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ANNUAL CYCLES IN BODY MASS AND REPRODUCTION OF ENDANGERED MT. GRAHAM RED SQUIRRELS

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Annual cycles in life-history traits often are interpreted as adaptations. The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) is an endangered species isolated in the Pinaleno Mountains of Arizona (United States) at the southernmost range terminus where the ecology is poorly known. I monitored annual cycles of reproduction and body mass in male and female Mt. Graham red squirrels. Males with scrotal testes were present during all months except October, with a peak in testis size in April. Lactating females were found from April to September. Male body mass was highest in winter and lowest in summer; females did not fluctuate seasonally in mass. Male body mass exceeded that of females during winter and was positively related to size of testes late in the breeding season. Annual cycles in reproduction and body mass of Mt. Graham red squirrels are similar to those of other red squirrels in similar life zones.

Key words: Arizona, body mass, energetics, mating systems, sex differences

In seasonal environments, annual cycles in life-history characteristics are considered adaptations to fluctuating climate and resource availability (Boyce 1988; Nylin and Gotthard 1998; Stearns 1992). Behavioral and physiological changes that occur in seasonal environments include increased communal nesting (Koprowski 1996; Merritt et al. 2001b); scatterhoarding and larderhoarding of foods (Vander Wall 1990); decreased periods of activity, hibernation, and torpor (Geiser 1994, 1998); reduced metabolic rates, decreased food consumption, and modified patterns of fat deposition and body mass (Bozinovic et al. 1990; Lindstedt and Boyce 1985; Rousseau et al. 2003); and changes in morphology of organs (Piersma and Lindstrom 1997). Demography of populations also is seasonal in such environments (Di Bitetti and Janson 2000; Merritt et al. 2001a; Millar 2001). Sex-specific strategies often differ in such seasonal environments, where distinct breeding seasons exist. Male mammals focus on access to mates, which are seasonally available as a limiting resource, whereas females increase reproductive success through enhanced litter size and quality related to food resources (Clutton-Brock and Harvey 1978; Koprowski 1998; Trivers 1972). Tree squirrels are excellent models in which to examine life in seasonal environments and sex-specific strategies that may result (Gurnell 1987; Koprowski 1998; Steele and Koprowski 2001).

Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) are found only in the highest-elevation forests of the Pinaleno Mountains of southeastern Arizona, United States (Hoffmeister 1986; Minckley 1968). The subspecies has been protected as an endangered species since 1987 (United States Fish and Wildlife Service 1993) and numbers remain <600 animals (T. Snow, pers. comm.). Red squirrels in coniferous forests of North America larderhoard large cone stores in conspicuous piles of cone scales known as middens that serve as a primary food source over winter (Finley 1969; Steele 1998). Biology of *T. hudsonicus grahamensis* is poorly known and this has necessitated use of information on other subspecies in conservation and management decisions (Buenau and Gerber 2004; United States Fish and Wildlife Service 1993). To rectify a paucity of data, an intensive livetrapping program was initiated in 2002 to monitor life history and demography of this endangered tree squirrel. These data permit an examination of sex-specific annual cycles of this rare subspecies in light of current theory. Herein, I report on annual cycles of sex-specific reproduction and body mass of endangered Mt. Graham red squirrels.

MATERIALS AND METHODS

Study area.—I studied Mt. Graham red squirrels in approximately 400 ha of mixed conifer and spruce–fir forest above 3,000 m elevation in the Pinaleno Mountains, Graham County, Arizona, near Columbine Visitor Center and Mt. Graham International Observatory. Forests are dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) at highest elevations, with Douglas-fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*) more frequent as elevation decreases (Hutton et al. 2003). Seasonal weather extremes include heavy winter snows from December until April (maximum depth 1992–2003: 156.7 cm ± 22.7 *SE*, range = 57–285 cm) and summer monsoon rains during July through

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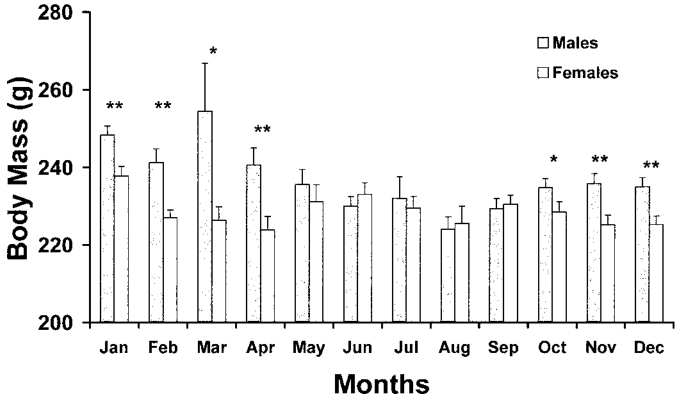

FIG. 1.—Mean body mass fluctuations for adult male and female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains, Arizona, April 2002 to December 2003. Asterisk (*) denotes $P < 0.10$, 2 asterisks (**) denote $P < 0.05$. Sample sizes (males, females): January, $n = 9, 11$; February, $n = 8, 10$; March, $n = 9, 11$; April, $n = 16, 18$; May, $n = 19, 25$; June, $n = 12, 15$; July, $n = 15, 21$; August, $n = 15, 21$; September, $n = 21, 23$; October, $n = 20, 22$; November, $n = 18, 24$; December, $n = 17, 23$.

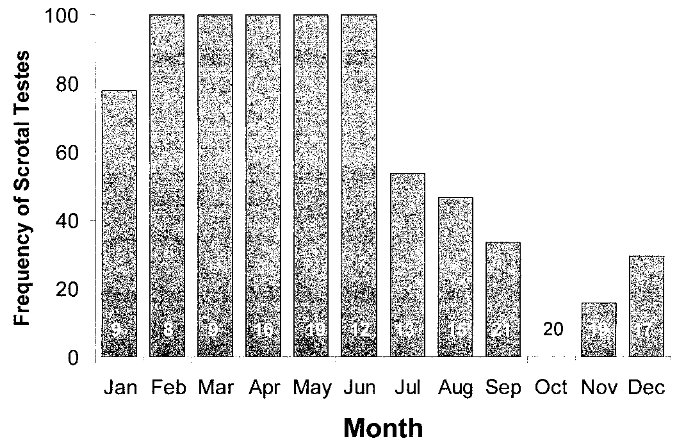

FIG. 2.—Frequency of scrotal testes in adult male Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains, Arizona, April 2002 to December 2003. Value at the base of each bar is sample size.

September (total accumulation 1996–2003: 241.2 mm ± 23.9 *SE*, range = 77.8–438.1 mm).

Live capture and handling.—I trapped *T. hudsonicus grahamensis* at middens each month from April 2002 until December 2003. Collapsible single-door live traps (model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanuts or peanut butter were checked every 2 h during daylight and closed to capture each night. Captured squirrels were transferred to a cloth handling cone (Koprowski 2002) of known mass and weighed ± 5 g with a Pesola spring scale (Baar, Switzerland); individuals were ear tagged with uniquely numbered tags (Monel #1, National Band and Tag, Newport, Kentucky). Reproductive condition was assessed through openings in the handling cone. For males, visual inspection of testis position (abdominal, inguinal, or scrotal) was used; greatest length of scrotal testes was measured ±1 mm. Scrotal testes >15 mm contain viable sperm (Layne 1954). For females, I inspected teats to assess degree of distension, alopecia, and pigmentation (Larsen and Taber 1980); inspected the vulva to determine swelling indicative of estrus (Layne 1954); palpated teats to express milk and confirm lactation; palpated the abdomen to confirm presence of late-term embryos; and palpated the pubic symphysis to assess closure, which indicates recent or impending parturition. Because of the endangered status of *T. hudsonicus grahamensis*, data were collected for only 5 min before I released animals, to minimize duration of restraint. As a result, incomplete data collection occasionally occurred.

Data analyses.—First capture of an animal during a month was used for analyses. Two-sample *t*-tests and analysis of variance (ANOVA) were applied to normally distributed body mass data. Tukey's multiple comparisons were used for post hoc pairwise comparisons. Simple linear regression was used to examine the relationship between testis length and body mass. Because of the endangered status of the study animal, sample sizes are generally small such that values of $P \leq 0.10$ are reported to indicate potential biological significance.

All research was conducted under permit from the University of Arizona's Institutional Animal Care and Use Committee, United States Department of Agriculture Forest Service, Arizona Game and Fish Department, and the United States Fish and Wildlife Service, Endangered Species Office, and in accordance with the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

RESULTS

I captured 70 adult Mt. Graham red squirrels (29 males and 41 females) on 409 occasions by using 1,350 trap nights over 116 days. The sexes differed in body mass at several times throughout the year as well as in seasonality of their annual cycle (Fig. 1). Body mass of females did not demonstrate significant seasonality (ANOVA: $F = 1.12$, *d.f.* = 11, 229, $P = 0.37$); however, male body mass varied over the seasons (ANOVA: $F = 3.36$, *d.f.* = 11, 178, $P \ll 0.01$). Males tend to be heavier in winter with a peak in March, and decline to lowest body mass in fall; male mass in March was greater than from June through September and January body mass also exceeded low August values (all other pairwise comparisons were not significant when using Tukey's multiple comparisons, $T > 4.69$, individual error rate $P = 0.0011$). Males were not lighter than females during any month and were heavier during winter months from October ($t = 1.78$, *d.f.* = 40, $P = 0.083$), November ($t = 3.03$, *d.f.* = 39, $P < 0.01$), December ($t = 3.06$, *d.f.* = 36, $P < 0.01$), January ($t = 3.05$, *d.f.* = 18, $P < 0.01$), February ($t = 3.53$, *d.f.* = 11, $P < 0.01$), March ($t = 2.20$, *d.f.* = 9, $P = 0.056$), and April ($t = 3.02$, *d.f.* = 29, $P < 0.01$) but not different during any other month (all $t < 0.80$, *d.f.* > 23, $P > 0.40$).

Some males possessed scrotal testes during all months of the year except October (Fig. 2). All males were considered reproductively active from February through June, after which a declining number of males with scrotal testes were found in the sample until the end of the year. Testis length differs seasonally (ANOVA: $F = 21.58$, *d.f.* = 10, 83, $P < 0.01$, no data from October when testes were not scrotal), with greatest length reached in April followed by a decline to an autumn low in November (Fig. 3). Mean length of testis did not differ from August to December nor from January to July; however,

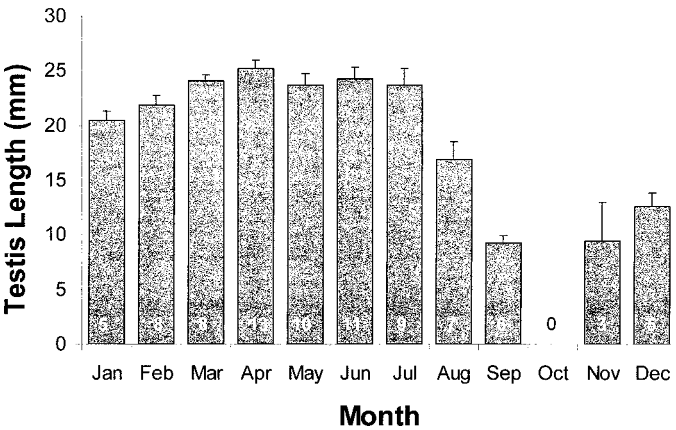

Fig. 3.—Mean maximum length of testes for adult male Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains, Arizona, April 2002 to December 2003. Value at the base of each bar is the sample size for animals with scrotal testes that could be measured.

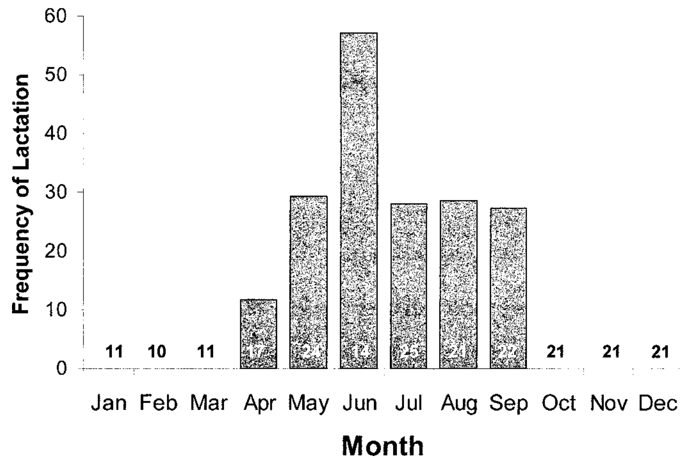

Fig. 4.—Frequency of lactation among female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains, Arizona, April 2002 to December 2003. Value at the base of each bar is sample size of adult females.

these 2 seasons differed from each other (Tukey's multiple comparisons, $T > 4.70$, individual error rate $P = 0.0014$). Size of testes was positively related to body mass only during May and July (May: $F = 7.17$, *d.f.* $= 1, 8$, $P = 0.032$, $R^2 = 43.5\%$; July: $F = 7.46$, *d.f.* $= 1, 8$, $P = 0.029$, $R^2 = 44.7\%$; June: $F = 3.26$, *d.f.* $= 1, 8$, $P = 0.11$, $R^2 = 22.0\%$: all other months $F < 1.57$, $P > 0.24$; Fig. 3). Note that May also is the putative peak in female receptivity at about 33 days before the peak in lactation (Ferron and Prescott 1977; Lair 1985; Fig. 4) and similar to the peak in testis size (Fig. 3). Lactating females were 1st found in April, with the prevalence of lactation peaking in June and declining until September; no lactating females were found from October to March (Fig. 4).

Discussion

Female body mass did not increase during winter in advance of spring and summer pregnancy and lactation nor did body mass decline significantly after the reproductive season. A lack of seasonality in female body mass has been noted in more northerly populations of red squirrels (Wood 1967; Zirul and Fuller 1970). Because nearly all female *T. hudsonicus grahamensis* reproduced, lack of seasonality is not confounded by including females of different reproductive classes. Seasonality in male body mass was similar to that reported for other populations of red squirrels with peaks in winter (Layne 1954; Wood 1967). A difference in body mass between the sexes at about 4–10% during winter months is nearly identical to that found in northern populations (Boutin and Larsen 1993). Annual fluctuations in male body mass suggest a peak in winter after testicular recrudescence, suggesting that males but not females may increase fat stores in anticipation of breeding, which involves considerable range expansion and exploitative and interference competition (Arbetan 1993; Koford 1982; Smith 1968).

Seasonality of reproduction for both male and female Mt. Graham red squirrels was similar to that of other populations in coniferous forests of northern and western North America (Steele 1998). Lactating females are reported in red squirrel populations from February to October (Becker 1993; Dolbeer 1973; Ferron and Prescott 1977; Hamilton 1939; Koford 1982; Lair 1985; Layne 1954; Millar 1970; Modafferi 1972; Rusch and Reeder 1978; Smith 1965; Zirul and Fuller 1970). Although eastern populations of red squirrels may show 2 peaks in reproduction (Hamilton 1939; Klugh 1927; Lair 1985, Layne 1954; Linzey and Linzey 1971; Wrigley 1969), red squirrels typically have a single reproductive season focused in late spring or early summer (Davis 1969; Dolbeer 1973; Gurnell 1987; Hatt 1929; Kemp and Keith 1970; Millar 1970; Modafferi 1972; Rusch and Reeder 1978; Smith 1968). Males with scrotal testes have been reported in populations during all months of the year, with a late summer–autumn period of testicular recrudescence as seen on Mt. Graham (Davis 1969; Layne 1954; Modafferi 1972; Rusch and Reeder 1978). Concordance of results of these studies is remarkably high and suggests that seasonality of reproduction in this endangered population of squirrels does not appear to differ from the reproductive ecology of the species in similar life zones.

Because red squirrels are typically solitary and territorial, males must assess status of reproductive females from a distance (Arbetan 1993; Koford 1982; Koprowski 1998; Smith 1968). Female eastern gray squirrels attract more attention from males about 5 days before estrus (Thompson 1977). Home ranges of male tree squirrels of many species are significantly larger than those of females; however, this trend does not appear to hold for most populations of red squirrels (Koprowski 1998). In a number of vertebrates, testis size is related to body mass and often is indicative of male reproductive success (Dunn et al. 2001; Evans and Goldsmith 2000; Millesi et al. 1998; Schulte-Hostedde and Millar 2004). On Mt. Graham during periods of peak reproductive activity of females, testis size is strongly related to body mass, suggesting potential for sperm competition ultimately to drive the cycle of testicular recrudescence and size of testes. Red squirrel mating behavior involves a scramble competition component because males must locate asynchronously estrous females during the breeding season and an interference competition component where males vigorously compete for access to females (Arbetan 1993; Koford 1982; Smith 1968). Testes in other species of squirrels are generally significantly larger than expected based upon body size, in apparent relation to their promiscuous mating system (Kenagy and Trombulak 1987).

Despite an extended period of isolation of perhaps 7,000–10,000 years (United States Fish and Wildlife Service 1993) on the southernmost portion of the species' range, the annual cycle of reproduction and body mass of endangered Mt. Graham red squirrels is similar to that reported for other subspecies. The divergence in body mass during winter, with males increasing in body mass before the breeding season suggests that this may be a tactic to prepare for greatly expanded home ranges, increased movement, and decreased feeding that characterize male tree squirrels during the breeding season (Koprowski 1998; Steele and Koprowski 2001). Annual cycles in body mass and reproduction must be considered in the formulation of informed strategies for the management and conservation of the endangered Mt. Graham red squirrel.

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