DOES PATERNAL CARE OF PUPS BENEFIT BREEDING FEMALE COYOTES?

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Post-partum care of offspring by male parents (paternal care), although rare among mammals generally, occurs commonly within the Carnivora, Primates, and Rodentia (Kleiman, 1977). Whereas lactation constrains female mammals to care for young, males are not similarly constrained (Trivers, 1972). Therefore, occurrence of paternal care in certain mammalian taxa suggests either strong benefits to males (male-choice hypothesis—Trivers, 1972; Gubernick et al., 1993) or benefits to females of sufficient magnitude to promote sexual selection for this trait in males (female-choice hypothesis—Orians, 1969; Wittenberger and Tilson, 1980). In the former case, paternal care primarily should enhance current reproductive success (i.e., of both sexes), whereas in the latter case, paternal care primarily should affect future reproductive success of the female (i.e., through increased survival or future fecundity). Among mammalian families, paternal care is most pronounced in the Canidae, in which males typically share in all pup-rearing behaviors except nursing (e.g., Kleiman, 1977). The relative benefits of these contributions to current and future reproductive success of females (or of males) have not been empirically investigated in this family.

Benefits of paternal care to current and future reproductive success of mates can be investigated by observing consequences to the female of male removal (Mock and Fujioka, 1990). In the absence of paternal care, one of 3 possible strategies for the female canid is predicted from life-history theory (Williams, 1966; Stearns, 1992). First, the female could abandon or kill her litter, thereby sacrificing all current reproductive potential to maximize future reproductive potential (Tait, 1980). Second, she could provide the same amount of care as she would have in the presence of paternal care, presumably sacrificing some of her current reproductive potential, but with no change in her future reproductive potential. Third, she could provide a greater than normal amount of care to compensate for the absence of paternal care, thus sacrificing no current reproductive potential, but reducing her future reproductive potential. The first strategy is most consistent with the male-choice hypothesis and the third strategy is most consistent with the female-choice hypothesis.

We used radiotelemetry and observations from a natural experiment of removals of male coyotes (Canis latrans) to investigate these strategies. Coyotes in our study area were routinely killed (regardless of whether they were radio-collared) by control personnel to reduce predation on domestic sheep (Sacks et al., 1999); this resulted in removal during pup-rearing of several paternal males and eventually some of their mates and pups, which were provided to us for post-mortem examination. We compared females with mates present to females
with mates removed with respect to den attendance, activity, body condition, and body mass of their pups. We also reported on fates of mateless mothers and a surviving offspring of a mateless female.

We conducted this study from March 1995 to September 1996 at the University of California Hopland Research and Extension Center, located in the north Coast Range in Mendocino Co., California (39°00' N, 123°05' W). The study area, coyote capture, and radiotelemetry methods were described elsewhere (Sacks, 1996; Sacks et al., 1999).

During pup-rearing periods of 1995 and 1996, presence or absence of 6 mates (n = 4, 1995; n = 2, 1996) of 5 radio-collared female coyotes was either known, when they were radio-collared (n = 2, 1995), or inferred through a combination of visual observations, paired territorial vocalizations (e.g., elicited by sirens—Okoniewski and Chambers, 1984), and paired sets of tracks associated with the female’s radio locations (Sacks, 1996). An uncollared breeding female also was assumed to be mated until just before she was removed. Her stomach contained scavenged coyote, linking her to a nearby den site where a breeding male and pup were shot (and their carcasses left behind) 9 days earlier. Our assessments, based on field data, of putative mates of radio-collared females in 1995 (i.e., all cases for which we had the necessary tissue samples) were confirmed by microsatellite DNA analysis, which identified each putative mate as the most likely father of the female’s offspring (90% confidence—K. M. Blejwas, in litt.).

To compare den (or rendezvous site) attendance by females with and without mates, we estimated the proportion of time each female spent attending dens in 1995, using the proportion of radio locations occurring ≤300 m (near) of the current den. We chose this distance to accommodate radiotelemetry error (92% of errors were <300 m; Sacks, 1996) and because the frequency distribution of locations sharply declined beyond 300 m (Harrison and Gilbert, 1985). Den attendance was quantified for 5 post-whelping periods of 4 weeks each, corresponding to nursing (periods 1, 2), postweaning (periods 3, 4), and pup independence (period 5), under normal (biparental) conditions (Andelt, 1985; Harrison and Gilbert, 1985).

Although we expected that time spent away from dens by females involved increased energetic expenditures (e.g., foraging and maintenance of territories), it was also possible that time away from dens indicated decreased energetic expenditures (e.g., respite from care of pups). To evaluate these hypotheses, we compared activity levels of females near and away from dens. Radio locations were classified as active or not active based on amplitude fluctuation and bearing shift (Andelt, 1985). We used a paired, 2-tailed t-test on arcsin-transformed proportions of locations coded as active (Zar, 1984).

To assess body condition of breeding females, we examined carcasses for fat on the hip (subcutaneous), on kidneys, mesentery, and omentum (visceral), and in femur marrow. We ranked coyotes by loss of body mass (difference between initial capture mass and death mass) with a rank of 1 assigned to the individual with the greatest loss; we then assigned a 1 (present) or 0 (absent) to each fat deposit category (subcutaneous, visceral, marrow). A condition index was calculated by summing mass-loss rank and fat-deposit points and dividing by the highest possible point value. Condition indices were compared between mateless and mated females using a 1-tailed Mann-Whitney U-test (Zar, 1984).

We used body masses of pups removed at dens to examine potential effects of male absence on pup growth. We estimated ages of pups from whelping dates (Sacks, 1996) and used the regression formula of Barnum et al. (1979) to calculate normal masses based on these ages. Ratios of observed to expected masses of pups were log-transformed prior to computation of confidence limits (Zar, 1984). The fate of a surviving (i.e., to independence) offspring of a mateless female (parentage determined by microsatellite DNA analysis—K. M. Blejwas, in litt.) was also reported.

We determined den locations and parturition dates (Sacks, 1996) for 4 female coyotes (F102, F104, F109, F203), all of which had mates present during the first nursing period. During the second nursing and 2 post-weaning periods, females whose mates were dead spent less time near dens than mated females (Fig. 1). No female abandoned her litter. During the fifth period (when we would no longer expect mated females to be associated with dens),
mateless females continued to be regularly located near dens, whereas the remaining mated female (F104) was apparently no longer associated with a den. Females generally were more active when away from dens than when near them ($\bar{x} = 13\%$, $t = 3.91$, $P = 0.038$, $n = 4$).

We examined the condition of 6 breeding female coyotes, which were killed during or shortly after pup-rearing. All were lean, but mateless females were in significantly poorer condition ($U = 9$, $P = 0.05$; Table 1). Numbers of uterine scars were similar between mateless and mated females, suggesting that litter size was not a confounding factor.

Average masses of pups removed from 2 litters with fathers present at the time (F102’s: $n = 2$, F104’s: $n = 1$) were not low ($\bar{x} = 1.10$, 1.21 of normal, respectively). Five pups from the fatherless litter (F109’s) were significantly underweight ($\bar{x} = 0.89$ of normal, 95% CL = 0.99). One of the surviving pups from this litter was captured 5 months post-independence and was in extremely poor condition. She had low body mass, many ectoparasites, apparently could not run, and was heavily parasitized by (ca. 300) heartworms (Dirofilaria immitis), as determined after she died 2 weeks later. She was killed by a mountain lion (Puma concolor), which was probably related to her poor condition.

Removal experiments have been used extensively in birds to elucidate benefits of male parental care to current and future reproduction (Mock and Fujikawa, 1990). However, few such studies have been conducted on mammals (Wynne-Edwards, 1987; Gubernick et al., 1993) and we know of no such study of a carnivore. The absence of removal studies of carnivores is likely due to the difficulty, expense, and controversial ethics associated with manipulative studies of these large, sparsely dispersed animals. Thus, although our study was based on a

![Proportion of radiotelemetry locations near dens (±1 SE)](image)

**Table 1**—Body condition of mateless and mated breeding female coyotes killed during or after pup-rearing (April through August), Hopland Research and Extension Center, 1995 and 1996.

<table>
<thead>
<tr>
<th>Breeding, Females</th>
<th>Number of uterine scars</th>
<th>Initial mass (kg)</th>
<th>Change in body mass (%)</th>
<th>Fat deposits</th>
<th>Condition Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mateless</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F102</td>
<td>4</td>
<td>11.2</td>
<td>-31.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>F109</td>
<td>9</td>
<td>10.8</td>
<td>-20.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>F203</td>
<td>9</td>
<td>12.2</td>
<td>-25.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Mated</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F104</td>
<td>5</td>
<td>9.2</td>
<td>-3.4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>F209</td>
<td>8</td>
<td>11.4</td>
<td>-11.7</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>F6</td>
<td>8</td>
<td>n/a</td>
<td>n/a</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

*a Marrow fat was considered absent when marrow was red and gelatinous.

*b Carcass partly decomposed when discovered; marrow fat could not be evaluated.
small number of individuals, our observations provided a rare opportunity to tentatively evaluate relative benefits of paternal care to female canids.

Our most basic finding was that females did not abandon their litters when mates were removed. There were several aspects particular to our study that may have promoted this result. First, food was relatively abundant (Neale, 1996), which may have facilitated pup-rearing by mateless females (Gubernick et al., 1993; Cantoni and Brown, 1997). Second, most males were removed after pups had been nursing for >2 weeks, such that remaining investment required of females to rear pups to independence was somewhat reduced (Bronson and Marsteller, 1985). Third, mortality from humans was generally high (Sacks et al., 1999), which reduced females' chances for future reproduction, thereby increasing the value of current reproduction (Williams, 1966).

Because females continued to rear litters after mates were removed, we were able to investigate relative benefits of paternal care to current versus future reproduction, by assuming that the magnitude of the male's contribution to the female was the same as the observed penalty to her in his absence (Mock and Fujioka, 1990). Female coyotes apparently attempted to compensate for absences of their mates through increased foraging or maintenance of the territory, based on den attendance and activity. Our observation that mateless females were in poorer physical condition than mated females suggests that such efforts exacerbated the already high energetic stresses of reproduction (e.g., lactation—Oppen and Gittleman, 1989). The apparently extended period of pup-rearing by mateless females also may have contributed to their poor condition. Heartworms, which also can reduce body condition in coyotes (Sacks and Blejwas, 2000), were found in similar intensities in both mated (range = 11 to 40 heartworms) and mateless (18 to 41) females (B. N. Sacks, in litt.) and therefore should not have confounded the comparison.

Survival of breeding females also seemed to be compromised by mate loss. In all 4 cases where mates were removed, females were removed within a few months. Two of these breeding females were caught in traps while on forays >2 km from their territories after removal of their mates (Sacks, 1996). Neither of these coyotes had made such forays prior to their mates' deaths (Sacks, 1996), suggesting that those forays were related to finding new mates or that mateless females were driven from their territories by incoming coyote pairs. Coyotes generally suffer higher mortality when outside of their territories (Windberg and Knowlton, 1990; Sacks et al., 1999) and, based on observations of other canids (Fritts and Mech, 1981; Moehlman, 1986), probably are more likely to leave or be expelled from territories when mateless.

The current reproductive success of females may also have been reduced by the absence of male mates. Low masses of pups from a mateless female and the poor condition and subsequent death of an older offspring of this same litter suggested that the female's efforts to provision pups did not compensate fully for her mate's absence. The death of the older offspring was unusual in that coyotes at our study site rarely died of natural causes (Sacks et al., 1999). Further, this individual was infected by far more heartworms than had ever been reported in coyote (Sacks, 1998), suggesting that she was immunosuppressed, possibly due to malnutrition (Gershin et al. 1985).

In conclusion, female coyotes attempted to compensate for the absence of paternal care at apparent costs to their own health, survival, and hence, future reproductive success. We also found evidence that current reproductive success of mateless females was reduced despite increased maternal efforts. Thus, female coyotes in our study apparently employed a life-history strategy emphasizing current over future reproductive success, which may not have been successful. Similar investigations of coyotes and other canids in different environments (e.g., lower human-caused mortality) are needed to further evaluate the propensity and ability of breeding females to rear pups in the absence of mates and, hence, to elucidate the adaptive significance of paternal care in canids.

Resumen—Comparamos hembras coyotes (Canis latrans) con machos presentes a aquellas con machos eliminados después del parir, para examinar los beneficios del cuidado paternal al éxito reproductivo actual y futuro de las hembras. Ninguna hembra abandonó su camada
como reacción a la ausencia de su macho. Aparentemente, las hembras pasaron más tiempo o forrajando o manteniendo el territorio cuando no habían machos, como indicado por relativamente más radiococolaciones lejos de los cúbiles, asociadas con aumentada actividad. Después de criar los cachorros, las hembras sin machos se encontraron en peores condiciones físicas que las hembras pareadas. Observaciones adicionales indicaron que los cachorros criados por hembras sin machos también estuvieron en relativamente peor condición física y padecían supervivencia disminuida. Estas observaciones sugieren que las hembras intentaban a compensar por las ausencias de sus machos en daño de su propia supervivencia, así acentuando el éxito reproductivo actual más de futuro.

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LITERATURE CITED


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