Ontogeny of black-footed ferret predatory behavior towards prairie dogs

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Abstract: To study the effects of environmental upbringing and predation experience on black-footed ferret (*Mustela nigripes*) predatory skills towards prairie dogs, we compared killing efficiency and behaviors of 32 black-footed ferret kits (from 24 different litters). Four treatment groups were established: group 1 (n = 8), kits raised in indoor cages and never exposed to live prey; group 2 (n = 8), kits raised in indoor cages and fed live hamsters twice a week beginning at 8 weeks of age; group 3 (n = 8), kits raised in indoor cages, fed live hamsters, and exposed to live prairie dogs in family trials once per week; and group 4, kits raised in outdoor enclosures with ad libitum access to live prairie dogs in natural burrows. Juvenile black-footed ferrets raised with exposure to live hamsters were more successful at killing prairie dogs than kits devoid of any predation experience. Previous experience with prairie dogs (in both indoor cages and outdoor pens) significantly increased predation efficiency. Witnessing a black-footed ferret mother performing a kill enhanced the kit's predatory skills. We conclude that the placement of the kill bite appears to be innate for black-footed ferrets, but the likelihood of killing and the efficiency at handling prey are substantially enhanced by experience.

Résumé : Nous avons étudié les effets des conditions d'élevage et de l'expérience de prédation sur les aptitudes prédatrices du Putois d'Amérique (*Mustela nigripes*) à l'égard des chiens de prairie en comparant le comportement de chasse et l'efficacité à tuer des proies chez 32 jeunes putois (de 24 portées). Quatre groupes expérimentaux ont été établis : groupe 1 (n = 8), jeunes élevés en cage à l'intérieur et jamais exposés à des proies vivantes; groupe 2 (n = 8), jeunes élevés en cage à l'intérieur et nourris de hamsters vivants deux fois par semaine à partir de l'âge de 8 semaines; groupe 3 (n = 8), jeunes élevés en cage à l'intérieur, nourris de hamsters vivants et exposés à la présence de chiens de prairie au cours de tests en famille une fois par semaine; et groupe 4, jeunes élevés dans des enceintes clôturées à l'extérieur avec accès ad libitum à des chiens de prairie vivants, dans des terriers naturels. Les jeunes putois exposés à la présence de hamsters vivants étaient plus habiles à tuer les chiens de prairie que les jeunes sans expérience préalable de prédation. L'exposition préalable à la présence de chiens de prairie (dans des cages à l'intérieur ou des enceintes à l'extérieur) augmentait considérablement l'efficacité de la prédation chez les jeunes. L'observation d'une mère en train de tuer une proie avait pour effet d'augmenter les capacités prédatrices chez les jeunes. La position de la morsure sur la proie semble instinctive chez le putois, mais la probabilité d'infliger une morsure mortelle et l'efficacité à manipuler les proies semblent fortement augmentées par l'expérience.

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Introduction

Complex behaviors, such as predation, develop as a result of interactions between an individual's genetic makeup and the environmental experience it has acquired throughout its life (Leyhausen 1973; Polsky 1975*b*, 1977). Neural mechanisms controlling an animal's predatory response are probably innately organized, although presumably modifiable by experience during development. An animal's experience preceding an actual killing test has a profound influence on its prey-killing behavior (Kuo 1930, 1938; Polsky 1975*a*, 1975*b*; Caro 1980*a*; Miller et al. 1992). Prior predation experience, such as killing per se or even witnessing a kill, considerably increases the chances of killing (Kuo 1930; Caro 1980*b*).

Experimental analyses of innate versus learned components of killing behavior in the European polecat (*Mustela putorius*) indicate that although the predation sequence is stereotyped (Gossow 1970), previous environmental experience (including play with siblings) has a strong influence on prey-killing behavior (Eibl-Eibesfeld 1956; Wüstehube 1960; Dresner 1981). Yet, while Wüstehube (1960) and Gossow (1970) maintained that the orientation of the kill bite to the nape of the neck is inborn, Eibl-Eibesfeld (1956) believed that it is learned through trial and error.

In domestic ferrets, predation experience significantly reduced the number of bites necessary to kill a cotton rat (*Sigmodon hispidus*), the number of adjustments of the kill bite, and the number of escapes by prey (Marshall 1984). Dresner (1981) found that although prey-naive European polecats were often successful at placing the kill bite in their first attack on mice, in ferrets, predation experience decreased kill latencies and increased killing efficiency. Also, Siberian ferrets (*Mustela eversmannii*) with predation expe-

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rience killed domestic laboratory mice better than control animals (Miller et al. 1992).

Because of the fossorial and secretive habits of this nocturnal carnivore, very few predation attempts by black-footed ferrets (*Mustela nigripes*) have been observed in the field (Hillman 1968; Henderson et al. 1974; Clark et al. 1986; Paunovich and Forrest 1987; Miller 1988; Clark 1989; B. Miller and B. Luce, personal communication). In addition, black-footed ferrets tend to consume prey in the same burrow where the kill is made (Richardson et al. 1987).

The following experiments were primarily designed to investigate the effects of upbringing in captivity and individual predation experience on black-footed ferrets' (referred to hereafter as ferrets) killing skills towards prairie dogs. We made the following predictions. (*i*) The captive environment will play an important role in the development of ferret predation skills towards prairie dogs. To test this prediction, we compared the predation skills of ferrets raised in outdoor pens with those of live prairie dogs and of ferrets raised in indoor cages and allowed to acquire different levels of predation experience (supplied with no prey, hamsters, and prairie dogs). (*ii*) Individual predation experience will increase killing success and help refine predation skills. To test this prediction, we evaluated predation behaviors and killing efficiency of ferrets exposed to prairie dogs in four subsequent trials. In addition, we describe the sequence of ferret predatory behaviors when confronting prairie dogs and discuss innate and learned components of ferrets' predation skills.

Materials and methods

These experiments were conducted as part of a research program designed to develop techniques for training captive-raised ferrets that were targeted for reintroduction into their native habitat (Vargas 1994). Experiments were carried out in compliance with the "Guidelines for the use of animals in research" (Anonymous 1991). In addition, husbandry of captive ferrets used in our research followed standards stipulated by the "Guidelines on the care of laboratory animals and their use for scientific purposes" (Universities' Federation for Animal Welfare 1990).

Effects of captive upbringing on predatory behavior

This study was conducted in 1992 at the Sybille Wildlife Conservation and Research Unit (now the National Black-footed Ferret Conservation Center) and involved trials with 32 ferret kits from 24 different litters. Litters were divided into four treatment groups: group 1 (*n* = eight kits, five litters), kits raised in indoor enriched cages and never exposed to live prey (fed standard Sybille diet (60% commercial mink chow and 40% ground domestic rabbit meat)); group 2 (*n* = eight kits, eight litters), kits raised in indoor enriched cages and fed live hamsters twice per week starting when kits were 8 weeks of age; group 3 (*n* = eight kits, five litters), kits raised in indoor enriched cages, fed live hamsters twice per week starting when kits were 8 weeks of age, and exposed to live prairie dogs weekly, in family trials starting at 13 weeks of age; group 4 (*n* = eight kits, six litters), kits raised in outdoor enclosures (each equipped with a release cage; Carlson 1993) with free access to prairie dog burrows and live prairie dogs. These litters were supplementarily fed live hamsters following the same regime used with the cage-raised kits.

Groups 1, 2, and 3 were raised in enriched cages with a surface area of 1.5 m^2 supported on 1-m legs (Vargas and Anderson 1996). Enriched cages had three nest boxes instead of two, an additional 3 m of tunnel material (ADS tubing, 10.2 cm in diameter), and two or more concrete blocks. Cage furnishings were rearranged once per week to increase environmental complexity, with the goal of stimulating curiosity and exploratory behavior (Vargas and Anderson 1998). Group 4 was raised in outdoor pens at the Sybille facility. Each pen had a surface area of 80 m^2, with enclosed prairie dog colonies contained by heavy gauge mesh "cyclone" fencing. This fencing extended 2.4 m underground and covered the bottom surface of the arena to prevent escape of the enclosed animals. Roofs were made of either fiberglass or corrugated metal and lighter gauge woven wire. Wild-caught prairie dogs were introduced first to establish burrow systems. Six pregnant ferret females were placed in release cages within the outdoor pens and allowed to whelp in the cages. Mother and litter were given access to the prairie dog burrows when the kits ranged between 52 and 60 days of age. Throughout summer and fall, four or five live white-tailed prairie dogs (*Cynomys leucurus*) were added weekly to the pens. Prairie dogs were quarantined for a minimum of 2 weeks to prevent potential transmission of infectious diseases, particularly sylvatic plague and tularemia.

In order to conduct predation trials in indoor cages, a mock prairie dog burrow was attached to the bottom of the ferrets' cage with 1 m of ADS tunnel (10.16 cm in diameter). Each mock burrow consisted of a wooden box (30 × 30 × 25 cm) with a removable Plexiglas front for viewing. The top lid was perforated with several breathing holes and hinged at an angle of approximately 35°. These boxes were partially filled with mortar mix configured into a burrow shape; the resulting inside chamber was approximately 22 × 22 ×15 cm. These dimensions were based on sizes of actual prairie dog burrows (L. Hanebury, personal communication). Attached to one of the burrow sides was a section of ADS tubing (45 cm in length) from which one side had been removed and replaced with Plexiglas to allow ferret activity in the tunnel to be viewed. All parts could be easily detached to facilitate cleaning and disinfection between trials.

Juvenile ferrets were individually exposed to live prairie dogs at the age of 16.5 weeks. All kits under evaluation were singly placed in the "trial cage" the day before the predation test. On that first day, the kit was given a live hamster, which was placed in the prairie dog nest box. The actual predation test took place the second night the kit was in the trial cage. That afternoon, a live prairie dog was placed in the mock burrow. A sliding door prevented the ferret from having visual or physical access to the prairie dog. Pieces of potato and (or) apple were placed in the burrow for the prairie dog's nourishment. In addition, a cloth covered the burrow's Plexiglas front wall to decrease potential disturbances to the prairie dog. Throughout the trial the mock burrow was illuminated with a 40-W red light bulb placed approximately 1 m away and 50 cm above the chamber's Plexiglas wall. Except for a low-light video camera (Panasonic WV 1850), all additional equipment was placed in the adjacent commissary – monitoring room. Between 22:00 and 23:00, the sliding door was removed and recording initiated. If after 8 h the ferret had not killed the prairie dog, both animals were removed from the testing arena.

To analyze these data, we focused on three main questions regarding the effects of the upbringing ferrets on their skills in killing prairie dogs: (1) how many animals managed to kill out of each group? (2) how "interested" were the ferrets in killing the prairie dog (interest was measured as the proportion of time that the ferret spent interacting with the prairie dog)? and (3) how efficient at handling the prairie dog were the ferrets that managed to kill? To determine differences among groups in the number of kits that managed to kill, we used a test of multiple proportions between the four experimental groups (Zar 1984). To test interest in killing, we calculated the percentage of time each kit spent interacting with the prairie dog (total number of minutes spent visually and (or) physically interacting with the prairie dog over the total number of

Table 1. Behavioral categories identified during trials in which black-footed ferrets killed prairie dogs.

Behavior	Description
Orient*	Directing head towards prairie dog from tunnel entrance
Approach*	Stalking prairie dog
Still*	Standing alert in tunnel, looking at prairie dog, but without making any body movement
Size up*	Standing alert in tunnel, focusing eyes on prairie dog while moving head up and down and occasionally from side to side
Sniff*	Placing nose within a few centimetres of prairie dog
Crawl up	Creeping slowly on top of sleeping prairie dog
Paw	Extending one forepaw and tapping prairie dog's side
Withdraw	Retreating from prairie dog's burrow into tunnel, but still visible in video picture
Leave	Departing from tunnel; not visible in video picture
Attempted bite	Opening mouth within a few centimetres of prairie dog without actually closing jaws on its body
Throat bite	Closing jaws around ventral side of prairie dog's neck (with lower jaw always placed on throat area)
Upper bite	Closing jaws anywhere on prairie dog's head except ventral side of neck (i.e., cheeks, chin, nose, nape of neck, top of head)
Other bites	Closing jaws on any other part of prairie dog's body except head or neck
Release bite	Opening closed jaws and letting go of prairie dog
Prairie dog unconsciousness	Prairie dog lying inert without apparent muscular tone

Note: Behaviors marked with an asterisk were combined into a single category: noncontact directive behaviors.

minutes that the trial lasted) and compared these percentages using a test of multiple proportions. Efficiency at killing the prairie dog was measured as the number of minutes elapsed since the ferret bit the prairie dog for the first time until all prey movements ceased (referred to as kill latency). Differences in kill latency among the experimental groups were contrasted using a nonparametric Kruskal–Wallis analysis of variance (Minitab, Inc. 1992). Kill latencies were compared between group 1 (prey deprived) and group 2 (exposed to hamsters) and between group 2 (exposed to hamsters) and group 3 (exposed to prairie dogs) using a Mann–Whitney test (Minitab, Inc. 1992).

Effects of individual predation experience

In this experiment, only kits belonging to group 3 (n = 8) were evaluated. Litters in this group had a mock prairie dog burrow permanently attached to their cages, but they had access to the system only once per week. Starting when the kits were 13 weeks of age, the family unit was exposed to a live prairie dog weekly, following the procedure utilized during the individual trials described previously. Individual kits to be used in these trials (different from the littermates involved in the upbringing experiment) were randomly chosen and marked with Nyanzol D fur dye for identification. Each kit was individually tested four times (at ages 13.5, 14.5, 15.5, and 16.5 weeks) with a live prairie dog.

We considered the following questions when analyzing this data set: (*i*) how many ferrets managed to kill during the first, second, third, and fourth individual exposures to prairie dogs? (*ii*) did interest in killing prairie dogs increase after repeated exposures to this prey? and (*iii*) did ferrets become more efficient at handling and killing prairie dogs after making subsequent successful kills? Killing success among trials and interest in killing the prairie dog with increasing experience were evaluated with a test of multiple proportions. Predation improvement from one kill to the next was calculated as the rate between latency to kill in one successful trial and the subsequent trial. Latencies to kill the prairie dog were compared with a Kruskal–Wallis one-way analysis of variance (Minitab, Inc. 1992).

Predation sequence

For the purpose of this study, we defined predatory behavior from both a functional and a descriptive viewpoint. From a functional perspective, predation involved those behaviors that resulted in killing of the prairie dog. From a descriptive viewpoint, predation consisted of a characterization of those movement patterns involved in the predation bout. We defined "kill bite" as the place on the prairie dog's body that the ferret was biting when the prey died. Fifteen ferret behaviors were identified during the test situation and considered for statistical analysis (Table 1).

Because killing efficiency differed greatly among kits, we conducted two separate lag sequential analyses based on the latency to kill prey. We considered "proficient kills" as those that lasted 2 min or less and "inefficient kills" as those that lasted 5 min or more. For analytical comparisons, we constructed two separate matrices for each group. On each matrix, preceding behaviors were entered on the vertical axis and subsequent behaviors on the horizontal axis (Vargas 1994). We then calculated transitional proportions and a binomial Z score for each cell (Bakeman and Gottman 1986). The frequencies of different categories of behavior needed to kill the prairie dog were compared between "proficient" and "inefficient" killers by means of a binomial test for equality of proportions (Zar 1984).

Prairie dog necropsies

To determine the actual cause of the prairie dog deaths, Dr. B. Williams (Wyoming State Veterinary Laboratory, Laramie) performed necropsies on 12 prairie dogs killed by ferrets. Prairie dogs were retrieved immediately after being killed, double-wrapped in a plastic bag, and kept either refrigerated or frozen until necropsy. Ferrets deprived of eating the prairie dog they had just killed were fed a live adult hamster instead.

Results

Effects of captive upbringing on predatory behavior

Juvenile ferrets from all four experimental groups (n = 8 kits per group) were individually tested against a live prairie dog during their 16th week of life. All ferrets that managed to kill the prairie dog did so with a bite to its throat. Two of the eight prey-naive juveniles (group 1) managed to kill the live prairie dog when tested at 16.5 weeks. Five kits from group 2 (previously exposed to live hamsters) were able to kill the prairie dog. Although these kits used the typical nape bite when killing hamsters (Vargas and Anderson 1998), they killed the prairie dogs with a bite to the ventral side of the neck.

Seven of eight kits exposed to live prairie dogs in family trials (group 3) killed prey in the individual trials. During

Fig. 1. Mean time spent by each experimental group of black-footed ferrets interacting with a prairie dog throughout the trial. Vertical lines represent SE. Treatment groups were as follows: group 1, cage-raised and not exposed to live prey; group 2, cage-raised and exposed to hamsters; group 3, cage-raised and exposed to a prairie dog; group 4, outdoor-raised and exposed to a prairie dog.

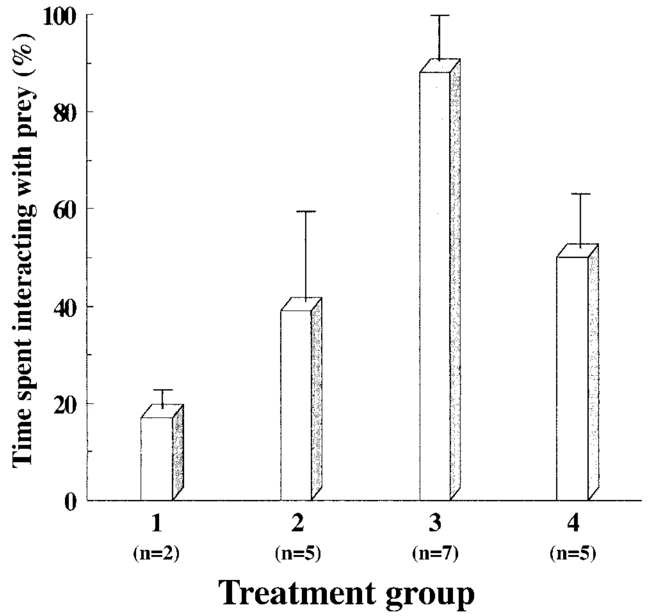
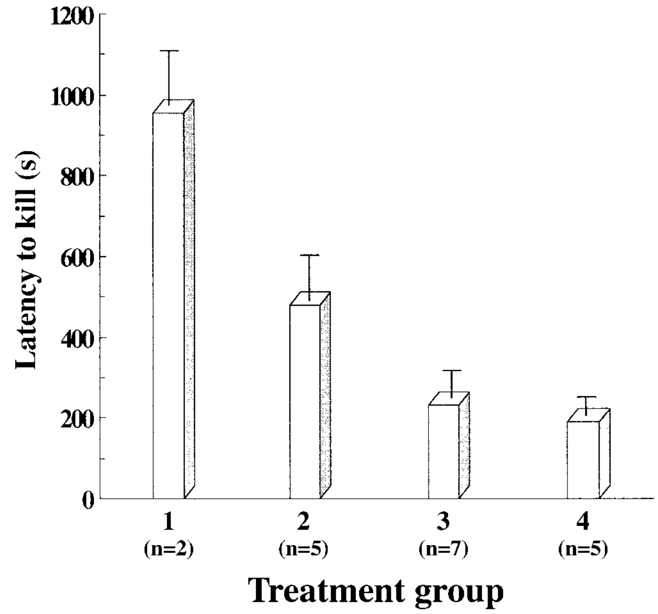


Fig. 2. Latencies to kill prairie dogs for black-footed ferrets according to rearing method. Vertical lines represent SE. For an explanation of treatment groups see Fig. 1.



the weekly family trials, the mother almost always delivered the final kill bite, although all kits generally participated in the predation process. After killing the prairie dog, the mother let the kits interact with the dead prey, allowing them to carry it from the mock burrow to the nest box. Of the five kits in group 4 (raised in outdoor enclosures) that managed to kill, four made efficient kills. Although there was no difference in the proportion of kits that killed in groups 2 and 4, there was a clear qualitative difference in the way the prairie dogs were handled.

The percentage of time that kits spent interacting with the prairie dog differed significantly among all four treatment groups ($\chi^2 = 413$, df = 3, $P < 0.001$) (Fig. 1). While group 3 showed the highest interest in prairie dogs (average interaction time (AIT) = 87% of trial length), most kits in group 1 showed little interest in interacting with prairie dogs (AIT = 12.8%).

Latency to kill, used as a measure of predation efficiency, was highest for the prey-deprived group and subsequently declined according to the complexity of the rearing environment ($H = 11.34$, df = 3, $P = 0.01$) (Fig. 2). Kill latencies did not differ between prey-deprived kits (group 1) and kits exposed to hamsters (group 2) ($W = 13.0$, $P = 0.081$). However, small sample sizes (only two of eight kits in group 1 managed to kill) may have led to a failure to detect a greater difference. Kill latencies were approximately the same for kits exposed to prairie dogs during their upbringing (groups 3 and 4), regardless of the type of captive environment in which they were raised (cage and outdoor pen, respectively).

We examined the influence of exposure to small and large prey on the ability to kill prairie dogs by comparing latencies to kill in groups 2 (exposed to hamsters) and 3 (exposed to prairie dogs). Results indicate that kits allowed to witness and participate in family kills were more efficient at killing prairie dogs when individually exposed to this prey than kits exposed to hamsters only ($W = 47.0$, $P = 0.023$).

Effects of individual predation experience

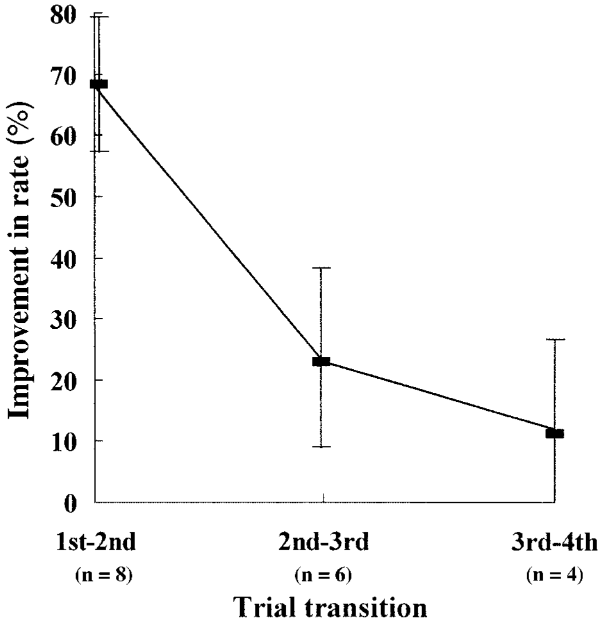
Success at killing prairie dogs (i.e., total number of ferrets that killed after one, two, three, or four individual exposures to prey) gradually increased during the first three trials. By the third exposure, killing success reached 100%. Interest level in prairie dogs steadily increased over subsequent trials. Once all kits had performed at least one successful kill, interaction time with the prairie dog reached 100%. In other words, once the ferrets detected the prairie dog, they proceeded to attack and did not leave the burrow until the prairie dog was dead.

Predation improvement was calculated as the ratio between the number of minutes spent "handling" the prairie dog during the first and second kills ($n = 8$), the second and third kills ($n = 6$), and the third and fourth kills ($n = 4$). Efficiency at killing prairie dogs was greatly enhanced after a single kill (Fig. 3). On average, ferrets managed to handle the prairie dog 62% more efficiently the second time they killed compared with the first time. Improvement rates decreased to 23 and 13% from the second to the third trial and from the third to the fourth trial, respectively. Latencies to kill prairie dogs decreased significantly with increasing predation experience ($H = 16.34$, df = 3, $P = 0.001$).

Predation sequence

Throughout these trials, ferrets were never injured by a prairie dog. We never observed a prairie dog using its powerful incisors to attack a ferret. The only defenses the prairie dogs utilized against ferrets were both forelegs and hind legs, undeniably equipped with a long, sharp set of claws. Prairie dogs defended themselves from the ferrets' bites by

Fig. 3. Improvement in predation rates shown by black-footed ferrets between trials. Vertical lines represent SE.



pushing and kicking with their hind legs and raking the ferret's head with their forepaws.

Although the behavior of ferrets when confronting a prairie dog was rather stereotyped, experienced and inexperienced kits differed in the number of movement patterns needed to subdue this prey. What we call proficient kills were characterized by a swift and well-integrated attack in which the ferret could subdue and kill a prairie dog within 2 min or less from delivery of the first bite. All ferrets that made proficient kills had previous predation experience in family or individual trials or came from the outdoor enclosures. Inefficient kills, which lasted 5 min or more, were typically slow and clumsy, often characterized by a series of uncoordinated strikes during which various parts of the prairie dog could be fiercely attacked prior to the delivery of the killing bite. We also observed a number of "intermediate kills," which were made by both experienced and inexperienced ferrets. Among experienced ferrets, intermediate kills took place when a prairie dog escaped from a bite and retaliated strongly.

When the total proportions of each of the behaviors that occurred during the predation sequence were compared, there were several noteworthy differences. Crawling over the sleeping prairie dog without waking it occurred more often among proficient killers than within the inefficient group (Z = 5.02, P = 0.0001). In addition, pawing at the sleeping prey after sneaking on top of it was more frequent among the proficient killers (Z = 2.66, P = 0.01). Proficient killers never withdrew from the prairie dog or left the chamber during an attack. In contrast, "withdraw" and "leave" constituted 5 and 8%, respectively, of the behavior categories recorded during inefficient killing sequences.

Skillful killers singled out the throat for attack remarkably more often than unskillful ones did (Z = 3.439, P < 0.001). While proficient killers directed 100% of all "non-throat" bites (17.2% of all bites) to the face or nape of the neck, inefficient killers often delivered bites to parts of the body other than the head, neck, and throat. Proficient killers needed fewer movements to get to the prey's throat, and once they bit the ventral side of the neck, they held on to it (sometimes with slight readjustments of the throat bite) until the prairie dog succumbed. Inefficient killers needed a greater number of behaviors to subdue a prairie dog, frequently lost the bite grip (throat bite and other bites), and withdrew or left the chamber significantly more often than proficient killers.

During various efficient kills, the prairie dog slumbered while the ferret entered the confined burrow chamber and crept slowly on top of its victim's curled body. It was not until the ferret gently tapped the prairie dog's shoulder that the unaware host woke up. As the prairie dog lifted its head, the ferret immediately gripped its jaws tightly on its victim's throat. While keeping a firm bite, the ferret generally rotated along its longitudinal axis (always progressing from head to tail). Slight bite readjustments were often necessary to secure the grip. A ferret often attempted to shake its head in response to the prey's struggles, when, for instance, the prairie dog braced both forelegs against the burrow's entrance hole. However, the prairie dog was always too strong to allow for a full head shake.

Ferrets reacted to the powerful prairie dog kicks by wrapping their supple body around the prairie dog in an attempt to cover as much of the surface of their prey as possible. If they succeeded in this "wrap-around assist," the prairie dog could be held immobile until it died. As the prey became weak, ferrets often used the burrow walls for leverage while mouth-pinning the ventral side of the prairie dog's neck tightly to the ground.

Once all prey movements ceased, the ferrets maintained the throat grip for a few more seconds (generally less than 1 min). Eventually they released the consummatory bite and left the chamber. Within a minute or two, they returned to their prey, briskly sniffed over the motionless carcass, and licked any conspicuous blood stains present. On several occasions, ferrets needed a short recovery period after a kill during which they laid flat on their stomach breathing rapidly after the strenuous effort.

Freshly killed prairie dogs were always carried to the bottom of the nest box for consumption. Ferrets always used a backward bound when carrying a prairie dog carcass, which was more often grasped by the nape of the neck than by the throat. Captive ferrets always began consuming prairie dogs by working their way from the kill wound (ventral side of the neck) to the thoracic viscera. All ferrets tested in this study consumed at least the prey's heart, lungs, and liver within hours of the kill. In some cases, such as when kills were performed by large family groups, we only recovered the prairie dog's paws and parts of the skull.

Prairie dog necropsies

All 12 prairie dog specimens examined post mortem had various levels of damage to the ventral side of the neck, including maceration of the throat muscles. Most damage was subcutaneous and the prey's skin was rarely pierced and never torn. The articulation between larynx and trachea (cricoid cartilage and tracheal rings) was torn in 67% of the carcasses examined. In three of the four cases in which this joint was not severed, coagulated blood was present in the throat, presumably due to the pressure exerted by the ferret's jaws. In the fourth case, there was profuse hemorrhaging around the larynx.

Ten prairie dogs exhibited severed masseter muscles. In seven of these, the ferret's canines had penetrated all the way through the muscle and punctured (four cases) or fractured (three cases) the mandible. One of the latter individuals also suffered a fractured zygomatic arch. The damaged masseter was always the left one, although in three instances both cheek muscles were affected.

Despite a damaged trachea, four (33%) of the prairie dogs may have died from causes other than suffocation. One subject, with a torn larynx and blood clots in the trachea, had been severely bitten on the thorax. Both the heart and lungs had been perforated and the animal had cardiac tamponade and hemothorax. Two other cases displayed subluxation of the cervical vertebrae, one between the atlas and the occipital condyles and the other between the atlas and the axis. These injuries were probably caused by the pressure exerted by the ferret's jaws while it was biting its victim's throat. It is likely that these two animals died of neural damage. Another prairie dog displayed two distinct bite wounds, one to the upper larynx (which was not ruptured) and another to the cranial sternum. The upper throat bite fractured the right lateral processes of several cervical vertebrae, while the lower throat bite fractured both the sternal manubrium and the right clavicle. This prairie dog might have died from damage to the spinal cord.

Discussion

Because every prairie dog kill that we witnessed ($n = 77$, 45 during individual trials and 32 during family trials) was performed with a bite to the ventral side of the neck, we concluded that use of the throat-killing technique when confronting large prey is innate in ferrets. Even prey-naive ferrets (group 1) killed prairie dogs on first opportunity with a bite to the throat. Both captive-rearing conditions and prior killing experience affected ferret predation abilities when they confronted live prairie dogs.

Effects of captive upbringing on predatory behavior

Killing success and interest in interacting with prey were higher for ferrets with prior hamster-killing experience than for prey-deprived kits. It seems that exposure to small live prey offered ferrets a predation advantage when they confront the larger prairie dogs. Kill latencies were longer for the prey-inexperienced group and decreased gradually with increasing rearing complexity. Although the proportions of ferrets in the hamster-exposed and outdoor-raised groups that managed to kill were the same, kill latencies were notably shorter for the outdoor group. It appears that some of the outdoor-raised ferrets might have never performed (or even witnessed) a kill, while others had probably had successful confrontations with prairie dogs and were adept at dispatching them.

Kits exposed to prairie dogs in family trials killed at a higher rate and displayed the greatest interest on "interacting" with prairie dogs. Latencies to dispatch prey were shorter and coordination of movements was more proficient than in any of the other cage-raised groups. Nonetheless, many of these kits had never had a prior opportunity to deliver a throat bite themselves. Ferret mothers were the ones that generally dispatched the prairie dog during the family trials, although kits observed (and frequently assisted) throughout the killing process. It seems that the prairie dog killing action performed by the mother during family trials induced more ferret kits to kill prairie dogs during individual trials. Kuo (1930) reported comparable results with cats, which always killed at least the same type of rat they saw their mother killing during family trials. Kittens exposed to live prey in the presence of their mother were capable of observational learning, showing higher killing rates both as juveniles and as adults (Caro 1980*b*).

Predatory efficiency did not differ between kits exposed to live prairie dogs in cages and in outdoor pens (Fig. 2). It seems that actual exposure to prairie dogs played a more important role in the refinement of killing skills than the environment (cage or pens) in which ferrets were raised. However, a naturalistic outdoor pen environment offered reintroduced ferrets a significant survival advantage after their reintroduction into prairie dog towns (Vargas 1994; Miller et al. 1996). Behavioral responses of free-ranging animals must be performed efficiently under a variety of simultaneous conditions (habitat characteristics, predator densities, prey abundance, etc.; Miller et al. 1998). Even though ferrets raised in cages and exposed to prairie dogs could kill as efficiently as ferrets raised in pens, the naturalistic pen environment seemed to enhance the development of a wider array of behaviors of important survival value (Vargas 1994) and therefore was a sounder approach to preparing ferrets for reintroduction.

Effects of individual predation experience

Interest in prey, as well as the likelihood of killing, increased after repeated individual exposures to prairie dogs. Also, killing efficiency greatly improved after a single kill. With experience, ferrets reduced the time needed to dispatch prairie dogs, and the frequency of behaviors employed during the killing act decreased. But only one successful kill was required for the ferrets to show a marked improvement in their predatory skills.

Several carnivores that kill prey larger than themselves use the throat-bite killing technique. For instance, silver-backed jackals (*Canis mesomelas*) utilize it when killing Thompson gazelles (*Gazella thompsoni*) (Ewer 1973), marbled polecats (*Vormela peregusna*) consistently use this method when killing laboratory rats (Ben-David et al. 1991), and cheetahs (*Acinonyx jubatus*) (Eaton 1970), lions (*Panthera leo*), and leopards (*Panthera pardus*) dispatch their prey with a bite to the throat (Kruuk and Turner 1967). The standard felid neck bite can be replaced by a safer throat grip when the animals confront large or dangerous prey (Ewer 1973). Under such circumstances, the predator can maintain its body clear from the prey's charges until the victim succumbs.

To maintain a positive energy balance throughout the winter, ferrets must ingest an average of 130 metabolizable kcal/day, which represents three field mice per day or one adult prairie dog every 6 or 7 days (Powell et al. 1985). Larger prey will provide greater caloric revenues only if the energy benefits obtained from the killed prey outweigh the costs of procuring it. Ferrets might have solved the problem of the high energy expenditures involved in killing a large and powerful prey by hunting at night (when the sleeping prairie dogs are easier to catch) and by using an energy-efficient way of dispatching their prey: the throat bite.

Predation sequence

Our data indicate that ferrets do not attack prey at random; rather, they direct their bites to the anterior region of the prey and aim at the nape or throat, depending upon prey size. Both inexperienced juvenile and adult ferrets managed to kill on their first encounter with live prey. Prey-deprived ferrets killed hamsters on the first opportunity, using the standard mustelid nape-bite technique. And kill bites performed by prairie-dog-naive ferrets were consistently placed on the ventral side of the neck.

These alternative killing methods are probably an adaptive response that depends upon the characteristics of the prey and the location of the kill. Because inflicting neural damage when biting the neck of small prey is swift and relatively easy, small mammals will most likely be killed with a nape bite regardless of where the kill takes place. We have observed ferrets killing hamsters both on the cage surface and in the mock prairie dog burrow, and they always dispatched them with a bite to the dorsal side of the neck.

In the wild, ferrets tend to ignore prairie dogs when roaming above ground (Hillman 1968; Henderson et al. 1974; Clark et al. 1986; Miller and Anderson 1993). On the rare occasions when ferrets were observed attacking prairie dogs in the open, they immediately took the prey into a burrow (Hillman 1968; Henderson et al. 1974; Clark et al. 1986; Paunovich and Forrest 1987). This is probably because the confinement of the tunnel walls offered the ferret a killing advantage. Nevertheless, while seizing prairie dogs above ground, ferrets tended to use a nape bite (Hillman 1968; Henderson et al. 1974; Clark et al. 1986). As is the case with weasels (Byrne et al. 1978), this type of bite prevents the ferret from getting kicked when the prey has a defensive advantage. Once in the burrow, the ferret probably switches to a throat bite to kill the prey. This is supported by the fact that most of the prairie dogs retrieved during studies in either Meeteetse, Wyoming, or in South Dakota had bloody throats (Hillman 1968; Henderson et al. 1974; Clark et al. 1986). Progulske (1969) observed a captive ferret killing prairie dogs with a neck bite, but he did not indicate whether or not a confined space, such as a burrow, was available.

Although attacks on small prey appeared to be visually triggered (sight of the moving rodent seemed to instigate the ferret's strike), motion was not necessary when they confronted large prey. In the wild, the nocturnal ferret must find and kill its prey in the absolute darkness of a prairie dog burrow. Under such constraints, visual sensory stimuli are nullified and the olfactory, tactile, and auditory senses become the only potentially useful ones. Whiskers and elbow vibrissae probably aid in underground orientation by helping ferrets perceive the tunnel's configuration. Locating prairie dogs by hearing might be difficult, since at night the auditory cues provided by stationary prey are probably absent (Minta 1990). Nevertheless, at close range, audition may help in detection of the prey's respiration. But the most likely guide that ferrets utilize when searching for prairie dogs is their refined and acute sense of smell. Indeed, olfaction is the most developed sense in the congeneric polecat and plays a crucial role in searching for prey (Poole 1970; Apfelbach 1978, 1986).

Once the ferret finds its victim, it probably relies on tactile stimulation to direct the consummatory killing act. Neurophysiological studies in the cat demonstrate that tactile stimulation of the lip region is essential for jaw opening, while tactile stimulation inside the cat's mouth induces closure of the jaws (Flynn et al. 1970). A similar neurological mechanism could operate in ferrets. During our trials, experienced ferrets placed themselves in a location adequate for delivering a bite without awakening the prairie dog. Once on top of their prey, they deliberately woke it up and aimed a swift and powerful bite to the throat area. Our impression is that all contact behaviors occurring during the predation act were triggered by tactile stimulation. Yet, because the red light seemed to provide the subjects with a certain degree of visibility, visual orientation of bites might have also played a role during the killing process. Thus, we cannot determine to what extent our experiments replicated the way in which ferrets kill prairie dogs under the "naturally blind" burrow conditions.

In conclusion, our study showed no differences in the way the kill bite materialized the first time it was performed (aimed at the dorsal or ventral side of the neck of small and large prey, respectively), but the likelihood of killing and the efficiency at handling prey increased with experience. Juvenile ferrets raised with exposure to live hamsters were significantly more successful at killing this prey than kits deprived of any predation experience. Experience with killing prairie dogs (whether kits were raised in indoor cages or outdoor pens) increased both the probability of killing and the efficiency with which the prairie dogs were handled. Even witnessing a ferret mother performing a kill enhanced the kits' predatory responses. Our data indicate that the placement of the kill bite appears to be innate in ferrets, but predation skills are greatly refined by social (mother's role) and individual predation experiences during the ferret's early development.

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