sec) among the successive FAs. Additionally, numbers of ingestion sites and amounts of mutton ingested were not useful variables for documenting feeding efficiency because of restricted variation and insufficient ranges during the feeding period.

DISCUSSION

Analysis of the behaviors displayed during coyote FAs of sheep in the current study seem to best fit operant conditioning principles (see Figure 2). That is, coyote detection, pursuit, attack, injury, immobilization, and ingestion of sheep can be likened to a typical operant chain (Stimulus$_0$ -- Response$_0$, S_1 -- R_1, S_2 -- S_2, ... S_x -- R_x), with release of the sheep into the enclosure serving as the S^d (discriminative stimulus) for reinforcement (food). Similar to findings of Sterner and Crane (In review), coyote predation behaviors in this study became more predictable after Æ2 FAs occurred; FAs occurred at increasingly more frequent intervals following an initial FA -- implying significant habituation or learning.

Adler (1955) stated that the success of observational learning is contingent upon the degree to which observed behaviors, or similar behaviors, exist in the animal's response repertoire. To the extent that similar behaviors have been practiced, enhancement of performance due to observations of conspecifics' behavior will be increased. This logic suggests several possible explanations for the current findings. First, we used wild-caught coyotes, with unknown sheep-predation histories. Future comparisons of observational-learning effects in coyotes should involve coyotes with known predation histories, preferably comparisons involving both pen-reared and wild-caught coyotes. Second, my findings agree with a number of earlier studies which have documented the complexities of predator-prey interactions (Adamec et al., 1980; Adler, 1955; Caro, 1980; Vincent and Bekoff, 1978). Observations of predator-prey interactions by conspecifics may not affect the incidence of predation directly in observers; rather, differences may occur for such variables as ontogenetic onset of behaviors and for size/species of prey.

Although a transitive effect for numbers of coyotes making FAs following Group I, II, and III exposures occurred, exposure of wild-caught coyotes to these demonstrations yielded no significant statistical effects upon the initiation or frequency of predation events. Larger sample sizes and the use of both wild-caught and pen-reared coyotes are needed to fully assess the Observational Learning Hypothesis in this context.

Finally, coyotes fed on sheep most frequently at the rib-flank-thigh junction. Whether this reflects nutritional selection by coyotes for the caloric content of mesentery fat, or some other dietary preference, remains unanswered. Still, the research and development implication of this result for coyote management suggests that components of entrails or mesentery warrant examination as possible olfactory/gustatory attractants for coyotes.

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Use of brand names does not imply endorsement by the U. S. Government.

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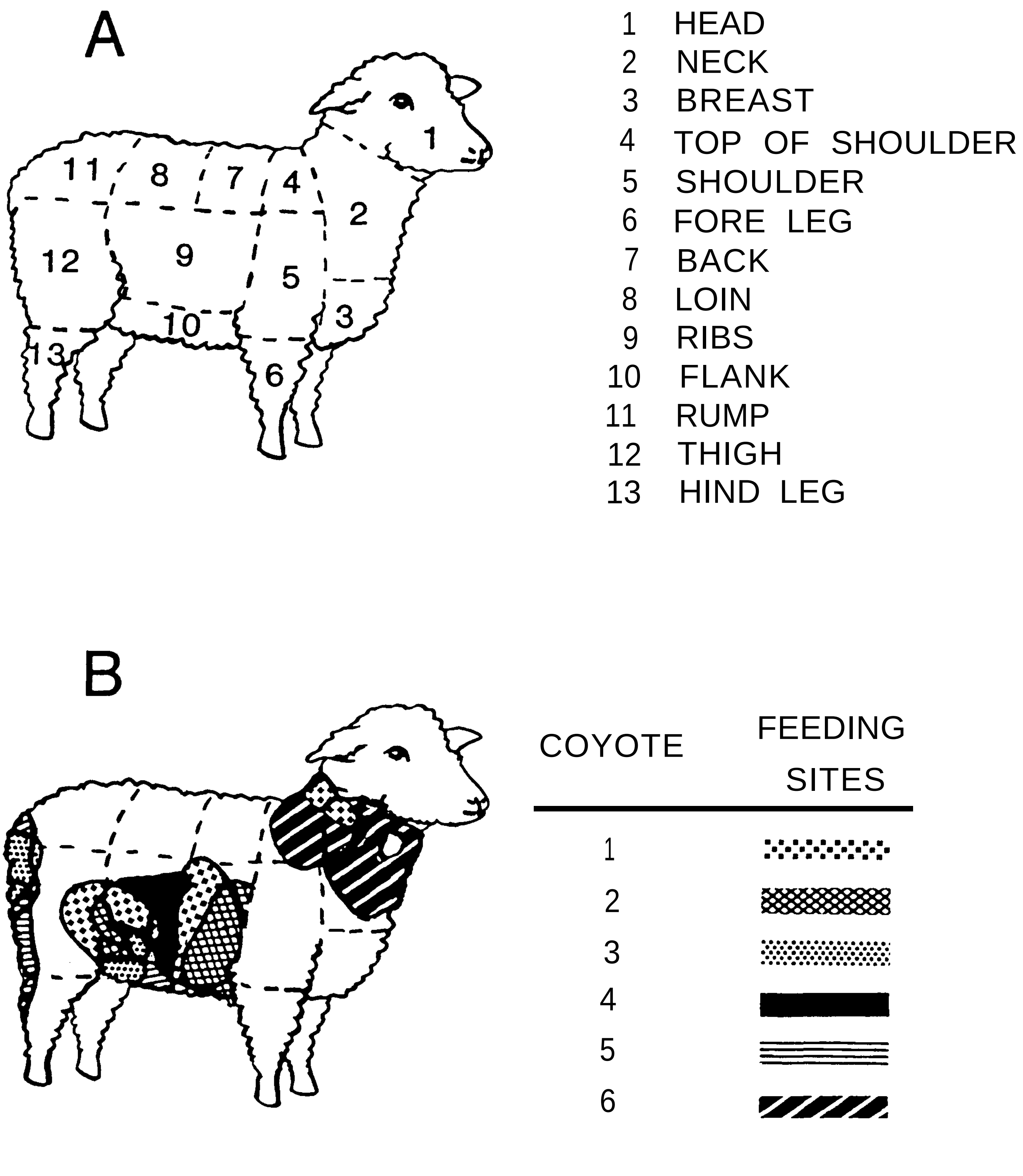
Figure 1. (la) Terms for Carcass Areas of Sheep Used in Sheep-grading Events (Ensminger, 1970). (1b) Approximate Locations/sizes of Feeding Sites Made by Each Coyote During Predation.



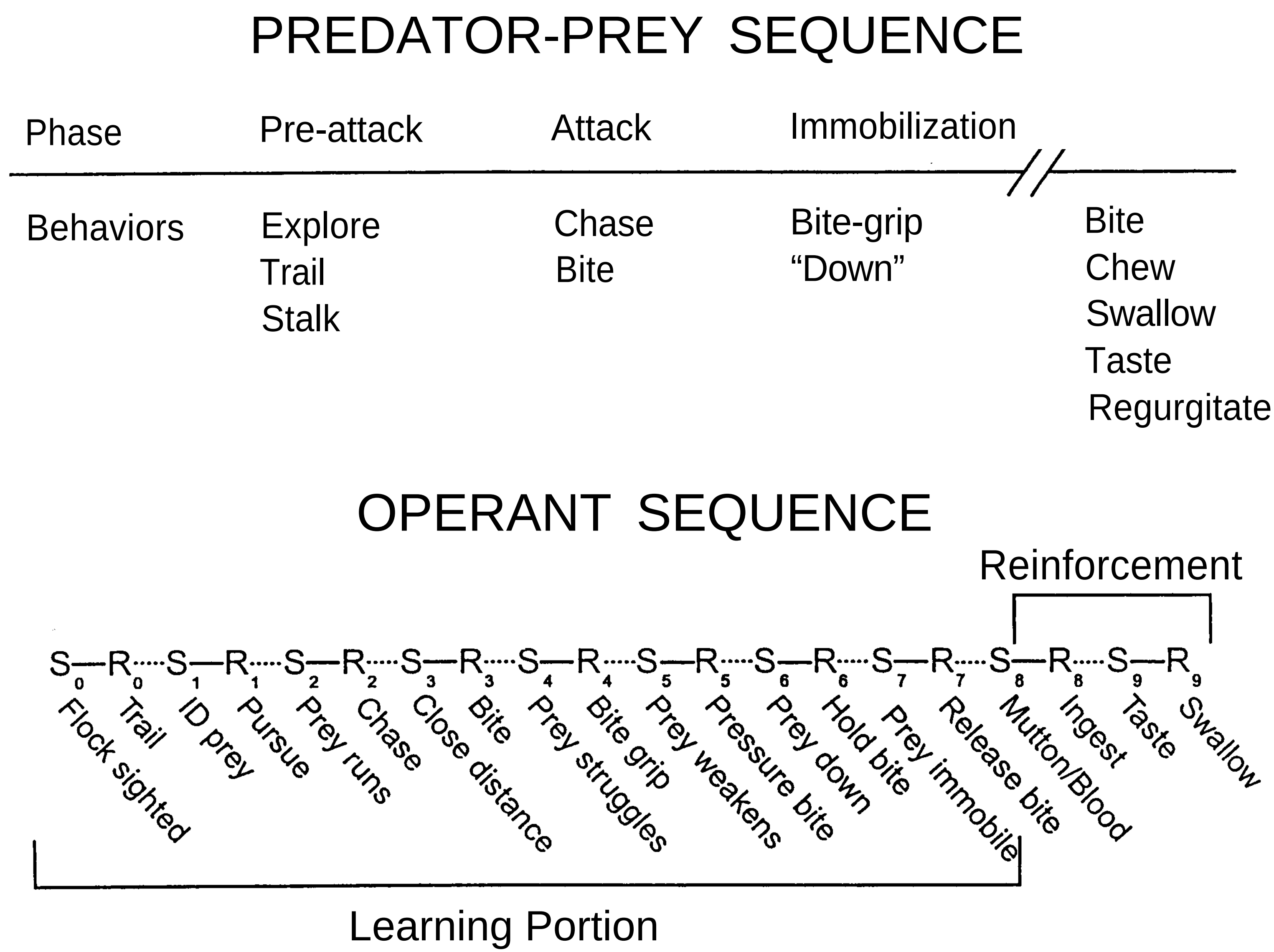


Figure 2. Schematic of a Predator-prey Sequence for Coyote Fas of Sheep (Top) and a Typical Operant Conditioning, Stimulus-response Sequence (Bottom).