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Maternal investment in sons and daughters: problems of methodology

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Summary. The prediction that mothers should invest more in sons than daughters was briefly examined in American bison (*Bison bison*) by Wolff (1988). He concluded that (a) male calves suckle more than females, (b) cows that had previously produced sons were more likely to be barren, and (c) cows that had male calves became estrous later in the year than other cows. In this paper we present data from two long term studies at different sites to show that Wolff's conclusions are equivocal at best and difficult to reconcile with predictions of the hypothesis because of questionable methods and assumptions.

Introduction

In polygynous mammals, mothers should invest more in sons than daughters to the extent that fitness is related to competitive ability in males but not in females (Trivers and Willard 1973; Maynard Smith 1980). This prediction has been examined in numerous species (e.g., Reiter et al. 1978; Clutton-Brock et al. 1981; Small and Smith 1984; Lee and Moss 1986; Trillmich 1986; Le Boeuf et al. 1989; McCann et al. 1989; Byers and Moodie 1990; Byers and Bekoff 1990); while some of these studies provide support, others do not.

Recently this prediction was examined by Wolff (1988, p 131), who found that "male American bison (*Bison bison*) apparently cost more to raise than do female calves." This conclusion was based on three sets of data that were interpreted as follows: (1) male calves suckled longer than females, (2) cows that produced sons the previous year were more likely to be barren in the current year than were cows that previously had daughters, and (3) cows that produced sons came into estrus later in the year than other cows.

We believe that Wolff's interpretations are unconvincing for reasons outlined below. Our goal is to identify problems of methodology and interpretation that may obscure the evaluation of sex-biased investment. Using our own data from two long term studies, we evaluate Wolff's methods for estimating calf age, suckling time, subsequent maternal reproductive status (in relation to sex of previous offspring), and estrus date.

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Methods

Bison were studied for 8 years (1982–1989) at Wind Cave National Park (WCNP; Green 1986, 1987; Green et al. 1989; Rothstein 1988; Green and Rothstein, in review) and 5 years (1985–1989) at Badlands National Park (BNP; Berger and Cunningham 1988; Berger and Kock 1988; Berger 1989), both in South Dakota, USA. The two sites are about 80 km apart, differing in some habitat characteristics. WCNP is situated at the interface between the Black Hills and the short-grass prairies, whereas BNP is drier, at lower altitude, and lacks forested areas. The WCNP bison population fluctuates between about 300 and 400 animals, due to biennial culling at roundups; at BNP, the population increased from about 300 to 775 between 1985 and 1988 in the absence of culling. The populations range over 114 km^2 (WCNP) and 250 km^2 (BNP).

Individuals at both study sites were identified through eartags and by natural variation in horn and hair growth, body shape, and coloration. Since juveniles are particularly difficult to recognize, some were marked temporarily with hair bleach at WCNP, using a bow and blunt arrows. At BNP, more than 200 individuals were known. All 145 females born before 1984 at WCNP were recognized and observed throughout the study. Birth dates during 1982–1984 for all WCNP calves were known to within 3 days, based on observed births or estimated from the last date on which the mother was previously seen and the calf's coordination and state of the umbilicus when first seen. For analyses, birth dates were grouped into weeks. All probabilities reported below are two-tailed.

Biases and evaluation of data

Calf age and suckling time

Wolff collected data during a 2.5-month period, beginning at least 1 month after the start of the calving season (see Rutberg 1984). His finding that male calves spent

more time suckling than females is questionable because the ages of the calves were unknown. Suckling time changes dramatically during the first few months; for example, female bison calves spend only 67% as much time suckling in the second month as in the first (Green 1986, 1987; see also Clutton-Brock et al. 1982 on *Cervus elaphus,* and Berger 1986 on *Equus caballus*). Because birth dates were unknown, Wolff estimated calf age by body size and coat color. Bison calves moult during the first few months, changing from rusty orange to the dark brown of adults. Wolff placed calves in two age categories based on their size and coat color as of August 1: small and "red-brown" or large and "brown-black."

Ages estimated from calf appearance are likely to be inaccurate for several reasons. In addition to the obvious problems associated with assuming age differences in calves of varying size, coat color does not change predictably with age in bison calves. At WCNP, the age at which 13 female calves began moulting varied from 5 to 14 weeks. During weeks 5–14, mean suckling time (bout duration/interbout interval) decreased by 45%. Thus, estimated suckling time based on coat color has little meaning. Moreover, specific biases are likely to occur. The age at which moulting was 90% complete was significantly related to birth date; calves born later moulted earlier ($r_s = -0.413$, $n = 23$, $P = 0.05$). Therefore, the appearance of later-born calves at 2 months of age may be similar to that of early-born calves at 4 months.

Without knowledge of calf age, Wolff was unable to control for sex differences in the time of birth. Although he stated that calf sex ratios did not differ significantly between the two age groups, his age-determination methods were not sufficiently precise to rule out the possibility that male calves suckled more because they were younger. That this may have been the case is suggested by the finding that, as shown in Fig. 1, male calves ($n = 78$) were born somewhat later than females ($n = 75$) at WCNP in 1982–1984 (Mann-Whitney U-test; $z = -1.74$, $P = 0.083$); data for each of the 3 years alone showed similar patterns.

The ability to control for calf age in examining patterns of maternal investment is also important in that benefits to offspring may vary greatly during the pre-

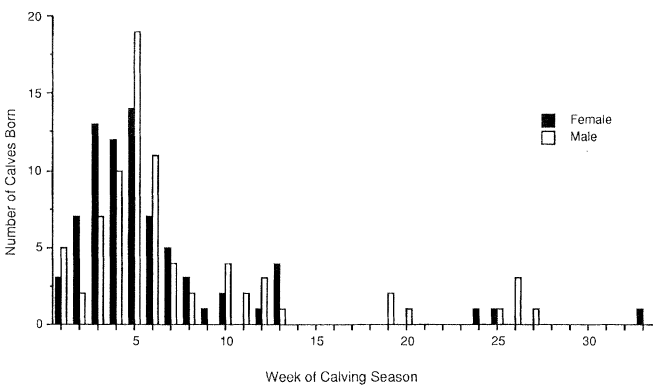

Fig. 1. Numbers of male and female calves born in each week of the calving season at WCNP in 1982–1984

weaning period. Early suckling time appears to be of particular importance at least for daughtes, perhaps in relation to peak lactation, which occurs in weeks 3–4 in domestic cattle (Oftedal 1985). For example, suckling time in the first month is correlated with the dominance rank of female bison during the first 2 years ($r_s = 0.793$, $n = 13$, $P < 0.01$). Data for a small sample also suggest that daughters with above- versus below-average early suckling time become more fecund (percentage of years in which calves were produced, age 2–6: $94.1 \pm 8.6\%$ vs $55.7 \pm 6.5\%$; $F = 4.93$, $df = 1,6$, $0.05 < P < 0.1$). In contrast, suckling time during months 1–5 was not significantly related to daughters' dominance ($r_s = -0.121$, $n = 13$, NS) or fecundity ($r_s = 0.077$, $n = 7$, NS). Similarly, growth rate in domestic lambs of both sexes was correlated with suckling frequency in the first 3 weeks but not later (Ewbank 1967).

Analysis of suckling data

Wolff's estimates of suckling time are weakened by his reliance on data pooled from identified and unidentified individuals. Because the sexes did not differ significantly in suckling frequency (interbout intervals), only bout duration was used to examine differences in suckling time. However, because data were pooled, the same individuals did not necessarily contribute to both bout duration and frequency. Animals that suckle less often tend to contribute fewer observations. Those with long interbout intervals usually require a long waiting period before the first nursing bout occurs and an even longer wait for the second bout; such intervals (and bouts) are therefore relatively unlikely to be sampled (see also Wehausen 1980). As a result, this method of measuring suckling time is likely to be biased toward animals that suckle more frequently. Suckling frequency decreases with age (i.e., interbout intervals increase); this pattern is reflected in Wolff's results for both sexes as well as in data on female calves at WCNP (ANOVA with months 1–5 as repeated measures: $F = 13.57$, $df = 4,32$, $P < 0.001$). If Wolff's male subjects were somewhat younger than the females, his finding that both sexes suckle at similar frequencies suggests that at the same age, females may suckle more frequently than males.

In measuring suckling time it is important to subtract interruptions in suckling from bout duration (see Green 1986), which Wolff apparently did not do, nor did he define suckling bout. Interruptions may account for substantial proportions of total bout length. For example, among 13 female calves at WCNP, intrabout pauses (while mothers continued to stand) totalled up to 160 s per bout. Mothers also moved up to 30 times per bout, each movement interrupting nursing for one or more seconds. The extent of such interruptions comprised a particularly variable aspect of nursing behavior. In the first month, for example, the mean and standard deviation for the total duration of calves' pauses per bout was 19 ± 24 s. While data on males are not available, this suggests that intersexual comparisons of suckling

time may be affected by individual variation in the proportion of time spent suckling during bouts.

Wolff's conclusions may also have been confounded by age-related differences among cows in nursing time. He made the assumption, based on Green (1986), that nursing time is comparable in cows aged 3–7 years. However, Green found that 3- and 4-year-old cows spent less time nursing their calves than did cows aged 7 and older. Whether 5- and 6-year-olds differ from those younger and older is unknown. Since body weight increases by about 5% annually in these age classes (see also Berger and Peacock 1988), it seems likely that milk production increases as well (based on data from domestic cattle: Dodd 1957; Oftedal 1985).

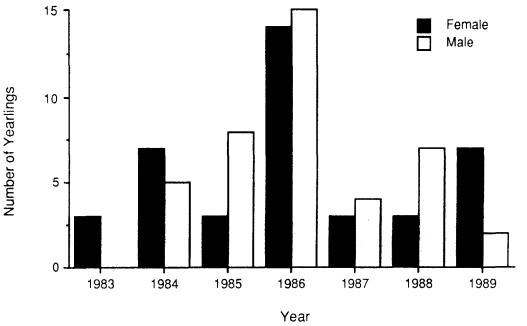

Fig. 2. Numbers of male and female yearlings whose mothers were barren at WCNP in 1983–1989

Fecundity and sex of previous offspring

Wolff stated that cows were barren more often after bearing male than female calves, indicating that sons cost more to produce. Four male and 16 female yearlings were reported to follow parturient cows (i.e., with new calves), whereas 9 male and 2 female yearlings were seen with barren cows. Wolff's conclusion was based on three assumptions: (1) the probability of a yearling's associating closely with its mother is independent of offspring sex and maternal reproductive status, (2) all yearlings that followed cows were their offspring, and (3) the ratio of sons to daughters produced by subsequently barren cows in a given year reflects patterns of sex-biased investment. One problem here is that Wolff did not define "following" or provide documentation for the mother-offspring associations on which (1) and (2) were based. More importantly, however, none of these assumptions is supported by more detailed examination.

1. The frequency with which yearlings associate with their mothers clearly depends on offspring sex as well as on maternal reproductive status. Since barren cows generally continue to nurse their yearlings, while parturient cows wean their offspring before calving again, the former dyads associate more closely and consistently than the latter (Green et al. 1989). After weaning, daughters associate with their mothers much more frequently than do sons. For example, 18 females spent 85% more time in the same groups with their mothers than with (randomly selected) control cows during their second year, whereas 13 males were observed in groups with their mothers only 3% more than with controls (Green et al. 1989; Rothstein, unpublished data). Thus, Wolff's observed sex ratio of yearlings with parturient cows (4:16) is not a reasonable representation of the calves born to all such cows in the previous year, but is likely to be biased toward females.

2. Yearlings may associate consistently with cows other than their own mothers. Some female and, to a lesser extent, male yearlings 'adopt' cows other than their mothers, particularly when their mothers are dead or close to term. For example, six females (out of 35 born in 1982–1983 at WCNP) maintained close, frequent and consistent contact with specific cows, just as they had with their mothers, for up to 8 months (Green 1987; Green et al. 1989). This emphasizes the fact that the only way to be sure of mother-offspring relationships is to follow subjects from early in life.

3. As with many questions of sex ratio variation, whether adult females are barren more often after bearing sons than daughters cannot be addressed in a 2.5-month study. Wolff's observation that more male than female yearlings were with barren cows is likely to have been due to year-to year variation. At WCNP, 41 male and 40 female calves were born to subsequently barren cows in the period 1982–1989. In individual years. however, the sex ratio of such offspring varied greatly (Fig. 2). Data from longer periods are clearly necessary to address this question.

Breeding date

In another test of the hypothesis that sons cost more to produce than daughters, Wolff predicted that mothers with sons should become estrous later in the season than those with daughters. The idea here is that females in relatively poor body condition enter estrus later than those in better condition (Berger 1989). Unfortunately, Wolff lacked data on estrus dates. Although he reported cumulative proportions of breeding cows (his Fig. 3, p 131), he witnessed only 10 copulations. He apparently assumed that males' tending (consorting) behavior could be used to predict when females were in estrus, reasoning that although tended females were not always in estrus, they generally became so before those not tended. The problem is that tending was not defined; therefore, it is impossible to know how male behavior was used to estimate estrus dates.

According to Lott (1974), tending occurs when a bull approaches and remains with a cow; consortships can end after a few seconds or last as long as 10 days. This being the case, the criteria used by Wolff to assess estrus are unclear. Because he could not identify many of his subjects, he based his cumulative breeding proportions on "the number of days of observations of animals... not the number of animals" (p 130). To evaluate Wolff's methods, estrus dates for 164 bison cows in BNP (Berger 1989) were reanalyzed using these criteria. More than 1400 tending events occurred among known individuals;

however, copulations took place in only 121. Non-breeding males (including those as young as 2 years old) participated in more than 1250 tending events. Copulations were also limited to shorter periods of time than were tending events. Tending is therefore a poor way to estimate the cumulative proportion of breeding females; in order to address questions of sex differences in rearing costs, it is critical to know when females are in estrus, not when they are tended.

The purpose of our paper has not been to decry the work of Wolff, who has presented some interesting data on possible ways in which mothers invest in offspring. Rather, our purpose has been to address problems of short term studies based on questionable assumptions, and of testing hypotheses about individual performance with large numbers of unidentified individuals. It may be that later studies will validate Wolff's major points. Nevertheless, we believe that the conclusions presented in his paper are not supported by the data and, therefore, are premature.

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