Natural History Miscellany

Selective Predation on Utah Prairie Dogs

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ABSTRACT: Predation always affects demography and population dynamics, but removal of certain types of individuals is especially consequential. Predators strike quickly and commonly avoid areas with human observers, however, and thereby make it difficult to document patterns of predation under natural conditions. At a colony of marked Utah prairie dogs (*Cynomys parvidens*), a high frequency of predation in 2005 provided an unusual opportunity to examine susceptibility of five types of individuals to predation by red foxes (*Vulpes vulpes*) and northern goshawks (*Accipiter gentilis*). Juveniles were more vulnerable than adults to predation by northern goshawks. Adults at the edge of the colony were more vulnerable than central adults to predation by both red foxes and northern goshawks. Recent immigrants, who were not yet familiar with the best routes for escape, were more likely than longtime residents to be captured by northern goshawks. Adult males, preoccupied with finding, impregnating, and guarding estrous females during the 17-day mating season, were easy targets for red foxes and northern goshawks. Pregnant females, who could not run quickly, were especially prone to predation by red foxes.

Keywords: Cynomys parvidens, northern goshawk, predation, red fox, Utah prairie dog, vulnerability.

Predation is an inevitable threat for animals of all species and sometimes can be the major cause of mortality (Sargeant et al. 1984; Crawley 1992; Caro 2005). Predation always affects demography and population dynamics, but

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removal of certain types of individuals is especially consequential (McGowan 1997; Barbosa and Castellanos 2005). Predation on pregnant and lactating females, for example, affects population size more than predation on juvenile females. Similarly, predation on sexually mature adult males affects population dynamics more than predation on juvenile males.

Assessing the vulnerability of different types of individuals to predation under natural conditions is difficult for at least three reasons. First, such assessment requires careful long-term research with animals for which we know age, sex, reproductive condition, body mass, and overall health (Caro 2005). Second, predators frequently rely on quickness and stealth for their hunting success—so detection of predation by human observers can be a formidable task (McGowan 1997; Caro 2005). Third, predators are usually less likely—but sometimes more likely (Boesch 1994)—to attack when behavioral ecologists are observing potential prey (Isbell and Young 1993).

At a colony of marked Utah prairie dogs (*Cynomys parvidens*), predations by red foxes (*Vulpes vulpes*) and northern goshawks (*Accipiter gentilis*) were unusually common in 2005. Consequently, we were able to examine rigorously the susceptibility of the following five types of individuals: juveniles, peripherals, immigrants, sexually mature males during the mating season, and pregnant females.

Foraging aboveground from dawn until dusk, Utah prairie dogs are rare, herbivorous, colonial, ground-dwelling squirrels (Pizzimenti and Collier 1975; Wright-Smith 1978; Hoogland 2003*a*). Within colonies, individuals live in territorial family groups called clans, which typically contain one breeding adult male (≥1 year old) and two to three breeding adult females. Predators on Utah prairie dogs are numerous and include American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), red foxes, golden eagles (*Aquila chrysaetos*), northern goshawks, and prairie falcons (*Falco mexicanus*).

When they first emerge from the nursery burrow in June, juvenile Utah prairie dogs are about 38 days old (Hoogland 2003*b*). For many weeks thereafter, juveniles cannot run as fast as adults and do not respond to alarm

calls as quickly as adults. Further, predators can more easily carry away juveniles, which in June weigh only about 25% as much as adults (208 ± 41.6 g [mean ± SD], $N = 1,064$, vs. 839 ± 141 g, $N = 449$; Hoogland 2003*b*). For these reasons, juvenile Utah prairie dogs, like juveniles of most species (Murie 1992; Adams et al. 1995; Doolan and Macdonald 1997; Caro 2005), should be more vulnerable to predation than adults.

A Utah prairie dog living in a central territory surrounded by other territories has many vigilant, alarm-calling conspecifics and numerous burrow entrances between itself and a predator that approaches from outside the colony site. An individual in a peripheral territory, by contrast, has fewer conspecifics and burrow entrances between itself and the predator and therefore should be more susceptible to capture (Kruuk 1964; Hamilton 1971; Vine 1971).

Most Utah prairie dogs remain in the natal colony for life, but occasionally an adult will emigrate into a new colony. Like other animals (Garrett and Franklin 1988; Van Vuren and Armitage 1994; Alberts and Altmann 1995; Belichon et al. 1996; Weisser 2001), Utah prairie dogs probably are highly susceptible to predation as they move between colonies because they are distant from burrows and conspecifics. We did not collect any data on this issue, but we were able to test the hypothesis that individuals should be highly susceptible shortly after arriving at a new colony site, when they are still unfamiliar with the locations of the best escape burrows (Metzgar 1967; Isbell et al. 1993; Belichon et al. 1996; Sapolsky 1996; Johannesen and Andreassen 1998; Weisser 2001).

During the short mating season, male Utah prairie dogs ardently search for, and then court, sexually receptive females (Hoogland 2001, 2003*a*). After mating with a female,

a male tries to prevent copulations with other males by chasing rivals away; after mating, the male also tries to sequester the female underground by perching on the mound of her burrow entrance. These behaviors reduce a male's vigilance for predators. Males during the mating season therefore should be highly vulnerable to predation (Dunbar et al. 1990; Lima and Dill 1990; Neuhaus and Pelletier 2001; Wolff and Van Horn 2003; see also Blumstein 1998; Dukas and Kamil 2000).

Like pregnant females of other ground-dwelling squirrels (Michener 1989; Macwhirter 1991; Hoogland 1995), pregnant female Utah prairie dogs emerge from their burrows earlier each morning and remain aboveground later each evening than do nonpregnant females (Hoogland 2001, 2003*a*). Further, as for other mammals (Trillmich et al. 2003; see also Trombulak 1989), pregnancy probably reduces running speed for Utah prairie dogs. Pregnant females therefore should be especially vulnerable to predation.

Methods

Our study colony of Utah prairie dogs at Bryce Canyon National Park, Utah, inhabited 5.8 ha and in early April 2005 contained 12 sexually immature adult males (all yearlings), 41 sexually mature adult males, and 70 sexually mature adult females (Hoogland 2001; Hoogland et al. 2004; table 1). Using binoculars and 4-m-high towers, we observed marked individuals every day from dawn until dusk for 124 consecutive days and recorded predations by red foxes and northern goshawks (fig. 1).

For permanent identification of individuals, we used fingerling ear tags (National Band and Tag, Newport, KY); for visual identification from a distance, we used Nyanzol

Table 1: Description of study colony of Utah prairie dogs at Bryce Canyon National Park in 2005

Type of individual counted	Count
Adults in early April	123[a]
Adults captured by predators in April and May	17
Adults in mid-June	89
Adults captured by predators in June and July	0
Juveniles in mid-June	116
Juveniles captured by predators in June and July	9
Adults in central/peripheral territories in early April	35/88
Adults captured by predators in central/peripheral territories in April and May	1/16
Immigrants in early April	2
Immigrants captured by predators in early April	2
Adult males captured by predators during mating season (17 days)	10
Adult males captured by predators before or after mating season (107 days)	0
Adult females captured by predators during period of pregnancy (29 or 30 days for each female)	4
Adult females captured by predators before or after period of pregnancy (94 or 95 days for each female)	1

Note: All captures were by red foxes and northern goshawks.

[a] 53 males, 70 females.

fur dye (Greenville Colorants, Clifton, NJ; Hoogland 1995, 2001). Our observations of marked individuals in 2005 began on March 7, as the prairie dogs were emerging from hibernation, and continued through July 8, 11 days after we had captured the last weaned juvenile; each of us watched for 1,100 h (× 4 persons = 4,400 person hours of observation). The mating season in 2005 extended from April 1 to April 17, but, as for other ground-dwelling squirrels (Schwagmeyer 1984; Sherman 1989; Boellstorff et al. 1994; Hoogland 1995, 1998; Murie 1996), each female Utah prairie dog was sexually receptive for only 4–5 h of a single day. After a pregnancy of 29 or 30 days, females reared their offspring in separate nursery burrows. From June 6 to June 20, 2005, 116 nearly weaned juveniles emerged from nursery burrows and appeared above-

ground. Research at the study colony began in 1995 and continued every year through 2005 (Hoogland 2001, 2003*b*).

We classified a territory as central if >50% of its boundary was contiguous with the boundaries of other territories and as peripheral if <50% of its boundary abutted other territories. All levels of probability (*P* values) result from two-tailed nonparametric statistical tests.

Results

Figure 2 supports the hypothesis that juvenile Utah prairie dogs should be more vulnerable than adults to predation. From the emergence of the first litter on June 6, 2005, until our last day of observations at the study colony on

Figure 1: *Top*, red fox on April 8, 2005, just after capturing adult male R12, who lived at the periphery of the study colony. *Bottom*, northern goshawk on April 7, 2005, in the process of killing adult male R44, who had immigrated into the study colony on April 5, 2005. Photos by Elaine P. Miller.
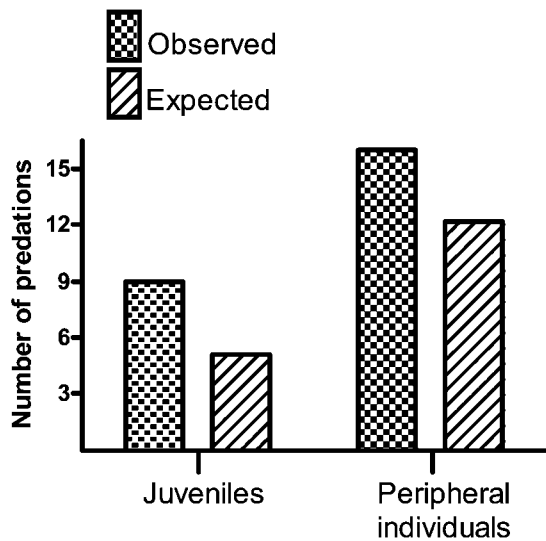
Figure 2: Observed versus expected predations for Utah prairie dogs ($P \leq .028$ for both comparisons; see text and table 1). Expected numbers result from the assumption that predation was equally likely for adults versus juveniles and for central versus peripheral individuals. Peripheral individuals lived at the edge of the study colony, in territories that were not surrounded by other territories.

July 8, 2005, we recorded nine predations, all by northern goshawks. All nine victims were juveniles ($P = .007$, 2×2 χ^2 test).

Individuals living in peripheral territories were more vulnerable to predation than individuals living in central territories (fig. 2). Specifically, all 14 adult Utah prairie dogs captured by red foxes, and two of the three adults captured by northern goshawks, lived in peripheral territories ($P = .028$, 2×2 χ^2 test).

Figure 3 supports the hypothesis that recent immigrants are more susceptible than longtime residents to predation. The only two immigrants in 2005, both adult males, were captured by northern goshawks within 2 days after we first noticed their arrivals ($P < .001$, 2×2 χ^2 test).

Males during the mating season were easy prey (fig. 3). The increased susceptibility was striking: red foxes captured seven adult males during the 17 days of the 2005 mating season, and northern goshawks captured another three, but we did not observe a single predation on adult males during the other 107 days of research in 2005 ($P < .001$, 2×2 χ^2 test).

Figure 3 supports the hypothesis that pregnant females are especially susceptible to predation. Four of the five adult females captured by red foxes in 2005 were pregnant, even though each female was pregnant for only 29 or 30 of the 124 days that we observed at the study colony (fig.

3; $P = .006$, 2×2 χ^2 test). The fifth victimized female copulated, but a visual examination on the day before predation showed that the female's vagina was closed and that her teats were small and nonturgid; that is, she either aborted pregnancy shortly after mating or failed to conceive.

Among adults, susceptibility to predation did not vary with age ($P = .962$, χ^2 goodness-of-fit test, df $= 4$). Further, none of the adult victims seemed weak or sick, as indicated by the following four lines of evidence. First, neither of the two male immigrants captured by northern goshawks appeared to suffer from poor condition that sometimes results from the perils of long-distance dispersal (Garrett and Franklin 1988; Van Vuren and Armitage 1994; Weisser 2001). Rather, up until the moment of predation, both males were persistently challenging other males for territories and for access to females; chases and fights involving these immigrant males were common. Second, of the males captured by northern goshawks and red foxes during the mating season, all 10 were defending territories and had a pigmented scrotum and thus were ready to mate (Hoogland 2001, 2003a); four of these males had already
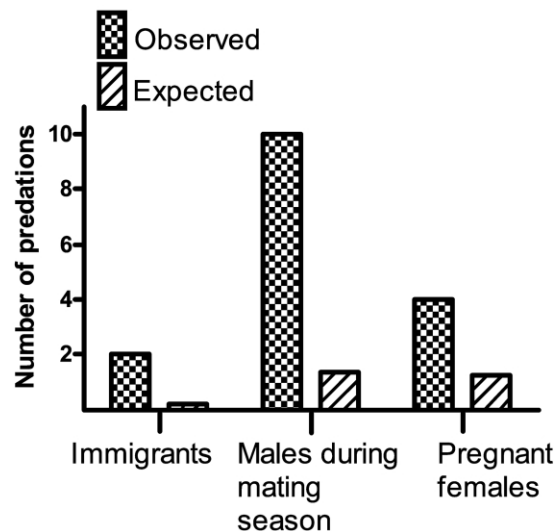

Figure 3: Observed versus expected predations for Utah prairie dogs ($P \leq .006$ for all three comparisons; see text and table 1). Expected numbers for males during the mating season and for pregnant females result from the assumption that predation was equally likely on all days of research (March 7, 2005–July 8, 2005); the expected number for immigrants results from the assumption that immigrants and longtime residents were equally susceptible to predation. Some of the 26 predations depicted in figures 2 and 3 applied to more than two analyses. A victimized pregnant female living at the periphery of the study colony, for example, affected analyses of predations regarding both center versus edge and pregnancy versus nonpregnancy.

mated at least once. Third, male victims of predation were heavier, and thus more likely to survive and reproduce in a typical year with less predation (Hoogland 2001, 2003b), than male survivors (874 ± 195 g [mean ± SD], $N = 10$, vs. 739 ± 130 g, $N = 42$; $P = .034$, Mann-Whitney U-test that compared body masses determined just before or during the mating season). Fourth, all five females captured by red foxes had mated, and four of the five at the time of predation were preparing for parturition and lactation.

For several days in April 2005, we tracked three different adults (one female, two males) that were emaciated (i.e., had a low body mass) and could not run quickly. We did not observe predation on any of these weak individuals, even though they spent most of each day aboveground like other, healthier adults. All three weak individuals soon disappeared, and we surmise that they died underground. The implication here is that weak Utah prairie dogs in poor condition are not inordinately susceptible to predation.

Discussion

Red foxes captured a total of 14 adult Utah prairie dogs from April 1 to May 3, 2005 (seven males, five females, and two individuals of unknown sex that we had not yet livetrapped for marking). For three reasons, we deduce that a single individual was responsible for all 14 predations. First, even though red foxes vary substantially in physical appearance (Lloyd 1981; Lariviere and Pasitschniak-Arts 1996), the red fox at our study colony always looked the same regarding body size and color of fur. Second, the red fox invariably showed little fear of humans observing from 4-m towers. Third, probably because it was returning to its den, the red fox consistently departed in the same direction away from the study colony after a predation. Similar devastation by a lone individual has been observed for other predatory species such as mountain lions (*Puma concolor*; Ross et al. 1997; Festa-Bianchet and Apollonio 2003), American badgers (Armitage 2004), and common grackles (*Quiscalus quiscula*; Brown and Brown 1996). We do not know how many different northern goshawks were responsible for killing 12 Utah prairie dogs (three adults from April 1 to April 7, 2005, and nine juveniles from June 18 to July 8, 2005).

Predations at the study colony in 2005 were unusually common—14 by red foxes and 12 by northern goshawks. We suspect that predation also caused the disappearance of several other individuals from certain peripheral areas that we could not easily observe in 2005. In 10 previous years of dawn-to-dusk research with Utah prairie dogs at this same colony, we observed only two predations by red foxes and only five predations by northern goshawks. Further, one of us (J.L.H.) observed only 26 predations during 15 years of intense research with black-tailed prairie dogs (*Cynomys ludovicianus*) at Wind Cave National Park in South Dakota (Hoogland 1995). Habituation and intrepidity to human observers probably explain the high frequency of predations in 2005 by the red fox, but we discovered no reason for the numerous predations by northern goshawks. In any event, our results illustrate the predicted hefty variation in usage of colony sites by predators and other animals that depend on a keystone species of the grassland ecosystem for survival (Kotliar et al. 2006).

When predators chase prey, adult victims are often the old and the weak (Mitchell et al. 1965; Kruuk 1972; Schaller 1972; Temple 1987; Pole et al. 2003). Perhaps our most important finding is that nonjuvenile victims of predation were not the old and the weak but rather young and middle-aged adult Utah prairie dogs in excellent condition. Another key discovery is that the rate of predation and the susceptibility of different types of individuals vary dramatically over time within the same year. Notice, for example, that sexually mature adult males were vulnerable only during a mating season that lasted a mere 17 days in 2005. Documenting these trends was possible because we knew the age, sex, body mass, and reproductive status for every resident within a natural colony that we observed daily.

Costs of reproduction include reductions in body mass, ability to endure the winter, probability of reproducing in the following year, and litter/clutch size in the following year (Reznick 1985; Nur 1988; Linden and Moller 1989; Stearns 1992). Utah prairie dogs experience some of these costs (J. L. Hoogland, unpublished data), but a more serious cost of reproduction is increased susceptibility to predation for both males (during the short mating season) and females (during pregnancy).

Our results identify five types of individuals that were vulnerable to predation. If we had terminated our research in 2004 (after 10 years) rather than 2005, we would not have discovered how predation can be so selective or how predation can have such a devastating impact on the demography and population dynamics of Utah prairie dogs. Our results thus demonstrate the importance of long-term research with marked individuals for understanding the effects of rare events and unusual years. Similar long-term research has led to the discovery of rare but important causes of mortality for cliff swallows (*Hirundo pyrrhonota*; Brown and Brown 1996), Darwin's finches (*Geospiza* spp.; Grant 1999), Belding's ground squirrels (*Spermophilus beldingi*; Morton and Sherman 1978; Sherman and Morton 1984), and yellow-bellied marmots (*Marmota flaviventris*; Schwartz et al. 1998; Van Vuren 2001).

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