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GENDER-RELATED DIFFERENCES IN NURSING BEHAVIOR BY ROOSEVELT ELK

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ABSTRACT—Parental investment declines with increasing age of offspring, producing a conflict between parent and offspring over amount of parental investment. The degree of parent-offspring conflict may be associated with the gender of the offspring, mating system such as polygyny, and variation in reproductive success among individuals. We examined the dynamics of maternal investment through time by observing nursing behavior in Roosevelt Elk (*Cervus elaphus roosevelti*). Suckling rate ($P = 0.031$) and suckling time per bout ($P = 0.014$) by calves decreased with calf age, and male suckling rate ($P = 0.047$) and suckling time per bout ($P = 0.008$) were greater than those for females. Maternal initiation of nursing was greater in the early nursing period ($P = 0.009$), and almost all suckling bouts were terminated by the mother. Our results were similar to those of studies on other polygynous ungulate species which exhibit differences in maternal investment in offspring based on gender.

Key words: *Cervus elaphus roosevelti,* Roosevelt Elk, nursing behavior, maternal investment, suckling, ungulate, northern California

Conflict arises when offspring demand more investment than parents are selected to provide (Trivers 1974). While all parental investment is beneficial to offspring fitness, parents reach a point when the benefit through increasing the fitness of current offspring is outweighed by a decrease in ability to invest in future offspring. In addition, lactation is the most energetically expensive component of maternal investment (Clutton-Brock and others 1989); therefore, maternal investment should decline over the nursing period. Time spent suckling and amount of milk ingested decreases with age, as has been observed in many ungulate species including Pronghorn (*Antilocapra americana,* Kitchen 1974), Moose (*Alces alces,* Reese and Robbins 1994), and White-tailed Deer (*Odocoileus virginianus,* Hirth 1985). In each of these studies, the greatest increase in time spent suckling and milk intake occurred in the early nursing period, followed by a gradual decline until weaning.

Trivers and Willard (1973) proposed that gender of offspring in a polygynous species also influences patterns of parental investment. Comparative reproductive success of females is not a function of condition at weaning, but slight improvements in a male's condition at weaning may disproportionately increase his future reproductive success (Trivers and Willard 1973). Males of polygynous species generally experience greater reproductive variance. Consequently, it is advantageous for a female of a polygynous species to invest more in male offspring due to greater lifetime reproductive potential (Trivers and Willard 1973).

Nursing behavior has been used as an indicator of maternal investment in numerous studies, including those on European Bison (*Bison bonasus,* Daleszczyk 2004), Bighorn Sheep (*Ovis canadensis,* Festa-Bianchet 1988), Pronghorn (Byers and Moodie 1990), and Red Deer (*Cervus elaphus elaphus,* Clutton-Brock and others 1981). Although evidence addressing the relationship between time spent suckling and maternal investment is conflicting (Mendl 1989; Cameron 1998; but see also Cassinello 2001), nursing behaviors were positively correlated with weight gain (a direct correlate of milk intake) in captive Woodland Caribou (*Rangifer tarandus caribou,* Lavigueur and Barrette 1992), River Buffalo (*Bubalus bubalis,* Paranhos da Costa and others 2000), Domestic Sheep (*Ovis aries,* Ewbank 1967), Domestic Pigs (*Sus scrofa,* Valros and others 2002), and Southern Elephant Seals

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(*Mirounga leonina,* Engelhard and others 2002). Additionally, nursing behavior is easily observable and a direct measure of maternal attentiveness and investment (Gauthier and Barrette 1985).

Clutton-Brock and others (1981) observed gender-biased investment in offspring in Red Deer; conversely, Kristan (1993) did not detect gender-biased nursing of offspring by Roosevelt Elk (*Cervus elaphus roosevelti*). Inconsistent findings in studies of maternal investment in *C. elaphus* spp. warrants further investigation. The objectives of this study were to: 1) describe the progression of nursing behavior of Roosevelt Elk calves, and 2) determine whether individual differences in nursing behavior were related to calf gender.

METHODS

Study Area

We conducted observations of nursing behavior between 25 May and 6 November 2000 in Sinkyone Wilderness State Park located in Mendocino County, California. The park, established in 1983, covers 2981 ha of coastal coniferous forest and coastal meadows, and is characterized by rugged terrain and elevations ranging from sea level to 610 m. Climate in this area is typified by warm springs and autumns, rainy winters, and foggy, cool summers. The park comprises approximately 20 km of coastline with no road access to the coast, except in the extreme northern and southern ends. The Roosevelt Elk herd in the park has approximately 60 to 80 individuals with an adult male to female sex ratio of approximately 0.28:1 (Wengert 2000). The study site is located in the northern part of the park along the coast in an area of approximately 8 km by 1 km. The Pacific Ocean is the western boundary of the study site, while the entire eastern edge consists of steep coniferous forest slopes. All observations took place in coastal meadows and associated riparian areas within the study site.

Nursing Behavior Observations

We used focal animal observation to record 211 h of nursing behavior for 4 male and 4 female Roosevelt Elk calves born between 24 May and 22 June 2000. Observation techniques were approved by Humboldt State University's Institutional Animal Care and Use Committee. At the 1st appearance of each newborn calf, we identified animals using natural markings (Bateson 1977; Weckerly 1998). Anogenital characteristics were used to determine calf sex. Exact birth dates of 3 calves were known through direct observation; ages of the other 5 were estimated to the nearest week based on size comparisons to calves of known birth date (Kristan 1993) and the date they joined the herd, usually at 18 to 20 d old (Altmann 1963).

Two to 10 observation sessions for each mother-calf pair were conducted at each age-class of the calf, once to twice every 10 to 15 d. We designated age-classes consisting of 14-d periods starting at 10 d (the youngest estimated age that any calf was observed), with age-class 1 including calves at age 10 to 23 d, age-class 2 including calves at age 24 to 37 d, and so on.

Observations of nursing behavior were conducted between sunrise and sunset, and each observation session lasted from 1 to 7 h. We observed elk with binoculars from distances of 50 to 200 m, distances at which we could obtain accurate measures but not influence elk behavior. Observations began when the focal calf was first located (Martin and Bateson 1986), and ended when both the calf and mother went out of view or the sun set. In each session we recorded the number of suckling attempts, success of each suckling attempt, total suckling time (in seconds) in each suckling bout, the identity of the individual in the mother-calf pair that initiated and terminated the bout, and total observation time (in hours). A successful suckling attempt was defined as a movement by the calf toward the mother's teat that resulted in a suckling bout, while an unsuccessful attempt did not result in a suckling bout. A suckling bout was defined as 1 or more suckles longer than 1 s with no interruption of 15 min or more (Clutton-Brock and others 1981; Kristan 1993). The suckling bout initiator was the pair member that vocalized first or moved toward the other pair member resulting in a suckling bout (Gauthier and Barrette 1985). The suckling bout terminator was the pair member that moved away during a suckling bout while the other remained stationary.

Because Trivers and Willard (1973) suggested that differential investment in offspring might be related to condition of the mother, we made a coarse field and photo assessment of each mother's overall condition. We based this

visual assessment on Riney (1960), which took into consideration visibility of certain anatomical structures such as pelvic girdle, backbone vertebrae, and ribs. Four non-biased observers ranked each mother into poor, medium, or good condition using photos of that mother.

Statistical Analysis

Response variables for nursing behavior included (1) suckling success defined as successful suckling attempts ÷ successful + unsuccessful suckling attempts (Gauthier and Barrette 1985), (2) proportion of suckling bouts terminated by the mother, (3) proportion of suckling bouts initiated by the mother, (4) total suckling time per bout defined as seconds suckling/bout, (5) suckling rate defined as seconds suckling/h of observation, and (6) suckling attempt rate defined as suckling attempts/h of observation.

To test for differences in suckling rate, suckling time per bout, suckling success, and suckling attempt rate at different calf age-classes and between genders, we used repeated measures analysis of variance with calf as subject, age as the repeated factor, and sex as the between factor. We used Geisser-Greenhouse adjustments for probability levels in order to meet the sphericity assumption (Grieve 1984). Proportion of suckling bouts initiated and terminated by the mother at different calf ages was analyzed using Pearson product moment correlation. The differences in frequency of suckling bouts initiated by the mother between the 1st and 2nd halves of the nursing period and between genders were compared using contingency tables. All statistical analyses were performed with NCSS (Number Cruncher Statistical Software, Kaysville, UT). We defined P-values <0.05 as statistically significant.

Results

All mothers were ranked in medium to good condition and none were considered by any observer to be in poor condition at the beginning of the nursing period. Therefore, we made the assumption that condition was not a confounding influence on nursing behavior in this study.

Nursing behavior observed in 48 suckling bouts by Roosevelt Elk calves varied throughout the nursing period. Mean suckling rate ($\bar{x}$ = 90.6 s/h, $s_{\bar{x}}$ = 8.8 s/h, age-class 2) and mean suckling time per bout ($\bar{x}$ = 228.4 s, $s_{\bar{x}}$ = 15.4 s, age-class 2) of all calves were both greatest at age-class 2. Suckling rate of calves declined linearly with increasing calf age ($F_{7,42}$ = 10.04, P = 0.031, Fig. 1a). Mean suckling time per bout also decreased linearly with increasing calf age ($F_{7,46}$ = 15.46, P = 0.014, Fig. 1b). Mean suckling success was greatest at age-class 1 ($\bar{x}$ = 1.0, $s_{\bar{x}}$ = 0.0), and declined with calf age ($F_{6,41}$ = 13.79, P = 0.024, Fig. 1c). Mean suckling attempt rate was greatest at age-class 6 ($\bar{x}$ = 2.15 attempts/h, $s_{\bar{x}}$ = 0.5 attempts/h) but was not significantly different among calf ages ($F_{7,43}$ = 0.66, P = 0.553, Fig. 1d).

The difference between genders in mean suckling rate was significant ($F_{1,42}$ = 6.24, P = 0.047, Table 1, Fig. 1a) as was the difference in mean time per suckling bout ($F_{1,46}$ = 14.87, P = 0.008, Table 1, Fig. 1b). Mean suckling success ($F_{1,41}$ = 0.31, P = 0.599, Table 1, Fig. 1c) and mean suckling attempt rate ($F_{1,43}$ = 0.27, P = 0.620, Table 1, Fig. 1d) did not differ between genders. The interaction term for gender and age-class was marginally non-significant for suckling time per bout ($F_{7,46}$ = 7.13, P = 0.051, Fig. 1b).

The proportion of suckling bouts initiated by the mother was not significantly correlated with calf age-class (r = −0.435, P = 0.282, Fig. 2). However, the likelihood of a mother initiating a suckling bout during age-classes 1 to 4 was significantly greater than the likelihood in age-classes 5 to 8 (X^2 = 6.76, df = 1, P = 0.009). Mothers were equally likely to initiate suckling bouts for female calves as for male calves (X^2 = 0.76, df = 1, P = 0.383). The proportion of suckling bouts terminated by the mother increased from 0.67 at age-class 1 to 1.0 at age-classes 4 through 8 and was significantly correlated with calf age-class (r = 0.829, P = 0.011, Fig. 2). Forty-four of 48 observed suckling bouts were terminated by the mother (Fig. 2), and mothers were equally likely to terminate suckling bouts for male calves as for female calves (X^2 = 1.31, df = 1, P = 0.252).

Discussion

The conflict between a mammalian mother and her offspring over the nursing period should increase resulting in decreased maternal investment (Trivers 1974). Our results are consistent with predictions from parental investment theory and many other studies on maternal investment in ungulates that found a

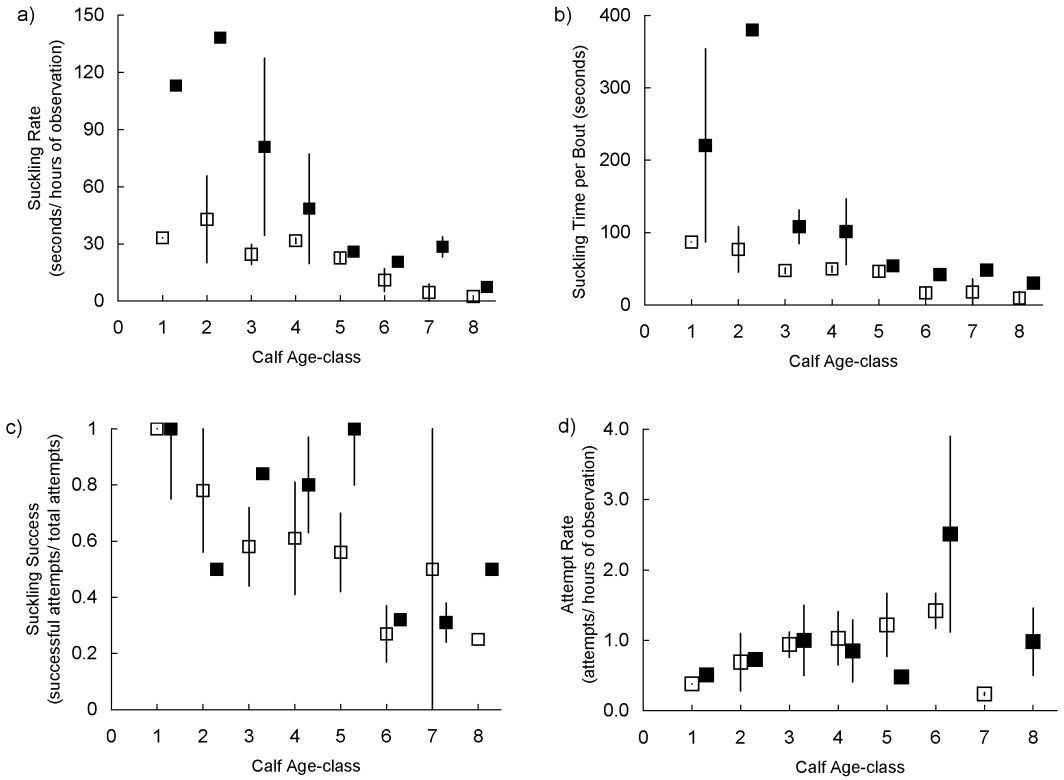

FIGURE 1. Changes in nursing behaviors (means) through the first 17 weeks of the nursing period for male (black squares) and female (white squares) Roosevelt Elk calves in Sinkyone Wilderness State Park, Mendocino County, CA, summer of 2000: a) suckling rate, b) suckling time per bout, c) suckling success, and d) suckling attempt rate. Error bars indicate ±1 *SE*. For values with no error bars, $n = 1$.

decrease in maternal investment through the nursing period (Martin 1984; Hirth 1985; Reese and Robbins 1994). Our results indicated a decline in suckling from 10 to 120 d of age and also supported the findings of Robbins and others (1981), who showed a peak in maternal investment by elk mothers at 21 d of age and a gradual decline over the following 60 d. We found no change in suckling attempt rate over the nursing period, suggesting that the decline in suckling success over this 120 d period was not confounded by increases in attempt rates as calves nursed less. However, attempt rates may be influenced by the calf's ability to supplement nursing with foraging (Cassinello 2001), an activity that we did not measure.

Bubenik (1982) showed that an elk mother's focus on nursing her calf began to wane when the calves were about 70 d old. We also found that the proportion of mother-initiated suckling bouts peaked at age-class 4, where it reached 0.875 and declined until age-class 8

TABLE 1. Means and standard errors (in parentheses) of nursing behavior measures of Roosevelt Elk calves in Sinkyone Wilderness State Park, Mendocino County, CA, summer of 2000. Those values that were significantly greater for males are indicated with an asterisk.

Nursing behavior measure	Males	Females
Mean suckling rate (s/h)	57.9 (9.4)*	21.6 (8.3)
Mean suckling time per bout (s)	123.0 (13.3)*	43.9 (11.9)
Mean suckling success (successful attempts/total attempts)	0.61 (0.12)	0.51 (0.11)
Mean suckling attempt rate (attempts/h)	1.1 (0.31)	0.86 (0.27)

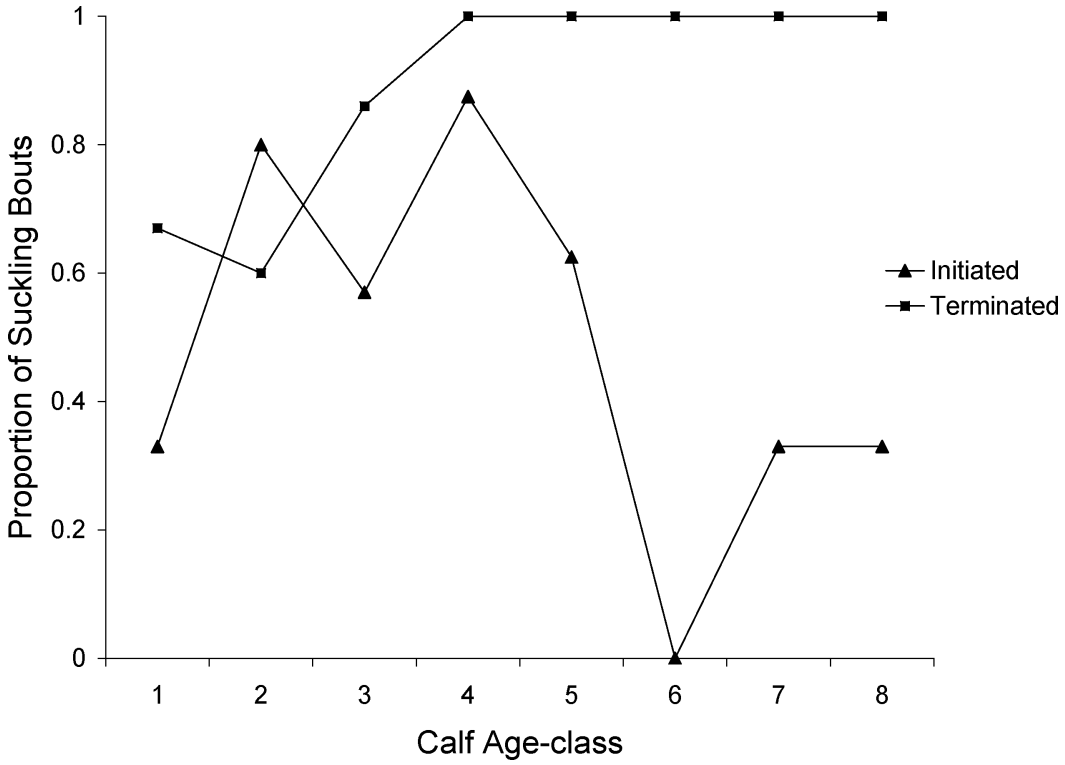

FIGURE 2. Proportion of all suckling bouts initiated and terminated by the mother in Roosevelt Elk in Sinkyone Wilderness State Park, Mendocino County, CA, summer of 2000.

(Fig. 2), though the decline over the nursing period was not significant. All but 4 suckling bouts were terminated by the mother, and in a majority of these instances we observed calves attempting to continue nursing. This behavior implied that the calf was not satiated and that it was the mother who determined the level of investment.

Hypotheses concerning differential maternal investment in genders are often specific to only 1 or a handful of closely related species (Trivers and Willard 1973; Smith 1980; Emlen 1997). Even within a species, no single theory can hold true in all situations of maternal investment in offspring, as environmental and physiological conditions may alter the expression of differential maternal investment (Festa-Bianchet 1988; Kojola 1998; Kohlmann 1999). Red Deer, a highly polygynous species, are reported to express differential maternal investment based on gender (Clutton-Brock and others 1981). Our results support this hypothesis and include observed differences in suckling rate and suckling bout length between male and female calves. These measures may have been biased by potential differences in the amount of milk obtained per second between male and female suckling times. Male Fallow Deer (*Dama dama*) fawns obtain more milk per second than females (Birgersson and others 1998). If Roosevelt Elk male calves suckle longer and also receive more milk per second than females, then gender differences in maternal investment could be greater than our results indicate. However, without actually measuring milk intake, possibly through doubly-labeled water, it is difficult to determine whether suckling behaviors are exactly representative of milk transfer.

Our results were unlike those found by Kristan (1993) in that we did find differences between genders in suckling rate and time per bout. However, Kristan (1993) did not present data on the condition of the mothers, and variation among females in body condition may confound results for differential investment through nursing. Some of our results were sim-

ilar to Kristan (1993) in that we found no differences in suckling success between male and female calves. Though suckling success could be influenced by differences in attempt rate (Festa-Bianchet 1988), we found no difference in attempt rate between male and female calves. Because male calves suckled longer, they may not have been compelled to attempt suckling more often than females.

The marginal statistical interaction between calf gender and suckling bout length indicates that the rate of decrease in maternal investment through the nursing period was different between the genders. Our results suggested that this interaction was driven by the large gender difference in nursing behaviors in the early nursing period (10 to 50 d), and a convergence of suckling rates in the later nursing period (50 to 120 d). In fact, the early nursing period was the only time when there was a difference in nursing behaviors between the genders. Perhaps the short period in which differential maternal investment occurred has special significance in the growth or social development of a male calf. It may be this period when extra nutritional investment has the most impact on his condition at weaning, his ability to maintain a healthy growth rate, or his social status among his male cohort. Analysis of these factors may help to explain why and when differential investment is important for male fitness over the long term.

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