2013

Den attendance patterns in swift foxes during pup rearing: varying degrees of parental investment within the breeding pair

Sharon A. Poessel
Utah State University, sharpoes@gmail.com

Eric M. Gese
Utah State University, eric.gese@usu.edu

J Ethol (2013) 31:193–201
DOI 10.1007/s10164-013-0368-y

ARTICLE

Den attendance patterns in swift foxes during pup rearing: varying degrees of parental investment within the breeding pair

Sharon A. Poessel · Eric M. Gese

Received: 27 October 2012 / Accepted: 7 February 2013 / Published online: 27 February 2013

Abstract Parental investment varies in mammalian species, with male care of young being more common in social and monogamous species. Monogamy is commonly observed in canid species, with both males and females, and often "helper" individuals, providing some degree of care for the young. Social units of the swift fox (*Vulpes velox*), a small North American canid species, usually consist of a male–female pair and occasionally helpers. The role of parental investment and behavior in swift fox society is currently poorly understood. We observed swift fox dens during the pup-rearing season in each of 2 years to evaluate attendance and frequency of visits to natal dens by adult males and females. Female foxes remained at dens longer and visited them more frequently than did male foxes. Female attendance and visitation decreased throughout the pup-rearing season as pups became older and more independent. Environmental factors, including climate and its effect on prey, appeared to contribute to differences in fox behavior between the 2 years. We observed only one fox outside of the breeding pair attending a den in each of the 2 years, both of which were males. We concluded that each of these two foxes were living within the social unit of the male–female pair as a trio, but not serving as a helper and contributing to the care of the pups. Our results increased knowledge of the ecology and behavior of the swift fox, a species of conservation concern in the Great Plains of North America.

S. A. Poessel (✉)
Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, USA
e-mail: sharpoes@gmail.com

E. M. Gese
USDA/WS/National Wildlife Research Center, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

Keywords Carnivore · Canid · Helper · Parental care · Sociality · *Vulpes velox*

Introduction

Knowledge of parental behavior is important in understanding the ecology of mammalian species. Females provide direct care to their young, while males provide direct care in 9–10 % of mammalian genera, with male care being common in social and monogamous species (Kleiman and Malcolm 1981; Clutton-Brock 1991). Within Canidae, monogamy is commonly observed (Kleiman 1977), with both parents, and often additional "helpers", providing some degree of care for the young. This care includes direct actions such as nursing, delivering food, guarding, and social interactions, combined with indirect behaviors such as territory maintenance and defense (Kleiman 1977). Shared parental duties have been documented in wolf (*Canis lupus*; Mech 1970), maned wolf (*Chrysocyon brachyurus*; de Melo et al. 2009), coyote (*C. latrans*; Bekoff 1977), and red fox (*Vulpes vulpes*; Storm et al. 1976) families. Pack size in African wild dogs (*Lycaon pictus*) has been shown to have a positive effect on the size of litters after den emergence (Gusset and Macdonald 2010). Additionally, kit fox (*V. macrotis*) parents, as well as their extra-pair helpers, have been observed attending pups (Ralls et al. 2001). Likewise, both male and female swift foxes (*V. velox*), as well as helpers, often use the same dens as the pups (Kilgore 1969; Egoscue 1979; Covell 1992; Olson and Lindzey 2002).

Expanding on the observation that most canids are monogamous, Moehlman (1986) suggested relationships between a species' body weight and key factors of their ecology, including feeding behaviors, mating system,

dispersal, and rearing of young. She suggested small canids are usually monogamous but also have a tendency towards polygyny, with females outnumbering males, male-biased dispersal, and female helpers in pup-rearing. While the mechanism driving this correlation (as it relates to neonate weight and litter size) has been questioned (Geffen et al. 1996; Macdonald et al. 2004), this description holds true for the small-sized swift fox as generally characterized in the literature.

Little knowledge exists regarding reproductive behavior and parental investment in swift foxes. The nocturnal swift fox is highly fossorial, giving birth to young below ground and using dens for long stretches of time each day (Kilgore 1969; Egoscue 1979). As a result, knowledge of parental care is one of the least understood aspects of swift fox social ecology. Swift fox social units are commonly comprised of a male–female pair maintaining an exclusive home range, with juveniles, especially females, occasionally remaining within a parent's home range (Rongstad et al. 1989; Covell 1992; Pechacek 2000). These juveniles may remain at the parents' den through the following breeding season, forming trios within the social unit. Mated pairs are identified as a male and female routinely located within the same den, particularly during the breeding season. Breeding occurs mid- to late winter, with pups being born between March and May (Kilgore 1969; Olson and Lindzey 2002). Litter size ranges from three to six pups (Egoscue 1979). Recently, Kitchen et al. (2006) used genetic analysis to discover swift fox mating strategies vary more than previously believed. While a mated male–female pair was still the most common bond, stable trios with both male and female helpers, as well as extra-pair copulations, were also common, suggesting that environmental factors, such as localized population density, may be important in determining swift fox mating strategies (Kitchen et al. 2006).

Among swift foxes, Covell (1992) concluded that pups associated with trios had a higher pre-emergence survival than those from pairs. Additionally, Olson and Lindzey (2002) observed an instance where a female who lost her mate joined her litter with that of another female, and they jointly raised their pups. In contrast, Kamler et al. (2004) concluded swift foxes had a primarily female-based social organization; while male foxes may occasionally assist with young, their presence is not vital to the success of a litter. Therefore, the swift fox may benefit from shared parental responsibility under certain conditions; however, an understanding of the extent of parental care and the resulting impact upon pup survival remains unclear.

Using night-time observations, we investigated swift fox den attendance and direct parental care at natal dens throughout the pup-rearing season. Factors of primary interest included identifying attending adults at the den and determining the percentage of time spent at dens and the frequency of den visitation for female and male swift foxes. We hypothesized females would spend a higher percentage of time at the den and make more frequent visits to the den than males, particularly during lactation. In addition, we hypothesized the percentage of time at the den and frequency of den visitation by adults would decrease as the pups grew older and became more independent.

Materials and methods

Study area

We conducted this study on the 1,040-km^2 U.S. Army Piñon Canyon Maneuver Site, Las Animas County, Colorado, USA. The climate was semiarid with a mean annual precipitation of 26–38 cm. Mean monthly temperatures ranged between −1 °C in January and 23 °C in July. Elevations ranged from 1,310 to 1,740 m. The topography included river canyons, basalt outcroppings, limestone breaks, and open plains. Vegetation communities (Shaw et al. 1989) included short-grass prairie dominated by blue grama (*Bouteloua gracilis*) and western wheatgrass (*Pascopyrum smithii*), shrub-grasslands dominated by fourwing saltbush (*Atriplex canescens*), greasewood (*Sarcobatus vermiculatus*), and tree cholla (*Cylindropuntia imbricata*), and woodlands dominated by pinyon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*). This site provided an ideal setting because of the number of swift fox studies conducted previously (e.g., Covell 1992; Kitchen et al. 1999, 2005a, b; Schauster et al. 2002a, b; Karki et al. 2007; Thompson and Gese 2007).

Trapping and collaring swift foxes

Swift foxes were captured with double-door box traps (80 × 25 × 25 cm; Tomahawk Live Trap, Tomahawk, WI, USA) baited with raw chicken, following Schauster et al. (2002a). Traps were deployed in the evening and checked the following morning. During periods when night-time temperatures were <−9 °C, traps were wired open to allow the fox to enter the trap, but prevented the trap from closing. To recapture certain individuals for changing their radio-collar, we used a trap-enclosure system (Kozlowski et al. 2003). Foxes were handled by personnel wearing thick leather gloves. Each fox was weighed, sexed, aged by tooth wear and body size, ear tagged, radio-collared, and released; no anesthesia was required during handling. Radio-collars were removed from animals at the end of the study. Trapping and handling protocols were approved by the Institutional Animal Care and Use Committees at the National Wildlife

Research Center (QA-930) and Utah State University (IACUC #1060).

Behavioral observations

We located swift fox dens during daylight hours beginning in mid-April and continued through mid- to late August. Locations consisted of following the signal until either a visual of the fox was obtained or a den was found, at which point a Universal Transverse Mercator grid coordinate was recorded using a global positioning system unit. Observations began at dens in mid-May soon after pups were born and continued until early August, or the point when pups began leaving the den for the entire night. Observation sessions were continuous through the night beginning at 1900 and ending at 0600 hours. One or two observers equipped with a night vision scope and spotting scopes and/or binoculars were located in a vehicle approximately 75–90 m from the den. Whenever feasible, researchers traveled to and from the den when foxes were not visible at the den and selected a location which afforded an unobstructed view of the den. We minimized movement, light, and noise within the vehicle. Observers scanned the den area with the night vision scope every 7–10 min until activity was detected, at which point monitoring became continuous. We also used radiotelemetry to monitor the activity of marked animals, which was helpful in alerting the researcher to animals as they approached the den during the night. We recorded fox presence/absence, frequency and length of den visits, whether a fox brought prey to the den, and whether the den was attended by one of the individuals in the adult pair or a helper. If an observation was interrupted because of weather, it was attempted the next night. For analysis and to determine whether fox den attendance and behavior varied throughout the night, we condensed observation periods into three approximately equal time periods of the night: early (1900–2200 hours), middle (2200–0200 hours), and late (0200–0600 hours). We also divided the pup-rearing season into three developmental phases, spanning late spring to late summer (phases 1, 2, and 3). In 2003, phase 1 was from 10 May to 1 June, phase 2 was from 6 June to 11 July, and phase 3 was from 12 July to 13 August. In 2004, phase 1 was from 14 May to 6 June, phase 2 was from 22 June to 13 July, and phase 3 was from 14 July to 3 August. These periods corresponded to complete pup dependence on the female (i.e., nursing) and den emergence (phase 1), weaning of the pups from the female (phase 2), and increased mobility of the pups and ingestion of solid foods from both parents (phase 3). These dates varied annually based upon observations at the dens and were adjusted accordingly. We counted the number of pups in a litter after pups emerged from the den in late summer; however, the number of pups born in a litter might have been higher due to the possibility of pup mortality before den emergence.

Small mammal trapping

We trapped small mammals near den sites using grids of Sherman live traps, following a protocol modified from Ribble and Samson (1987), to determine prey abundance. Each grid consisted of 64 stations deployed at 10-m intervals, and each station consisted of one live trap. We baited traps with a mixture of sweetened rolled oats and birdseed, and we also filled them with a handful of wood shavings for bedding and insulation. We opened traps shortly before dusk, checked them at dawn, and closed them throughout the day. Traps were active for three consecutive nights, weather permitting; in inclement weather, traps were closed and opened again on the next suitable night. We ran three small mammal grids on each fox territory. We placed grids at a random compass bearing from each natal den under observation at a distance of 500–700 m, which allowed for each trapping survey to be directly correlated with a fox's known territory, while allowing enough distance that young pups did not interfere with the traps.

Statistical analyses

We statistically analyzed the percentage of time female and male foxes attended natal dens and the frequency of visits to natal dens within each of the 2 years and within each developmental phase and time period. We ran two generalized linear mixed models, one with percentage of time attending dens as the response variable and the other with frequency of visits to dens (measured as number of visits/h) as the response variable, with the den number as a random-effects predictor variable and sex, year, phase, and time period as fixed-effects predictor variables. In the mixed model, total variance was partitioned into three components: variance among dens, variance among animals within dens, and variance among repeated observations on animals within dens. The sex factor was assigned to animals within dens. Year, phase, and time period factors were assigned to repeated observations on animals. We also included litter size and number of small mammals trapped near a den site as fixed-effects covariates measured on repeated observations. Because only one fox outside of the adult pair was observed at a den during each year, we did not include fox status (i.e., adult pair or helper) as a predictor in the models. We used percentage of time attending dens (in contrast to total amount of time attending dens) and frequency of visits to dens (in contrast to number of visits to dens) as our response variables because not all observation periods were of equal length. We used a logit

transformation on the percentage of time response variable and a square root transformation on the frequency of visits response variable to meet distributional assumptions. For any significant interactions or main effects, we analyzed specific pairwise comparisons with *t* tests, correcting *p* values with a Bonferroni adjustment. Only adjusted *P* values that were significant are reported. We set the significance level to 0.05 for all statistical tests, which were two-tailed. We used SAS v.9.3 for all statistical analyses (SAS Institute 2011).

Results

Swift foxes and dens

We captured and monitored 14 adult swift foxes (seven females, seven males) at seven natal dens during 2003 and 2004. We collected 680 h of observation at the dens. Each den was observed an average of 97 h (range 22.5–167.25 h) and nine nights (range 2–15 nights). Average litter size was 3.5 pups/litter in 2003 and 4.2 pups/litter in 2004. Female visits to dens (37.7 min ± 42.5 SD) were, on average, twice as long as male visits to dens (18.6 ± 22.8 min; Table 1). The percentage of time dens were left unattended by any adult fox increased over time (Table 1). We observed the fox outside of the adult pair in 2003 at the den two times for an average of 52 min per visit, and we observed the extra-pair associate in 2004 at the den three times for an average of 19 min per visit. For the 2003 fox, 99 % of the time spent at the den was concurrent with the female's den attendance, and for the 2004 fox, 62 % of the time spent at the den was concurrent with the female's den attendance. Excluding the extra-pair associates, adult fox pairs attended the den concurrently only 0.60 and 2.20 % of the time observed in 2003 and 2004, respectively. One den was only monitored in 2003, and another den was only monitored in 2004; in addition, four of the seven dens were not monitored during every phase/time period combination. Thus, we had 172 observations in our dataset.

Table 1 Den attendance patterns for female and male swift foxes (*Vulpes velox*) in the Piñon Canyon Maneuver Site, Colorado, 2003 and 2004

	2003			2004		
	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3
Den attendance (% of time)						
Concurrent[a]	2.37	0.70	0.21	4.84	0.32	2.33
Unattended[b]	67.38	85.47	92.68	68.89	78.69	87.95
Average length of den visit (min)						
Females	44.02	22.55	18.47	45.00	55.90	46.30
Males	21.00	16.45	14.36	22.71	16.00	18.50

Phase 1 corresponds to complete pup dependence, *Phase 2* to weaning of pups, and *Phase 3* to increased mobility of pups and ingestion of solid foods

[a] Percentage of time dens were attended by both female and male foxes

[b] Percentage of time dens were not attended by any adult fox

Percentage of time attending dens

Percentage of time attending natal dens differed between female and male swift foxes, and also differed among the three developmental phases (Table 2). Females and males also differed in den attendance across the pup-rearing season (Table 2, sex × phase interaction). Den attendance varied within phases and time periods, pooled across both sexes and both years (Table 2, phase × time interaction), as well as within years, phases, and time periods, pooled across both sexes (Table 2, year × phase × time interaction). No other interactions or main effects were significant. Litter size ranged from three to five pups across both years, and number of prey animals captured at den sites

Table 2 Tests of main effects and interactions for the model analyzing percentage of time swift foxes attended natal dens, Piñon Canyon Maneuver Site, Colorado, 2003 and 2004

Effect	Numerator *df*	Denominator *df*	*F*	*P* value
Sex	1	6	33.62	**0.001**
Year	1	126	0.53	0.469
Sex × year	1	126	0.36	0.548
Phase	2	126	11.82	**<0.001**
Sex × phase	2	126	5.32	**0.006**
Year × phase	2	126	1.09	0.341
Sex × year × phase	2	126	2.48	0.088
Time	2	126	0.33	0.723
Sex × time	2	126	0.50	0.607
Year × time	2	126	1.58	0.210
Sex × year × time	2	126	0.45	0.637
Phase × time	4	126	3.32	**0.013**
Sex × phase × time	4	126	0.30	0.875
Year × phase × time	4	126	4.92	**0.001**
Litter	1	126	0.04	0.842
Prey	1	126	0.99	0.321

Predictor variables for the model included sex of swift foxes, either male or female (*sex*), year of study, either 2003 or 2004 (*year*), phase of pup-rearing season, either 1, 2, or 3 (*phase*), time of night, either early, middle, or late (*time*), interactions among these four variables, size of litter at a den (*litter*), and number of small mammals trapped at a den site (*prey*)

Bold denotes significance at the 0.05 level

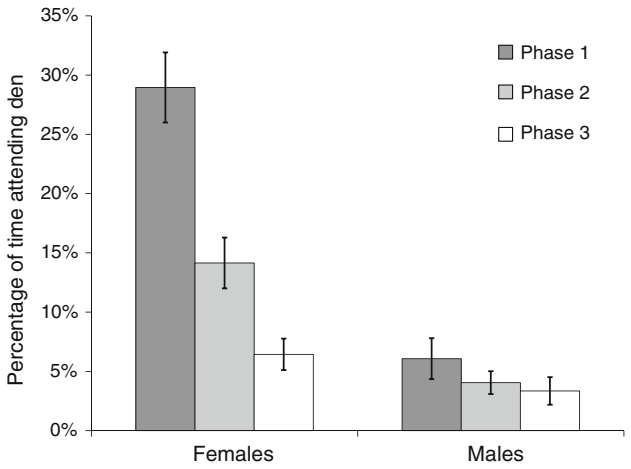

Fig. 1 Percentage of time female and male adult swift foxes (*Vulpes velox*) attended to dens during the three phases of the pup-rearing season (spanning late spring to late summer), Piñon Canyon Maneuver Site, Colorado, 2003 and 2004. *Bars* standard error around the mean. *Phase 1* corresponds to complete pup dependence, *Phase 2* to weaning of pups, and *Phase 3* to increased mobility of pups and ingestion of solid foods

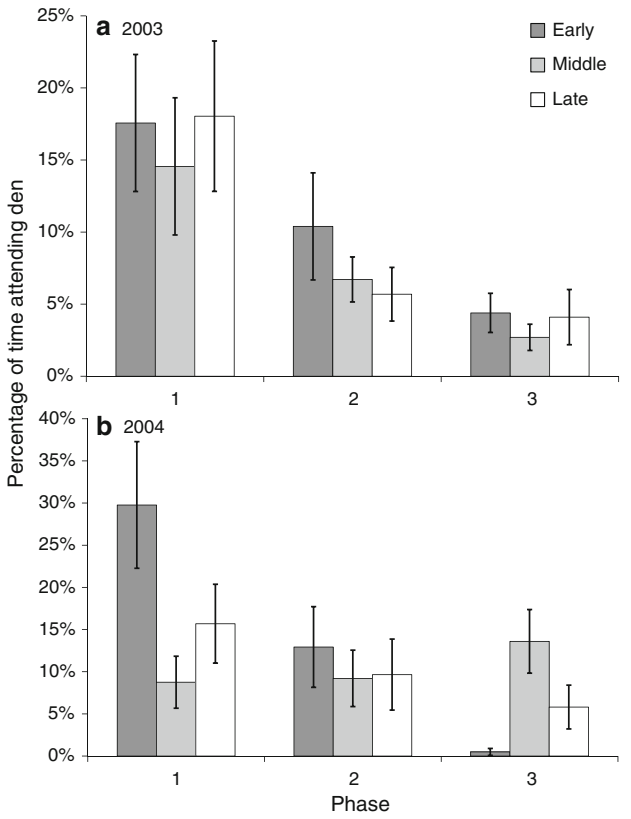

Fig. 2 Percentage of time adult swift foxes attended to dens during the three phases of the pup-rearing season (spanning late spring to late summer) and during each of the three observation time periods (early, middle, and late) in **a** 2003 and **b** 2004, Piñon Canyon Maneuver Site, Colorado. *Bars* standard error around the mean. *Phase 1* corresponds to complete pup dependence, *Phase 2* to weaning of pups, and *Phase 3* to increased mobility of pups and ingestion of solid foods

ranged from 0 to 23 individuals; neither variable had an effect on percentage of time foxes spent at dens.

Female den attendance was higher than male attendance ($t_6 = 5.80$, $P = 0.001$), and time spent at dens across both sexes in phases 1 and 2 was higher than in phase 3 (phase 1: $t_{126} = 4.82$, $P < 0.001$; phase 2: $t_{126} = 2.82$, $P = 0.017$). The phase difference observed was primarily due to female foxes (Fig. 1). Female attendance was higher in phases 1 and 2 than in phase 3 (phase 1: $t_{126} = 5.72$, $P < 0.001$; phase 2: $t_{126} = 3.15$, $P = 0.019$; Fig. 1); female attendance was also higher than male attendance in phase 1 ($t_{126} = 6.34$, $P < 0.001$; Fig. 1) and phase 2 ($t_{126} = 3.93$, $P = 0.001$; Fig. 1). The percentage of time male foxes spent at dens did not differ throughout the pup-rearing season (Fig. 1).

The primary difference in den attendance within phases and time periods occurred across phases in the early time period, with percentage of time in both phases 1 and 2 higher than in phase 3 (phase 1: $t_{126} = 5.45$, $P < 0.001$; phase 2: $t_{126} = 3.16$, $P = 0.036$). Den attendance did not differ across phases in the middle or late time periods. Time spent at dens did not vary within phases and time periods in 2003 (Fig. 2a), but in 2004, attendance was higher in both phases 1 and 2 than in phase 3 during the early time period (phase 1: $t_{126} = 5.35$, $P < 0.001$; phase 2: $t_{126} = 3.51$, $P = 0.022$; Fig. 2b) and was higher in the middle time period than in the early time period during phase 3 ($t_{126} = 4.85$, $P < 0.001$; Fig. 2b).

Frequency of visits to dens

The results for the analysis of frequency of visits to natal dens were similar to the results for the analysis of percentage of time attending dens. Visit frequency differed between females and males, and also differed among the three developmental phases (Table 3). Females and males also differed in frequency of visits across the pup-rearing season (Table 3, sex × phase interaction). Visit frequency varied within years, phases, and time periods, pooled across both sexes (Table 3, year × phase × time interaction). No other interactions or main effects were significant. Litter size and number of prey animals captured at den sites had no effect on frequency of visits to dens.

Females had a higher visit frequency to dens than did males ($t_6 = 4.16$, $P = 0.006$), and visit frequency across both sexes in phase 1 was higher than in phase 3 ($t_{126} = 4.02$, $P < 0.001$). The phase difference observed was primarily due to female foxes (Fig. 3). Female frequency of visits was higher in phase 1 than in phase 3 ($t_{126} = 4.80$, $P < 0.001$; Fig. 3); visit frequency for females was also higher than for males in phase 1 ($t_{126} = 4.77$, $P < 0.001$; Fig. 3). Den visit frequency for male foxes did not differ throughout the pup-rearing season (Fig. 3).

Table 3 Tests of main effects and interactions for the model analyzing frequency of visits by swift foxes to natal dens, Piñon Canyon Maneuver Site, Colorado, 2003 and 2004

Effect	Numerator *df*	Denominator *df*	*F*	*P* value
Sex	1	6	17.32	**0.006**
Year	1	126	0.06	0.812
Sex × year	1	126	0.92	0.338
Phase	2	126	8.13	**0.001**
Sex × phase	2	126	3.84	**0.024**
Year × phase	2	126	0.35	0.708
Sex × year × phase	2	126	2.72	0.070
Time	2	126	0.59	0.556
Sex × time	2	126	0.22	0.802
Year × time	2	126	2.08	0.129
Sex × year × time	2	126	0.42	0.657
Phase × time	4	126	2.19	0.074
Sex × phase × time	4	126	1.18	0.324
Year × phase × time	4	126	3.77	**0.006**
Litter	1	126	0.41	0.524
Prey	1	126	1.73	0.191

See Table 2 for a description of the predictor variables in the model
Bold denotes significance at the 0.05 level

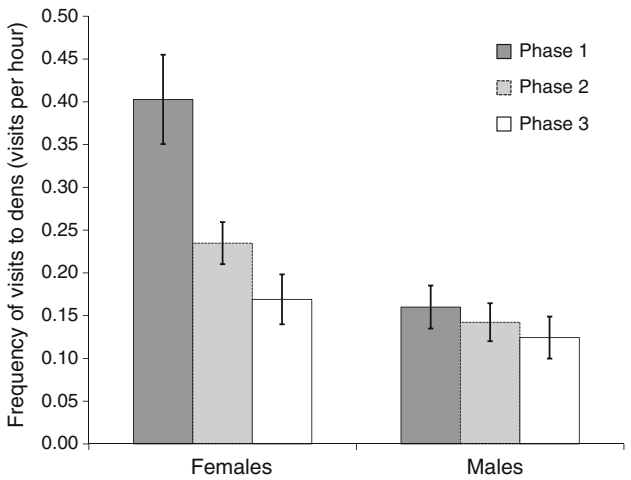

Fig. 3 Frequency of visits to natal dens by female and male adult swift foxes during the three phases of the pup-rearing season (spanning late spring to late summer), Piñon Canyon Maneuver Site, Colorado, 2003 and 2004. *Bars* standard error around the mean. *Phase 1* corresponds to complete pup dependence, *Phase 2* to weaning of pups, and *Phase 3* to increased mobility of pups and ingestion of solid foods

Frequency of visits to dens did not vary within phases and time periods in 2003 (Fig. 4a), but in 2004, visit frequency was higher in phase 1 than in phase 3 during the early time period ($t_{126} = 4.61$, $P < 0.001$; Fig. 4b) and

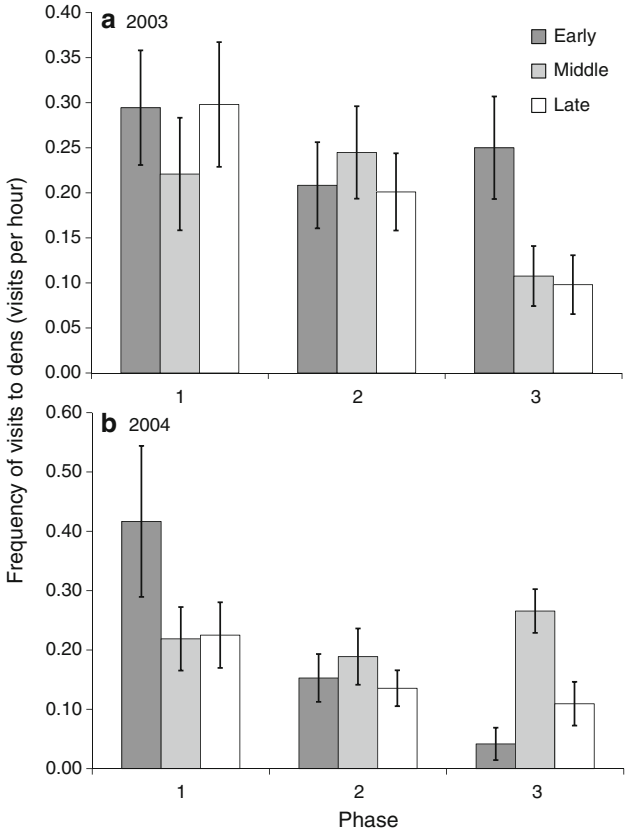

Fig. 4 Frequency of visits to natal dens by adult swift foxes during the three phases of the pup-rearing season (spanning late spring to late summer) and during each of the three observation time periods (early, middle, and late) in **a** 2003 and **b** 2004, Piñon Canyon Maneuver Site, Colorado. *Bars* standard error around the mean. *Phase 1* corresponds to complete pup dependence, *Phase 2* to weaning of pups, and *Phase 3* to increased mobility of pups and ingestion of solid foods

was higher in the middle time period than in the early time period during phase 3 ($t_{126} = 3.71$, $P = 0.011$; Fig. 4b).

Discussion

Female swift foxes visited and attended natal dens more than did male foxes. Females nurse their young pups, whereas males occasionally deliver food to dens for females and pups. In 2003, we observed three male foxes on eight separate occasions, and only one female fox on one occasion, delivering prey to dens. We also observed regurgitation of prey by both female and male adult foxes. Thus, female swift foxes are critical to the survival and care of young, consistent with the female-based social organization discussed by Kamler et al. (2004), whereas male foxes infrequently provision young with food but generally play a less important role in their direct care. Instead, adult male swift foxes likely spend more time during the pup-rearing season maintaining territories

(Kitchen et al. 2005a) and monitoring for predators, such as coyotes, which are a leading cause of mortality in swift foxes (Schauster et al. 2002a). Alternatively, 52 % of swift fox litters result from extra-pair copulations (Kitchen et al. 2006); hence, males may not provide direct care to offspring because of uncertainty regarding paternity.

Den attendance and visit frequency by females decreased throughout the pup-rearing season (Figs. 1, 3). Female parental investment was greatest early in the season when the altricial pups were new-born and highly dependent on their mothers for nutrition and care, but decreased as pups became older and more independent. Towards the end of the pup-rearing season, females were more likely to spend longer periods of time away from dens each night foraging for prey. In late summer, swift foxes feed primarily on insects, especially Orthoptera (Kitchen et al. 1999), which are not large enough to deliver to dens (Geffen and Macdonald 1992), and which likely would be available prey for weaned pups (Kamler et al. 2004). Male visitation to dens did not change during the season, further supporting our conclusion that male parental investment was not as important to the direct care of pups as female investment.

The most prominent decrease in den attendance throughout the pup-rearing season occurred in the early time period (1900–2200 hours). Swift foxes are quite active during this time period (Kitchen et al. 1999), so the significant decrease in time spent at dens during late summer could have been due to high activity and movement rates by adult foxes out foraging for insects as soon as darkness fell. This trend was most notable in 2004, a year that was somewhat cooler (mean temperature: 20.9 °C ± 0.8 SE, $n = 21$ days; United States Geological Survey 2012) and wetter (mean precipitation: 4.05 mm ± 2.4 SE) during late summer than in 2003 (temperature: 25.2 ± 0.4 °C, $n = 33$ days; precipitation: 2.31 ± 1.4 mm; United States Geological Survey 2012) which might have resulted in an increase in insects (Capinera and Horton 1989; Branson 2008). In addition, fox attendance and visitation to dens was higher in late summer of 2004 during the middle time period (2200–0200 hours) than during the early time period (Figs. 2, 4). Perhaps successful foraging earlier in the evening resulted in foxes returning to dens sooner than they might have otherwise and then venturing out again during the late time period (0200–0600 hours).

Male and female parental care in other fox species varies. Attendance of natal dens was higher for females than males in arctic foxes (*V. lagopus*; Garrott et al. 1984), gray foxes (*Urocyon cinereoargenteus*; Nicholson et al. 1985), and red foxes (Vergara 2001), but higher for males than females in bat-eared foxes (*Otocyon megalotis*; Wright 2006). For arctic foxes, both males and females brought prey back to the dens, but females provided a larger proportion of food than males, and females also visited dens more frequently than males, with den visits decreasing as pups grew older (Garrott et al. 1984). Gray fox females spent more time in or near natal dens than did males, and females visited dens with food at night more frequently than did males (Nicholson et al. 1985). For red foxes, females visited dens more frequently and for longer periods of time than did males, whereas males spent more time than females in vigilant behavior near dens (Vergara 2001). In contrast, bat-eared fox males spent more time near natal dens than did females and were involved in all aspects of pup care except lactation; paternal den attendance was the best predictor of the number and proportion of pups surviving to weaning age (Wright 2006). Thus, although parental investment between the sexes does vary among fox species, our results for swift foxes are consistent with the majority of other fox species in that direct parental investment of females was greater than that of males.

We observed only one extra-pair associate attending a den in each of the 2 years, with the fox in 2004 attending the same den on three separate occasions. Both of these foxes were males. This result was in contrast to Moehlman (1986), who suggested that small canids usually have female helpers, and Macdonald (1979), who documented female helpers in fox societies. Additionally, Covell (1992) observed five different swift fox pairs with female helpers and none with male helpers. However, Kitchen et al. (2006) observed three trios of foxes consisting of two males and one female. Male helpers are considered to be favored over female helpers in large canid societies because they are able to handle larger prey and bring more food to the pups (Geffen et al. 1996; Macdonald et al. 2004), and they do not compete with adult females for breeding opportunities. However, although male swift foxes occasionally delivered food to the pups, our results demonstrated that males did not play an important role in direct pup care. Hence, each of these two male foxes might have been related to the adult male in the pair, with each group of two males and one female likely living as social groups of three individuals (Kitchen et al. 2006). Because only one extra-pair associate visited a den during each year of this study, we were unable to test for any influence of helpers on adult female or male den attendance or visitation.

Other canid species vary in their use of helpers. Beta helpers in black-backed jackals (*C. mesomelas*) supplied both the adult female and pups with food, and their presence increased pup survival (Moehlman 1979). Similarly, pups in coyote packs with helpers received a higher rate of food provisioning and were attended more often than pups in packs without betas (Hatier 1995). In contrast, von Schantz (1984) questioned whether the presence of an additional helper raised reproductive success in red fox

families. Similarly, arctic fox helpers provisioned pups very little (Strand et al. 2000), and Geffen and Macdonald (1992) found no evidence that Blanford's fox (*V. cana*) helpers contributed to the care of young at any stage of development. Hence, our results for swift foxes are consistent with other fox species in that helpers do not appear to play a critical role in pup care.

In summary, our results demonstrate the importance of female parental investment in a small canid, the swift fox. Female foxes visited and attended natal dens more than did male foxes, and female attendance and visitation decreased throughout the pup-rearing season as pups became older and more independent. Environmental factors, including climate and availability of prey, contributed to differences in fox behavior between years. While male foxes, including males outside of the adult pair, occasionally visited dens and delivered food to pups, their direct contribution to pup care and survival appears to be marginal in swift fox society. Instead, males are more likely to provide indirect care to pups through territory maintenance and predator detection. To our knowledge, this study is the first to document parental care and investment of adult female and male swift foxes. Understanding parental behavior in swift foxes will increase knowledge of the ecology and behavior of this and other social mammalian species.

Acknowledgments Funding and logistical support was provided by the U.S. Army, Directorate of Environmental Compliance and Management, Fort Carson, Colorado, through the U.S. Fish and Wildlife Service, Colorado Assistance Office, Denver, Colorado. Additional support was provided by the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center at Utah State University, Logan, Utah. We thank E. Joyce, C. Thompson, J. White, E. Cleere, M. Watkins, D. Degeranno, A. Larkins, C. Roemer, D. Fletcher, W. Ulrey, S. Schopman, C. Gazal, A. Knipps, J. Garner, and C. Briggs for field assistance. We also thank S. Durham for statistical assistance.

References

Bekoff M (1977) *Canis latrans*. Mamm Species 79:1–9

Branson DH (2008) Influence of a large late summer precipitation event on food limitation and grasshopper population dynamics in a northern Great Plains grassland. Environ Entomol 37:686–695

Capinera JL, Horton DR (1989) Geographic variation in effects of weather on grasshopper infestation. Environ Entomol 18:8–14

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Covell DF (1992) Ecology of the swift fox (*Vulpes velox*) in southeastern Colorado. MS thesis, University of Wisconsin, Madison

de Melo LFB, Sábato MAL, Magni EMV, Young RJ, Coelho CM (2009) First observations of nest attendance behavior by wild maned wolves, *Chrysocyon brachyurus*. Zoo Biol 28:69–74

Egoscue HJ (1979) *Vulpes velox*. Mamm Species 122:1–5

Garrott RA, Eberhardt LE, Hanson WC (1984) Arctic fox denning behavior in northern Alaska. Can J Zool 62:1636–1640

Geffen E, Gompper ME, Gittleman JL, Luh H, Macdonald DW, Wayne RK (1996) Size, life-history traits, and social organization in the Canidae: a reevaluation. Am Nat 147:140–160

Geffen E, Macdonald DW (1992) Small size and monogamy: spatial organization of Blanford's foxes, *Vulpes cana*. Anim Behav 44:1123–1130

Gusset M, Macdonald DW (2010) Group size effects in cooperatively breeding African wild dogs. Anim Behav 79:425–428

Hatier KG (1995) Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming. MS thesis, Montana State University, Bozeman

Kamler JF, Ballard WB, Gese EM, Harrison RL, Karki S, Mote K (2004) Adult male emigration and a female-based social organization in swift foxes, *Vulpes velox*. Anim Behav 67:699–702

Karki SM, Gese EM, Klavetter ML (2007) Effects of coyote population reduction on swift fox demographics in southeastern Colorado. J Wildl Manag 71:2707–2718

Kilgore DL Jr (1969) An ecological study of the swift fox (*Vulpes velox*) in the Oklahoma panhandle. Am Midl Nat 81:512–534

Kitchen AM, Gese EM, Schauster ER (1999) Resource partitioning between coyotes and swift foxes: space, time, and diet. Can J Zool 77:1645–1656

Kitchen AM, Gese EM, Karki SM, Schauster ER (2005a) Spatial ecology of swift fox social groups: from group formation to mate loss. J Mammal 86:547–554

Kitchen AM, Gese EM, Waits LP, Karki SM, Schauster ER (2005b) Genetic and spatial structure within a swift fox population. J Anim Ecol 74:1173–1181

Kitchen AM, Gese EM, Waits LP, Karki SM, Schauster ER (2006) Multiple breeding strategies in the swift fox, *Vulpes velox*. Anim Behav 71:1029–1038

Kleiman DG (1977) Monogamy in mammals. Q Rev Biol 52:39–69

Kleiman DG, Malcolm JR (1981) The evolution of male parental investment in mammals. In: Gubernick DJ, Klopfer PH (eds) Parental care in mammals. Plenum, New York, pp 347–387

Kozlowski AJ, Bennett TJ, Gese EM, Arjo WM (2003) Live capture of denning mammals using an improved box trap enclosure: kit foxes as a test case. Wildl Soc Bull 31:630–633

Macdonald DW (1979) 'Helpers' in fox society. Nature 282:69–71

Macdonald DW, Creel S, Mills MGL (2004) Society: canid society. In: Macdonald DW, Sillero-Zubiri C (eds) The biology and conservation of wild canids. Oxford University Press, Oxford, pp 85–106

Mech LD (1970) The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis

Moehlman PD (1979) Jackal helpers and pup survival. Nature 277:382–383

Moehlman PD (1986) Ecology of cooperation in canids. In: Rubenstein DI, Wrangham R (eds) Ecological aspects of social evolution. Princeton University Press, Princeton, pp 64–86

Nicholson WS, Hill EP, Briggs D (1985) Denning, pup-rearing, and dispersal in the gray fox in east-central Alabama. J Wildl Manag 49:33–37

Olson TL, Lindzey FG (2002) Swift fox survival and production in southeastern Wyoming. J Mammal 83:199–206

Pechacek P (2000) Activity radii and intraspecific interactions in the swift fox (*Vulpes velox*). Biologia (Bratislava) 55:201–205

Ralls K, Pilgrim KL, White PJ, Paxinos EE, Schwartz MK, Fleischer RC (2001) Kinship, social relationships, and den sharing in kit foxes. J Mammal 82:858–866

Ribble DO, Samson FB (1987) Microhabitat associations of small mammals in southeastern Colorado, with special emphasis on *Peromyscus* (Rodentia). Southwest Nat 32:291–303

Rongstad OJ, Laurion TR, Andersen DE (1989) Ecology of swift fox on the Pinon Canyon Maneuver Site, Colorado. Final report to

the U.S. Army, Fort Carson. Wisconsin Cooperative Wildlife Research Unit, University of Wisconsin, Madison

SAS Institute (2011) SAS/STAT user's guide. Release 9.3. SAS Institute, Cary.

Schauster ER, Gese EM, Kitchen AM (2002a) Population ecology of swift foxes (*Vulpes velox*) in southeastern Colorado. Can J Zool 80:307–319

Schauster ER, Gese EM, Kitchen AM (2002b) An evaluation of survey methods for monitoring swift fox abundance. Wildl Soc Bull 30:464–477

Shaw RB, Anderson SL, Schulz KA, Diersing VE (1989) Plant communities, ecological checklist, and species list for the U.S. Army Piñon Canyon Maneuver Site, Colorado. Colorado State University, Department of Range Science, Science Series No. 37, Fort Collins

Storm GL, Andrews RD, Phillips RL, Bishop RA, Siniff DB, Tester JR (1976) Morphology, reproduction, dispersal, and mortality of midwestern red fox populations. Wildl Monogr 49:3–82

Strand O, Landa A, Linnell JDC, Zimmermann B, Skogland T (2000) Social organization and parental behavior in the arctic fox. J Mammal 81:223–233

Thompson CM, Gese EM (2007) Food webs and intraguild predation: community interactions of a native mesocarnivore. Ecology 88:334–346

United States Geological Survey (2012) National water information system. http://waterdata.usgs.gov/co/nwis/inventory/?site_no=372319104073301 and http://waterdata.usgs.gov/co/nwis/inventory?site_no=373004104032001. Accessed 13 February 2012

Vergara V (2001) Comparison of parental roles in male and female red foxes, *Vulpes vulpes*, in southern Ontario. Can Field Nat 115:22–33

von Schantz T (1984) 'Non-breeders' in the red fox *Vulpes vulpes*: a case of resource surplus. Oikos 42:59–65

Wright HWY (2006) Paternal den attendance is the best predictor of offspring survival in the socially monogamous bat-eared fox. Anim Behav 71:503–510