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COMMUNAL DENNING OF CLIFF CHIPMUNKS (*TAMIAS DORSALIS*)

ALLYSSA L. KILANOWSKI* AND JOHN L. KOPROWSKI

School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721-0001 (ALK, JLK)

Present address of ALK: Department of Biology, University of Kentucky, Lexington, KY 40506-0225

**Correspondent: allyssa.kilanowski@gmail.com*

ABSTRACT—Rodents are a diverse group that display a range of social systems. Cliff chipmunks (*Tamias dorsalis*) are documented as solitary across their range; however, we report here observations of communal denning outside of the breeding season in southeastern Arizona. We radiocollared and tracked nursing females and their offspring to locate nocturnal dens from June to October 2013 and 2014. We observed codenning in juvenile siblings, and juveniles and adults. Our social denning observations indicate that cliff chipmunks demonstrate behavioral plasticity.

RESUMEN—Los roedores son un grupo taxonómico diverso que incluye una amplia gama de sistemas sociales. Las ardillas rayadas de barranca (*Tamias dorsalis*) son documentadas como solitarias a través de su área de distribución, sin embargo aquí reportamos observaciones de las ardillas ocupando madrigueras comunales fuera de la temporada de reproducción en el sureste de Arizona, EE.UU. Colocamos collares transmisores y rastreamos a las hembras lactantes y a sus crías para localizar madrigueras nocturnas desde junio hasta octubre del 2013 y 2014. Observamos anidación conjunta entre hermanos juveniles y entre juveniles y adultos. Nuestras observaciones de las madrigueras comunales indican que las ardillas rayadas de barranca demuestran plasticidad de comportamiento.

Rodents (Mammalia: Rodentia) are a diverse taxonomic group that displays a range of social systems from highly territorial and solitary (Rayor and Armitage, 1993; Wolff and Sherman, 2007) to dense, highly social aggregations (Hoogland, 1981; Rayor and Armitage, 1993; Wolff and Sherman, 2007). Previous explanations for the evolution of sociality focused on generating hypotheses for highly social

species and testing those same hypotheses within similar or the same species (Ebensberger, 2001). By examining species within the middle of the sociality continuum in conjunction with species at the extremes of the continuum, we can test alternative hypotheses because these moderately social species are intermediate forms (Ebensberger and Blumstein, 2006; Flores-Prado, 2012).

Rodents have been the focus of many studies of social evolution, but most of this research has focused on ground squirrels (subfamily Xerinae; Ebensperger, 2001; Armitage, 1999) and tree squirrels (subfamily Sciurinae; Koprowski, 1996; Edelman and Koprowski, 2005; Williams et al., 2013; Selonen et al., 2014). Within Sciuridae, the genus *Tamias* has been documented as asocial and solitary (Snyder, 1982; Hart, 1992; Best, 1993a, 1993b; Best and Granai, 1994; Burt and Best, 1994; Clawson et al., 1994). Herein, we report observations of communal denning in the cliff chipmunk (*Tamias dorsalis*) on Mt. Graham in the Pinaleno Mountains in southeastern Arizona, and we propose that further investigation of these observations could provide insight into the evolution of sociality.

The cliff chipmunk is a granivorous rodent that ranges from Mexico to Utah, with populations as far east as New Mexico and west into Nevada (Hart, 1992). Although this species is considered fossorial, the Mt. Graham population has been documented climbing trees to forage (often stealing food that was cached by the Mt. Graham red squirrel, *Tamiasciurus hudsonicus grahamensis*; Edelman et al., 2005), nesting in tree cavities, and using tree cavities for maternal nests (Hoffmeister, 1956, pers. observ.). The female chipmunk home range averages 0.8 ha (Hart, 1976) and likely this value differs among the sexes, but there is no information on male home range size (Hart, 1992). Juveniles disperse about a month after emerging from the maternal nest, June–August (Hart, 1992). Female-biased sexual dimorphism is prevalent in the genus *Tamias* (Levenson, 1990), and the size difference of male and female adult cliff chipmunks is generally 10% (Levenson, 1990; Hart, 1992). The population on Mt. Graham has females that are, on average, 11% larger than males (pers. obser.).

Our study was conducted in 200 ha of mixed conifer forest above 3,000 m on Mt. Graham, an isolated 3,267-m peak in the Pinaleno Mountains, Graham County, Arizona (2°42'5.87"N, 109°52'18.87"W). The dominant trees are Douglas-fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strobiformis*), and corkbark fir (*Abies lasiocarpa* var. *arizonica*), mixed with Engelmann spruce (*Picea engelmannii*), aspen (*Populus tremuloides*), and ponderosa pine (*Pinus ponderosa*, Sanderson and Koprowski, 2009). Climate is highly seasonal (Koprowski, pers. observ.) with temperature lows in December and January (2013: –20.8°C, 2014: –16.4°C) and temperature highs during June and July (2013: 25.6°C, 2014: 24.7°C). Rainfall occurred from May to September (monthly average and range, 2013: 52.76 mm, 0–132.2 mm; 2014: 36.96, 0–114.8). Snowfall occurred from December to April (average accumulated depth, 2013: 0.0–78.0 cm; 2014: 0.0–42.0 cm).

From May to October 2013 and 2014, we used 7.62 × 8.89 × 22.86 cm large folding galvanized Sherman traps (H.B. Sherman Traps, Tallahassee, Florida) to capture 237 unique adults and 36 unique juveniles for a total of

1,121 total captures (approximately 7.56 animals captured per trap session). We marked individuals with ear tags (Monel #1, National Band & Tag, Newport, Kentucky) and colored washers, and recorded reproductive status and mass. We collared (SOM 2070, Wildlife Materials, Murphysboro, Illinois) 11 nursing females and 17 juveniles (2 males, 15 females). We used radiotelemetry to locate female dens before juveniles first emerged (median: one den per month; range: one to four den locations per month) and we used observations to determine the first emergence of juveniles from the den (20 total observations, average duration of 102 min). To determine if radiocollared animals were sharing a den, we used homing to locate the nocturnal den of mothers and offspring (median: one den location per month, range: one to three den locations per month), and we observed maternal and juvenile dens multiple days at sunrise throughout the year to count the individuals sharing a den in case there were nonradiocollared individuals sharing a den (37 observations, average duration of 98 min). We observed different dens each day, but did observe some dens on consecutive days. Dens only were observed if we tracked an individual to that location or if we were attempting to locate an individual with a radiocollar that had ceased to work. Former dens of radiocollared individuals were not observed after an individual moved to a new den.

We only were able to capture juveniles for 8 of the 11 nursing females. From juvenile nest emergence through dispersal, we observed 13 instances of communal denning and 8 instances of solitary denning (16 observations were unable to see chipmunks emerge from a den). We observed one instance of two adults (one nursing female, one unknown sex) denning with three juveniles (one female, two unknown sex) during nursing. During juvenile dispersal, we observed two instances of juveniles and their mother sharing a den (group size range including adult female: three to five individuals). One of these events included a male juvenile in the codenning group; the other group contained only females. Juvenile siblings denned together after dispersal from the maternal nest six times (2013: four individuals, 2014: two individuals). Group size of codenning juveniles averaged 2.6 individuals (range: two to three individuals) and included both males and females. After dispersal, we observed four instances of juveniles returning to share a den with their mother; however this was only observed with all female groups.

Dispersal occurred approximately from July to August, the warmest months at our study area (range, monthly minimum: 5.8–7.7°C; monthly maximum: 19.8–24.7°C). During the fall, juveniles continued to den communally with other juveniles and with adults. The observations of female juveniles returning to den with their mother occurred in August and September (range, monthly minimum: 4.2–6.8°C; monthly maximum: 18.7–20.4°C).

We were unable to follow individuals until hibernation because of radiocollar life so we have no evidence of communal denning during winter.

This is the first reported observation of communal denning in cliff chipmunks, which have been described as territorial near the main den, but social away from the main den, with the territorial distance varying by individual (Hart, 1992). Our observations indicate that this territoriality is relaxed in the Mt. Graham population, with siblings of both sexes and mothers sharing a den throughout the summer season and female siblings and mothers sharing a den during the fall. Communal nesting of chipmunk mothers and offspring is not uncommon during the dependent period (Snyder, 1982; Best, 1993a, 1993b; Best and Granai, 1994; Burt and Best, 1994; Clawson et al., 1994); however, the extension of communal denning after weaning is uncommon. It is possible that communal denning in *T. dorsalis* is common and the species is not well studied. Another possibility is that the climate on Mt. Graham promotes communal denning behavior.

Our social denning observations might indicate that cliff chipmunks on Mt. Graham are a behavioral transition between social and asocial species and display considerable variation in social behavior (Lott, 1991). Mechanisms proposed to explain communal nesting outside the mating season include thermoregulation (Williams et al., 2013), kin selection (Clutton-Brock et al., 2001), reduced predation (Ebensperger et al., 2012), mate guarding (Selonen et al., 2014), limited nest and den sites (Johnson et al., 2005), or information sharing (Dall, 2002). These mechanisms are not mutually exclusive and future research on chipmunk communal denning could test hypotheses about these mechanisms leading to the evolution of social behavior. A genetic analysis of codenning individuals could determine if groups of individuals are closely related. More research is needed to determine the location of *T. dorsalis* along the continuum of sociality, but this species provides a unique opportunity to test hypotheses on the evolution of sociality.

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SEASONAL CIRCADIAN RHYTHM SHIFT AND LUNAR CHRONOBIOLOGY OF THE NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*)

ERIC N. GREEN,* DANA M. GREEN, SEAN P. MAHER, AND LYNN W. ROBBINS

Department of Biology, Missouri State University, Springfield, MO 65897

**Correspondent: EG.Biology@gmail.com*

ABSTRACT—Nine-banded armadillos (*Dasypus novemcinctus*) are nocturnal, semifossorial, insectivorous mammals that historically live in warm climates but have been moving northward over the past 150+ y. As armadillos move into more-temperate climates, behavioral adjustments occur in response to decreasing temperatures. Observations in northern latitudes have noted more activity during the daytime in the winter, indicating a shift in circadian rhythm. Such behavioral plasticity may allow individuals to forage when temperatures are optimal for thermoregulation. We recorded armadillo activity for 6 mo using game cameras. We created nocturnal, crepuscular, and diurnal activity indices and then plotted them as a function of time. We compared temperatures of when armadillos were photographed to temperatures when other animals were photographed. Analyses suggest that a seasonal shift in circadian rhythm does occur and that air temperature is an important factor. Although armadillos have previously been reported to have lunar phobia, we saw no evidence of this.

RESUMEN—Los armadillos de nueve bandas (*Dasypus novemcinctus*) son mamíferos semi-fosoriales, nocturnos, insectívoros, que viven históricamente en climas cálidos, pero se han estado trasladando hacia el norte a lo largo de los últimos 150 años más o menos. Mientras armadillos se trasladan hacia climas más templados, los ajustes de comportamiento se producen en respuesta a la disminución de las temperaturas. Las observaciones en las latitudes del norte han registrado una mayor actividad durante el día en el invierno, lo que indica un cambio en el ritmo circadiano. Dicha plasticidad de comportamiento puede permitir que los individuos se alimenten cuando las temperaturas son óptimas para la termorregulación. Registramos la actividad de armadillos por seis meses usando cámaras de vida silvestre. Calculamos índices de actividad nocturna, crepuscular, y diurna, y después los graficamos como una función del tiempo. Comparamos las temperaturas cuando los armadillos fueron fotografiados a las temperaturas cuando fueron fotografiados otros animales. Los análisis sugieren que un cambio estacional en el ritmo circadiano sí se produce, y que la temperatura del aire es un factor importante. Aunque se ha dicho previamente que los armadillos tienen fobia lunar, no vimos ninguna evidencia de esto.

The nine-banded armadillo, *Dasypus novemcinctus*, is the only mammal in the family Dasypodidae in the United States. Over the past 150 y, its range has expanded greatly, encompassing much of the southeast and central United States (Taulman and Robbins, 1996, 2014; Van Dellen et

al., 2002). This expansion has been promoted by many factors such as decreased hunting by humans, natural barriers either being removed or bypassed, and roads acting as dispersal corridors (Taulman and Robbins, 1996, 2014; Feng and Papeş, 2015).

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