Raising pups of urban San Joaquin kit fox: relative roles of adult group members

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ABSTRACT.—Maternal care of young is the norm in mammals because of internal gestation and lactation by females. Care by adults other than the mother is rare in most mammals but is common in primates, rodents, and carnivores. We studied parental care in an urban population of the San Joaquin kit fox (*Vulpes macrotis mutica*), a small canid endemic to the San Joaquin Desert in California. Kit fox family groups typically consist of a mated pair, the young-of-the-year, and occasionally older offspring from previous years known as helpers. The relative contributions of the parents and helpers to the rearing of young are unknown in San Joaquin kit foxes. We determined the relative time investment (den attendance), the tasks performed (e.g., provisioning and guarding), and the chronology of participation and tasks performed by adult group members in pup rearing. We classified group members into 3 categories (mother, father, and helper) and monitored them for 3 periods of the reproductive season (preparturition, nursing, and weaned). There was no difference in den attendance between periods, but there was a significant difference in den attendance by role. Mothers spent significantly more time at the den than either fathers or helpers. There was no significant difference between average provisioning events per hour per individual by role, but provisioning rates were significantly lower during the nursing period compared to the weaned period. Mothers provided the most direct care to young, while the role of fathers was primarily to guard the family and maintain the territory. Assistance provided by helpers supplemented the efforts of the mother and father and consisted primarily of guarding and some social interaction, especially play. Pups in groups with helpers were left unattended significantly less than pups in the group with no helpers, which may result in lower predation levels on pups. Helpers were likely tolerated because of a superabundance of food in the urban environment, but their presence may reduce pup-rearing costs for parents and enhance the successful rearing of the current litter. Future research should compare parental care in urban and nonurban kit foxes and determine whether helpers increase pup survival rates.

RESUMEN.—El cuidado materno de las crías es la norma en los animales mamíferos como consecuencia de la gestación interna y de la posterior lactancia. El cuidado por parte de adultos que no sean la madre es inusual en la mayoría de los mamíferos. Sin embargo, ocurre en primates, roedores y carnívoros. Analizamos el cuidado parental en una población urbana de zorrita del desierto de San Joaquín (*Vulpes macrotis mutica*), pequeños cánidos endémicos del desierto de San Joaquín en California. El grupo familiar de la zorrita del desierto se compone, típicamente, de la pareja reproductiva, crías nacidas ese año y, en ocasiones, crías mayores conocidas como ayudantes. Desconocemos la contribución relativa de los padres y de los ayudantes en la crianza de los cachorros, en la población de zorritas del desierto de San Joaquín. Determinamos la inversión de tiempo (presencia en las madrigueras), las tareas realizadas (por ejemplo, el suministro de alimentos y la vigilancia), la cronología de participación y la realización de tareas por los miembros adultos del grupo en la crianza de los cachorros. Clasificamos a los miembros del grupo en tres categorías (madre, padre y ayudante) y los monitoreamos durante los tres períodos de la época reproductiva: preparto, lactancia y destete. No encontramos diferencias en cuanto a la presencia en las madrigueras entre los períodos, pero sí hubo una diferencia significativa en cuanto a la atención de las madrigueras por rol. Las madres pasaron considerablemente más tiempo en las madrigueras que los padres o los ayudantes. No hubo diferencias significativas en el promedio de eventos de provisión de alimentos por hora por individuo según el rol. Sin embargo, las tasas de suministro fueron más bajas durante el período de lactancia comparadas con el período de destete. Las madres brindaron mayor atención directa a las crías, mientras que el papel de los padres fue principalmente el de proteger a la familia y preservar el territorio. La asistencia proporcionada por los ayudantes complementó los esfuerzos de la madre y del padre y consistió principalmente en la vigilancia y en cierta interacción social, especialmente durante el juego. Los cachorros en grupos con ayudantes significativamente permanecieron sin atención menos tiempo que aquellos en grupos sin ayudantes, lo que podría resultar en niveles menores de depredación de los cachorros. Es probable que los ayudantes fueran tolerados debido a la sobreabundancia de alimentos en el entorno urbano, pero su presencia puede reducir los costos de la crianza para los padres y promover el éxito de la crianza de la camada actual. Investigaciones futuras deberán comparar el cuidado parental de la zorrita del desierto de San Joaquín en ambientes urbanos y no urbanos, para determinar si los ayudantes promueven la tasa de supervivencia de los cachorros.

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Maternal care of young is typical in mammals because of internal gestation and lactation by females. Females typically invest greatly in offspring, while care of the young by other adults is relatively rare (Kleiman and Malcolm 1981, Clutton-Brock 1991, Woodroffe and Vincent 1994). Paternal care in mammals is most common in primates, rodents, and carnivores (Woodroffe and Vincent 1994). Paternal care occurs in about 40% of primate genera and has been described for many species (Muller and Thompson 2012, Huck and Fernandez-Duque 2013). There is also extensive information on paternal care in small rodents (Dulac et al. 2014, Saltzman and Ziegler 2014), but there are relatively few studies on carnivores compared to those on primates and rodents.

Among carnivores, male parental care is most common in canids, and fathers are thought to provide some form of care for the young in most species (Malcolm 1985). Canid young typically have a prolonged period of dependence following birth, and in some species, pup survival is markedly enhanced by care from 2 parents versus a single parent (Macdonald et al. 2004). Parental care in mammals can be classified into direct and indirect behaviors (Kleiman and Malcolm 1981). In canids, types of direct care include watching for or defending young against predators; provisioning and attending young (remaining with young while other group members forage); carrying, retrieving, grooming, and cleaning young; resting and huddling with young; and playing or socializing with young. Indirect care includes den construction, alerting group members to danger, provisioning pregnant or lactating females, and territorial maintenance (Malcolm 1985).

Alloparenting (i.e., care provided by adults other than the mother or father) is also relatively rare in mammals, but common among canids (Macdonald and Sillero-Zubiri 2004). Such care is typically provided by young-of-the-year, who occasionally remain in their natal range and assist parents with rearing future litters (Moehlman 1989, Ralls et al. 2001, Macdonald et al. 2004). Alloparenting by philopatric young has been described in black-backed jackals (*Canis mesomelas*), Ethiopian wolves (*C. simensis*), African wild dogs (*Lycaon pictus*) (Macdonald et al. 2004), golden jackals (*C. aureus*), bat-eared foxes (*Otocyon megalotis*) (Moehlman 1989), red foxes (*Vulpes vulpes*) (Soulsbury et al. 2010), swift foxes (*V. velox*) (Poessel and Gese 2013), and arctic foxes (*V. lagopus*) (Elmhagen et al. 2014). While alloparenting is known to increase pup survival for black-backed jackals (Moehlman 1989), evidence of the benefits of helpers to pup survival in many other canid species is lacking (Macdonald et al. 2004). In many smaller foxes, such as swift and arctic foxes, the assistance provided by helpers does not seem to be substantial or necessary (Kruchenkova et al. 2009, Poessel and Gese 2013). Although alloparenting can provide multiple benefits from an evolutionary perspective (Moehlman 1989, Macdonald et al. 2004), the behaviors and contributions of helpers have not been well described for most canid species.

We studied San Joaquin kit foxes (*V. macrotis mutica*), small canids that typically inhabit arid and semiarid habitats including desert scrub, chaparral, and native and nonnative grasslands in central California (Macdonald and Sillero-Zubiri 2004, Moehrenschlager et al. 2004, Cypher 2010). Unlike most other canids, which only use dens for pup rearing, kit foxes use earthen or subterranean dens all year (Koopman et al. 1998, Moehrenschlager et al. 2004, Cypher 2010). Dens are used to escape predators, to avoid temperature extremes and water loss, for diurnal resting, and for pup rearing (Ralls and White 2003, Moehrenschlager et al. 2004, Cypher 2010). Kit foxes typically have multiple dens within their home range that are maintained by family groups (Morrell 1972, Ralls and White 2003). A kit fox family group typically consists of a mated pair and their current year's offspring (Ralls and White 2003, Cypher 2010). Occasionally, groups include additional adults (helpers) that are typically previous year's offspring, though this is rare and only occurs approximately 10% of the time in exurban kit foxes (Ralls et al. 2001).

Kit foxes are mostly monogamous, with occasional cases of polygyny, and they generally mate for life (Spiegel and Tom 1996, Moehrenschlager et al. 2004, Ralls et al. 2007). They mate from late November to early December, and young are born in dens from late January to early March (Morrell 1972, Moehrenschlager et al. 2004, Cypher 2010). Litters consist of 1–7 pups, with an

average of 4 (Moehrenschlager et al. 2004, Ralls et al. 2007). Pups emerge from the den at 4 weeks, are weaned at 8 weeks, and become independent at 5–6 months (Morrell 1972, Moehrenschlager et al. 2004, Ralls et al. 2007). At that time, young will either disperse or continue to occupy their natal ranges for variable time periods, and may even take over the range, usually when one or both parents die (Ralls et al. 2001, 2007, Cypher 2010).

We observed San Joaquin kit foxes in Bakersfield, California, to determine the contributions of parents and helpers in pup rearing. Bakersfield (population 376,380) encompasses 391 km^2 with only 25% to 30% of its limits abutting natural habitat (Cypher 2010). Nevertheless, the city has a substantial population of San Joaquin kit foxes living within its limits (Smith et al. 2006, Cypher 2010). The goals of our study were to determine (1) the relative time invested by each adult group member in pup rearing, (2) the tasks performed by each adult member in pup rearing (e.g., provisioning and guarding), and (3) the changes in adult behaviors over time as the pups matured. We hypothesized that parental care differs among mothers, fathers, and helpers, predicting that mothers would provide the most direct care, fathers would provision more than other group members, and helpers would provide less care to pups than parents. Finally, we predicted that all group members would spend less time at the den in order to forage for more food as the pups grew older and larger.

Methods

Study Area

Bakersfield is located in the southeastern San Joaquin Valley in Kern County, California. Bakersfield is within the San Joaquin Desert and receives an average of 145 mm of precipitation between November and March, resulting in dry, hot summers and moist, cool winters (Germano et al. 2011). Our study sites within Bakersfield were Stockdale High School (SHS); California State University, Bakersfield (CSUB); and Bakersfield College (BC). We monitored family groups at school campuses because ambient light was sufficient to observe foxes without the aid of night vision equipment. Additionally, foxes living on campuses were relatively accustomed

to human presence, not disturbed by the presence of an observer, and observable without the use of binoculars. Campuses were relatively safe and quiet at night so observations could be conducted without interference. All dens we monitored were located in landscaping beds and open manicured lawns.

Field Methods

We trapped foxes during late December 2010 to mid-January 2011 and in early January 2012 with wire-mesh box traps (38 × 38 × 107 cm; Tomahawk Live Trap, Hazelhurst, WI) that we baited with cat food, hot dogs, and sardines. We placed traps in secure locations away from well-trafficked areas and covered them with oiled cloth tarps to guard against the elements. We assessed each fox to determine age, sex, and reproductive condition and applied a uniquely numbered ear-tag to every individual. Females were ear-tagged on the right and males were ear-tagged on the left to help distinguish sexes at a glance. Over the study, we collected hair samples from all foxes for potential genetic analysis. In addition to hair samples, we began collecting tissue samples during the second year of the study when we realized that genetic analysis would be necessary to determine parentage in some groups (Westall 2015). We collected tissue samples from one ear using a 2-mm disposable biopsy punch (Inegra® Miltex®, Model 33-31, York, PA) and stored them in 95% ethanol.

To determine individual contributions to pup rearing, each adult fox in a family group needed to be easily identifiable. We marked each fox with a unique pattern using a black permanent nontoxic dye (Nyanzol-D; Albinal Dyestuff, Inc., Jersey City, NJ) to allow for the identification of individuals over the course of the project. In addition to dye markings, we attached very high frequency (VHF) collars (Model E2C 162A; Sirtrack, Havelock North, New Zealand) to adult foxes in order to locate foxes and dens. We only collared adult foxes (>2 years old) that were exhibiting signs of breeding (e.g., swollen vulva, enlarged testes). The VHF signal could be tracked with a receiver (Communications Specialists, Inc., Model R1000, Orange, CA) paired with a 3-element antenna (AF Antronics, Inc., Model F150-3FB, Urbana, IL) or omnidirectional antenna (Telonics, Model RA-5A, Mesa, AZ).

TABLE 1. Definitions of behaviors (adapted from Kleiman and Malcolm 1981) observed in San Joaquin kit foxes (*Vulpes macrotis mutica*) during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA.

Behavior	Definition
QUANTIFIED BEHAVIORS	
Den attendance	
Present	Inside the den or present outside the den, including patrolling while pups were outside the den
Absent	Not present at the den
Care behaviors	
Huddling	Makes body contact with pups, such as cuddling or nursing
Grooming	Nibbles and/or licks pups to clean them
Retrieving	Calls pups to the den, herds pups to the den, or bodily retrieves pups and returns them to the den
Guarding	Watches over pups and/or patrols the area around the den to ensure safety
Playing	Initiates or engages in chasing or wrestling with pups
Provisioning	Provides food to the pregnant or lactating female and to pups
Active defense	Actively defends the den or pups from a perceived threat
Den modification	Digs at the den to remove waste or modify the den
Noncare behaviors	
Socializing	Interacts with other adults without the presence of pups
Resting	Rests or naps at the den without the presence of pups
OPPORTUNISTICALLY OBSERVED BEHAVIORS	
Resource maintenance	Patrols throughout the territory, scent marking via urination and/or defecation
Sentinel and antipredator behavior	Patrols the territory looking for threats and actively defends the territory from intruders

Once we were reasonably sure that we had captured most, if not all, adult foxes from a family group, we began collecting data by conducting direct observations. During observation sessions, we recorded times when adult foxes were present and absent from the den, as well as behaviors performed above ground while foxes were at the den (Table 1). We also noted behaviors that we observed opportunistically while foxes were away from the den (Table 1). We observed the foxes at each den for a 2-h session 1–2 times a week between January and May in 2011 and 2012. Because kit foxes are nocturnal and remain in underground dens during the day, we tracked target foxes to the den they were currently using at least 0.5 h prior to sunset. If adults were tracked to more than one den, the den with the mother in it was observed, as this was most likely to be the natal den. After tracking foxes to the den, we found a nearby location with a clear view of the den from which to conduct observations. Generally, these locations were 30–50 m from the den, but there was one group that was so accustomed to the presence of humans that observers could sit on a bench 10 m from the den, as these foxes behaved normally even with foot traffic occurring within 3 m of the den. Our 2-h observation session began as soon as a fox emerged from the den.

We recorded the number of minutes that each adult fox was present or absent from the den; foxes were considered present when they were in the den or above ground at the den. We divided the amount of time each adult fox was present into 3 behavior categories: time in the den, time performing care behaviors above ground, and time performing noncare behaviors above ground (care and noncare behaviors adapted from Kleiman and Malcolm 1981) (Table 1). While observing the den, we recorded the number of times each fox provisioned food at the den, as well as what item was provisioned if it could be determined.

We categorized foxes into 3 roles: mother, father, or helper. For family groups with female helpers, we initially used nursing behavior to identify the mother. For one family group with a male helper, we used genetic analysis (Westall 2015) to determine which male was the father and which male was a helper. We estimated the date of birth of the pups by counting back 4 weeks from the date of emergence. To determine changes in behavior over time, we divided the reproductive season into 3 periods: preparturition, nursing, and weaned.

Preparturition lasted from the start of observations to the birth of the pups. The nursing period began at the estimated date of birth and ended at 8 weeks of age. The final period, weaned, began when the pups reached 8 weeks of age and lasted until the pups began to leave the den with their parents. Splitting the breeding season into these 3 periods allowed us to monitor changes in adult kit fox contributions to pup rearing as the needs of the pups changed.

Statistical Analysis

We analyzed the amount of time adult foxes were present (i.e., in the den and at the den above ground) and absent (i.e., away from the den), as well as how much time was spent performing care or noncare-related behaviors while at the den above ground. To determine relative care contributions, we calculated the average number of minutes each fox was present per observation session. We standardized observation sessions to 2 h and used counts of minutes for statistical analyses. A 2-way analysis of variance (ANOVA) was used to test for differences in the amount of time individuals were present by role and between periods, as well as any interactions between role and period. Tukey's pairwise comparisons with P values adjusted for multiple comparisons were used to determine differences between roles and between periods. We treated groups with and without helpers the same, except when analyzing the amount of time dens were left unattended. We analyzed the amount of time dens were left unattended overall and across periods using a Kruskal–Wallis test with P values adjusted for ties to compare between the family groups with helpers and the family group without helpers.

We used an arcsine transformation to normalize the proportion of time present that each fox spent in the den, providing care while above ground (huddling, grooming, retrieving, guarding, playing, provisioning, den modification, and active defense), or performing noncare-related behaviors while above ground (resting or socializing while pups were not present) (Table 1). We used a general linear model to test for differences in the proportion of time present by role, period, and behavior, as well as any interactions between role, period, and behavior. Tukey's pairwise comparisons with P values adjusted for multiple

comparisons were used to determine differences in behavior between roles and between periods. Behaviors observed while foxes were present were only compared between the nursing and weaned periods, because care could not be provided during the preparturition period.

We summarized the number of provisioning events per hour per individual by role in 2-week increments to determine how provisioning events changed to meet the increasing energetic needs of the pups as they matured. We used a Kruskal–Wallis test with P values adjusted for ties to compare the average provisioning events per hour per individual between periods, as well as between roles. We used Minitab (Minitab 17, Minitab Inc., State College, PA) for all statistical analyses ($\alpha = 0.05$ for all tests).

Results

In 2011, we monitored one family group from Bakersfield College (BC-2011) and one family group from Stockdale High School (SHS), and in 2012 we monitored one family group from Bakersfield College (BC-2012) and 2 family groups from California State University, Bakersfield (CSUB-S and CSUB-C) (Table 2). The SHS group did not produce pups, so we were unable to include it in this analysis. Two helpers from the BC-2011 group were not captured and marked before the breeding season began (6525 ♀ and 6523 ♂) and our permits do not allow us to trap during the breeding season. Because these foxes were indistinguishable, the individuals had to be excluded from the analysis for this group. The BC-2011 and BC-2012 groups were monitored at the same natal den during consecutive years, but the breeding pair from 2011 both died of vehicle strikes before the 2012 reproductive season. Two groups, BC-2012 and CSUB-S, had 2 mothers with communal litters raised in the same den. Each group with communal litters was treated as a single family group. We used a total of 4 groups for all our analyses.

Den Attendance

The average proportion of time spent at the den ranged from 43.2% to 67.4% for mothers, from 20.0% to 32.4% for helpers, and from 9.5% to 14.5% for fathers. Kit foxes
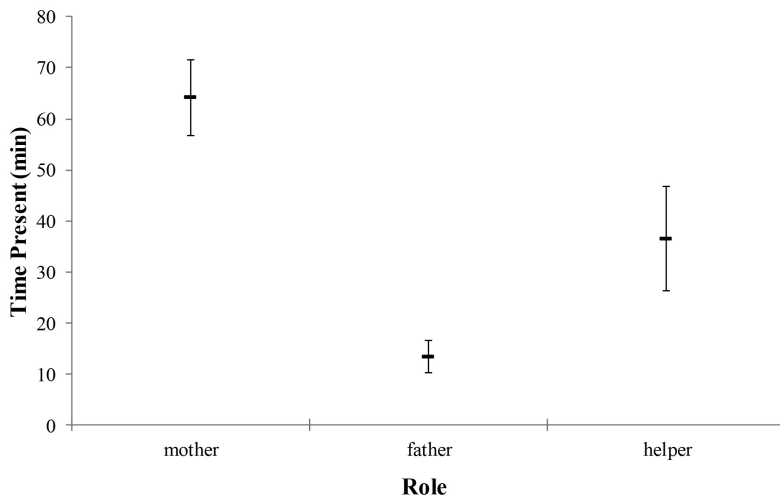
Fig. 1. Average number of minutes that adult San Joaquin kit foxes (*Vulpes macrotis mutica*) were present at the natal den by role during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA. Vertical bars represent 95% confidence intervals.

TABLE 2. San Joaquin kit fox (*Vulpes macrotis mutica*) family group members and number of observation days during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA. NA = not applicable.

Family group	Mother	Father	Helper	No. pups	Pups sampled	Observation days		
						Preparturition	Nursing	Weaned
BC-2011	6069 ♀	6547 ♂	6521 ♀ 6523 ♂* 6525 ♀* 6566 ♀	3	6522 ♀ 6524 ♂ 6584 ♂	6	14	13
BC-2012	6566 ♀ 6525 ♀	6524 ♂	6584 ♂	10	6595 ♂ 6596 ♀ 6606 ♀ 6607 ♂ 6677 ♀ 6678 ♂	1	7	4
CSUB-S	6700 ♀ 6309 ♀	6065 ♂	6585 ♀	6	6593 ♀ 6594 ♀ 6676 ♂ U177	8	8	5
CSUB-C	6592 ♀	6578 ♂	NA	4	none	3	7	4

*Individuals not included in statistical analyses

spent significantly different amounts of time at the den based on role ($F_{2, 33} = 11.06$, $P < 0.001$), but similar amounts of time across the 3 periods ($F_{2, 33} = 1.46$, $P = 0.247$). There was no significant interaction between role and period ($F_{4, 33} = 0.24$, $P = 0.913$). Mothers spent significantly more time at the den than helpers ($t = 2.54$, df = 8, $P = 0.042$) and fathers ($t = 4.64$, df = 8, $P < 0.001$; Fig. 1). The amount of time that helpers and fathers spent at the den was not significantly different ($t = 1.92$, df = 8, $P = 0.148$; Fig. 1).

The group without helpers left the natal den unattended significantly more than the groups with helpers ($H = 11.18$, df = 1, $P = 0.001$). On average, the group without helpers left the natal den unattended 46.2% (median 47.5%) of the time, while the groups with helpers left the natal den unattended 18.3% (median 15.0%) of the time. There was no significant difference in the time that dens were left unattended across periods ($H = 1.90$, df = 2, $P = 0.388$).
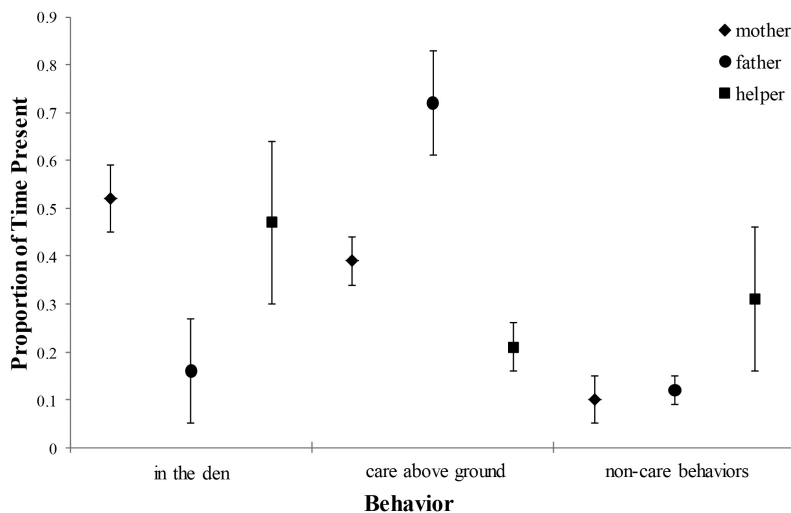
Fig. 2. Average number of minutes present at the natal den that adult San Joaquin kit fox (*Vulpes macrotis mutica*) mothers, fathers, and helpers spent in the den, providing care above ground, or performing noncare behaviors during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA. Vertical bars represent 95% confidence intervals.

Behavior While at the Den

Proportion of time spent performing each behavior differed ($F_{2,66}$ = 13.79, P < 0.001), but role ($F_{2,66}$ = 0.00, P = 1.000) and period ($F_{1,66}$ = 0.00, P = 1.000) were not significant factors. There were also significant interactions between role and behavior ($F_{4,66}$ = 7.97, P < 0.001) and between period and behavior ($F_{2,66}$ = 11.42, P < 0.001). Mothers and helpers spent a significantly larger proportion of their time present in the den than fathers did, while fathers spent a significantly larger proportion of their time present providing care above ground (Fig. 2). All adult group members spent a significantly larger proportion of time in the den when pups were nursing and a larger proportion of time providing care above ground when pups were weaned (Fig. 3). There were no significant interactions between role and period ($F_{2,66}$ = 0.00, P = 1.00) or between role, period, and behavior ($F_{4,66}$ = 1.37, P = 0.254). All foxes spent significantly less time performing noncare behaviors (resting and socializing) than they spent in the den (t = −3.20, df = 34, P = 0.006) or providing care at the den above ground (t = −5.21, df = 54, P < 0.001). The amount of time foxes spent in the den and providing care above ground did not differ significantly (t = −2.00, df = 54, P = 0.120).

The amount of time mothers spent in the den and at the den providing care did not differ significantly, but mothers spent less time performing noncare behaviors than they spent in the den or providing care above ground at the den (Table 3). While present at the den, fathers spent significantly more time providing care above ground than in the den or performing noncare behaviors above ground (Table 3). Fathers also spent a significantly larger proportion of their time when present at the den providing care above ground compared to helpers (Table 3). The proportion of time at the den that helpers spent providing care above ground did not differ significantly from time in the den or time performing noncare behaviors above ground (Table 3). The amount of time all foxes spent providing care above ground at the den in the nursing period did not differ significantly from time in the den or time performing noncare behaviors; however, there was a significant difference in the amount of time foxes spent in the den and the amount of time they spent performing noncare behaviors (Table 3). During the weaned period, foxes spent significantly more of their time present providing care above ground at the den than they spent in the den or performing noncare behaviors above ground at the den (Table 3).
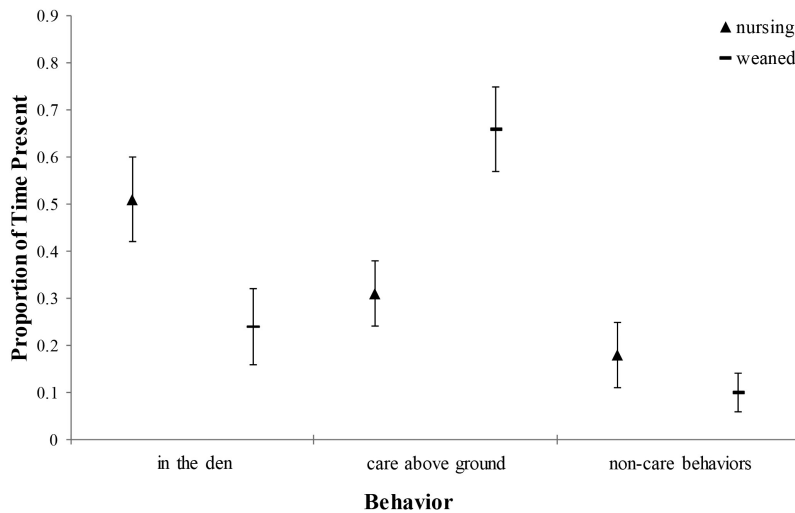
Fig. 3. Average proportion of time present at the natal den that adult San Joaquin kit foxes (*Vulpes macrotis mutica*) spent in the den, providing care above ground, or performing noncare behaviors during the nursing period and the weaning period during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA. Vertical bars represent 95% confidence intervals.

TABLE 3. Tukey's pairwise comparisons with adjusted *P* values analyzing differences in proportions of time that adult San Joaquin kit foxes (*Vulpes macrotis mutica*) spent in the natal den or performing care- and noncare-related behaviors above ground at natal dens in Bakersfield, California, USA, during the nursing and weaned periods of the 2011 and 2012 reproductive seasons.

| Comparison	df	*t*	*P*
Behavior within roles			
(father in the den) – (father care)	4	−5.17	<0.001
(father noncare) – (father care)	4	−5.52	<0.001
(father noncare) – (father in the den)	4	−0.35	1.000
(mother in the den) – (mother care)	4	0.36	1.000
(mother noncare) – (mother care)	4	−3.72	0.012
(mother noncare) – (mother in the den)	4	−4.09	0.004
(helper in the den) – (helper care)	4	1.60	0.801
(helper noncare) – (helper care)	4	0.05	1.000
(helper noncare) – (helper in the den)	4	−1.55	0.829
Behavior between roles			
(mother in the den) – (father in the den)	4	3.09	0.068
(father in the den) – (helper in the den)	4	−2.66	0.184
(mother in the den) – (helper in the den)	4	0.18	1.000
(mother care) – (father care)	4	−2.90	0.107
(father care) – (helper care)	4	4.11	0.003
(mother care) – (helper care)	4	1.60	0.799
(mother noncare) – (father noncare)	4	−0.19	1.000
(father noncare) – (helper noncare)	4	−1.46	0.871
(mother noncare) – (helper noncare)	4	−1.78	0.693
Behavior within periods			
(nursing in the den) – (nursing care)	2	1.81	0.467
(nursing noncare) – (nursing care)	2	−1.19	0.839
(nursing noncare) – (nursing in the den)	2	−3.00	0.042
(weaned in the den) – (weaned care)	2	−4.64	<0.001
(weaned noncare) – (weaned care)	2	−6.17	<0.001
(weaned noncare) – (weaned in the den)	2	−1.53	0.648
Behavior between periods			
(nursing in the den) – (weaned in the den)	2	−2.64	0.102
(nursing care) – (weaned care)	2	−3.81	0.004
(nursing noncare) – (weaned noncare)	2	1.17	0.850
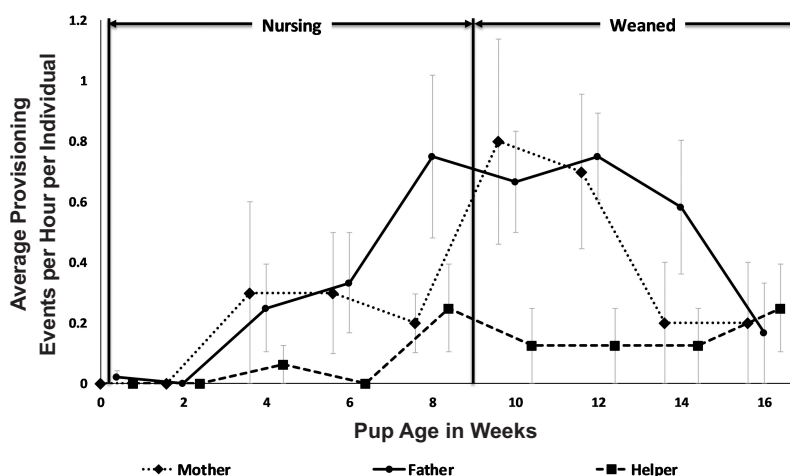
Fig. 4. Average provisioning events per hour per individual performed by San Joaquin kit fox (*Vulpes macrotis mutica*) mothers, fathers, and helpers as pups matured during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA. Vertical bars represent standard errors.

TABLE 4. Direct and indirect care behaviors (after Kleiman and Malcolm 1981) performed by mother, father, and helper San Joaquin kit foxes (*Vulpes macrotis mutica*) during the 2011 and 2012 reproductive seasons in Bakersfield, California, USA.

Behavior	Mother	Father	Helper
Direct care behaviors			
Huddling	X		
Grooming	X		
Retrieving	X		
Guarding	X	X	X
Playing		X	X
Provisioning	X	X	X
Active defense	X	X	
Indirect care behaviors			
Resource maintenance		X	
Den modification	X	X	X
Sentinel and anti-predator behavior		X	

We observed 80 provisioning events, of which 42 (52.5%) were by mothers, 29 (36.3%) were by fathers, and 9 (11.2%) were by helpers. Only a single provisioning event occurred during preparturition, so data were only compared between the nursing and weaned periods. Average provisioning events per hour per individual was not significantly different based on role ($H = 2.86$, df = 2, $P = 0.240$). The average number of provisioning events per hour per individual was significantly lower during the nursing period when compared to the weaned period ($H = 5.39$, df = 1, $P = 0.020$). Provisioning events per hour per individual by foxes of all roles increased when the pups were fully weaned at 8 weeks of age (Fig. 4). Sample sizes were too small to determine differences in provisioning rates by role across periods. We documented kit foxes provisioning many anthropogenic items including pizza, potato chips, fast food, and various refuse that had no nutritional value. Kit foxes also provided natural food items including desert cottontails (*Sylvilagus audubonii*), California ground squirrels (*Otospermophilus beecheyi*), rats (*Rattus* sp.), birds, and American bullfrogs (*Lithobates catesbeianus*).

Although some direct care behaviors were performed by foxes of all roles, others were not (Table 4). Sample sizes were too small for statistical analysis, so we only report trends for these data. Only mothers were observed huddling with young, grooming young, and retrieving young. While mothers sometimes physically retrieved pups, they also frequently herded them toward the den or alerted them to return to the den by barking. Only mothers and fathers engaged in active defense of the pups by warding off perceived threats, such as cats or people. Only fathers and helpers were regularly observed playing with the pups. Foxes of all roles were observed guarding and provisioning pups. Fathers were regularly seen away from the den urinating and defecating to mark the territory, and one father was observed warding

off a red fox that had entered the territory. Foxes of all roles performed den maintenance and modifications by digging and cleaning out the entrances throughout the breeding season.

DISCUSSION

Parental Care by Role

While all individuals in the study provided some level of care to pups, their role was the most relevant factor in predicting the types and amount of care provided. Mothers spent more time at the den than other family members and provided the most direct care to the pups. Mothers were the only family members to huddle with pups, groom them, and retrieve them when they were too far from the den. Behaviors that were performed by mothers as well as other group members included guarding pups, defending the den from threats, and provisioning pups with food. Mothers guarded the young by vigilantly watching the pups and the surrounding area, and they frequently patrolled around the den in wide circles, stopping at regular intervals to scan the area. If a threat was perceived, the mother would vocalize a warning and the pups would immediately return to the den. Perceived threats included cats, dogs, and humans (e.g., students, security staff, grounds keepers). Occasionally, mothers would actively defend the den from cats and humans by stalking them until they were out of the area, but at other times they would simply wait for the threat to pass and would then signal, presumably through vocalization, for the pups to exit the den again.

The only direct care behavior that mothers did not regularly perform was play. Mothers rarely played with pups and sometimes aggressively bit them if they persistently tried to initiate play. Mothers modified dens but were not seen performing other indirect care behaviors, such as resource maintenance (e.g., scent-marking the territory) or sentinel and antipredator behavior, which would have required being away from the den. It is noteworthy that foxes of all roles performed den maintenance, as it has been suggested that den construction in other canids is performed exclusively by breeding females (Malcolm 1985).

Fathers spent significantly less time at the den than mothers, but most of their time at the den was spent providing care to the pups.

Fathers primarily guarded pups, actively defended the den, and provisioned mothers and pups. While guarding pups at the den, fathers exhibited the same vigilance as mothers; however, they defended the territory more frequently and more aggressively than mothers. One father was observed snarling and growling at a red fox that had wandered into the territory near the natal den. Red foxes, which are considerably larger than kit foxes, have been documented killing adult kit foxes (White and Ralls 1993, Clark et al. 2005) and are known to limit reproductive success in arctic foxes by killing their pups (Hersteinsson and Macdonald 1992, Tannerfeldt et al. 2002). Nevertheless, the father in this group continued his aggressive behavior until the red fox left the area. The only direct care behavior that fathers performed more frequently than mothers was playing with the pups. Indirect care behaviors performed by fathers included maintaining the territory through urination and defecation, den modification, and sentinel and antipredator behavior away from the den. Male kit foxes are known to scent mark more than females, and a greater proportion of their marks are in boundary areas of home ranges (Murdoch 2004).

Although helpers are sometimes found in nonurban populations (Koopman et al. 2000, Ralls et al. 2001, Moehrenschlager et al. 2004), they are much less common than in the Bakersfield population (Cypher 2010). Only about 10% of the mated pairs in exurban environments have helpers (Ralls et al. 2001), whereas helpers were present in 3 of the 4 groups we monitored. Not only did most of our groups have helpers present, but one group had 4 helpers. The abundant food supply in Bakersfield ensures that most mated pairs can share their territories with one or more other adults at little or no cost to themselves or their future litters.

Helpers spent significantly less time at the den than mothers, but not fathers. Although fathers and helpers spent similar amounts of time at the den, helpers spent significantly less time providing care to pups than fathers. Most of the time helpers spent at the den was spent resting, although occasionally they would guard the pups or provision them. Helpers were never observed actively defending the den or the territory. When guarding,

helpers tended to be less vigilant than mothers and fathers, sometimes playing with pups instead of watching them.

Playing with the pups was the only direct care behavior that helpers seemed to perform more than other roles. Play is an important preparation for adult life (Bekoff 1995), and the father in the group with no helpers played with the pups, whereas in the other groups it was mostly the helpers that played with pups. The frequent presence of the helper(s) at the den may have enabled the parents, especially the fathers in these groups, to spend less time playing with pups at the den, freeing them for other activities. Play between individuals can also serve to establish dominance (Cordoni 2009). As kit foxes can breed at 1 year of age (Cypher et al. 2000), a pup can potentially take over the territory of its parent the following reproductive season. It may be important for the helpers to establish dominance over the pups in the event an opportunity arises to take over the territory.

Although helpers provided little direct care for the pups, they often attended them while neither parent was present. Groups with helpers left the den unattended for less time than the group without helpers, so helpers may increase pup survival by reducing the opportunity for predation on pups. Only 2 pups died during the course of our study, one to raptor predation and one to unknown causes, so we did not have sufficient data to determine the effect of helpers on pup survival. It is also worth noting that behavior occurring inside the den could not be observed, and that there may therefore be other direct care behaviors performed by helpers. The only indirect care behavior that helpers were observed performing was den modification.

While the exact benefits of helpers are hard to define, there are some potential benefits documented in kit foxes. Helpers provide insurance for the breeding pair and their future offspring. In the event that one of the breeding pair dies, helpers are potential mates for the breeding adult of the opposite sex. When this adult is the parent of the helper, inbreeding can result, but it has nonetheless been documented in this urban kit fox population (Westall 2015). Helpers could also potentially care for the pups if something happened to either or both of the parents. Kit fox helpers sometimes adopt and raise pups following the death of a parent (Spiegel and Tom 1996). Finally, helpers could also potentially benefit the mated pair if they inherit the territory and produce offspring related to the pair.

Behavioral Changes Over the Reproductive Season

Den attendance patterns by role did not change, and there was no difference in the amount of time the pups were left unattended while above ground as the pups grew older. When pups first emerged, one or more adult foxes were usually present at the den when pups were above ground, and pups would go back into the den almost immediately when an adult fox left the area. As the pups grew older, the frequency and duration of periods where the pups were left unattended increased, but this was a result of pups spending more time above ground rather than the den being left unattended for longer periods of time. Behaviors of adults while they were present at the den did change. During the nursing period, adult group members spent a larger proportion of their time present in the den. During the weaning period, adults spent more of the their time present providing care above ground. While pups were younger and more vulnerable, adults would stay in the den, presumably to provide care; then, as the pups grew older and spent more time out of the den, care took place above ground.

There was a noticeable change in provisioning events as the pups matured. The number of provisioning events per individual per hour surged during the weaned period compared to the nursing period. Kit fox pups are fully weaned after 8 weeks, and because pups no longer receive nutrition via lactation, but are not old enough to hunt for themselves, parents are required to bring more food to the den to meet the growing energetic demands of pups. During this time, provisioning events increased markedly, but by 14 weeks of age, pups began venturing farther from the den, and at that point provisioning at the den tapered off.

Comparisons to Other Fox Species

In general, our den attendance observations on kit foxes were consistent with observations on other socially monogamous fox species,

although there were some differences. As in most other monogamous canids, including swift (Poessel and Gese 2013), arctic (Garrott et al. 1984, Strand et al. 2000), and red foxes (Vergara 2001, Soulsbury et al. 2010), breeding females spent the most time with pups and also provided the most direct care, while breeding males spent little time at the den but spent considerable time foraging to provision pups and lactating females. Den attendance patterns of kit foxes did differ compared to patterns of the similarly sized bat-eared foxes, but this is likely related to available prey. Bat-eared fox males spent significantly more time with pups than mothers did, and males also performed many of the behaviors that female kit foxes perform, such as guarding, huddling, playing, retrieving, and grooming offspring (Maas and Macdonald 2004, Wright 2006). Bat-eared foxes rely primarily on insects for food, and lactating females must spend large portions of the night away from the den to obtain enough nutrients to produce milk as well as meet their own energetic needs (Maas and Macdonald 2004, Wright 2006). In contrast, because kit foxes rely primarily on rodents in exurban environments and on relatively large prey and anthropogenic food items in urban environments, adults are able to forage for food that can easily be brought to the den to provision pups and lactating females.

In our study, den attendance patterns remained the same throughout the breeding season, but different trends have been recorded for swift foxes, which are an ecologically similar species. Male swift foxes did not change their den attendance patterns over the course of the breeding season, although females did (Poessel and Gese 2013). Female swift foxes spent more time with pups early in the breeding season and spent less time at the den as the pups grew older, probably because of the high consumption of insects by adults later in the breeding season (Poessel and Gese 2013). Because insects cannot be carried back to the pups, adult swift foxes regurgitated food for their offspring (Poessel and Gese 2013), a behavior that has not been documented in kit foxes. It is likely that female kit foxes in our study were able to spend a relatively constant amount of time with the pups because the ample and consistent supply of resources in the urban environment allows females to gather the necessary nutrients for producing milk in a relatively short amount of time. Fathers also provided food items for both pups and mothers, allowing mothers to remain at the den to provide direct care to their offspring throughout the breeding season.

The increased frequency of helpers and the greater number of helpers per group in the urban environment seems to be consistent with observations on other species, though a larger sample size is required for a statistical analysis. Arctic foxes accept additional family members in years of high prey availability (Strand et al. 2000) and live in groups more frequently when food availability increases, either naturally or with supplemental feeding (Elmhagen et al. 2014). Red foxes have also been documented with higher occurrences of philopatric young when resource availability and habitat stability are high (Gosselink et al. 2010).

Similar to kit foxes, helpers in other species, including arctic foxes (Strand et al. 2000), Blanford's foxes (*Vulpes cana;* Geffen and Macdonald 1992), and red foxes (von Schantz 1984), seem to provide little or no care to the pups but are still tolerated due to potential benefits to the breeding pair. The presence of helpers benefits the long-term reproductive success of the breeding female in arctic foxes (Kruchenkova et al. 2009). The presence of helpers may also increase pup survival by reducing the amount of time the natal den is left unguarded. Erlandsson et al. (2017) found that arctic fox pup survival was negatively correlated with the proportion of time pups were left unattended. In our study, the presence of helpers decreased the amount of time the den was left unattended and may have reduced the predation risk to the pups.

This is the first study to document parental care behaviors in the San Joaquin kit fox. The enhanced observability of kit foxes in the urban environment provided a good opportunity to obtain detailed data on parental and alloparental care. Future research could compare parental care between urban and exurban kit foxes. Questions of particular interest include determining whether helpers increase the survival of pups and whether group composition (particularly the presence of helpers) varies with natural fluctuations in resource availability.

ACKNOWLEDGMENTS

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