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Foraging and reproductive behavior of Arizona gray squirrels (*Sciurus arizonensis*): impacts of climatic variation

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Optimal timing of reproduction is critical to ensure adequate conditions for raising young. However, factors influencing timing of reproduction may differ between sexes. Harsh seasonal environments offer unique opportunities to link timing with resource availability and strategies of the sexes. The Arizona gray squirrel (*Sciurus arizonensis*) inhabits arid forests in which precipitation is highly seasonal and exceptionally variable; however, no data are available on diet or reproduction. We investigated annual variation in foraging and reproductive habits of Arizona gray squirrels to assess responses to extreme seasonality. We found that Arizona gray squirrels have a diverse diet, with consumption of major food items shifting between years. Reproduction also varies between years. Reproductive output was greater in 2008, with more females successfully reproducing and males remaining in reproductive condition for extended periods. Males shifted timing of reproductive behaviors in response to female receptivity, which tracked food availability. This shift likely reflects variation in food production due to precipitation, because rainfall varied greatly, with most years prior to and during our study recording below-average rainfall. With drought conditions and extreme rainfall events predicted to increase with climate change, understanding the relationship between climatic events, phenology of food production, and impacts on reproduction is critical when attempting to manage and conserve species.

Key words: Arizona, climate, food availability, resource limitation, *Sciurus arizonensis*, squirrel, timing of reproduction

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Optimal timing of reproduction is critical in order to ensure adequate environmental and climatic conditions and resources for raising young (Cumming and Bernard 1997; Lewis and Kappeler 2005; Love et al. 2010). One vital resource is food, both for ensuring adequate body condition for adults as well as providing energy for growth of juveniles (Lack 1968; Perrins 1970; Rubenstein and Wikelski 2003; Talbot and Talbot 1963). However, the relative importance of these resources may differ between sexes. In mammals, females dedicate more to parental investment due to high costs of pregnancy and lactation; consequently, food availability is recognized as a key limiting resource in female fitness (Clutton-Brock and Harvey 1978; Ostfeld 1985). As a result, female reproduction is often timed so that periods of high energy demand coincide with periods of high food availability (Bowyer 1991; Kenagy et al. 1989; Lewis and Kappeler 2005; Racey 1982). Alternatively, males dedicate little energy to parental investment, and fitness is instead limited by access to mates (Clutton-Brock and Harvey

1978; Ostfeld 1985; Trivers 1972). Consequently, male reproduction is timed to maximize the number of reproductive opportunities (Emlen and Oring 1977; Michener 1983).

Sex-biased differences in reproductive investment are especially evident in tree squirrels, where females enter estrus for only a single day, resulting in scramble competition among males for the opportunity to mate (Gurnell 1987; Koprowski 1998). Males shift behaviors annually to maximize interactions with females during the breeding season by increasing movements and, consequently, home-range sizes (Cudworth and Koprowski 2010; Gurnell 1987; Halloran and Bekoff 2000; Pasch and Koprowski 2006; Steele and Koprowski 2001) and remaining reproductively active throughout the breeding season, potentially displaying descended testes during



all months of the year (Gurnell 1987; Steele and Koprowski 2001). Reproduction for females, however, is more energetically demanding. Consequently, females must demonstrate a positive energy balance before acquiring reproductive condition (Gurnell 1987), and breeding may completely cease following food shortages (Nixon and McClain 1969, 1975). When food is abundant, however, females may be able to breed precociously (Smith and Barkalow 1967), attain reproductive condition earlier in the year, and maintain adequate body condition to raise 2 litters in a breeding season, effectively doubling reproductive output (Gurnell 1983, 1987).

Mast-producing trees are an especially important food resource for tree squirrels (Gurnell 1987; Koprowski and Corse 2001; Moller 1983). Individuals may suffer decreased body mass and increased juvenile mortality in poor crop years (Koprowski 1991). Caching of mast provides a store of food essential for overwinter survival when such food resources are scarce (Gurnell 1987; Thompson and Thompson 1980; Vander Wall 1990); consequently, food availability may be a limiting factor for many populations (Brown 1984). Because the production of mast crops is influenced by rainfall (Calama et al. 2008; Koenig et al. 1996; Sork et al. 1993; Zlotin and Parmenter 2008), extreme variability in rainfall within and among years, such as is seen in the deserts of the southwestern United States and northwestern Mexico, can have drastic impacts on vegetation and availability of mast crops (Germaine and McPherson 1998; Zlotin and Parmenter 2008).

The Arizona gray squirrel (*Sciurus arizonensis*) is a tree squirrel restricted to the mountainous sky islands of the southwestern United States and northwestern Mexico (Hoffmeister 1986). Populations are found at elevations above 1,120 m (Best and Riedel 1995) within riparian areas of deciduous or mixed forest in a number of mountain ranges within the Madrean Archipelago, including the Huachuca Mountains, which are believed to have among the highest densities throughout the range of the species (Brown 1984; Hoffmeister 1986). Despite being a species of conservation concern in Mexico and portions of the United States (*S. a. catalinae*—Álvarez-Castañeda and Patton 1999; Best and Riedel 1995), the species is still virtually unknown, with a paucity of information on diet and reproduction, both of which are critical for the conservation and management of populations. Anecdotal information suggests that Arizona gray squirrels consume tree nuts, fungi, insects, and flower parts, and the onset of reproduction is timed with the availability of flowering parts, with a peak in breeding activity in April and May. However, litters in the fall have not been documented for Arizona gray squirrels, and females appear to be constrained to a single litter per season and may even forgo breeding in some years (Brown 1984; Theobald 1983). Consequently, Arizona gray squirrels provide an excellent species with which to assess behavioral responses to extreme variation in precipitation in arid forest environments. Therefore, our objective was to describe foraging and reproductive behavior of Arizona gray squirrels and investigate what impacts climatic variation may have on the annual timing of these behaviors.

MATERIALS AND METHODS

Study area.—We investigated foraging and reproductive behavior of Arizona gray squirrels from April 2007 to December 2008 on Fort Huachuca Military Reservation on the northwestern portion of the Huachuca Mountains in southwestern Cochise County, Arizona. The Huachuca Mountains are approximately 26,000 ha and range from 1,500 to 2,880 m in elevation. We primarily restricted data collection to a population of squirrels in the oak–juniper (*Quercus–Juniperus*) forests of lower Huachuca Canyon between 1,555 and 1,860 m. This is the lowest forested community in the Huachuca Mountains and an area where we would expect variation and limitation in precipitation to be the greatest. An ephemeral stream runs through the canyon from late summer through winter. Major tree species include Arizona white oak (*Quercus arizonica*), Emory oak (*Q. emoryi*), silverleaf oak (*Q. hypoleucoides*), alligator juniper (*Juniperus deppeana*), and Arizona sycamore (*Platanus wrightii*). Arizona walnut (*Juglans major*), Fremont cottonwood (*Populus fremontii*), piñon pine (*Pinus edulis*), manzanita (*Arctostaphylos pungens*), and Arizona madrone (*Arbutus arizonica*) also are present in lower densities (Wallmo 1955). Rainfall at Fort Huachuca varied greatly the years prior to and during our study, with 3 years recording drought conditions (2004, 2005, and 2007) and only 2 years recording near-average rainfall (2006 and 2008; Fig. 1). Our study encompassed both drought and average years, with 2007 receiving 30.08 cm of rainfall and 2008 receiving 38.55 cm of rainfall. Most rainfall occurred during the monsoon season (July–September), with monsoon months recording 60% of rainfall on average (Fig. 1).

Trapping and telemetry.—We placed Tomahawk live traps (model 104; Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter and peanuts at the base of large-diameter trees to capture squirrels. We transferred all

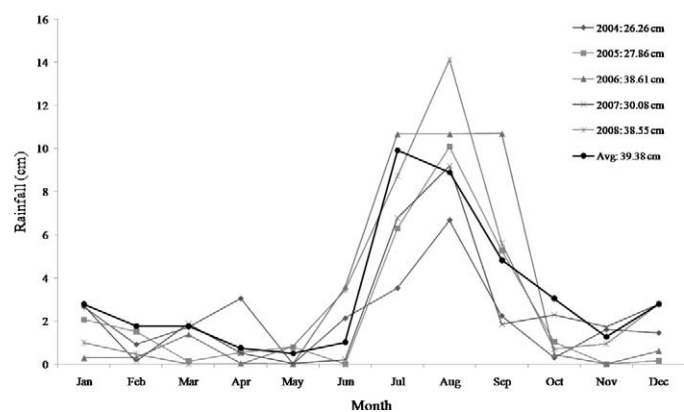


FIG. 1.—Monthly rainfall (cm) by year for 2004–2008 and average monthly rainfall (cm; thick line) from 1954 to 2003 for Huachuca Canyon, Fort Huachuca Military Reservation, Cochise County, Arizona. Total rainfall for each year and average total rainfall are included in the legend. December rainfall values were missing for 2007 and 2008; consequently, values are taken from mean December value from 1954 to 2003.

captured squirrels to a cloth handling cone (Koprowski 2002) for analysis and affixed unique combinations of metal ear tags and colored washers (1 cm; model 1005-3 and model 1842, respectively; National Band and Tag Co., Newport, Kentucky) to allow for individual identification. We radiocollared adult squirrels (≥ 540 g; model SOM 2380; Wildlife Materials Inc., Murphysboro, Illinois; $< 5\%$ of body mass) and released all individuals at the capture site. For each squirrel captured, we recorded sex, age class (juvenile, subadult, or adult), and reproductive status. Males were either nonreproductive (abdominal), inguinal, or scrotal; we also measured testes size for reproductively active males. Females were either nonreproductive, in estrus, pregnant, or lactating (current, recent, or past). Trapping and telemetry data were collected throughout the duration of the study to allow for analysis of annual cycles in reproduction.

We homed to collared individuals multiple times throughout the day at a minimum of 2-h intervals. We used a yagi antenna (model F164-165-3FB; Wildlife Materials Inc.) and receiver (model R-1000; Communications Specialists Inc., Orange, California) for all telemetry work. For each observation, we recorded location with a global positioning system unit as well as noting behaviors, including intra- and interspecific interactions and foraging. Each individual was only observed long enough to positively determine identity and behavior. Trapping and handling procedures were approved by The University of Arizona Institutional Animal Care and Use Committee (IACUC protocol 08-025) and Arizona Game and Fish Department and in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Food habits.—Foraging was defined as feeding, caching, or traveling with a food item. Marked individuals provided the majority of foraging observations, although we also recorded foraging events opportunistically on unmarked squirrels. When comparing food habits between years, we discarded those observations for which we were unable to determine food type. Because of the difficulty in ascertaining species when individuals were caching or traveling, we combined all oak species into a single acorn group for analyses.

Timing of reproduction.—Homing allowed us to document behaviors, classify reproductive status between trapping attempts, and locate maternity nests. We recorded mating chases opportunistically and documented all marked and unmarked squirrels involved in each chase. Because of the low number of observed mating chases in 2007 ($n = 2$), we only use results from 2008 when describing participation in mating chases. We also checked all known maternity nests systematically to record date of 1st emergence for each litter. Once juveniles were observed outside the maternity cavity, we actively monitored each nest to determine litter size. We only include results from litters for which we were confident we had successfully counted all juveniles.

Data analysis.—We used a contingency analysis to compare proportion of foraging observations for top food items ($\geq 10\%$ of total observations) between sexes and years for marked individuals. We averaged litter sizes within years and used a t -

test to compare litter sizes between years. We further divided the year into 4 seasons based upon rainfall and temperature data from Fort Huachuca (Fig. 1; winter: January–March; spring: April–June; summer: July–September; fall: October–December). Although we were able to collect data on some individuals in multiple seasons throughout the study, this occurred at a low rate that precluded us from using repeated-measures analysis. Therefore, we averaged body mass within each season for each adult and used single-factor analyses of variance to investigate the effects of sex, season, and year on variation in body mass. We used a contingency analysis to compare the frequency of reproductive adult males and females between years and among seasons within each year using only marked individuals. Because we were interested in the variation in time spent in foraging and reproductive behaviors (i.e., mating chases, in maternity nest, or gathering nesting materials for maternity nest), we used a chi-square analysis to compare the number of observations for each of these behaviors to other behaviors (e.g., traveling, resting, and other intra- and interspecific interactions); we report the percentage of time spent in each behavior for each comparison. For summary statistics, we report means ($\pm SE$). We conducted all statistical analyses in JMP version 7 (SAS Institute Inc. 2007), Minitab version 14 (Minitab Inc. 2005), and SigmaPlot version 11 (Systat Software Inc. 2008).

RESULTS

Food habits.—We recorded 392 foraging observations (2007: $n = 195$; 2008: $n = 197$) for which we were able to ascertain food type. Diet was diverse and included 17 unique foods (Table 1). Most important food items ($\geq 10\%$ of observations) for both years included juniper seeds, acorns,

TABLE 1.—Food items and percentage of foraging observations ($n = 392$) for Arizona gray squirrels (*Sciurus arizonensis*) by year from May 2007 to December 2008 in the Huachuca Mountains, Cochise County, Arizona.

Food item	2007	2008
<i>Quercus</i> (acorns)	44.62	35.03
<i>Q. arizonica</i>	18.46	12.69
<i>Q. emoryi</i>	14.87	4.06
<i>Q. hypoleucoides</i>	2.05	5.08
<i>Quercus</i> spp.	9.23	13.20
<i>Juniperus deppeana</i> (seeds)	20.51	42.13
<i>Juglans major</i> (nuts)	14.36	12.69
Insect galls	11.79	0.00
<i>Pinus edulis</i> (seeds)	0.00	3.55
Tree bark/sap	3.08	0.51
Fungi	1.54	1.02
Minerals from rocks	0.00	2.03
<i>Platanus wrightii</i> (seeds)	1.03	1.02
<i>Arctostaphylos</i> (seeds)	1.54	0.00
<i>Arbutus arizonica</i> (seeds)	0.51	0.51
<i>Pseudotsuga menziesii</i> (seeds)	0.51	0.51
<i>Acacia</i> (seeds)	0.00	0.51
Lichen	0.00	0.51
Egg—songbird	0.51	0.00

TABLE 2.—Top food items ($\geq 10\%$ of total foraging observations) and percentage of foraging observations ($n = 335$) for marked male and female Arizona gray squirrels (*Sciurus arizonensis*) by year from May 2007 to December 2008 in the Huachuca Mountains, Cochise County, Arizona.

Food item	Female		Male		Sexes combined	
	2007	2008	2007	2008	2007	2008
<i>Quercus</i> (acorns)	47.57	28.13	53.03	43.14	49.70	37.35
<i>Juniperus deppeana</i> (seeds)	25.24	54.69	21.21	45.10	23.67	48.80
<i>Juglans major</i> (nuts)	12.62	17.19	18.18	11.76	14.79	13.86
Insect galls	14.56	0.00	7.58	0.00	11.83	0.00

and walnuts. Insect galls in cottonwood leaves also were an important food item in 2007 (Table 2). Foraging habits of Arizona gray squirrels differed significantly when proportion of observations for each important food item was compared between years ($\chi^2_3 = 37.27$, $P < 0.001$). Insect galls were used exclusively and acorns were used 1.3 times more often in 2007, juniper seeds were used 2.1 times more often in 2008, and walnuts were consumed equally between years. Foraging habits of males followed this same trend between years, with insects used more often in 2007 and junipers used more often in 2008, although walnuts also were used 1.5 times more often in 2007 ($\chi^2_3 = 16.12$, $P = 0.001$). Foraging habits of females also differed between years ($\chi^2_3 = 22.98$, $P < 0.001$), with insects used exclusively and acorns used 3.1 times more often in 2007, and walnuts used 1.4 times and juniper seeds used 2.2 times more often in 2008. Foraging habits were similar between males and females overall ($\chi^2_3 = 6.02$, $P = 0.111$) and did not differ between males and females in 2007 ($\chi^2_3 = 3.02$, $P = 0.389$) or 2008 ($\chi^2_2 = 3.95$, $P = 0.139$; Table 2).

Body mass.—Between April 2007 and December 2008, we trapped and uniquely marked 48 individuals (21 females and 27 males). Of these marked individuals, we routinely monitored 32 individuals (16 females and 16 males) in 2007, and 34 individuals (14 females and 20 males) in 2008. Adult body mass was similar between sexes ($F_{1,91} = 0.65$, $P = 0.422$) and seasons ($F_{3,89} = 1.50$, $P = 0.220$), but individuals averaged 21.3 g (± 10.7 g) heavier in 2008 ($F_{1,91} = 3.98$, $P = 0.049$; Fig. 2). Females tended to be 23.9 g (± 10.7 g) heavier on average in 2008 ($F_{1,49} = 3.34$, $P = 0.074$; Fig. 2); male body mass did not differ between years ($F_{1,40} = 0.91$, $P = 0.347$; Fig. 2).

Timing of reproduction.—All radiocollared males ($n = 19$) were reproductively active for at least a portion of each mating season (January–July) in 2007 and 2008 based upon descended testes or participation in mating chases. Proportion of males in reproductive condition was consistent among seasons in 2008 ($\chi^2_3 = 1.40$, $P = 0.706$). However, proportion of males in reproductive condition differed among seasons in 2007 ($\chi^2_2 = 6.17$, $P = 0.046$), with the proportion steadily decreasing from spring to fall (Fig. 3). We observed 2 mating chases in 2007, both of which occurred in May (Fig. 4). We observed 9 mating chases in 2008, which occurred between 12 February and 7 August (Fig. 4). Mating chases contained 1 female pursued by 2–9 males, with an average of 5.3 (± 0.6) males per mating chase. We documented 12 of 15 marked males participating in mating chases in 2008. Five males were marked and observed

in the study area throughout the entire mating season and were involved in an average of 2.6 (± 1.0) mating chases each (range 0–6 chases).

Sixteen of 17 radiocollared females for which we had sufficient data reproduced at least once from May 2007 to December 2008 based upon participation in mating chases, documentation of lactation, or emergence of young. The proportion of females breeding differed between years, with a lower proportion breeding in 2007 than in 2008 (9 of 13 females and 10 of 10 females, respectively, $\chi^2_1 = 3.73$, $P = 0.054$). The proportion of lactating females differed among seasons in 2008 ($\chi^2_3 = 9.05$, $P = 0.029$), with fewer females lactating in winter than any other season. The proportion of

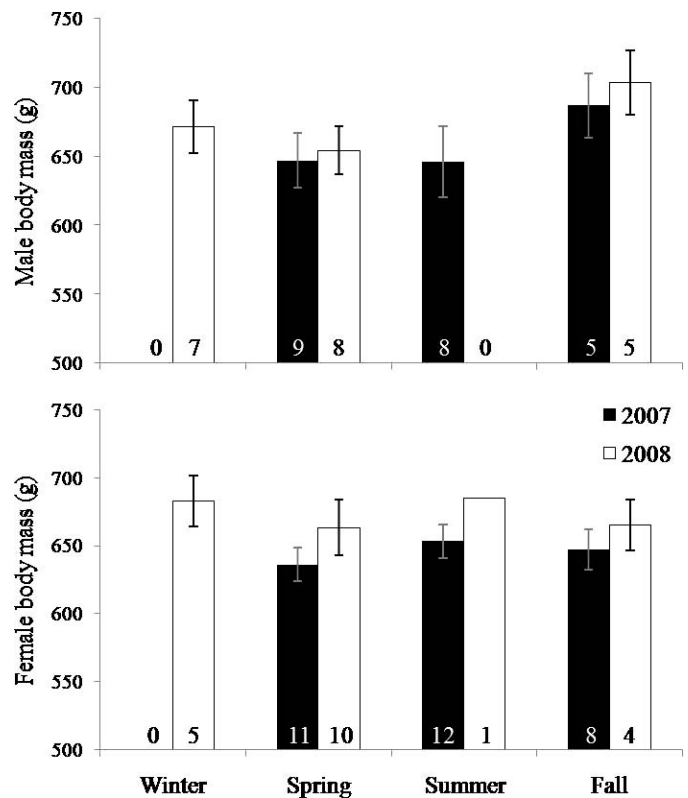


FIG. 2.—Mean ($\pm SE$) body mass of adult (>540 g) male and female Arizona gray squirrels (*Sciurus arizonensis*) among seasons from April 2007 to December 2008 in the Huachuca Mountains, Cochise County, Arizona. Sample sizes are shown at the base of each bar. Winter = January–March, spring = April–June, summer = July–September, fall = October–December.

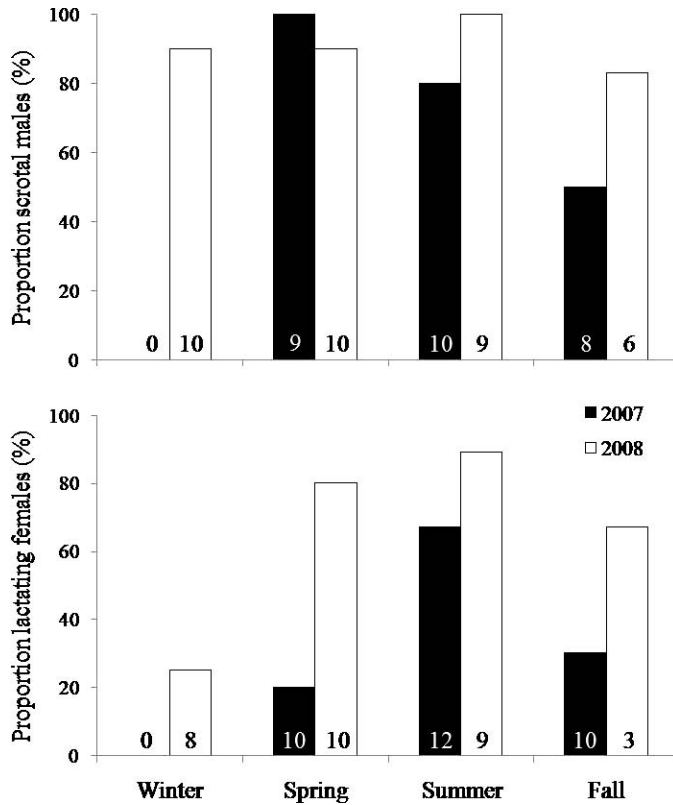


FIG. 3.—Proportion of Arizona gray squirrel (*Sciurus arizonensis*) males with scrotal testes and females in lactation among seasons from April 2007 to December 2008 in the Huachuca Mountains, Cochise County, Arizona. Sample sizes are shown at the base of each bar. Winter = January–March, spring = April–June, summer = July–September, fall = October–December.

females lactating also tended to differ among seasons in 2007 ($\chi^2_2 = 5.61$, $P = 0.061$), with more females lactating in summer than any other season; however, we did not have reproductive data for winter of that year (Fig. 3).

We monitored 6 females throughout breeding seasons in both 2007 and 2008. Only 3 females reproduced in 2007; another 2 females were suspected to have entered estrus but showed no indication of having given birth or lactating. Conversely, 5 females successfully raised litters to emergence in 2008, and the other female was lactating at the time of her death. We were able to record emergence of litters for 2 females in both years, both of which had young emerge ≥ 2 months earlier in 2008. In addition, although no females were observed reproducing > 1 time in 2007, 3 females were known to enter estrus twice in 2008. Two females successfully weaned 3 young each and were observed in mating chases while their young were still in the nest; 1 female was not collared and the other died before we could observe the fate of 2nd litters. The 3rd female lost her 1st litter (we found a juvenile approximately 4 weeks old with no signs of predation dead outside the maternity cavity), but successfully weaned 2 young on her 2nd attempt.

We were able to determine litter size for 14 litters, which included 2 opportunistic observations outside the study area. Litter size ranged from 2 to 4 young and did not differ between

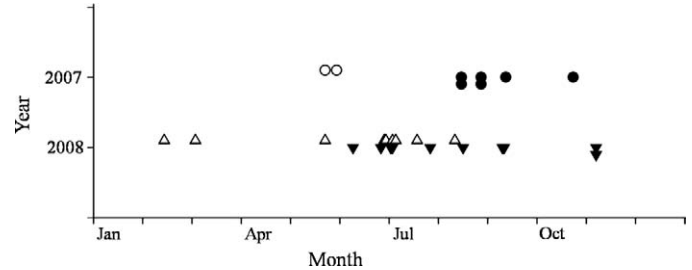


FIG. 4.—Seasonal distribution of mating chases (open symbols; $n = 11$) and 1st emergence for known litters (closed symbols; $n = 14$) of Arizona gray squirrels (*Sciurus arizonensis*) in the Huachuca Mountains, Cochise County, Arizona, from May 2007 to December 2008.

years ($t_{12} = 1.18$, $P = 0.261$). Mean litter size when years were combined was $3.1 (\pm 0.2)$ young. Emergence of litters was constrained to a 1-month period in 2007, with 5 known litters from marked females in our study area emerging between 12 August and 8 September and 1 late litter on 19 October (Fig. 4). In contrast, litters emerged over a 3-month period in 2008, with 7 known litters emerging between 6 June and 6 September and 2 late litters on 1 November (Fig. 4). In 2007, we observed 1 litter for which we had documented the date of birth and emergence, suggesting approximately 50 days between birth and 1st emergence. We observed 3 females for which we had dates of mating chases and emergence, which averaged $114 (\pm 3.5)$ days from copulation to litter emergence.

Time budgets.—When behavioral observations of all marked squirrels were combined, the number of observations for foraging, reproductive behavior, and other activities differed between 2007 and 2008 ($\chi^2_2 = 42.16$, $P < 0.001$), with individuals observed foraging 1.2 times more often in 2007 (2007: 27.0%, 2008: 22.1%) and in reproductive behaviors 2.6 times more often in 2008 (2007: 5.8%, 2008: 15.0%); individuals spent similar amounts of time in other behaviors (2007: 67.2%, 2008: 62.9%). We observed this same pattern between years for males ($\chi^2_2 = 20.07$, $P < 0.001$) and females ($\chi^2_2 = 54.55$, $P < 0.001$), with females observed foraging 1.3 times (2007: 26.5%, 2008: 20.8%) and in other behaviors 1.2 times (2007: 65.0%, 2008: 52.4%) more often in 2007 and in reproductive behaviors 3.2 times more often in 2008 (2007: 8.5%, 2008: 26.8%). Behavioral observations also differed between sexes, with males observed 1.2 times more often in other behaviors (males: 69.5%, females: 59.9%) and females observed 2.7 times more often in reproductive behaviors (males: 6.0%, females: 15.9%; $\chi^2_2 = 49.78$, $P < 0.001$); males and females spent similar amounts of time foraging (males: 24.5%, females: 24.2%). We observed this same pattern between males and females in both 2007 ($\chi^2_2 = 19.35$, $P < 0.001$) and 2008 ($\chi^2_2 = 64.19$, $P < 0.001$).

DISCUSSION

Arizona gray squirrels consume a diverse diet, ranging from acorns, seeds, and nuts, to insect galls, tree bark and sap, and fungi. Although we did not directly measure food availability,

foraging observations likely reflect relative availability of food items in our study area, because tree squirrels maximize the rate of patch-specific energy intake by spending more time foraging on the most abundant species (Lewis 1980), thus minimizing travel and search time necessary to locate widely dispersed, less abundant foods. This also is supported by the similar foraging habits observed for both sexes in our study. The most important food items consumed by Arizona gray squirrels, including acorns, seeds, and nuts, are similar to major food items of other species of *Sciurus* (Gurnell 1987). Although tree squirrels are known to consume insects in small quantities (Koprowski 1994; Koprowski and Corse 2001; Korschgen 1981; Shealer et al. 1999), the extensive consumption of insect galls in 2007 appears to be relatively uncommon and may represent a unique foraging behavior. We did not observe the same abundance of insect galls in 2008, suggesting that Arizona gray squirrels were likely taking advantage of a fluctuating resource. This is further supported by the seasonality of food consumption: although acorns and juniper seeds were consumed throughout the year, walnuts and insect galls were consumed exclusively in the summer, with only 1 foraging observation for walnuts in late spring, likely reflecting their availability throughout the year. The overall diverse diet of Arizona gray squirrels mirrors that of the closely related Chiricahua fox squirrel (*S. nayaritensis chiricahuae*—Koprowski and Corse 2001), an endemic subspecies restricted to a neighboring mountain range. This diversity likely reflects the large variation in spatial and temporal availability of food items resulting from variable production of food crops.

Rainfall is known to influence production of mast crops (Calama et al. 2008; Koenig et al. 1996; Sork et al. 1993; Zlotin and Parmenter 2008), and rainfall varied significantly in the years prior to and during our study, with lower than average rainfall recorded in 2004, 2005, and 2007. Total rainfall in the growing year prior to acorn production has been suggested to influence acorn yield (Koenig et al. 1996; Zlotin and Parmenter 2008), and larger crop yields for pines, oaks, and junipers have been reported following years with high rainfall (Zlotin and Parmenter 2008). However, seeds of the juniper species in this study, *J. deppeana*, mature in 2 years (Felger et al. 2001), suggesting that rainfall 2 years prior to crop production likely influences current yields. The rainfall patterns observed in our study area conform to these predictions: acorns were consumed more in 2007 and juniper seeds more in 2008, suggesting a higher rainfall in 2006, which was the only recent year prior to our study that recorded average rainfall (Fig. 1). Given this pattern and the below-average rainfall recorded in 2004 and 2005, 2007 was likely the 1st year to display average to high acorn crop production in ≥ 3 years in our study area.

Timing of female reproduction is driven by availability of food resources for a variety of mammals, including bats (Arlettaz et al. 2001), snowshoe hares (O'Donoghue and Krebs 1992), mink (Ben-David 1997), and squirrels (Becker 1993). Female Arizona gray squirrels appear to conform to these patterns by shifting reproductive habits in response to food

availability. Acorns provide among the highest energy return per handling time of a variety of seeds available to tree squirrels (Steele and Koprowski 2001), and walnuts provide a food item high in fat (Smith and Follmer 1972). The consumption of insects has been suggested to provide supplemental food during crop-poor years (Nixon 1970); however, 2007 was not a year of mast crop failure. Instead, insect galls were likely sought out for their high caloric content (Korschgen 1981; Shealer et al. 1999) as observed for other species, such as grizzly bears (*Ursus arctos*) feeding on cutworm moths (*Euxoa auxiliaris*—French et al. 1994; Mattson et al. 1991). We documented Arizona gray squirrels entering estrus between February and early August, with most litters emerging between June and early September. Because female squirrels must demonstrate a positive energy balance before reproducing (Gurnell 1987), females likely did not achieve this level of energy balance prior to the breeding season in 2007 and instead exchanged reproduction in favor of foraging, as seen in our behavioral observations, especially following 2 years of below-average rainfall. Because food availability can influence the onset of the breeding season for squirrels by allowing females to breed earlier in good crop years (Gurnell 1983), the greater use of acorns and insects in 2007 may have provided the energy reserves necessary to maintain better body condition throughout the winter and thus allow more females to reproduce, enter estrus earlier, and produce 2nd litters in 2008. The body mass observed for females supports this conclusion, because females tended to be heavier in 2008, likely as a result of increased food availability and consumption the previous year.

All radiocollared males were reproductively active for at least a portion of each mating season (January–July) throughout the study. However, the proportion of reproductive males differed throughout the year. Contrary to 2008, males were not consistently in reproductive condition among seasons in 2007, when the proportion of scrotal males steadily decreased from spring to winter. Although we were not able to collect reproductive data in winter of 2007, the abbreviated length and late timing of litter emergence suggests that we were still able to accurately capture timing of reproduction for males in 2007. Despite differences in food consumption, males maintained consistent body mass between years, suggesting that food availability was not responsible for this variation in male reproduction. Because males time reproduction in order to maximize reproductive opportunities (Emlen and Oring 1977; Michener 1983), the difference in reproductive behavior between years is likely explained by differences in the timing of estrus for females, because females entered estrus earlier and remained in estrus longer in 2008, effectively increasing the length of the breeding season. This pattern also is reflected in the space use of male Arizona gray squirrels. Males maintain home ranges that are larger than female home ranges throughout the year, likely in response to temporal variation in female reproduction within and among years (Cudworth and Koprowski 2010). Males devote time to seeking and mating with females at the expense of other behaviors, with males in

our study participating in a minimum of 0–6 mating chases per year. However, energetic demands due to reproductive investment are most likely considerably less for males than for females (Clutton-Brock and Harvey 1978; Ostfeld 1985; Trivers 1972). Although males spent a similar amount of time foraging as did females, males spent significantly less time in reproductive activities overall. Consequently, in years when females display prolonged reproductive seasons, the fitness benefits of remaining reproductively active throughout the year may outweigh the energetic costs for male Arizona gray squirrels.

Reproductive timing in Arizona gray squirrels appears to follow the pattern of male reproduction tracking female distribution and receptivity, female reproduction tracking food availability, and food availability tracking rainfall. However, the southwestern United States is currently in a decade-long drought, with drought conditions generally increasing in intensity (Zlotin and Parmenter 2008). Global climate change models predict these drought conditions and extreme rainfall events to continue to increase (Easterling et al. 2000; Intergovernmental Panel on Climate Change 2007; Karl et al. 1995), which may further impact the production of mast crop yields. This has the potential to shift the timing of food availability, both within and among years, potentially uncoupling timing of availability and timing of requirements for food resources (Both et al. 2006; Durant et al. 2007; Visser et al. 1998; Winder and Schindler 2004). Consequently, understanding the relationship between climatic events, such as rainfall, phenology of production of food, and their subsequent impacts on reproduction, is critical when attempting to manage and conserve species.

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