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SHEEP-PREDATION BEHAVIORS OF WILD-CAUGHT, CONFINED COYOTES: SOME HISTORICAL DATA

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ABSTRACT: As part of efforts to develop The Livestock Protection Collar (U.S. EPA Reg. No. 56228-22), we videotaped sheep-predation events by 23 (15♂ and 8♀) wild-caught, confined coyotes (*Canis latrans*) in a 31 x 41 m enclosure. Coyotes were paired individually with a sheep (*Ovis aries*) during 1 h daily trials. Nineteen (13♂ and 6♀) of the coyotes made 75 fatal attacks of 1 to 7 sheep each; 4 coyotes (2♂ and 2♀) made no fatal attacks despite 19 to 39 daily pairings. Of coyotes that made fatal attacks, 13 (9♂ and 4♀) always attacked at the neck of sheep; 5 (4♂ and 1♀) always attacked by nipping at the legs/head/back of sheep; and 1 attacked at the legs/head/back of sheep during two initial events, but subsequently attacked at the neck of sheep. Greater time in captivity was not correlated with trials preceding a fatal attack ($\rho = +0.23$). Among coyotes making ≥ 2 fatal attacks, subsequent predation events occurred after fewer intervening pairings with sheep. Initial feeding sites occurred most frequently at the flanks/ribs of sheep. Although collected between 1976 to 1980, these observations represent a never-to-be-acquired-again data set that remains timely. Data showed that not all coyotes display sheep-predation behaviors or kill sheep efficiently. Instrumental learning and stimulus-habituation models of coyote predation behavior are discussed.

KEY WORDS: predation behavior, coyotes, *Canis latrans*, sheep, *Ovis aries*, learning, habituation

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INTRODUCTION

Observations of coyote (*Canis latrans*) predation behaviors directed towards sheep (*Ovis aries*) are rare. Essentially, these are limited to: 1) anecdotal descriptions by ranchers or biologists that witnessed coyote-sheep attacks on open rangeland (Davenport et al. 1973; Hawthorne 1980); 2) reconstructed accounts inferred from post-mortem examinations of carcass wounds on predator-killed sheep (Gluesing et al 1980; Klebenow and McAdoo 1976; Nass 1977; Nesse et al. 1976; Tigner and Larson 1977); and 3) direct observations of coyote-sheep attacks involving confined coyotes (Jansen 1974; Connolly et al. 1976; Timm and Connolly 1980). Of these accounts, only the latter afford detailed analyses of how coyotes perform these attacks.

Jansen (1974) studied the sheep-selection patterns, sheep-attack sequences, and sheep-attack gaits of one wild-caught and two pen-reared coyotes using small flocks in a pen facility. He reported that the coyotes invariably developed a "throat-bite grip" during each kill, with times to death varying greatly (1.2 to 27.0 min). Analyses of "chase patterns" showed that the coyotes typically galloped along behind a sheep flock, then ran and bit onto the backs of the sheep at the flock's periphery during changes of direction—if a sheep broke from the flock, the coyote typically pursued this animal. Little, if any, increased efficiency of predation was noted during three kills each by these coyotes.

Connolly et al. (1976) described incidents of sheep predation by 12 pen-reared coyotes in enclosures. Trials involved 1 to 4 coyotes paired with 1 to 6 sheep; these ranged from 1 to 216 h in length. Nine of the coyotes killed 24 sheep, while three pups never made a kill. Without exception, coyotes that killed during individual pairings with a sheep always clamped their jaws dorsally behind the ears and held or improved this neck bite until

the sheep succumbed. In trials involving multiple coyotes, slashing and biting at the sides or backs of sheep by coyotes were noted, with one mauling death reported. Timm and Connolly (1980) published a photo series illustrating certain data from Connolly et al. (1976).

Over 20 years ago, as part of efforts to develop "specific" methods for the management of coyotes that prey upon sheep, we videotaped 75 sheep-predation events of 23 wild-caught coyotes within a enclosure. Efforts led to the registration of The Livestock Protection Collar (U.S. EPA Reg. No. 56228-22). These data remain the most extensive database of empirical information available on the sheep-predation behaviors of coyotes—key data for biologists attempting to devise novel, effective, sheep-mounted devices that will protect sheep from canids. This paper identifies patterns of attack used by lone coyotes paired with lone sheep and quantifies the frequency, duration, and anatomical site of sheep-attack and -ingestion responses by wild-caught, confined coyotes.

MATERIALS AND METHODS

Animals

Twenty-three coyotes (15♂ and 8♀) weighing between 9.5 and 17.0 kg at the start of trials were used. Coyotes were captured in four states: Colorado (1♂ and 2♀), Kansas (7♂ and 2♀), New Mexico (6♂ and 4♀), and Texas (1♀). Upon capture, coyotes were held individually in portable wire kennels (0.92 x 0.46 x 0.35 m).

Following transport to the research facility, coyotes were inoculated for rabies and quarantined for ≥ 60 days. During non-test periods, they were housed either individually or as opposite-sex pairs in chain-link pens (3.0 x 1.5 x 1.8 m) with attached shelter boxes (1.0 x 0.8 x 0.7 m), and were provided Purina® Dog Chow® (Purina

Mills, St. Louis, MO) and water ad libitum. During predation trials, coyotes were moved to a set of eight of these same pens and housed individually; dietary restriction was used during these trials (i.e., in general, ~0.5 kg of Purina® Dog Chow® was provided every 2 to 3 days in the home cage and ~1 to 3 kg portions of prey were ingested following predation events).

Various breeds of domestic sheep served as prey. Sheep (12 to 50 kg) were held within fenced pastures at the site and grazed on available grass or were fed a daily ration of baled hay in winter. Water was available to the sheep ad libitum.

Test Enclosure

Predation trials were conducted in a 41 x 31 m (0.13 ha) behavioral enclosure. Sides of the enclosure were 2.4 m high and composed of two joined sections of 1.2 m wide, woven V-wire fence. A 0.91 m chain-link overhang extended inward at the top of the enclosure fence. Brick observation buildings (3.1 x 2.0 x 2.9 m), fitted with one-way glass windows near the roof, were located in the southeast and southwest corners of the enclosure. A 1.2 m high V-wire fence surrounded each building to prevent animals from entering blind areas. Coyotes were moved to and from the release pen through a wire-enclosed walkway (14 x 1.2 x 2.0 m) along the kennel-housing area. About 0.04 ha of the southeast corner of the enclosure was enclosed with 4.8 m high V-wire fence; this formed a release pen for coyotes between the enclosure and their housing cage. The release pen was equipped with entry-exit guillotine doors that were operated by the observer in the southeast building.

Procedures

Coyotes were paired individually with a sheep during 1 h daily trials. A three-phase procedural sequence was used: acclimation, sheep-predation assessment, and/or sheep-predation maintenance.

Acclimation involved between one and six daily 1 h trials to familiarize the coyote with the enclosure and handling procedures. These trials consisted of moving a coyote to and from the enclosure through the walkway and release pen, plus 1 h in the enclosure without a sheep present.

Sheep-predation assessment involved a series of consecutive, daily, 1 h pairings of a sheep and a coyote in the enclosure. Most trials were videotaped (Model VC-150, AKAI Corp., Tokyo, Japan) for behavioral analysis. Trials consisted of placing a sheep into the enclosure, moving a coyote through the walkway into the release pen and releasing the coyote into the enclosure. Trials were scheduled to last 1 h; however, if predation occurred, trials lasted until the coyote had attacked, immobilized and fed on the sheep for 15 to 20 minutes. If sheep survived attack, they were euthanized via a cranial blow upon completion of the trial. Trials occurred on successive days, except for Coyotes 13, 14, 16, 17, 22 and 23; these animals experienced interruptions of 1, 1, 5, 13, 1 and 6 no-trial days during the assessment schedule, respectively.

Sheep-predation maintenance involved a series of trials in which coyotes that fatally attacked a sheep were

held without sheep pairings for various numbers of days (no dietary restriction) and were then retested for predation behaviors (dietary restriction). Maintenance procedures were used with 12 (i.e., Coyotes 1, 2, 3, 4, 5, 6, 10, 11, 13, 14, 15 and 16); trial interruptions for these coyotes varied between 1 and 126 successive days (\pm SD=22.1 \pm 33.7). Upon retest, trial procedures were the same as described for the initial sheep-predation assessment.

Data Analyses

Written narratives, descriptive statistics (i.e., frequencies, $\bar{x} \pm$ SDs, minimums-maximums, percentages and proportions), and illustrative tables/graphs/charts were used to characterize sheep-attack, -fatal-attack, and -ingestion patterns of the coyotes. A Spearman Rank Order Correlation (Kirk 1990) was computed between months in captivity and trials preceding the initial fatal attack of sheep by coyotes.

Precise operational definitions for observed behaviors were derived prior to scoring of the videotapes. "Attack" was defined as any physical contact of the coyote's jaws/mouth with the sheep. "Attack trial" referred to any 1 h trial during which ≥ 1 attack occurred (i.e., some coyotes made numerous attacks during a trial, but this was scored as only one attack trial). "Fatal attack" referred to any 1 h trial in which predation occurred—the sheep was immobilized and consumed by the coyote or was euthanized by the investigator; this was a carefully derived definition because severe injury or death was not a prerequisite to ingestion of prey by some coyotes. "Fatal attack" and "predation event" were synonymous.

RESULTS

Incidence of Predation

Of the 23 coyotes observed, 19 (83%) fatally attacked ≥ 1 sheep; predation events occurred following between 3 and 31 ($\bar{x} \pm$ SD=13.6 \pm 7.1) 1 h pairings with sheep (Table 1). Altogether, 75 trials involved fatal attacks of a sheep; this included 55 fatal attacks during the predation-assessment trials and 20 fatal attacks by the 12 coyotes used to study maintenance of predation behaviors.

Minimum-maximum fatal attacks by individual coyotes varied between 1 and 7 for the 19 coyotes that caused predation events ($\bar{x} \pm$ SD=3.9 \pm 1.9). Thirteen of these also displayed attack behaviors (e.g., bites, nips) prior to completing a fatal attack; whereas, 6 of these 19 coyotes made fatal attacks without displaying prior attack behaviors (see Table 1).

Incidence of Non-predation

Four coyotes (17%; 2♂ and 2♀) did not fatally attack a sheep despite 19 to 39 ($\bar{x} \pm$ SD=29.2 \pm 8.4) 1 h pairings with a sheep. Interestingly, two of these coyotes attacked sheep twice, but neither ever caused predation of a sheep (see Table 1).

Predation Behaviors

All predation events on sheep involved either a neck-attack or a body-attack sequence. The neck-attack sequence involved a bite to the neck that usually downed, immobilized and appeared to cause the sheep's death prior to feeding by coyotes. Prolonged pursuit with

Table 1. Months captive, test length, sheep-attack (A)¹ and fatal attack (FA) data for coyotes.

Coyote (¹ Body- attack)	Months Captive	Total Days of Test	Total 1 h Trials with Sheep	Total As/FAs of Sheep	As/FAs of Sheep— Assessment	As/FAs of Sheep— Maintenance
1(♂)	8	22	10	0/3	0/2	0/1
2(♂)	8	155	26	0/4	0/2	0/2
3(♂)	8	36	17	4/3	3/2	1/1
4(♂)	4	30	19	2/3	2/2	0/1
5(♂) ¹	13	123	29	6/7	5/3	1/4
6(♂)	10	23	12	1/6	1/4	0/2
7(♂)	5	14	9	1/2	1/2	None
8(♂)	12	30	25	1/2	1/2	None
9(♀) ¹	10	23	18	2/5	2/5	None
10(♀)	12	178	45	1/7	1/3	0/4
11(♀)	13	65	26	4/5	4/3	0/1
12(♂) ¹	7	49	40	3/1	3/1	None
13(♂)	9	48	38	7/7	4/5	3/1
14(♀)	16	44	30	1/5	1/4	0/1
15(♂) ¹	10	47	20	0/4	0/3	0/1
16(♀) ¹	25	45	14	1/4	1/3	0/1
17(♂)	11	40	35	0/1	0/1	None
18(♀)	10	18	13	0/3	0/3	None
19(♂) ¹	10	22	17	0/3	0/3	None
				Σ=34/75	Σ=29/55	Σ=5/20
20(♂)	5	24	19	2/0	2/0	None
21(♀)	4	32	27	0/0	0/0	None
22(♀)	9	37	32	0/0	0/0	None
23(♂)	11	40	39	2/0	2/0	None

intermittent bites to the back, flanks, and legs of the sheep distinguished the body-attack sequence.

Of the 19 coyotes that made fatal attacks, 13 (68%) displayed the neck-attack sequence during 51 of the 75 (68%) predation events recorded. The neck-attack sequence was characterized by four distinct behaviors: 1) initial activity (e.g., walking, sniffing, rolling) after release into the enclosure which appeared undirected towards the sheep ($\bar{x} \pm SD = 9:47 \pm 14:43$ min:sec); 2) pursuit of the sheep, with intermittent bites to the head,

neck, shoulders, etc. that usually slowed and stopped the sheep (0.5 to 5 min); 3) a prolonged, pressure-type bite to the neck of the sheep, with frequent adjustment and intensified pressure to the ventral-lateral area ($\bar{x} \pm SD = 10:10 \pm 5:16$ min:sec) which continued until the sheep was "downed" (i.e., lost its footing and fell); and 4) a pause following release of the pressure-type bite prior to feeding ($\bar{x} \pm SD = 7:20 \pm 6:51$ min:sec).

Five of the 19 killer coyotes (26%; Coyotes 5, 9, 12, 15 and 19) invariably used the body-attack sequence

during 20 of the 75 (27%) predation events observed; whereas, the remaining killer coyote (Coyote 16) used the body-attack sequence in two initial fatal attacks, but changed to the neck-attack sequence in the remaining two predation event—the only observed shift of predation pattern by any coyote. This sequence involved: a) initial activity including walking, sniffing, and rolling ($\bar{x} \pm SD = 12:04 \pm 15:52$ min:sec); and b) lengthy periods of intermittent chasing, biting, and nipping directed at the head, legs, sides, back, and flanks of sheep which rarely downed or proved fatal prior to feeding by the coyote.

Predation Efficiency

Durations of fatal attack sequences were highly variable for both neck- and body-attack sequences, and no coyote displayed a transitive, consistent decrease of fatal-attack durations during successive kills. The 14 coyotes (including Coyote 16) that displayed the neck-attack sequence during 53 fatal attacks took a mean ($\pm SD$) of 10:10 ($\pm 5:16$) min:sec to complete these behaviors (minimum-maximum=00:25 and 27:00 min:sec, respectively). Of course, the body-attack sequences cannot be called efficient; generally, these lasted the entire 1 h trial, with the investigator having to euthanize the sheep.

Times from the start of neck attacks until the sheep were "downed" took a mean ($\pm SD$) of 3:42 ($\pm 4:20$) min:sec, with minimum and maximum times of 00:05 and 19:30 min:sec, respectively (Figure 1). These times were also variable; no coyote displayed consistently quicker downing of sheep during successive fatal attacks.

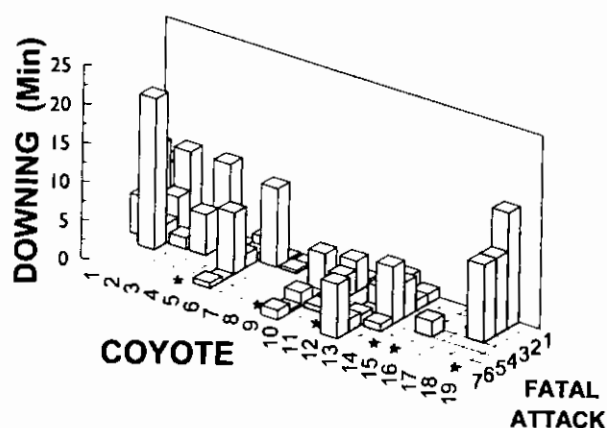


Figure 1. Time-to-downing of 52 sheep (three missing data elements) recorded for 14 of the coyotes that used the neck-attack sequence. [* Coyotes which used the body-attack sequence—times not computed; note that Coyote 16 used the body-attack sequence for the first two fatal attacks, then used the neck-attack sequence for the remaining two fatal attacks.]

The number of pairings with sheep intervening multiple predation events decreased sharply after coyotes made one or two fatal attacks. That is, the daily trials preceding or intervening successive predation events by the coyotes decreased dramatically following initial predation (see Table 2). Mean ($\pm SD$) trials preceding or intervening the first, second, third, fourth, fifth, sixth, and seventh fatal attacks by those coyotes completing multiple sheep predation events were 13.4 (± 7.0), 3.1 (± 2.0), 1.7 (± 0.8), 2.6 (± 2.5), 1.3 (± 0.5), 3.5 (± 4.4), and 4.7 (± 3.5). Nevertheless, conduct of maintenance-of-sheep-predation trials somewhat obscured this effect; occurrence of no-trial days seemed to delay resumption of predation.

Captivity and Predation Events

Months in captive for the coyotes did not predict the rank order of trials preceding a fatal attack of sheep ($\rho = +0.23$, NS, two-tailed Critical Value_{0.05}=0.46). Length of captivity for the 19 coyotes completing fatal attacks and the four coyotes that engaged in no predation differed by about three months ($\bar{x} \pm SD = 10.6 \pm 4.5$ and 7.2 ± 3.3 mo., respectively).

Prey-ingestion Behaviors

To evaluate typical sheep-ingestion behaviors, feeding sites on sheep were plotted on a standard sheep-grading chart (Figure 2A). Sites were recorded for 67 of the 75 predation events; these comprised a total of 112 distinct carcass-feeding sites, with 32 events involving multiple (≥ 2) sites (Figure 2B). The greatest proportion of all feeding sites occurred at the ribs (0.22), neck (0.19), flanks (0.16), and head (0.13) of sheep; the coyotes never fed at the back or the top-of-shoulder.

Regarding the first feeding sites on carcasses, preferred sites (based on decreasing proportions) were: flanks (0.26), ribs (0.23), head (0.13), neck (0.13), and thighs (0.13) (Figure 2C). No initial feedings were noted at the top-of-shoulder, fore leg, back, loin, or hind leg.

DISCUSSION

Not surprisingly, the neck-attack sequence characterized the predation pattern for most of the coyotes; whereas, about a fourth of the coyotes consistently attacked sheep by making multiple bites at the legs/back/flanks. While the neck-attack sequences extend prior descriptions of how coyotes typically kill sheep, the relatively high number of body attacks involving lone coyotes was unexpected (see Jansen, 1974; Connolly et al. 1976). Although Connolly et al. (1976) noted body attacks in several multiple-coyote/multiple-sheep trials, the incidence of body-attack behaviors is previously unreported. Interestingly, this body-attack sequence resembles that described for dogs (*Canis familiaris*)—a noteworthy finding for wildlife managers attempting to determine post-mortem cause of death for livestock claims or predation surveys (see Hawthorne, 1980).

Table 2. Number of daily 1 h trials preceding or intervening successive fata attacks (FAs) by coyotes.

Coyote	FA1	FA2	FA3	FA4	FA5	FA6	FA7
1	9	1 ¹	1				
2	12	4 ¹	1	2			
3	13	2 ¹	2				
4	13	5 ¹	1				
5	13	2	1 ¹	1	1	10	1
6	3	6	1	1 ¹	1	1	
7	7	1 ¹					
8	23	1 ¹					
9	10	3	3	1	1 ¹		
10	22	2	2	9 ¹	1	1	8
11	18	5	2	1 ¹	2		
12	31 ¹						
13	19	4	2	2	1 ¹	2	5
14	19	5	3	2 ¹	2		
15	8	7	1 ¹	4			
16	10	1	2 ¹	3			
17	4 ¹						
18	11	1	1 ¹				
19	11	3	3 ¹				
\bar{x}	13.4	3.1	1.7	2.6	1.3	3.5	4.7
(\pm SD)	(\pm 7.0)	(\pm 2.0)	(\pm 0.8)	(\pm 2.5)	(\pm 0.5)	(\pm 4.4)	(\pm 3.5)

¹Denotes last predation event of the sheep-predation assessment; subsequent events were recorded during the sheep-predation maintenance and involved varied periods of no-trial days intervening between subsequent predation events.

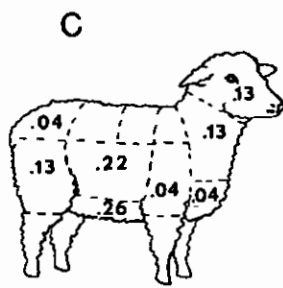
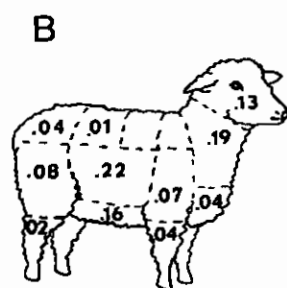
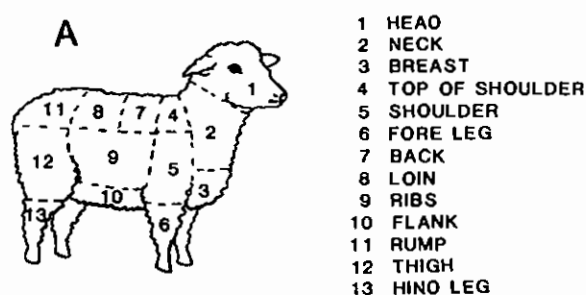


Figure 2. (A) A drawing of 13 sheep-carcass zones used in sheep-grading events (see Ensminger 1970). (B) Proportionate locations of 112 feeding sites obtained for 67 FAs by 19 sheep-attacking coyotes. (C) Proportionate locations of 23 feeding sites identified for sheep-attacking coyotes during predation events.

We found little, if any, alterations in predation patterns with greater experience of the coyotes. The only evidence for new learning in our sample was the qualitative change from the use of a body-attack sequence to a neck-attack sequence by Coyote 16. Still, the rapid decrease in trials intervening successive fatal attacks of sheep once predation occurred supports a learning/habituation model. Demonstration of altered, more effective predatory behaviors in confined (or wild) coyotes may require >7 events; it is probably a lengthy process.

A key finding of these observations is that not all coyotes displayed sheep-predation behaviors during this enclosure-type assessment. Although Connolly et al. (1976) reported a similar finding (i.e., 3 of 12 pen-reared coyotes never killed sheep), this is the first report of wild-caught coyotes not displaying predation behaviors despite food restriction. This result implies that some wild coyotes may not have learned to kill sheep in the wild or simply will not kill large prey such as sheep. Gese et al. (1996) reported that intrinsic (social dominance) and extrinsic factors (weather) impact foraging areas and time budgets of wild coyotes, with sub-dominants (betas) and pups excluded from certain prey-foraging areas by adult coyotes.

Based upon the carcass-feeding responses that we observed, development of "selective, specific"

coyote-management devices (i.e., effective for canids and targets sheep-attacking canids) of lures/baits derived from viscera/entrails of sheep deserves consideration for the development of coyote attractants. Moreover, neck-attack frequencies show that affixing delivery systems for toxicants, repellents, and aversive agents to the necks of sheep offers the most specific oral delivery to coyotes—about 70% of sheep-attacking coyotes should contact such chemicals.

In conclusion, we believe that coyote predation in confined (and probably unconfined) situations can (in essentially 80% of cases) be explained using instrumental learning principles (Skinner 1938; Sterner 1997). Under this model, coyotes are viewed to learn prey identification, selection, pursuit, attack, immobilization, release, ingestion, taste, and satiation responses. This can be likened to a serial stimulus-response chain (i.e., Stimulus₀-Response₀, S₁-R₁, S₂-R₂, etc.), with the source of reinforcement associated with release into the enclosure (movement into range or pasture) and occurrence of prey (i.e., discriminative stimulus or S^d). Confinement stimuli (e.g., human presence, enclosure fence) function to inhibit these stimulus-response chains initially, but nutritional incentives eventually increase drive and yield predation. Subsequent reinforcement then makes recurrence of the stimulus-response chain more frequent.

ENDNOTES

This research was conducted during the late 1970s with the support of the U.S. Fish and Wildlife Service, Department of the Interior, and the U.S. Environmental Protection Agency (IAG-D6-0910) as part of a larger effort to develop novel selective (canids only), specific (responsible canid) methods of coyote management. Care and maintenance of animals met all Animal Welfare Guidelines in effect at that time.

At the time of the research, the authors were at the Denver Wildlife Research Center (DWRC); the DWRC transferred to the Animal and Plant Health Inspection Service (APHIS), U.S. Department of Agriculture (USDA) on March 3, 1986 and was closed on August 4, 1997.

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