

greater ($P=0.03$) than the expected value for random pairing (0.50). The size differences between nestmates and non-nestmates were not significantly different ($P>0.20$), and thus size differences do not appear to account for the observed pairing ratio in group-2 males.

It is not obvious to us why we documented the ability of male *P. fuscatus* to recognize male nestmates, while Ryan et al. (1984) did not. Nor is it apparent why the nestmate preference in group-2 males was detected only after a few days of study. In Table I we give several potentially important differences in the experimental conditions for group-1 males, group-2 males, and the males of Ryan et al. (1984), which may have affected recognition.

The disparate results in Table I can be at least partially explained if male recognition ability or male preference for nestmates declines with age. (The males of Ryan et al. (1984) were considerably older than either the group-1 or group-2 males.) Alternatively, since the males of group 2 and Ryan et al. (1984) were exposed to their nestmates for a lengthy period of time prior to observations, the delayed male nestmate preference, or lack of it, may reflect the effects of habituation. Finally, males spending extended periods of time in a homogeneous laboratory environment (e.g. the males of Ryan et al. 1984 and group-2 males) may acquire common environmental odours, which might temporarily mask other recognition odours. Additional studies are required to test these and other hypotheses and to ascertain the adaptive significance, if any, of a male's ability to recognize its male nestmates.

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Instances of Female-like Behaviour in a Male Ungulate

In sexually reproducing vertebrate species, males generally differ from females in some if not numerous aspects of their behaviour, and such differences have proved valuable for naturalists to use in categorizing individuals according to sex (especially in birds). Among non-human male mammals, few cases of effeminate behaviour have been reported from wild populations, although abnormal behaviour may develop in individuals (of either sex) and for any number of proximate reasons. In this note I report several cases of female-like behaviour in wild male bighorn sheep, *Ovis canadensis*, and then suggest a possible cause for this aberrant behaviour.

Bighorn sheep were studied in Oregon, California, and British Columbia in 1976 and 1977 (Berger 1979a,b), although only in the latter study area did male sheep behave unusually. The population of approximately 400 was located in the Chilcotin region of the central interior of British Columbia, where I followed numerous bands almost daily from April into November. To indicate how several Chilcotin sheep acted anomalously, it is necessary to summarize briefly what is considered 'normal' patterns of behaviour.

In northern bighorn populations, breeding is seasonal, with males and females segregating by sex except during the rut—a period that usually extends from mid-fall into early winter (Geist 1971; Bunnell 1982). Young males typically emigrate

from ewe bands between the ages of 2 and 3 years, whereupon they often join small groups containing older rams (Geist 1971). Although subtle variations upon this theme occur, observations on other populations substantiate the above scenario (Shackleton 1973; Wehausen 1980, and references therein). Differences in the dispersion of the sexes have been noted, and these arise primarily because of ecological conditions. For instance, in desert environments breeding periods are longer than in northern mountains (Berger 1982; Bunnell 1982), and desert rams tend to associate with females for longer periods of time than in northern bighorns (Lenarz 1979). However, the overall picture that emerges from studies of northern bighorns is that they are seasonal breeders and the sexes are segregated throughout much of the year (Geist 1971; Shank 1982).

In the Chilcotin sheep that I observed, over 50% of the rams whose horns curled half way around their heads (e.g. class II rams of Geist 1971), more than 90% of the class III (e.g. horns curled 3/4 of the way), and all full-curved rams were segregated from ewe bands prior to the fall rut. Periodically, some larger rams appeared with ewe groups during the spring and summer, but none ever remained longer than 3 days. This agrees well with Geist's (1971) portrayal of northern bighorn society. However three rams, A, B and C (whose ages I estimated to be 2-3, 3-4, and 4-5 years respectively on the basis of their horn sizes) deviated considerably in their behaviour from that of other rams of similar ages. Instead of dispersing and joining other rams, individuals A-C remained in ewe bands. These rams, all individually recognizable, were repeatedly observed throughout the study. Two were in basically the same home area and the third used a different home range. Individuals B and C were the largest members observed regularly in ewe groups; in fact, all three of these rams were larger in both horn and body size than some rams which were found in all ram groups. Thus these three rams differed from others of similar size and age in that they failed to emigrate.

Rams A, B and C also differed from other similarly-aged males in interactions with conspecifics of either sex. All three dominated ewes only about 50% of the time ($N=51$ feeding displacements), whereas smaller rams who had been segregated from ewe bands dominated adult females in over 85% of their feeding encounters ($N=41$; $\chi^2=12.03$, $df=1$; $P<0.001$; heterogeneity test of 2×2 contingency table, see Zar 1984). Rams A-C were not as able to supplant females as were rams who had previously lived within ram bands.

Additionally, despite their advantages in body and horn size, A, B and C were subordinate to

smaller and younger rams who had lived away from ewe groups. At least once, individuals A and C each adopted crouched (female-like) urination postures during or immediately after aggressive interactions with both larger and smaller rams, rather than assuming the traditional male-stretched urination posture described by Geist (1971). It may not be unusual that males of both bighorn and barbary sheep (*Ammotragus lervia*) occasionally indicate submissiveness by adopting female urination stances (Geist 1971). What is different here is that when A and C urinated in female postures, it was in response to conspecifics of varying sizes, not only larger ones as had been found previously (Geist 1971).

Besides failing to disperse, reacting submissively to females and smaller males, and occasionally adopting female-like urination postures, individuals A-C were not very aggressive. They also differed significantly from other males in the behaviour patterns they used. Similar-sized rams that had lived regularly in ram bands tended to stand during interactions when approached by larger males, but rams A-C withdraw significantly more often ($N=122$; $\chi^2=27.90$; $df=1$; $P<0.001$). Since the extent to which ewes withdrew from larger rams was not quantified, it remains unknown whether rams A-C were supplanted in a proportion similar to that of females. However, Geist (1971, page 161) stated that 'Whereas small rams stand and allow larger ones to display or even mount them, non-oestrous females withdraw'. In this respect, the three non-dispersing Chilcotin rams were once again effeminate in their behaviour since they avoided interactions in much the same ways as did non-oestrous females.

Hence, on the basis of the above four factors, individuals A-C were not 'normal' rams, despite the attainment of half and nearly 3/4 curled horns, and the associated body and chest size development. Effeminate behaviour in males from natural populations of non-human mammals has not been described (to my knowledge), and whether or not it may be adaptive remains to be seen.

There is no simple way to determine the causes of such behaviour, and numerous speculations are possible. Perhaps androgen levels were abnormally low in rams A-C. If this were true, it is unclear whether androgen levels were low since birth or whether normal hormonal secretions became interrupted at some point during later growth. If a hormone deficiency hypothesis was correct in explaining the low levels of 'male-like' behaviour observed in several Chilcotin rams, then one still needs to explain why physical maturation had progressed (since body and horn growth continued) but associated social processes had not.

Additional study of the behaviour of known individuals in natural and experimental settings and the establishment of endocrinological profiles may provide the answers.

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