Surplus-killing by endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) is linked to a local population decline of endangered giant kangaroo rats (*Dipodomys ingens*)

Author(s): Rachel L. Endicott, Laura R. Prugh, and Justin S. Brashares
Source: The Southwestern Naturalist, 59(1):110-115. 2014.
Published By: Southwestern Association of Naturalists
DOI: http://dx.doi.org/10.1894/N01-JKF-39.1
URL: http://www.bioone.org/doi/full/10.1894/N01-JKF-39.1

NOTES

THE SOUTHWESTERN NATURALIST 59(1): 110–115

SURPLUS-KILLING BY ENDANGERED SAN JOAQUIN KIT FOXES (*VULPES MACROTIS MUTICA*) IS LINKED TO A LOCAL POPULATION DECLINE OF ENDANGERED GIANT KANGAROO RATS (*DIPODOMYS INGENS*)

RACHEL L. ENDICOTT, LAURA R. PRUGH,* AND JUSTIN S. BRASHARES

Department of Environmental Science, Policy, and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720 (RLE, JSB)
University of Alaska Fairbanks, Institute of Arctic Biology, Fairbanks, AK 99775 (LRP)
**Correspondent: lprugh@alaska.edu*

ABSTRACT—We describe surplus-killing of endangered giant kangaroo rats (*Dipodomys ingens*) by endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) and consider the conditions that may have promoted such killing. We also use results of extensive mark-recapture surveys of rodents to document a decline in local density of the giant kangaroo rat that was likely caused by surplus-killing.

RESUMEN—Describimos la matanza excedente de ratas canguro gigantes (*Dipodomys ingens*), que están en peligro de extinción, por el zorro de San Joaquín (*Vulpes macrotis mutica*), también en peligro de extinción, y consideramos las condiciones que pueden haber promovido la matanza. Además, usamos los resultados de muestreos extensivos de marcaje y recaptura de roedores para documentar una disminución de la densidad local de ratas de canguro gigantes que fue probablemente causada por matanza excedente.

Surplus-killing occurs when a predator kills more prey than it can eat, leaving carcasses unconsumed (Kruuk, 1972; Meuller and Hastings, 1977). Although surplus-killing has been documented in predators ranging from canids to birds of prey (Nunn et al., 1976), the frequency and extent of this behavior among individual predators is unknown. Additionally, the effects of surplus-killing on the population dynamics of prey are poorly studied. We report surplus-killing of giant kangaroo rats (*Dipodomys ingens*) by a family of San Joaquin kit foxes (*Vulpes macrotis mutica*) in the Carrizo Plain National Monument, California, and explore the ecological causes and consequences of this event.

On 25 May 2011, 91 carcasses of the giant kangaroo rat were found at two dens, located ca. 30 m apart, of the San Joaquin kit fox. The carcasses appeared to have been ejected from the dens, with 61 carcasses found near a den on one of our study plots and 30 carcasses counted at the second den (Fig. 1). A family of San Joaquin kit foxes with at least three juveniles and two adults was seen near these dens during spotlighting-surveys conducted on 16, 17, and 19 May 2011. Kit foxes maintain multiple active dens, with an average home range in the Carrizo Plain of 11.9 km^2 (White and Ralls, 1993). Thus, both dens were likely used by a single family of San Joaquin kit foxes. The majority of carcasses of the giant kangaroo rat were intact with no signs of consumption, and they ranged in condition from freshly killed to mummified. It is unknown how long the bodies had been stored underground. Observers noted that carcasses were still at the entrances of dens in August, and they emitted a strong rotting odor.

We documented these surplus-killings as part of a long-term study in the Carrizo Plain to understand relationships among giant kangaroo rats, cattle grazing, and other species in a grassland community. The surplus-kills were found on and immediately adjacent to one of our 30 study plots where a variety of surveys are conducted each year, including biannual mark-recapture surveys of giant kangaroo rats. Each study plot is 140-x-140 m in size (1.96 ha). Trapping occurs in April and August for three consecutive nights on each plot (see Prugh and Brashares, 2010, for details of the trapping protocol). Our study was approved by the University of California Animal

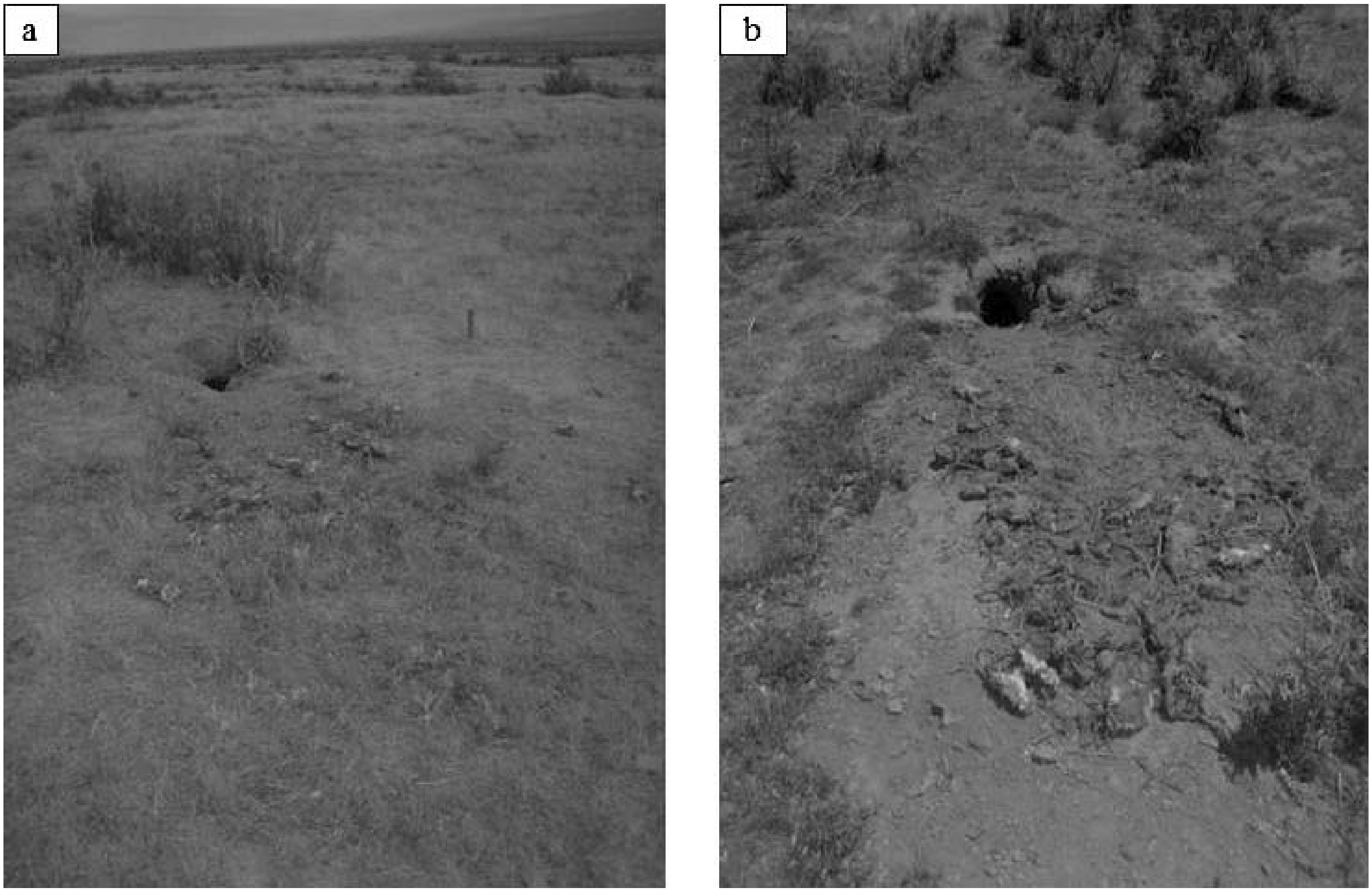

Fig. 1—Dens of the San Joaquin kit fox (*Vulpes macrotis mutica*) in the Carrizo Plain National Monument, California, during 2011 a) on study plot C5 with at least 61 carcasses of the giant kangaroo rat (*Dipodomys ingens*) and b) 30-m from C5 with at least 30 carcasses.

Care and Use Committee (R304) at the University of California, Berkeley, and followed guidelines of the American Society of Mammalogists (Sikes et al., 2011).

Giant kangaroo rats are a primary food for San Joaquin kit foxes in the Carrizo Plain, where they are the most common nocturnal rodent (Grinnell et al., 1937; McGrew, 1979; Prugh and Brashares, 2012). Giant kangaroo rats completely dominate the community of nocturnal rodents in our study area; only 29 of 24,895 captures from 2007–2012 were of species other than *D. ingens*. Although locally abundant, the giant kangaroo rat and San Joaquin kit fox are federally endangered due to extensive loss of habitat (United States Fish and Wildlife Service, in litt.). Thus, insight into the predator-prey dynamics between these species may aid the development of plans for their recovery.

San Joaquin kit foxes have been studied extensively in the Carrizo Plain and surrounding areas (e.g., White and Ralls, 1993; White et al., 1996; White and Garrott, 1997, 1999; Cypher et al., 2000). In the mid-1990s, during a year of unusually high density of kangaroo rats, observers found carcasses of kangaroo rats ejected from several natal dens in the nearby Elk Hills (B. Cypher, pers. comm.). However, no more than a dozen carcasses were found at any given den, and the heads of the carcasses had been consumed. Our observation of 91 ejected carcasses from two nearby dens is, therefore, an unusually large surplus-killing event for this species. In addition, this is the first case of surplus-killing we have discovered in 5 years of intensive fieldwork. Thus, surplus-killing does not appear to be a widespread behavior among San Joaquin kit foxes.

If carcasses are not ejected from dens, then surplus-killing may remain undetected. However, we suspect foxes would eject carcasses in most cases due to the stench and parasitic outbreak that would result from dozens of rotting carcasses. Additionally, the entrances of dens remain littered with bones of giant kangaroo rats 2 years after the event, indicating that these events should be detectible for a long period of time. While canids often cache prey for later use by themselves or their pups (Samelius and Alisauskas, 2000), these caches were not utilized in the case we report.

Three factors have been proposed as triggers of surplus-killing events: severe weather; poor condition of prey; super-abundant prey. Surplus-killing is often linked to environmental conditions, such as deep snows or heavy storms (Patterson, 1994). These conditions can impede

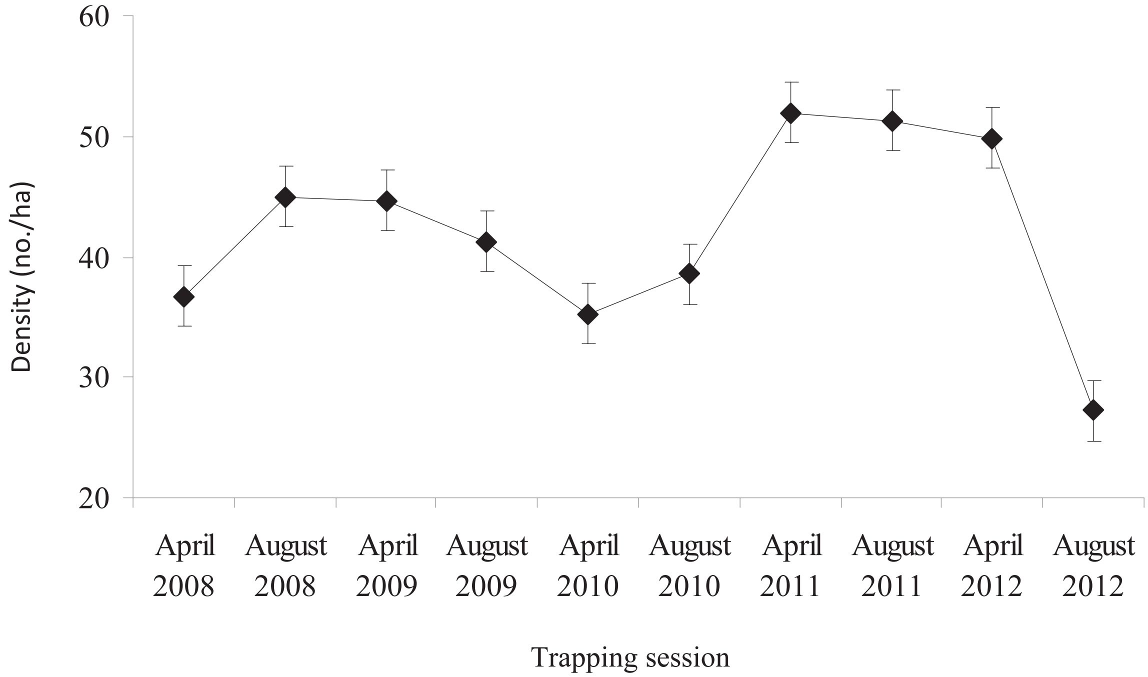

Fig. 2—Average density of populations of the giant kangaroo rat (*Dipodomys ingens*) over 5 years (2008–2012) on 30 study plots in the Carrizo Plain National Monument, California, during each trapping session with standard error bars. The surplus-killing event occurred between the sessions in April and August 2011.

the ability of prey to escape and hide from predators. Additionally, extreme weather or chronic shortage of food can drive prey to engage in behavior that exposes them to a high risk of predation (Delgiudice, 1998). However, these factors are not always associated with surplus-kills. For example, Miller et al. (1985) found in their observation of surplus-killing by wolves (*Canis lupus*) that depredated calves of caribou (*Rangifer tarandus*) were in good physical condition. In addition, when prey are unusually abundant, their increased presence may trigger predation past the point of satiation (Miller et al., 1985). Kruuk (1972:12) argues that "satiation in carnivores does not inhibit further catching and killing, but it probably does inhibit searching and hunting. Thus carnivores are able to procure an 'easy prey' but normally satiation limits numbers killed."

Of the three potential triggers, super-abundant density of giant kangaroo rats is the most likely cause of the incident of surplus-killing we report. Density of the giant kangaroo rat was estimated in trapping sessions during April and August each year using the robust design with heterogeneity estimator in program RMark (J. Laake and E. Rexstad, http://www.phidot.org/software/mark/docs/book). The density of giant kangaroo rats on the plot where the surplus-killings occurred (plot C5) increased by 34% between August 2010 and April 2011. The dynamics of the giant kangaroo rat on plot C5 reflected a general trend across all 30 sites; the average density of giant kangaroo rats increased by 35% during this time period (from 38 giant kangaroo rats/ha to 52/ha; R. L. Endicott and L. R. Prugh, in litt.). Densities in April 2011 were significantly higher than in any previous year of the study (Fig. 2), and survival over winter was highest between August 2010 and April 2011. Giant kangaroo rats were, therefore, unusually abundant in April 2011.

There were no apparent plot-specific environmental conditions or events of extreme weather that would have rendered giant kangaroo rats on plot C5 especially vulnerable to predation. Additionally, giant kangaroo rats captured on plot C5 during our live-trapping sessions had similar body condition (as measured by the ratio of the body weight to the skull length) as giant kangaroo rats captured on our other plots. The average body-condition index of adults on C5 in April 2011 was 2.84 ($n = 52$; 95% confidence interval, CI, = 2.79–2.89), and the average condition of adults on all 30 plots combined also was 2.84 ($n = 1{,}380$; 95% CI = 2.83–2.85). It is possible that a research-effect may have increased activity of foxes on our plots, because San Joaquin kit foxes are drawn to novel items such as Sherman traps and plot stakes (B. Cypher, pers. comm.). However, this issue should have affected all our plots equally.

The consequences of surplus-killing for populations of prey have not been previously reported. We used our mark-recapture dataset to examine the change in density of the giant kangaroo rat following the surplus-kills. Of our 30 plots, the plot where surplus-killing was observed (C5) had the largest decline in density between the April and August 2011 trapping sessions, from 56 individuals/

Table 1—Density (number per hectare) of giant kangaroo rats (*Dipodomys ingens*) on 30 study plots in the Carrizo Plain National Monument, California, during 2011, and average change in density from April–August during 5 years (2008–2012). The first 20 plots were part of a study of grazing by cattle, and an additional 10 plots were located in an ungrazed pasture. Mark-recapture estimates, with 95% confidence intervals (CI) in parentheses, are given as well as the change in density over time.

Plot	Plot treatment	Density estimate (95% CI)		Change in density in 2011	Mean change in density 2008–2012
		April 2011	August 2011		
C1	Grazed	54 (52–59)	57 (54–64)	3	5.0
E1	Ungrazed	41 (40–45)	20 (18–24)	−22	−3.8
C2	Grazed	54 (53–58)	69 (68–73)	15	−8.8
E2	Ungrazed	55 (53–61)	52 (50–59)	−3	−5.0
C3	Grazed	54 (53–58)	61 (59–66)	7	1.4
E3	Ungrazed	54 (53–57)	48 (46–52)	−6	−4.4
C4	Grazed	40 (39–42)	63 (61–66)	23	−3.0
E4	Ungrazed	46 (45–49)	60 (58–64)	14	−9.4
C5	Grazed	56 (56–58)	31 (29–34)	−26	−18.2
E5	Ungrazed	52 (52–54)	42 (41–45)	−10	−12.4
C6	Grazed	40 (39–43)	32 (31–36)	−8	−12.0
E6	Ungrazed	50 (49–52)	35 (34–39)	−15	−14.0
C7	Grazed	47 (46–51)	55 (53–61)	8	−6.8
E7	Ungrazed	52 (50–58)	55 (52–62)	3	−3.6
C8	Grazed	52 (51–55)	68 (66–72)	16	−2.6
E8	Ungrazed	58 (57–61)	64 (62–69)	6	2.2
C9	Grazed	48 (47–50)	62 (60–66)	14	5.8
E9	Ungrazed	44 (44–46)	43 (42–46)	−1	0.6
C10	Grazed	73 (71–76)	73 (70–78)	0	2.0
E10	Ungrazed	63 (62–66)	72 (69–76)	9	5.6
S1	Ungrazed	57 (56–59)	71 (70–75)	14	−0.6
S2	Ungrazed	73 (73–75)	51 (49–54)	−23	−5.8
S3	Ungrazed	56 (55–59)	60 (58–64)	4	−7.2
S4	Ungrazed	56 (55–58)	54 (53–58)	−1	−5.4
S5	Ungrazed	51 (50–53)	35 (34–39)	−15	−6.6
S6	Ungrazed	50 (49–53)	38 (37–41)	−12	−2.0
S7	Ungrazed	58 (57–64)	58 (57–64)	0	5.0
S8	Ungrazed	31 (31–33)	24 (23–26)	−8	5.6
S9	Ungrazed	35 (35–37)	33 (32–35)	−3	5.2
S10	Ungrazed	52 (51–54)	43 (42–46)	−9	−0.8
Average		52 (49–55)	51 (46–56)	−1	−3.0

ha in April (95% CI = 56–58) to 31/ha in August (95% CI = 29–34; Table 1). Densities on a paired plot (E5) located 60 m away, in contrast, were 52 in April (95% CI = 52–54) and 42 in August (95% CI = 41–45). Densities of the giant kangaroo rat also sharply declined on plot E1 (Table 1), which was located several kilometers from plot C5, and on which no surplus-kill was detected. However, a family of San Joaquin kit foxes had active dens on plot E1, so heavy predation also may have been involved in that decline.

The fact that populations of giant kangaroo rats declined on plots such as E1, where no surplus-kill was found, raises the possibility that heavy predation rather than surplus-killing caused the steep decline observed on plot C5. Indeed, populations on plots often declined between April and August across all 5 years of our study (2008–2012), though the average decline was minimal (Table 1). The population of giant kangaroo rats on plot C5 was unusual in that it declined from April–August during each of the 5 years and had the steepest average decline among the 30 plots (Table 1). Thus, dynamics on this plot appear to differ from those on other plots.

To further examine the possibility that the steep declines on plot C5 could have been caused by heavy predation rather than surplus-killing, we evaluated the dynamics of giant kangaroo rats on each plot in relation to the distance to the nearest known natal den or family group of San Joaquin kit foxes from 2008–2012. If populations of giant kangaroo rats tend to steeply decline on all plots close to natal dens of San Joaquin kit foxes, this would indicate that heavy predation rather than surplus-killing may have caused the local decline observed on plot C5. Active dens were recorded opportunistically by project-staff each year. Additionally, locations of family groups were recorded during spotlighting surveys conducted during four consecutive nights in May and July each year. We used a hierarchical linear model to examine the effect of distance to nearest den or sighting on the change in density of the giant kangaroo rat from April–

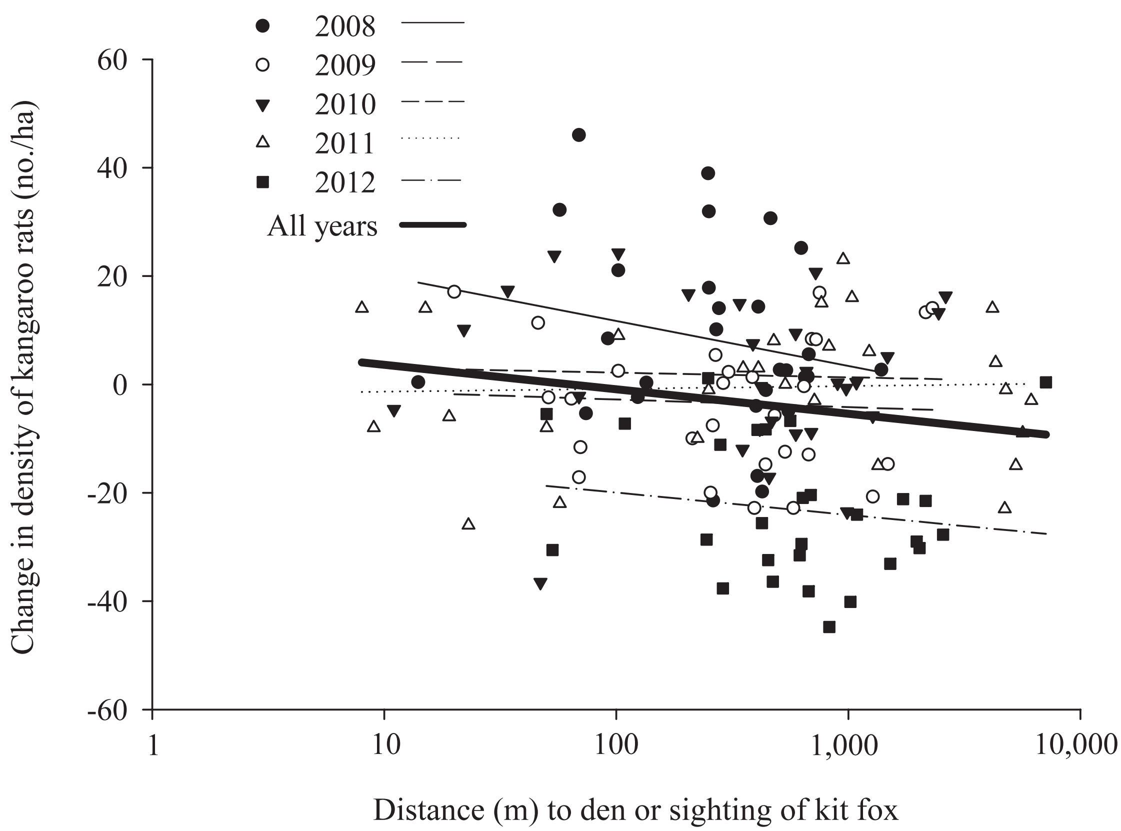

Fig. 3—Change in density of the giant kangaroo rat (*Dipodomys ingens*) from April–August on each plot each year (2008–2012) in relation to the nearest den or sighting of a family of San Joaquin kit foxes (*Vulpes macrotis mutica*) in the Carrizo Plain National Monument, California. Locations of dens were recorded opportunistically each year, and locations of family groups were recorded during spotlighting surveys each year ($n = 8$ surveys/year).

August on each plot each year. Distances were log-transformed prior to analysis. Year was entered as a random effect, plot was entered as a nested (within year) random effect (Pinheiro and Bates, 2000), and analyses were conducted using the lme function in program R.

We found no relationship between distance to the nearest den or sighting of the San Joaquin kit fox and change in density of the giant kangaroo rat (Fig. 3; $F_{1,134} = 0.70$, $P = 0.40$). Thus, local declines in populations of the giant kangaroo rat do not appear to be caused by proximity to natal dens of San Joaquin kit foxes.

While other factors may have been involved in the steep decline in the density of giant kangaroo rats on plot C5, it is likely that surplus-killing by one family of San Joaquin kit foxes played a major role. Our finding supports previous studies documenting strong impacts of individuals or small groups of predators (Linnell et al., 1999). For example, a single cougar (*Puma concolor*) killed 9% of the adults and 26% of the lambs in a population of bighorn sheep (*Ovis canadensis*) in Alberta during a single winter (Ross et al., 1997). Our observation indicates that surplus-killing by a small group of predators can similarly have a marked impact on the dynamics of populations of targeted prey. Because cases of surplus-killing may occur sporadically and are difficult to document, it is unknown how widespread this behavior may be among individual predators and how often such incidents occur. Our findings highlight the importance of long-term and large-scale studies in the field for documenting events such as surplus-killing because these rare events may have stronger ecological impacts than previously thought.

Funding and logistical support was provided by the Bureau of Land Management and the United States Department of Agriculture. We thank assistants in the field who collected data for this study (S. Kong, A. Ross, G. Taylor, R. Lyon, and A. Matea). B. Cypher and an anonymous reviewer provided helpful comments on an earlier version of this manuscript. L. Withey translated the abstract into Spanish.

Literature Cited

Cypher, B. L., G. D. Warrick, M. R. M. Otten, T. P. O'Farrell, W. H. Berry, C. E. Harris, T. T. Kato, P. M. McCue, J. H. Scrivner, and B. W. Zoellick. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. Wildlife Monographs 145:1–43.

DelGiudice, G. D. 1998. Surplus killing of white-tailed deer by wolves in Northcentral Minnesota. Journal of Mammalogy 79:227–235.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Kit foxes. Pages

417–418 in Fur bearing mammals of California. Volume 2. University of California Press, Berkeley.

Kruuk, H. 1972. Surplus killing by carnivores. Journal of Zoology (London) 166:233–244.

Linnell, J. D. C., J. Odden, M. Smith, E. R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: do "problem individuals" really exist? Wildlife Society Bulletin 27:698–705.

McGrew, J. C. 1979. Vulpes macrotis. Mammalian Species 123:1–6.

Meuller, D. L., and B. C. Hastings. 1977. A clarification of surplus killing. Animal Behaviour 25:1065.

Miller, F. L., A. Gunn, and E. Broughton. 1985. Surplus killing as exemplified by wolf *Canis lupus* predation on newborn caribou *Rangifer tarandus groenlandicus*. Canadian Journal of Zoology 63:295–300.

Nunn, G. L., D. Klem, Jr., T. Kimmel, and T. Merriman. 1976. Surplus killing and caching by American kestrels (*Falco sparverius*). Animal Behaviour 24:759–763.

Patterson, B. R. 1994. Surplus killing of white-tailed deer, *Odocoileus virginianus*, by coyotes, *Canis latrans*, in Nova Scotia. Canadian Field-Naturalist 108:484–487.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-plus. Springer Verlag, New York.

Prugh, L. R., and J. S. Brashares. 2010. Basking in the moonlight? Illumination increases the capture success of the endangered giant kangaroo rat. Journal of Mammalogy 91:1205–1212.

Prugh, L. R., and J. S. Brashares. 2012. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology 81:667–678.

Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Canadian Journal of Zoology 74:771–775.

Samelius, G., and R. T. Alisauskas. 2000. Foraging patterns of arctic foxes at a large arctic goose colony. Arctic 53:279–288.

Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

White, P. J., and R. A. Garrott. 1997. Factors regulating kit fox populations. Canadian Journal of Zoology 75:1982–1988.

White, P. J., and R. A. Garrott. 1999. Population dynamics of kit foxes. Canadian Journal of Zoology 77:486–493.

White, P. J., and K. Ralls. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. Journal of Wildlife Management 57:861–867.

White, P. J., C. A. V. White, and K. Ralls. 1996. Functional and numerical responses of kit foxes to a short-term decline in mammalian prey. Journal of Mammalogy 77:370–376.

Submitted 28 November 2012. Acceptance recommended by Associate Editor Jennifer K. Frey 20 May 2013.

The Southwestern Naturalist 59(1): 115–117

REPRODUCTIVE CYCLE OF BAIRD'S POCKET GOPHER (*GEOMYS BREVICEPS*) IN NORTHERN LOUISIANA

Matthew B. Connior,* Douglas C. Cagle, Heather E. Peek, Christopher R. Ellington, and John L. Hunt

Health and Natural Sciences, South Arkansas Community College, El Dorado, AR 71730 (MBC)
University of Arkansas at Monticello, Monticello, AR 71656 (DCC, HEP, CRE, JLH)
**Correspondent: mconnior@southark.edu*

Abstract—We examined the reproductive status of Baird's pocket gophers (*Geomys breviceps*) in Union Parish, Louisiana, for 18 months in 2010 and 2011. We found that pocket gophers were potentially reproductively active throughout the year, although the number of reproductively active gophers peaked during late spring through autumn. Our results are similar to those of studies of Baird's pocket gopher in other states and of other pocket gophers in the genus *Geomys*.

Resumen—Examinamos tuzas de Baird (*Geomys breviceps*) de Union Parish, Louisiana, durante 18 meses en 2010 y 2011 para determinar su estado reproductivo. Encontramos que las tuzas fueron potencialmente activas reproductivamente durante todo el año, aunque el número de tuzas reproductivamente activas fue más alto desde finales de la primavera hasta el fin del otoño. Nuestros resultados son similares a los encontrados en estudios en otros estados, así como para otras especies del género *Geomys*.

Baird's pocket gopher (*Geomys breviceps*) occurs from eastern Louisiana and Arkansas westward into central Texas and Oklahoma (Sulentich et al., 1991) and is the only species of pocket gopher that occurs in Louisiana (Lowery, 1974). Because pocket gophers are fossorial, solitary rodents exclusive of short durations during the breeding season (Chase et al., 1982), limited information regarding reproductive patterns and ecology is known.