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Cover: Coromandal Sacred Langur *Semnopithecus priam* - made with acrylic paint. © P. Kritika.



Observations of Gray Fox *Urocyon cinereoargenteus* (Schreber, 1775) (Mammalia: Carnivora: Canidae) denning behavior in New Hampshire, USA

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Abstract: Dens are important for mammals because they provide protection for dependent young from weather and predators. Gray Foxes *Urocyon cinereoargenteus* are an understudied mesocarnivore that range across North and Central America, and have limited information available on demographics and denning behaviors. We monitored a Gray Fox den in New Hampshire over the course of three years (2017–2020) to quantify behaviors and document visitation and activity patterns of Gray Foxes and other mammal species. We observed Gray Fox pairs intensively using the den during parts of the first and second years of the study. Across the 949 trap nights over which we monitored the den, use by adult Gray Foxes peaked in spring – coinciding with the pup-rearing season. During this time, the adults were diurnal with peaks in the afternoon, opposed to being crepuscular at other times of the year. We did not observe any puppies during the first breeding season, but during the second year we documented a puppy emerging from the den on 24 May 2018. All excursions by the puppy outside the den for the first five days were restricted to the immediate area near the den entrance and the puppy was always with an adult when outside the den. During the puppy's second solo excursion, however, we documented a Bobcat *Lynx rufus* pounce and kill the puppy, after which the adults abandoned the den. We also observed the common (squirrels and rabbits) and uncommon (a bat) prey items brought to the den, and the den being shared among multiple species. Our observations highlight the importance of dens for protecting young, and our observations of visitation and activity patterns, as well as common and uncommon prey, help inform our understanding of the denning behavior of Gray Foxes.

Keywords: Activity patterns, den, mammal, neonatal, predation, prey.

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INTRODUCTION

Dens are important for mammals as a means to protect the dependent young from weather and predators. Most canids primarily use dens (generally holes dug in the ground) for raising young, and while they may visit den sites throughout the year, activity often peaks from mid-winter to early summer (Egoscue 1956; Chesemore 1969; Uraguchi & Takahashi 1998). During this period, the pair bonds are often the strongest and the mating pair act as central place foragers, which exhibits itself as the pair often making foraging forays away from the den and returning with food (Nicholson et al. 1985; Way et al. 2001; Allen & Moll 2023). Behaviors at the den are often difficult to observe, and while there are many studies on canid den selection, there are fewer studies documenting behaviors at dens (but see Way et al. 2001; Elbroch & Allen 2013; Mukherjee et al. 2018).

Gray Foxes *Urocyon cinereoargenteus* are an understudied mesocarnivore that ranges across North and Central America (Allen et al. 2022), and has limited information available on demographics and denning behaviors (Allen et al. 2021). The breeding cycle is generally thought to be from January through April, with later dates in more northern areas (Sheldon 1949). The exact gestation period is unknown and is often estimated as the same 53 days as Red Foxes *Vulpes vulpes* (Sheldon 1949). Litter size ranges from one to six, with averages of three to four puppies (Sheldon 1949; Sullivan 1956; Wood 1958; Weston & Brisbin 2003; Glenn et al. 2009). While Gray Foxes were traditionally thought to be monogamous, more recent research shows that up to half of the litters exhibit multiple paternity (Glenn et al. 2009).

Gray Fox dens can be in all areas, including ground dens, cavities among rock piles or ledges, brush piles, under buildings, and hollow logs (Sullivan 1959; Nicholson et al. 1985). However, the use of dens appears to vary based on the stage of puppy rearing, with only underground dens used during the weaning period, but hollow logs used during whelping and nursing periods (Nicholson et al. 1985). Female movements are similarly restricted by rearing stage, with movements greatly reduced during whelping and nursing stages (Nicholson et al. 1985). Given that Gray Foxes are often associated with forested habitats (Allen et al. 2021, 2002), it is likely that den sites are often selected in forested areas similar to Red foxes (Uraguchi & Takahashi 1998). However, Gray Foxes prefer denning among denser cover and closer to water sources (Sullivan 1959).

We monitored a Gray Fox den in New Hampshire

over three years to quantify behaviors and document visitation patterns of Gray Foxes and other species. We calculated the relative abundance for all species using the den and the relative abundance, temporal patterns, and duration of visits for Gray Fox adults and puppies. We also documented predation of a puppy and prey items brought to the den by adult Gray Foxes.

MATERIALS AND METHODS

Study Area

We monitored a Gray Fox den in a mixed forest area on private land in Strafford County, New Hampshire (43.114, -70.918). Common tree species surrounding the den site include Eastern White Pine *Pinus strobus*, Northern Red Oak *Quercus rubra*, Red Maple *Acer rubrum*, American Elm *Ulmus americana*, and Black Birch *Betula lenta*. The surrounding area is a low-density suburb consisting of generally wooded lots, with a number of adjacent undeveloped conservation properties owned by municipal, state, and non-profit landowners. Temperatures in the area reach wintertime lows below 0°C and summertime highs above 25°C. Rainfall is moderate and relatively consistent throughout the year, with monthly lows of approximately 70 mm in the winter and around 100 mm in the spring and fall, but overall precipitation is highest in the winter due to monthly snowfall that can exceed 300 mm. Mammal species in the area are typical of the northeastern USA, including Black Bears *Ursus americanus*, Bobcats *Lynx rufus*, Coyotes *Canis latrans*, Fishers *Pekania pennanti*, Raccoons *Procyon lotor*, Red Foxes, Striped Skunks *Mephitis mephitis*, Virginia Opossums *Didelphis virginiana*, White-tailed Deer *Odocoileus virginianus*, and Woodchucks *Marmota monax*.

Field Methods

We first sighted a Gray Fox traversing the property and entering the den in early February 2017, and again in early April 2017. Following the second sighting, we set up a camera trap to monitor the presence and activity of Gray Foxes and other species. We used a Browning Recon Force (Model no. BTC-7FHD; Birmingham, AL, USA) to record a burst of four images with two seconds between images when triggered, with a 1-minute delay between bursts. We ran the camera trap continuously from 13 April 2017, until 7 March 2020, with brief and infrequent gaps in coverage due to dead batteries. The camera trap was mounted on a nearby tree 55 cm off the ground and approximately 4.2 m from the den entrance.

The field of view was approximately 5 m wide by 2.5 m high, and centered on the den entrance.

We observed Gray Fox pairs intensively using the den during parts of the first and second years of the study, but not during the third year (after which we ended the study). The den was situated on a well-drained slope alongside a poorly drained and seasonally flooded gully adjacent to several residential properties. Near-surface and emergent granitic bedrock creates a variety of ledges, crevices, and other structures along the slope. We could only confirm one entrance to the den, although its interior structure is unknown and it is possible other entrances might exist along the rocky ledge.

Statistical Analyses

We used program R version 4.2.2 (R Core Team 2022) for all statistical analyses. We calculated relative abundance (RAB) on a monthly scale as:

$$\text{RAB} = \text{visits} / \text{trap nights}$$

to quantify the average number of visits per day for each species, as well as gray fox adults and puppies. We calculated the duration of visits to the nearest minute and calculated a monthly average.

We used kernel density estimation to quantify temporal activity patterns (Ridout & Linkie 2009). Our two comparisons were the overlap between adults and puppies during the period when the puppy was active outside of the den (24 May 2018 to 30 May 2018), and the overlap between adults during times when they were intensively using of the den (April and May during 2017 and 2018) versus their use during the rest of the year. We used the time each visit started as our values, after changing the time of each visit to radians that corresponded to sun time. We then used the 'overlap' package (Meredith & Ridout 2017) to fit the data to a circular kernel density. We estimated the activity among time periods from the kernel density distribution. For our first comparison, we used \hat{D}_1 due to small sample sizes, and in the second comparison, used \hat{D}_4 .

RESULTS

Across the 949 trap nights we monitored the den, we documented 27,072 photos, representing 3,205 independent visits by animals. During the first year, the presumptive female (based on smaller size) was distinctive by having a thin, uneven, and light-colored coat with minimal characteristic markings. We observed the pair immediately and consistently following

installation of the camera trap on 13 April 2017, through 26 May 2017 (Figure 1a). Thereafter, the Gray Foxes were observed only occasionally near the den entrance and presumably had vacated the den. We did not observe any puppies during the first breeding season.

After the den was vacated in May 2017, a pair of Gray Foxes began visiting and using the den periodically from October 2017 through March 2018, before taking up regular residence again in April 2018 (Figure 1a). Both animals had more typical coats and markings, suggesting that either the presumptive female from the first year had matured or regained health, or that one or both individuals were different from those that had used the den the previous spring.

During the second year of observation, we first documented a puppy emerging from the den on 24 May 2018. For the first five days, the movement of the puppy was restricted to the immediate area near the den entrance and the puppy was always with an adult when outside the den. We never documented more than one puppy, and we assume all observations were of the same individual. Overall, this encompassed a total of 27 visits with an average duration of 21.9 minutes per visit. The puppy was most active in the afternoons (Figure 2a), and during this time the activity of adults was nearly a perfect mirror for activity of the puppy ($\hat{D}_1 = 0.95$).

On 29 May at 0451 h, the puppy made its first solo excursion outside of the den, spending less than one minute outside alone. On 30 May, the puppy emerged for its second solo excursion at 0215 h and explored around the den entrance until 0225 h, when we documented a Bobcat pounce and kill the puppy (Image 1). This was the first visit we documented by a Bobcat since 9 May 2017. But the Bobcat returned again twice on 30 May 2018 at 0253 h and 0322 h, both times appearing to search around the den, with follow up visit on 01 and 02 June 2018.

Overall, use of the den by adult Gray Foxes peaked in spring, coinciding with the breeding and pup-rearing season (Figure 1a). Use of the den became more frequent each year in November, but was substantially more frequent in April and May (Figure 1a). However, after Bobcat predation of the puppy in May 2018, there was little activity at the den, with a few visits in January, February, and March 2019 but no visits in any other months. During the two months that adult foxes were actively using the den (April and May), they were most active during the daytime, with peaks in the afternoon (Figure 2b). At other times of the year, the activity of adult Gray Foxes was strongly crepuscular.

We documented adults returning to the den with 51

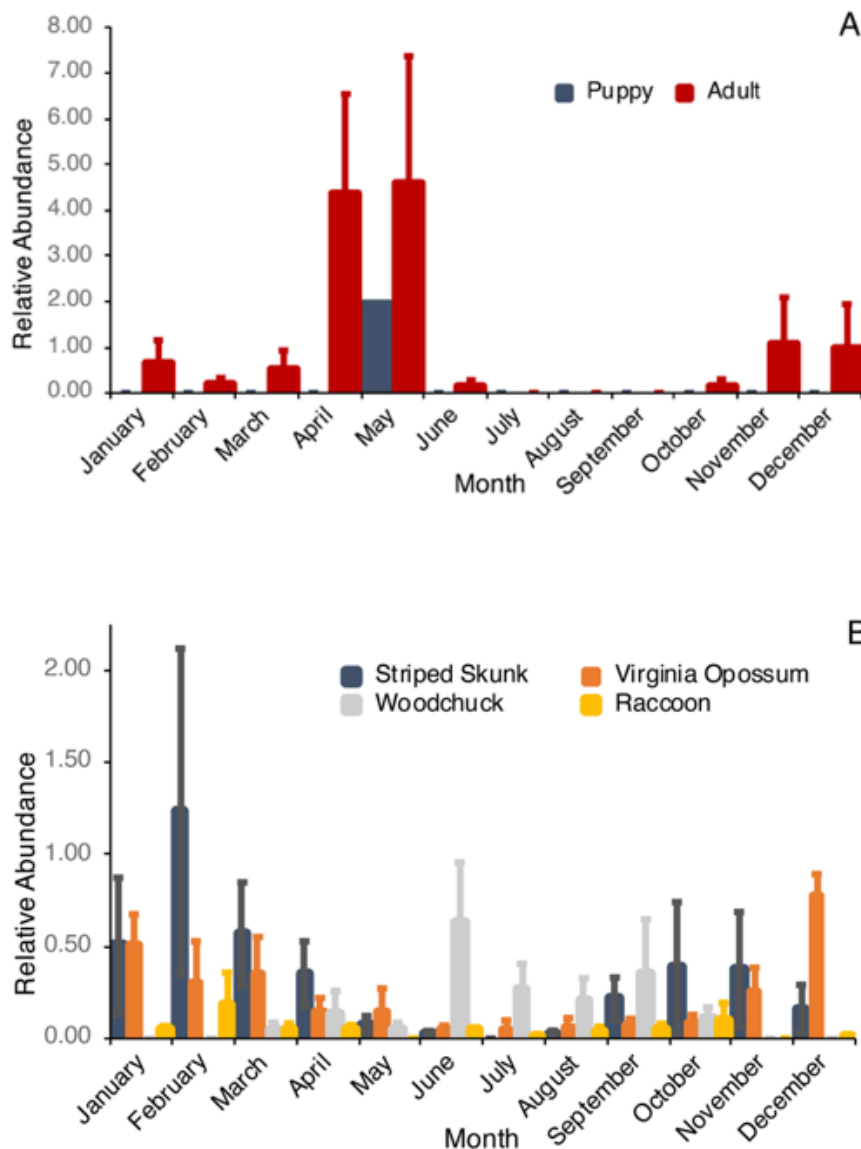


Figure 1. The relative abundance (visits per trap night) by month for: A—Gray Foxes (adults and puppy) | B—other species that also use the den (Raccoon, Striped Skunk, Virginia Opossum, and Woodchuck).

prey items. Most of the prey items ($n = 35$) were not identifiable in the photographs. The most common prey we could identify was Eastern Gray Squirrels *Sciurus carolinensis* ($n = 12$) followed by Eastern Cottontails *Sylvilagus floridanus* ($n = 3$). The other notable prey item that we observed was a bat of indeterminate species (Image 2).

Besides Gray Foxes ($n = 1,029$ visits), we documented visits by multiple species that also used the den, including Striped Skunks ($n = 316$), Virginia Opossums ($n = 207$), and Woodchucks ($n = 140$). Skunks and opossums used the den more frequently in the winter, presumably for protection from the weather, whereas Woodchucks more frequently used the den in summer and fall prior

to hibernation (Figure 1b). Notably, we observed Gray Foxes, skunks, opossums, and Woodchucks using the den close in time to one another, reflecting den-sharing among these species. We also documented other carnivores near the den site including Domestic Dog *Canis lupus familiaris* ($n = 51$), Northern Raccoon ($n = 44$), Domestic Cats *Felis catus* ($n = 20$), Bobcats ($n = 14$), Coyotes ($n = 5$), Red Foxes ($n = 5$), Long-tailed Weasels *Neogale frenata* ($n = 2$), and a Fisher ($n = 1$). We also documented other mammals, the most frequent of which included Eastern Gray Squirrels ($n = 731$), Eastern Chipmunks *Tamias striatus* ($n = 454$), and White-tailed Deer ($n = 79$).

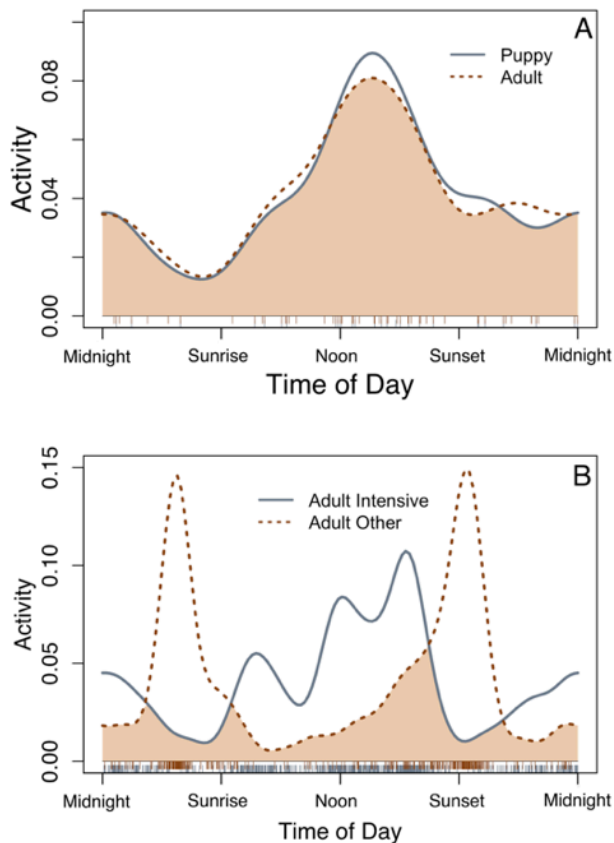


Figure 2. The activity patterns of gray foxes at the den site, adjusted to sun time. **A**—comparison of the activity of the puppy and adults in the period the puppy was active outside the den | **B**—comparison of the activity of adults during their intensive use of the den (April and May) and the rest of the year.

DISCUSSION

We documented Gray Foxes acting as central place foragers and using the den as their focal area of activity. The use of the den by Gray Foxes in the first and second year of monitoring peaked in April and May, which coincides with the birthing season. We first documented a puppy emerging from the den on 24 May in the second year, and this was approximately the same time the den was vacated during the previous year although we did not observe any puppies during the first year. This could have been due to the female being immature or ill (e.g., mange), the pair moving to a new birthing den, or the puppies dying in the den before emergence. After the puppy was killed by the Bobcat in the second year, the adults vacated the den and did not use it again the following year.

Our observations highlight the importance of using dens for protecting young. Initially the Gray Fox puppy was using the area outside of the den in the company

of a parent, with the activity patterns of the parents mirroring that of the puppy. This protection is helpful because parents can signal danger to young (in which case young can retreat into the den) and also potentially fight off other predators. When puppies are outside of the den in the absence of parents, they are likely more prone to predation and the second time we observed the puppy by itself outside of the den it was killed by a Bobcat. The typical survival rates of juvenile Gray Foxes (0.34) are often half that of adults (0.77) (Farias et al. 2005), with predation being a common source of mortality for Gray Foxes. Predation is most often attributed to Coyotes (Weston & Brisbin 2003; Farias et al. 2005), although Bobcat predation has also been documented (Farias et al. 2005), along with legal harvest, vehicle collisions, and disease (see review in Allen et al. 2021). While Gray Foxes are well known for their ability to climb trees to escape predation, puppies are unlikely to be coordinated enough to climb trees, emphasizing the importance of the den for safety.

Adult Gray Foxes are thought to leave dens for short (~ one hour) hunting forays at crepuscular times to hunt for food (Nicholson 1985). Although we found that Gray Foxes were crepuscular at most times of year, they tended to be diurnal during times they were intensively using the den (Figure 2b). We did not distinguish between behaviors like sunning themselves outside of the den and hunting forays, and these behaviors may occur at different times of day. We did document adults frequently returning to the den with prey items, with larger prey (such as squirrels and cottontails) and distinctive prey (bats) easier to identify. The bat is notable because the scavenging of bats can lead to the transmission of rabies (Theimer et al. 2017) and bringing a bat back to the den increases risk for the entire family. It also raises the question of how the Gray Fox acquired the bat. Eight species of bats reside in New Hampshire, several of which roost primarily or opportunistically in trees where Gray Foxes may hunt, but Gray Foxes are also known to scavenge bats (Theimer et al. 2017). Young animals need large quantities of food, so parents likely bring whatever food is available back to the den. While Gray Foxes often focus on common prey (e.g., squirrels, small rodents, and rabbits), they have been documented bringing prey back to the den ranging from Banana Slugs *Ariolimax columbianus* to deer (Elbroch & Allen 2013).

In addition to our detailed observations of Gray Fox behavior, we also documented interspecific den-sharing among different combinations of Gray Foxes, Striped Skunks, Virginia Opossums, and Woodchucks.



Image 1. Documentation of Bobcat *Lynx rufus* predation on a Gray Fox puppy, during the puppy's second solo excursion outside of the den.



Image 2. Gray Fox returning to den with a bat, an uncommon prey species.

Den-sharing entails trade-offs between costs such as competition for space and increased pathogen exposure, and benefits such as information sharing and

thermoregulation (Zeus et al. 2017). The balance of these trade-offs will vary among the species in question and might not be reciprocal. For example, Cape Ground

Squirrels *Xerus inauris*, Suricates *Suricata suricatta*, and Yellow Mongooses *Cynictis pencilatus* commonly share burrows in Namibia (Waterman & Roth 2007). Ground Squirrels benefit from warning vocalizations by Suricates, but are at risk of predation on their juveniles by Yellow Mongooses. Both Suricates and Yellow Mongooses benefit from aggressive predator mobbing behavior by Ground Squirrels. Bats can preferentially select roosts occupied by conspecifics or heterospecifics due to the information conveyed about habitat quality (Zeus et al. 2017). However, den-sharing among different species of Spiny Lobsters *Panulirus* spp. and Moray Eels *Gymnothorax* spp. in shallow, tropical marine systems might be driven by habitat limitation rather than any clear costs or benefits of cohabitation (Lozano-Álvarez et al. 2007; Lozano-Álvarez et al. 2010). The extent to which den-sharing among the species observed in this study represents costs-benefit trade-offs or habitat limitation (i.e., lack of ideal dens) is unclear but may affect the activity and conservation of these species.

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