

THE EVOLUTION OF HORNEDNESS IN FEMALE RUMINANTS

by

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Summary

Females of many ruminant species possess horns or hornlike organs, but their precise function remains largely unclear. In this paper, four previous explanations for female hornedness are compared with a new hypothesis, the Female Competition Hypothesis, which suggests that horns initially evolved for reasons of intrasexual competition for resources with conspecifics, the level of competition being correlated with female group size. Each hypothesis is first reviewed and necessary predictions arising from each are generated. In order to test between these hypotheses, the incidence of female hornedness across the ruminants is then examined using a comparative method which takes account of the evolutionary history of each species, in order to control for effects of phylogenetic correlation. Group size and body size are found to be the only variables which predict hornedness successfully; however, when the influence of the other predicting variable is removed, only group size remains as a significant predictor. This analysis is found to support the Female Competition Hypothesis and is shown to be robust both in relation to adjustments in phylogenetic construction (e.g. the position of *Aepyceros* and *Booceros*) and to intraspecific variation in horned condition (e.g. horned and hornless races of *Oreotragus*).

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Introduction

Overview

The extraordinary appearance and diversity in form of cranial appendages have long been a source of fascination for ungulate biologists. An extensive literature has accumulated which documents the occurrence of cranial appendages in both fossil and living taxa and proposes a variety of functional explanations for their evolution. Attention has primarily been focused on males, in which appendages are more common, larger and often more complex than in females of the same species. In males at least, it is generally accepted that these structures (including true horns, antlers and hair-covered ossicones but hereafter termed horns, *sensu* Geist, 1966) function as weaponry for intra-specific combat (Darwin, 1871; Walther, 1958; Geist, 1965, 1966, 1968; Bubenik, 1968; Barrette, 1977; Clutton-Brock, 1982; Clutton-Brock *et al.*, 1980; Packer, 1983) which may win greater access to receptive females for high-calibre males (Clutton-Brock *et al.*, 1982). In the modern cervids and bovids, for example, horn size relative to body weight is larger in polygynous species, as variance in male mating success increases and male-male competition becomes more intense (Clutton-Brock *et al.*, 1980; Popp, 1985).

In comparison, the evolution of hornedness in females has received little interest. One consequence is that, in contrast to males, no general consensus regarding functional explanations exists. The three most recent attempts (Packer, 1983; Kiltie, 1985; Estes, 1991b) to explain the occurrence of female weapons have each reached a different conclusion. In this paper, I examine the evolution of horns in females of the families of higher ruminants in order to test between existing hypotheses. In contrast to previous studies, I use a comparative method which takes account of the evolutionary history of each species (Pagel & Harvey, 1988, 1989; Harvey & Pagel, 1991) in order to control for effects of phylogenetic correlation which may have partially confounded previous cross-specific comparisons (see Clutton-Brock & Harvey, 1984; Berger, 1988). The findings of this analysis are then applied to the problem of female hornedness in the East African race of *Oreotragus*.

Classification

This paper considers female horn evolution in families of the higher ruminants (infraorder *Pecora*, Linnaeus, 1758), which are distinguished from the primitive traguloid ruminants by larger body size and possession of horns amongst all living species except the Moschidae (Janis, 1982). The relationships of the pecoran families have been discussed by Webb & Taylor (1980), who regarded the possession of horns as a synapomorphy uniting eupecoran families and placed the hornless Moschidae as a sister-group to the *Eupecora*. More recently it has become clear that horns have evolved several times in parallel (Janis, 1982; Leinders, 1983; Scott & Janis, 1987) and that their presence is in fact not a synapomorphy among the *Ruminantia* (Janis & Scott, 1987). I therefore follow Janis & Scott (1987) by including among the living *Pecora* the following five families: Giraffidae, Bovidae, Antilocapridae, Cervidae and Moschidae. A cladogram illustrating the inter-relationships of these families is shown in Fig. 1.

The classification of the Bovidae has provided considerable problems for systematists in the past (Simpson, 1945) and although the growing use of cladistic, biochemical and genetic methods is beginning to aid its resolution (e.g. Lowenstein, 1986; Miyamoto *et al.*, 1989; Georgiadis *et al.*, 1991; Gentry, 1992; Gatesy *et al.*, 1992) present classifications remain some-

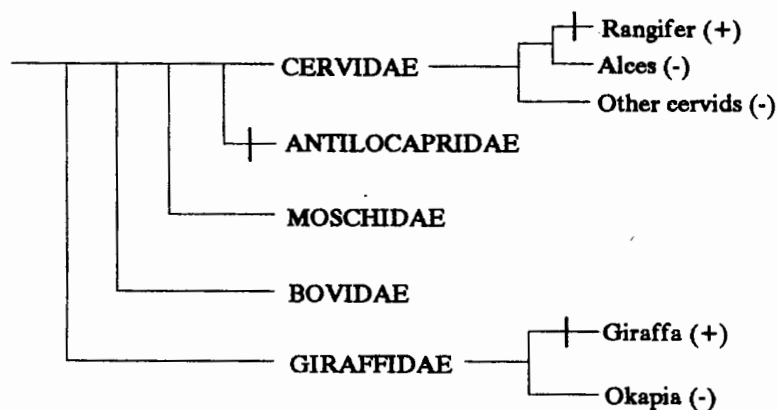


Fig. 1. Cladogram of the extant pecoran families (after Janis & Scott, 1987). Bars denote evolutionary events at which horns became expressed. (+) signifies horned females; (-) shows that females are hornless.

what unsatisfactory (Gentry, 1992). In this analysis, I have adopted the most recent summary of tribal phylogeny (Fig. 2), which comes from the cladistic and phenetic analyses of Gentry (1992). In this classification the position of five genera (*Pantholops*, *Oreamnos*, *Capricornis*, *Nemorhaedus* and *Rupicapra*) remain undetermined, and these are not considered here. Generic classification follows Nowak & Paradiso (1983), with the exception of *Aepyceros* which is taken from the *Alcelaphini* and placed within the tribe *Aepycerotini* (after Gentry, 1992). The position of *Rangifer* as closest to *Alces* within the cervids is that advocated by early morphological (Frick, 1937) and more recent classifications (Baccus *et al.*, 1983; Gustafson, 1985; but see Groves & Grubb, 1987), including those based on genetic evidence (Cronin, 1991).

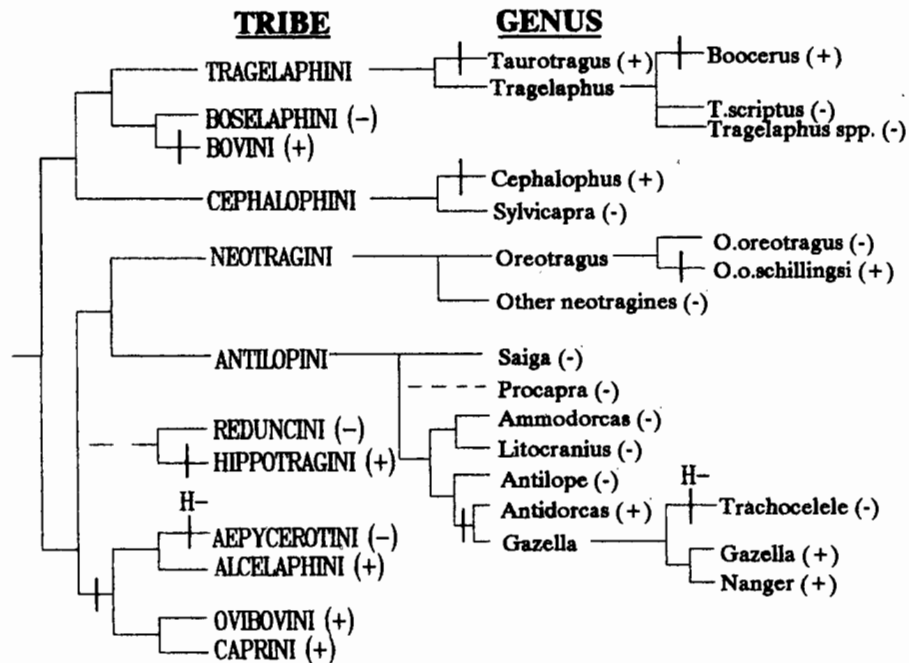


Fig. 2. Phylogeny of the Bovidae. Tribal relationships, and generic relationships in the Antilopini, are from Gentry (1992). Bars marked H- denote events where a reversal to hornlessness is probable.

Taxonomic distribution of hornedness

Kiltie (1985) has reviewed the taxonomic distribution of horns and horn-like organs in recent ungulate genera. He notes that the horned or hornless condition amongst females is essentially uniform at the generic level (see also Packer, 1983). For example, 22 of 60 pecoran genera in which males are horned contain only horned females, while 34 are exclusively hornless. Within the bovids, of a total of 41 genera from 12 tribes, 19 genera in 8 tribes contain only horned females while 18 genera from 6 tribes contain only hornless females (see Table 1).

Intragenetic polymorphism in hornedness is rare but occurs in five bovid genera. Most species of *Cephalophus* have horned females, but populations of *C. maxwelli* and *C. monticola* contain some hornless females (Aeschlimann, 1963; Ralls, 1973; Kingdon, 1982). Only one of eleven races of *Oreotragus oreotragus* has horned females (Stevenson-Hamilton, 1947; Haltenorth, 1963; Kingdon, 1982). *Gazella* contains ten female horned species, and intraspecific variation in only one, *G. subgutturosa*, in which only the Arabian populations have horned females (Nowak & Paradiso, 1983; Habibi *et al.*, 1993). Some populations of *Ovis orientalis musimon* also have hornless females (Schaller, 1977). The last case, *Tragelaphus*, is included in this section by virtue of the position of *Boocerus* as a subgenus of *Tragelaphus*, which is not the case in some other classifications. The other six species of *Tragelaphus* are all female hornless.

Amongst non-bovid families there are two other documented examples of polymorphism in hornedness: *Rangifer tarandus* (Lent, 1965a; Geist & Bromley, 1978) and *Antilocapra americana* (O'Gara, 1969). Whilst several other cervid and bovid species are sometimes recorded as possessing horns in females at a very low frequency in the population (*e.g.* *Odocoileus*: Dixon (1927), Berry (1932), Cowan (1946), Wislocki (1954, 1956), Doutt & Donaldson (1959); *Alces*: Henshaw (1968); *Cervus*: Murie (1951); *Capreolus*: Tegner (1951); *Ovis*: Jensen *et al.* (1988); *Aepyceros*: Benzon (1935); *Kobus*: Jenkins (1929), Buechner *et al.* (1968); *Redunca*: Venter (1984)), it seems that these isolated cases are in some way aberrant manifestations of a latent ability to produce them, possibly as a result of abnormally high androgen levels (Henshaw, 1968; but see Lincoln & Tyler, 1992). Although examples of this phenomenon are more common in the North American cervids, this is perhaps a consequence of interest gener-

TABLE 1. *The incidence of female hornedness and socioecological variables found in pecoran genera^a (adapted from Kiltie, 1985)*

Taxa	Female horns ^{b,c}	Body weight (kg) ^d	Shoulder height (mm) ^d	Habitat ^f	Food ^g	Group ^g	Typical group size ^e	Maximum group size ^e	Sexual assoc. ^f
Bovidae									
Boselaphini									
<i>Boselaphus</i>	0	216	1080	2	2	2	6	10	2
<i>Tetracerus</i>	0	19	600	2	1	1	1	2	3
Bovini									
<i>Bubalus</i>	X	950	1700	2	3	3	133	251	3
<i>Syncerus</i>	X	700	1350	2	3	3	266	2000	1
<i>Bos</i>	X	692	1479	1	2	2	17	525	3
<i>Bison</i>	X	675	1750	2	2	3	57	200	2.5
Tragelaphini									
<i>Tragelaphus</i>	0	137	1050	2	1	2	10	20	3
<i>Boocerus</i>	X	185	1250	1	1	2	9 ^g	44 ^g	3
<i>Taurotragus</i>	X	700	1400	2	1	3	34	600	3
Cephalophini									
<i>Cephalophus</i>	X [†]	35	550	1	1	1	1	2	3
<i>Sylvicapra</i>	0	18.5	575	2	1	1	1	2	3
Neotragini									
<i>Oreotragus</i>	0 [†]	13.5	525	3	1	2	2	3	1
<i>Ourebia</i>	0	17.5	600	3	3	2	3	5	1
<i>Raphicerus</i>	0	10.5	500	2	2	1	1	2	3
<i>Neotragus</i>	0	8.5	300	1	1	1	1	2	3
<i>Madoqua</i>	0	4.5	355	2	1	1	2	2	1

TABLE 1. (Continued)

Taxa	Female horns ^{b,c}	Body weight (kg) ^d	Shoulder height (mm) ^d	Habitat ^e	Food ^e	Group ^e	Typical group size ^e	Maximum group size ^e	Sexual assoc. ^f
<i>Dorcatragus</i>	0	10	630	3	2	2	4.5	7	1
<i>Pelea</i>	0	25	748.5	3	3	2	7	30	3
Antilopini									
<i>Antilope</i>	0	37	812	3	3	3	23	129	3
<i>Ammodorcas</i>	0	30.5	826	3	1	2	3	9	3
<i>Litocranius</i>	0	43.5	975	3	1	2	4	7	3
<i>Antidorcas</i>	X	34	800	3	2	3	28	2000	2
<i>Gazella</i>	X†	48.5	800	3	2	3	12	274	2
<i>Procapra</i>	0	30	690	3	2	3		8000	3
<i>Saiga</i>	0	47.5	700	3	2	3	35	9000	2.5
Reduncini									
<i>Kobus</i>	0	175	1020	2	3	3	24	370	2.2
<i>Redunca</i>	0	57.5	825	3	3	2	6	10	3
Hippotragini									
<i>Hippotragus</i>	X	180	1040	2	3	3	14	65	3
<i>Oryx</i>	X	155	1150	3	3	3	23	800	1
<i>Addax</i>	X	92.5	1050	3	3	3	20	200	1
Aepycerotini									
<i>Aepyceros</i>	0	42.5	887.5	2	2	3	55	200	2.5
Alcelaphini									
<i>Damaliscus</i>	X	102	1040	2	3	3	17	606	2
<i>Alcelaphus</i>	X	162.5	1300	2	3	3	13	1400	2.5
<i>Connochaetes</i>	X	207.5	1225	3	3	3	49	1100	2

TABLE 1. (Continued)

Taxa	Female horns ^{b,c}	Body weight (kg) ^d	Shoulder height (mm) ^d	Habitat ^c	Food ^c	Group ^c	Typical group size ^e	Maximum group size ^e	Sexual assoc. ^f
Ovibovini									
<i>Budorcas</i>	X	252.5	915	2	2	3	8 ^h	100	2
<i>Ovibos</i>	X	305	1355	3	2	3	15	100	2
Caprini									
<i>Hemitragus</i>	X	75	835	2	2	3	4	23	3
<i>Capra</i>	X	84	850	2	2	3	13	100	3
<i>Pseudois</i>	X	52.5	830	3	2	3	11	400	3
<i>Ammotragus</i>	X	47.5	935	3	2	2			3
<i>Ovis</i>	X	110	960	2	2	3	4 ⁱ	100	3
Giraffidae									
<i>Giraffa</i>	X	800	3100	2	1	2	6	100	3 ^j
<i>Okapia</i>	0	225	1600	1	1	1	1	2	1
Antilocapridae									
<i>Antilocapra</i>	X [†]	48	832.5	3	2	3	23	1000	3
Cervidae									
<i>Muntiacus</i>	0	21	515	1	2	1	1	4	3
<i>Elaphodus</i>	0	33.5	600	1	2	1	1	2	3
<i>Dama</i>	0	70	925	2	2	2		30	
<i>Axis</i>	0	68.5	800	2	2	3	7.5	200	2

TABLE 1. (Continued)

Taxa	Female horns ^{b,c}	Body weight (kg) ^d	Shoulder height (mm) ^d	Habitat ^f	Food ^f	Group ^f	Typical group size ^e	Maximum group size ^e	Sexual assoc. ^f
<i>Cervus</i>	0	129	875	2	2	2	57	750	3
<i>Elaphurus</i>	0	175	1150		2				2
<i>Odocoileus</i>	0	118.5	825	2	2	2	4		2
<i>Blastocerus</i>	0	125	1150	2	2	2	3.5	6	1
<i>Ozotoceras</i>	0	35	725	2	2	2	3		3
<i>Hippocamelus</i>	0	55	785	1	2	2		8	1
<i>Mazama</i>	0	16.5	550	1	2	1	1	2	3
<i>Pudu</i>	0	8.5	367.5	1	2	2			
<i>Alces</i>	0	512.5	1875	2	2	1	1	24 ^k	3
<i>Rangifer</i>	X	81	1135	2	2	3	6 ^l	79 ^l	2
<i>Hydropotes</i>	0	12	500	2	2	1			
<i>Capreolus</i>	0	32.5	712.5	2	2	2			2

^a Classifications are based on Nowak & Paradiso (1983), Janis & Scott (1987) and Gentry (1992).

^b X denotes females in genus are horned, 0 denotes generic hornlessness.

^c From Kiltie (1985). Variables are subdivided into three categories: Habitat, 1 = forests; 2 = intermediate or both forested and open habitats; 3 = open habitats. Food habits, 1 = browsing and frugivory; 2 = intermediate grazing/browsing; 3 = predominantly grazing.

^d Group size, 1 = solitary or in groups of 2-5; 2 = groups of 5-15; 3 = large groups (> 15) or very large herds.

^e Calculated from Nowak & Paradiso (1983); data represent the mid-points of ranges provided, and scaled according to sexual size dimorphism when necessary.

^f Data calculated from Jarman (1974) and Nowak & Paradiso (1983), and represent mid-points of the ranges provided.

^g Based on Estes (1991a). 1 = sexes usually associated (some males alone or in bachelor herds); 2 = bisexual groups for some proportion of the year (outside the breeding season or during migration); 3 = sexes usually segregated.

^h Hillman (1986); ⁱ Morris (1965); ^j Geist (1971), Bon *et al.* (1990); ^k Macdonald (1984), Estes (1991b); ^l Peek *et al.* (1974); ^m Bergerud (1974).

† Some degree of polymorphism in hornedness exists within these genera. The most common condition is described here.

ated by sport hunting, and we might expect more records from Old World species in the future. Nonetheless they serve to illustrate the remarkable plasticity that exists with regard to hornedness and its latent potential for rapid adaptation in response to changing selective pressures.

Existing hypotheses for female horns in ruminants

1. Predator Defence Hypothesis

The Predator Defence Hypothesis suggests that female horns function as a means of defence against predator attack (Darling, 1937; Kingdon, 1982, p. 43; Packer, 1983). This may indeed be the original function of cephalic weaponry in both males and females. According to Walther (1966, p. 60), "it could be — a few facts point in this direction — that phylogenetically the initial impetus to the development of primitive, small, daggerlike horns actually was for enemy defence".

While this function is thought not to be a primary factor in further male horn evolution (Walther, 1966; Clutton-Brock, 1982), it is sometimes considered to be more important in females because of their greater opportunity and incentive to defend vulnerable offspring (Packer, 1983).

Packer's (1983) study of sexual dimorphism in horn size and shape within the African bovids led him to conclude that horns in each sex functioned in very different ways. Male horns are thicker and more complex and adapted for intrasexual combat (see also Clutton-Brock, 1982); female horns on the other hand are straighter and would function better as offensive stabbing weapons which could be used against predators. It is important in this respect that although female horns tend to be less complex structurally, their maximum reach (*i.e.* straight-line distance from base to tip) was found to be the same as males.

Packer also found a relationship between body weight and hornedness amongst females. The smaller species (< 25 kg; which rely on crypsis and flight to avoid predators) tend to have hornless females while about 75% of those species over 40 kg (which flee from predators or may actively defend themselves) are female-horned. Furthermore, except perhaps in the smaller monogamous species, females certainly invest much more in each offspring than do males and might be expected to defend them vigorously.

Packer's findings have been discussed in detail by Estes (1991a), who finds little evidence to support the hypothesis (see also Walther, 1966). Briefly, he notes that observations of active defence are rare and restricted to only two or three bovid species, that in many species horn shape is inappropriate for effective defence, that there is no evidence for prey selection by predators that is biased towards female-hornless species and that in the most heavily selected species in the East African ecosystem (*Gazella thomsonii*) there seems to be a trend towards horn loss in females (p. 408-412). There is also good reason to suppose that hornedness should evolve to a greater extent in the smaller lineages (Predator Defence Hypothesis Prediction 1): "small antelopes and their young are vulnerable not only to the same predators as large antelopes, but also to a whole array of smaller ones down to the size of eagles; these small antelopes can and do attack in defence of their offspring. One could even argue that enhancement of their defensive capability would make horns most useful for small species" (Estes, 1991a, p. 411).

Furthermore, if predator defence is influential in the evolution of hornedness, hornedness should be negatively related to group size (Predator Defence Hypothesis Prediction 2) because of decreased vulnerability to predation in larger groups (Dehn, 1990), and to male association (Predator Defence Hypothesis Prediction 3), because greater proportions of time spent with armed males decreases the frequency with which females are compelled to use horns defensively against predators.

2. *Andromimicry Hypothesis*

The Andromimicry Hypothesis is due to Estes (1991a) and proposes that the primary function of horns (and other male secondary sexual characters) in females is to mimic those of their juvenile male offspring. Estes (1991a) suggests that this may increase the exposure of despotic males within the group to male gender badges, thereby raising the threshold for aggression elicitation against male offspring. This may pay considerable dividends to females in terms of offspring survival if this is successful in postponing the stage of sons' dispersal from the natal group and mother's home range to bachelor herds or solitary lifestyles. Concurrently, reduced despotic aggression by adult males may permit horn growth to begin at an earlier date, which is advantageous to young males in terms of peer competition.

There are good reasons to expect females to attempt to delay their sons' dispersal date, as male mortality at dispersal is high and can lead to a strongly skewed sex ratio (Greenwood, 1980; Pusey, 1987). Delayed dispersal stage and the ability to initiate horn development earlier will lead to increased offspring survival and reproductive success, and hence increase the mother's fitness. The combined advantages gained through natural and sexual selection to offspring of horned mothers would cause expression of the hornedness gene to spread rapidly through a population once it appeared (Estes, 1991a, p. 424).

One of the founding principles of this hypothesis are the strong correlations between isomorphism and spatio-temporal association of the sexes and between sexual dimorphism and adult segregation which is evident within the Bovidae (Estes, 1991b). Species which form bisexual groups for large parts of the year (e.g. *Syncerus caffer*, *Addax nasomaculatus*) are isomorphic while those in which sexes are usually segregated (e.g. *Capra falconeri*, *Tragelaphus angasi*) are highly dimorphic. Estes (1991a) summarises these trends using a novel method for scoring dimorphism and by dividing 54 gregarious bovid species into one of three 'degree of bisexual association' classes (his Fig. 3, p. 430). If the Andromimicry Hypothesis is correct as an explanation for the presence of female horns we would expect a positive relationship between hornedness and prolonged bisexual association (Andromimicry Hypothesis Prediction 1).

As Estes points out, the hypothesis fails to explain a number of cases where dimorphic species associate in mixed herds. He suggests (Estes, 1991a, p. 427) that in some dimorphic species, bisexual aggregations may occur as males abandon resource-based territories (*Saiga*, *Cervicapra*, southern *Aepyceros*), during migration (*Gazella thomsonii*, *G. granti*, *Kobus megaceros*) or because of localised and specialised habitat requirements (*Kobus ellipsiprymnus*, *K. leche*). However, with the possible exception of migrations, these aggregations occur during significantly large proportions of the year and it is in precisely these contexts that females would be expected, according to the Andromimicry Hypothesis, to have evolved horns. In addition, the cited cases of reduction in sexual dimorphism in response to forming bisexual groups (smaller horns in southern *Aepyceros*, pelage colour change in male *Cervicapra*) are solely corollaries of the male mating system and bear absolutely no relation to male mimicry by females.

In fact, in the case of *Cervicapra* the change is more likely an example of temporary gynomimicry by males in order to reduce either energetic costs of intrasexual aggression (cf. Wickler, 1967; Burley, 1981) or male-biased predation (cf. Geist & Bromley, 1978).

Similarly, the hypothesis fails to explain examples of very isomorphic, sexually segregated species. Estes (1991a, p. 428) notes that *Capricornis sumatraensis*, *Oreamnos americanus*, *Hippotragus equinus* and *Alcelaphus busephalus* (all isomorphic) are usually segregated because they do not tend to aggregate or migrate in large herds, but offers no explanation for andromimicry in these cases. It is in just these (and similar) species that females are *not* under great selection pressure to mimic males (*i.e.* become isomorphic). The fact that in each of these examples females are horned suggests that andromimicry is not a satisfactory hypothesis for horn evolution.

Moreover, Estes (1991a, p. 441) states that the Andromimicry Hypothesis may not account for the evolution of horns in females of non-gregarious species where horns may rather function in reducing harassment or feeding competition with males (see below). However there are good reasons to expect females of non-gregarious species to mimic male offspring even more than gregarious ones (Andromimicry Hypothesis Prediction 2). Firstly, the degree of bisexual association reaches its pinnacle among some of the non-gregarious species (*Oreotragus oreotragus*: Dunbar & Dunbar, 1974, 1980; Tilson, 1980; *Madoqua kirki*: Hendrichs & Hendrichs, 1971; Hendrichs, 1975). Aggression towards male offspring may begin as soon as horns become visible in these species (in contrast to polygynous species) and at a much earlier age than towards females (5 months in males, 13 in females: Roberts, 1994), enforcing earlier dispersal from the natal territory (Norton, 1980). In contrast to gregarious species where ousted young males may then join bachelor groups (Jarman, 1979; Gosling, 1974), males remain solitary until they can successfully acquire both a territory and a mate. In addition, while bachelor groups can travel relatively freely through a ranging area occupied by dominant males, young males of non-gregarious species are usually chased on sight by territorial pairs and may sustain serious injury if they do not retreat. In consequence, they are forced to occupy sub-optimal areas where they may be susceptible to higher levels of predation and poor nutrition.

Lastly, the hypothesis makes assumptions regarding the inability of males to distinguish juvenile males and female andromimics. As Gosling suggests (in Estes, 1991a, p. 424), olfactory cues are more reliable than visual ones and will be used by most males. The olfactory ability of male ungulates is well-documented (e.g. Gosling, 1985). For example, males are capable of very precise monitoring of females' reproductive states by means of lipcurl (Estes, 1972; Adams, 1980). It therefore seems likely that males will be selected to use non-visual cues for monitoring group composition.

3. *Intraspecific Competition Hypothesis*

The Intraspecific Competition Hypothesis proposes that female horns function as weapons in order to reduce feeding competition with males (Geist, 1977; Janis, 1982). Espmark (1964a), for example, has demonstrated that female *Rangifer tarandus* can displace males from feeding sites during winter, after males have cast their antlers. In Janis' (1982) view, the Intraspecific Competition Hypothesis may particularly apply to the smaller monogamous species where pair bonding and bisexual association are exceptionally close (Dunbar & Dunbar, 1980; Tilson & Tilson, 1986). Estes (1991a, p. 441) suggested that this group was one possible exception to the Andromimicry Hypothesis.

Another formulation of this hypothesis states that female horns may discourage unwanted sexual harassment by subadult males (Geist, 1974a, b, 1977). Estes (1991a, p. 413) dismissed this hypothesis for two reasons: "Sexual harassment by immature males does not appear to be a serious problem in any of the species with which I am familiar, including those whose herds often include a number of subadult or older males... It is also noteworthy that even the highest degree of isomorphism represented in these species (by the alcelaphines and oryx) has not given females dominance over immature males; males become dominant once they get as big as females, which occurs well before maturity".

Furthermore, the eviction of subadult males in some other species usually occurs when horns become longer than ear length (Estes, 1991a) which is either prior to or contemporaneous with achieving dominance over females. While it could be argued that female horns in these species have become sufficiently large to maintain social dominance over immature males until they are forced to leave their natal groups (this is a similar argument to that

explaining the developmental stage to which females 'track' male characters under the Andromimicry Hypothesis) it fails to explain hornlessness in those species which are accompanied by horned male offspring for much of the year (*e.g. Tragelaphus*).

Although these two formulations have often been treated together, they differ qualitatively in the predictions they generate. I therefore subdivide the Intraspecific Competition Hypothesis into two: the Male Displacement and the Male Harassment Hypotheses.

The Male Displacement Hypothesis asserts that hornedness in females will correlate with prolonged bisexual association (Male Displacement Hypothesis Prediction 1) and smaller groups where the accompanying male is responsible for a greater proportion of feeding competition with the females (Male Displacement Hypothesis Prediction 2). In contrast, the Male Harassment Hypothesis would predict that hornedness is positively related to group size (Male Harassment Hypothesis Prediction 1) because there are likely to be more young males in larger herds. It might also predict a negative relationship between hornedness and bisexual association with female herds (Male Harassment Hypothesis Prediction 2) as adult males may act aggressively towards harassing juvenile males.

4. Female Competition Hypothesis

Rationale

Although very close in spirit to the Intraspecific Competition Hypotheses described above, I have termed this the Female Competition Hypothesis in order to differentiate it from those proposed by Geist (1974a, 1977) which deal exclusively with intersexual competition. The Female Competition Hypothesis asserts that female horns have evolved as weapons to reduce competition for limiting resources with *any* group members. Competing group members may be adult males or immature animals of either sex (as in the Intraspecific Competition Hypotheses) but will most commonly be other adult females. In the majority of cases the limiting resource which accounts for aggressive competition is likely to be food or feeding sites, but under certain circumstances position within the herd (Hamilton, 1971) or attractive mates (Balmford *et al.*, 1992) may become worth competing for. In times of drought, limited access to drinking sites can also provoke high

levels of aggression between females of both horned and hornless species (*e.g. Taurotragus oryx* and *Aepyceros melampus*, respectively: pers. obs.).

In contrast to the Male Displacement Hypothesis (Geist, 1974b, 1977), the Female Competition Hypothesis also accounts for between-group as well as within-group competition as a driving force of horn development. This will be relevant to species where female groups actively defend resources and collectively contest for them with other groups. Between-group resource defence by female bovids may not be as common a phenomenon as in other taxa (*e.g.* lions: Packer, 1986; primates: Garber, 1988; van Schaik, 1989) but has been reported in *Hippotragus equinus* (Joubert, 1974) and might apply to smaller territorial species such as the cephalophines and neotragines.

The Female Competition Hypothesis is founded on the premise that females' fitness is limited by the number of offspring produced and raised to become reproductively active, in contrast to males whose limiting factor is the number of inseminations achieved (Emlen & Oring, 1977). It is well-known that the nutritional state of females can determine fertility (Williamson, 1991; Heydon *et al.*, 1992; Langbein & Putman, 1992) and offspring birth weight and sex ratios (Clutton-Brock *et al.*, 1986). In addition, the high energetic costs of gestation and especially lactation (Hanwell & Peaker, 1977; Oftedal, 1985; Clutton-Brock *et al.*, 1989) can place a strong burden on female body condition and hence the ability to breed successfully in subsequent years (Clutton-Brock *et al.*, 1982, 1983) or even survive (Putman & Langbein, 1992).

Evolutionary theory asserts that females are usually distributed within a habitat in such a way as to maximise their access to limiting food resources and hence their reproductive success (Emlen & Oring, 1977; Wrangham, 1979, 1980) while simultaneously minimising the risks of predation (Rauch, 1988; van Schaik, 1989). The spatial distribution that females adopt is the optimal pattern which balances these selective pressures and it shapes the social and mating systems of the population (Rubenstein & Wrangham, 1986; Clutton-Brock, 1989; Dunbar, 1989; Davies, 1991). In most cases, this cost-benefit analysis means that the size of social groups is constrained by the distribution and abundance of food resources (*e.g.* Warrick & Krausman, 1987; Berger, 1988; Bon *et al.*, 1990), but that given this constraint, group size is the maximum possible in order to reap the benefits of in-

creased detection rates and dilution effects associated with large groups (Foster & Treherne, 1981; Dunbar, 1988; van Schaik, 1989; Dehn, 1990). In this way, most smaller species occur solitarily or in small groups because they rely on low-bulk, high-energy foods which are spatially and temporally patchy (Jarman, 1974; Geist, 1974a, b), and therefore rely on crypsis and flight as a predator-avoidance strategy (Estes, 1974). Larger species feed on less patchy resources which relaxes the constraint on solitariness; predation pressure then selects for maximum possible group size (van Schaik, 1989).

Female competition for resources

Evidence that females actively compete for resources is nevertheless substantial and is becoming more commonplace (Berglund *et al.*, 1993). The most convincing example of female weaponry being used in contest for limited feeding sites is perhaps the development of antlers in female *Rangifer* (Clutton-Brock, 1982; Geist, 1994). The possession and large size of antlers can confer dominance over conspecifics of either sex (Espmark, 1964a, b; Lent, 1965a; Henshaw, 1968; Kojola, 1989; Geist, 1994). Gravid females shed antlers much later during the winter than barren ones or males (Lent, 1965a, b; Bergerud 1974; Leader-Williams, 1988) and can retain social rank and dominance over subordinate barren females and even males during periods when feeding sites are limited to snow craters, which are highly valuable and monopolisable resources (Henshaw, 1968, 1969). Successful defence of feeding sites by lactating mothers has been shown to maintain body weight (Kojola, 1989) and reduce disease and mortality of their calves (Thing *et al.*, in Reimers, 1993). Henshaw (1968, 1969), Clutton-Brock (1982) and Geist (1994) have suggested that female antlers are used in agonistic behaviours against both males and other females. Use of horns against adult males also occurs in some caprids (Risenhoover & Bailey, 1985; Lovari, 1985).

Within-group sex ratios are, however, nearly always strongly female-biased (Jarman, 1974; Gosling, 1986) and it is towards other females that most aggression by any one female will be directed. The presence of female dominance hierarchies, so important amongst some other taxa (*e.g.* primates: Dunbar, 1988; Harcourt, 1989; perissodactyls: Rubenstein, 1986), is now also known to be an integral dimension of the social or-

ganisation of many artiodactyl ungulates. A number of studies have found and described female dominance hierarchies (*Bos*: Schein & Fohrmann, 1955; *Odocoileus*: Dasmann & Taber, 1956; Browman & Hudson, 1957; *Rangifer*: Espmark, 1964a; *Capreolus*: Espmark, 1974; *Hippotragus*: Joubert, 1974; Thompson, 1993; *Cephalophus*: Ralls, 1974; *Bison*: Rutberg, 1983; *Cervus*: Altmann, 1952; Hall, 1983; Mourik, 1985; Thouless & Guinness, 1986; *Ovis*: Eccles & Shackleton, 1986; *Rupicapra*: Ingold & Marbacher, 1991; *Gazella*: Alados & Escös, 1992) which can confer priority of access to feeding sites (e.g. Hall, 1983) and enhanced fecundity and offspring survival in highly ranked females (Alados & Escös, 1992). A plethora of other studies have recorded encounters where females behave very aggressively to other females (e.g. Lent, 1965b; Jungius, 1971; Herbert, 1972; Houston, 1974; Sinclair, 1974; Murray, 1981; *Raphicerus*: Novellie *et al.*, 1984; Risenhoover & Bailey, 1985; Lovari, 1985; Prins, 1989; Locati & Lovari, 1990; Lovari & Locati, 1993) and where passive displacements occur between conspecific females (e.g. Espmark, 1964a; Prins, 1989; Thouless, 1990; Alados & Escös, 1992). Dominance status has been shown to correlate with horn length in *Gazella cuvieri* (but not *G. dama*, Alados & Escös, 1992). Furthermore, ritualised displays have evolved in females of some species as advanced behavioural mediation of overt aggression by dominant individuals (Joubert, 1974; Lovari, 1985; Lovari & Locati, 1993).

In species exposed to relatively high predation risk, and where position within the herd can significantly affect the individual's risk of predation, competition may also occur between group members for the safest positions (Rauch, 1988; van Schaik, 1989). Predation is usually highest at group margins (e.g. Tenaza, 1971) so members of a 'selfish herd' compete for central positions (Hamilton, 1971; Bertram, 1978). In addition, central animals can afford to spend less time vigilant than peripheral members (Jennings & Evans, 1980; Bertram, 1980; Prins & Iason, 1989; Dehn, 1990) and therefore more time foraging (Underwood, 1982). Underwood (1982) has shown that vigilance and foraging rates in a number of bovids are extremely sensitive to position within the herd, and Prins (1989) recorded a relationship between herd position and food intake rates. Further study is required to investigate whether social ranking and contest competition in ungulate herds can secure preferred central positions as it does in some

primate groups (Robinson, 1981; Collins, 1984). If it does, this would provide firm support for the Female Competition Hypothesis.

Contest for safety is unlikely to be a factor in horn evolution among females of solitary or pair-living species, but as male companions in these species may in fact provide a special vigilance service for females (Dunbar & Dunbar, 1980; Dunbar, 1984) females might compete for proximity and access to males (Dunbar, 1980; Sigg, 1980) who are supervigilant or trustworthy. The latter quality is an important one if females reduce look-up rates while feeding on the assumption that the male is vigilant and will alert her should a predator be spotted (Dunbar & Dunbar, 1980). Dunbar (1985) noted that the efficiency of these vigilance partnerships improves with experience and age, so that loss of an established mate would bear significant costs. Female aggression against unpaired females and daughters might thus be interpreted as a form of mate guarding.

Predictions

The particular spacing system adopted by a species in a defined ecosystem dictates the level of competitive encounters to which individual females are exposed (Harcourt, 1989). The Female Competition Hypothesis predicts that a strong selective pressure exists for the development of female weaponry in those species which have a high opportunity rate for aggressive encounters with conspecifics (Female Competition Hypothesis Prediction 1). Females of solitary or pair-living species are exposed to a very low frequency of direct, aggressive encounters (*e.g. Oreotragus oreotragus*: 0.09 h^{-1} , Dunbar & Dunbar, 1974; 0.074 h^{-1} and 0.065 h^{-1} , Roberts, 1994). In more gregarious species, inter-individual distances are small (*e.g. Risenhoover & Bailey, 1985; Prins, 1989*) and the opportunity for aggressive displacement is high (*Bison*: 2.2 h^{-1} , Rutberg, 1983; *Gazella cuvieri*: 2.8 h^{-1} , *G. dama*: 1.2 h^{-1} , Alados & Escös, 1992; *Rupicapra pyrenaica*: 6.1 h^{-1} , Lovari & Locati, 1993). Hall (1983) showed that the frequency of aggression in red deer hinds increased markedly (0.09 h^{-1} vs 7.6 h^{-1}) between groups of hinds offered natural grazing conditions to those forced to converge at artificially provided clumped feeding stations.

The incidence of hornedness among gregarious species should therefore be positively related to group size (Female Competition Hypothesis Prediction 2). Kiltie (1985) showed in his cross-specific analysis that group

size accounted for hornedness better than any variable except body size, although neither variable reliably predicted hornedness independent of the other. Estes (1991a, b) has shown that female hornedness is more common in gregarious species, but suggested that this is due to closer association between sexes during large aggregations rather than a specific effect of larger group size at these times.

Analysis

Predictions

The predictions used to test between the five competing hypotheses are summarised in Table 2. It is clear that each hypothesis yields a contradictory set of predictions, allowing us to make a rigorous comparison between them. Neither the Andromimicry, Male Displacement or Female Competition Hypotheses make predictions regarding the influence of body size *per se* but we may expect indirect, positive correlations between body weight and shoulder height with group size (Janis, 1982, 1990) which are not expected with the Male Harassment Hypothesis. No specific predictions are generated for habitat or food type variables.

TABLE 2. *Summary of predictions arising from five main hypotheses for female hornedness*

	Body weight	Shoulder height	Group size	Sexual association
PDH	negative	negative	negative	negative
AMH	(+)	(+)		positive
MDH	(+)	(+)	negative	positive
MHH			positive	negative
FCH	(+)	(+)	positive	

Negative and positive denote direction of correlation with hornedness.

PDH: Predator Defence Hypothesis; AMH: Andromimicry Hypothesis; MDH: Male Displacement Hypothesis; MHH: Male Harassment Hypothesis; FCH: Female Competition Hypothesis. Parentheses denote possibility of an indirect positive relationship with hornedness which may arise by correlation with group size or sexual association.

Methodology

Data with which to test each hypothesis were collated from the literature and are presented in Table 1. Generic data on body weight and shoulder height represent the mid-points of the ranges provided by Nowak & Paradiso (1983) and are scaled for sexual size dimorphism when necessary. The categories of habitat use, food selection and group size were those used by Kiltie (1985). Typical and maximum group sizes come mainly from Nowak & Paradiso (1983) and Jarman (1974); these data were collected for each species of the genus and then averaged. The measure of sexual segregation is based on Estes' Fig. 3 (1991a, p. 430), with additional values (mainly non-bovids) based on Nowak & Paradiso (1983).

The analysis of these data was done using the comparative method of Pagel & Harvey (1989) and Harvey & Pagel (1991) which controls for the confounding effects of phylogenetic relationships on comparative tests between species or populations. In contrast to the previous studies of horn evolution in females, this method identifies distinct evolutionary 'decision' points where the horned character developed in one lineage but not in its most closely-related line. In effect, this method thus identifies a series of independent comparisons between closely related lineages which differ in the character of interest.

The method inherently relies on the construction of a phylogenetic tree which portrays as accurately as possible the evolutionary inter-relationships of the living species under study (Pagel & Harvey, 1989; Mace & Pagel, 1995). There is a growing consensus that horns have evolved independently a number of times within the ruminants (Heintz, 1969; Janis, 1982; Janis & Scott, 1987; Gentry & Hooker, 1988), a fact that supports the methodology of identifying a number of independent evolutionary events in which hornedness appeared. However, identification of independent contrasts to be used in the analysis depends on the decision rule that is adopted regarding the stability of hornedness once it has evolved.

We cannot yet be certain that ancestors of modern female hornless species were never horned, although as yet there is no palaeontological evidence to suggest that reversals from presence to absence of horns have occurred in any lineage (Janis, 1982, p. 280, 1990). Kiltie's (1985) assertion that this could be true during the evolution of the Antilopini and Alcelaphini has been refuted by Janis (1990), although the situation is not

yet resolved. For this reason the interpretation of the constructed phylogeny was first tested using two decision rules. The first assumed that secondary reversals to hornlessness once hornedness is established have not occurred. The second assumed maximum parsimony (interpreting the phylogeny in a way that minimises the number of evolutionary events required to achieve the present distribution of hornedness within the ruminants) and allowed reversal to hornlessness.

In fact, both interpretations yielded the same number of evolutionary events (thirteen) and an identical series of paired independent contrasts. Figures 1 and 2 present the most realistic model based on current phylogenies, and postulate eleven horn gains and two horn losses during the evolution of the Ruminantia. The first horn loss (within *Gazella subgutturosa*) appears most plausible as all eleven congeners are horned and because some *G. subgutturosa* populations are still horned (Nowak & Paradiso, 1983). The second assumes horn loss in ancestral lineages of modern *Aepyceros* subsequent to their divergence from the alcelaphines. The validity of this assumption is difficult to test, as there are no known fossils close to the alcelaphine-aepycerotine common ancestor (Vrba, 1984), but there is some evidence to suggest a decrease in horn core size in early aepycerotines (Gentry, 1976; Vrba, 1984) which might represent a trend towards hornlessness in females. Nonetheless, a 'no-reversal' model (in which hornedness developed independently in the ovibovine-caprine lineage and within Alcelaphini after divergence from an alcelaphine-aepycerotine hornless common ancestor) would be equally parsimonious and would generate the same paired contrasts produced by the model shown in Figs 1 and 2.

The thirteen independent contrasts identified from this phylogeny are presented in Table 3, and data used to perform the analysis are summarised in Table 4. In cases where these contrasts involve comparisons at nodes above the generic level (e.g. *Bovini* vs *Boselaphini*) the generic scores from Table 1 are averaged (see Mace & Pagel, 1995). In the analysis of continuous measures from Table 4, data were natural log-transformed and then compared using a pairwise *t*-test (Jaccard & Becker, 1990). In order to separate the positive influences of body size and group size on hornedness, a series of regression analyses were carried out in which the dependent and independent variables were alternated between the two body size and the two group size measures. For each alternation, the standardized

TABLE 3. *Independent contrasts to test between competing hypotheses*

Contrast number	Horned	Hornless
1	<i>Boocerus</i>	<i>Tragelaphus scriptus</i>
2	<i>Taurotragus</i>	<i>Tragelaphus</i> ^a
3	Bovini	Boselaphini
4	<i>Cephalophus</i>	<i>Sylvicapra</i>
5	<i>O. o. schillingsi</i>	<i>O. oreotragus</i>
6	Hippotragini	Reduncini
7	Alcelaphini	Aepycerotini
8	Ovibovini/Caprini	Neotragini ^b /Antilopini ^c
9	<i>Antidorcas</i>	<i>Antilope</i>
10	<i>Gazella/Nanger</i>	<i>Trachocelele</i>
11	<i>Rangifer</i>	<i>Alces</i>
12	<i>Antilocapra</i>	Cervidae ^d
13	<i>Giraffa</i>	<i>Okapia</i>

^a except *T. scriptus*.

^b except *Oreotragus*.

^c except *Antidorcas*, *Gazella* and *Antilope*.

^d except *Rangifer* and *Alces*.

residuals from the regression line were taken and tested using paired *t*-tests. Categorical data were subdivided into two classes: 1-1.9 and 2-3, and set in a 2 × 2 table. These distributions were tested using both a χ^2 analysis and the non-parametric Fisher's exact test (Siegel & Castellan, 1988).

Results

Tables 5 and 6 present a summary of the findings of the analysis. Each of the three measures of group size are found to predict hornedness in females to within a 98% confidence level. Body weight and especially shoulder height are also good predictors of hornedness. The other socioecological variables (habitat type, food type and degree of sexual association) appear to have very little influence on horn development.

The strong predictive value of both body size and group size suggests a possible intercorrelation between the two variables. In his analysis, Kiltie (1985) concluded that these factors were reasonably good predictors of hornedness in combination, but that neither was reliable when considered independently. However, Pearson correlations (Table 7) revealed that these variables were not significantly correlated. Analysis of the residuals from

TABLE 4. Candidate variables to account for hornedness in female ruminants

Contrast number	Taxa	Body weight (kg)	Shoulder height (mm)	Habitat	Food	Group	Typical group size	Maximum group size	Sexual assoc.
Horned									
1	<i>Boocerus</i>	185	1250	1	1	2	9	44	3
2	<i>Taurotragus</i>	700	1400	2	1	3	34	600	3
3	Bovini	754	1570	1.8	2.5	2.8	118	744	2.4
4	<i>Cephalophus</i>	35	550	1	1	1	1	2	3
5	<i>O. o. schillingsi</i>	14	525	3	1	2	2	3	1
6	Hippotragini	143	1080	2.7	3	3	19	355	1.7
7	Alcelaphini	157	1188	2.3	3	3	26	1035	2.2
8	Ovibovini								
	Caprini	176	1009	2.5	2	2.9	9	137	*2.7
9	<i>Anidorcas</i>	34	800	3	2	3	28	2000	2
10	<i>Gazella</i>	49	800	3	2	3	12	274	2
11	<i>Rangifer</i>	81	1135	2	2	3	6	79	2
12	<i>Antilocapra</i>	48	833	3	2	3	23	1000	3
13	<i>Giraffa</i>	800	3100	2	1	2	6	100	3
Hornless									
1	<i>T. scriptus</i>	50	875	1	2	1	1	4	3
2	<i>Tragelaphus</i>								
	(exc. <i>T. scriptus</i>)	154	1085	2	2	1	10	20	3
3	Boselaphini	118	840	2	1.5	1.5	4	6	2.5
4	<i>Sylvicapra</i>	19	575	2	1	1	1	2	3
5	<i>O. oreotragus</i>	14	525	3	1	2	2	3	1
6	Reduncini	116	923	2.5	3	2.5	15	190	2.6
7	Aepycerotini	43	888	2	2	3	55	200	2.5

TABLE 4. (Continued)

Contrast number	Taxa	Body weight (kg)	Shoulder height (mm)	Habitat	Food	Group	Typical group size	Maximum group size	Sexual assoc.
8	Neotragini/ Antilopini ^a	25	660	2.7	1.7	2	8	2130	2.5
9	Antilope	37	812	3	3	3	23	129	3
10	Trachocolele ^b		635	3	2	3	6	61	2
11	Alces	513	1875	2	2	1	1	24	3
12	Other cervids	64	749	1.6	2	1.8	10	125	2.3
13	Okapia	225	1600	1	1	1	1	2	1
	Revisions								
	<i>Boocerus</i> \								
	<i>Taurotragus</i> ^c	443	1325	1.5	1	2.5	22	322	3
	<i>Tragelaphus</i> (inc. <i>T. scriptus</i>) ^c	137	1050	2	2	1	10	20	3
	Ovibovini\ Caprini\ Alcelaphini ^d Neotragini\ Antilopini ^d	170	1068	2.4	2.3	2.9	15	430	2.4
		26	669	2.8	1.6	2.6	24	3443	2.8

^a Contains all genera with the exception of *Oreotragus*, *Antilope*, *Antidorcas* and *Gazella*.

^b Data from Habibi *et al.* (1993).

^c Revision 1: *Boocerus* placed with *Taurotragus*.

^d Revision 2: *Aepyceros* placed in Antilopini.

TABLE 5. *Predictive value of continuous variables for hornedness in females*

Variable	Student's <i>t</i>	df	<i>p</i>
Body weight	2.04	11	0.066
Shoulder height	2.30	12	0.040
TGS ^a	2.86	12	0.014
MGS ^b	3.05	12	0.010

^a Typical group size.

^b Maximum group size.

TABLE 6. *Predictive value of categorical variables for hornedness in females*

Variable	χ^2	<i>p</i>	Fisher's exact <i>p</i>
Habitat	0	NS	0.355
Food type	0	NS	0.312
Group size	5.57	< 0.02	0.014
Degree of sexual association	0	NS	0.407

TABLE 7. *Independent predictive values of body size and group size*

Dependent variable	Independent variable	Pearson <i>r</i>	<i>r</i> ²	Analysis of residuals		
				<i>t</i>	df	<i>p</i>
TGS ^a	Weight	0.274	0.075	2.08	11	0.062
	Height	0.201	0.041	2.56	12	0.025
MGS ^b	Weight	0.253	0.064	2.28	11	0.043
	Height	0.239	0.057	2.72	12	0.019
Weight	TGS	0.274	0.075	1.35	11	0.203
	MGS	0.253	0.064	0.87	11	0.402
Height	TGS	0.201	0.041	1.72	12	0.112
	MGS	0.239	0.057	1.53	12	0.153

^a TGS = Typical group size.

^b MGS = Maximum group size.

a regression analysis between group and body sizes show clearly that while the predictive value of group size remains significant after the confounding influence of body size has been removed, body size is a poor indicator of hornedness when considered independently of group size (Table 7).

A comparison between the direction of these results and the predictions generated by competing hypotheses in Table 2 would appear to support the Female Competition Hypothesis as the best explanation for the taxonomic distribution of hornedness in female ruminants. The only other hypothesis which predicts a positive trend with increasing group size is the Male Harassment Hypothesis; however, this also predicts a negative relationship between hornedness and sexual association, which is not present. The most recently proposed hypothesis, the Andromimicry Hypothesis, makes no prediction regarding group size, but requires a strong positive correlation between hornedness and the degree of association between the sexes, which is not present.

Discussion

The evolution of hornedness

Horn-like organs are thought to have evolved independently between three and seven times in the pecorans, and in each family with the exception of the Moschidae (Janis, 1982; Janis & Scott, 1987; Gentry & Hooker, 1988). They are thought to have evolved initially in males only (Janis, 1982; Kiltie, 1985); for example, hornless skulls of the first true bovid, *Eotragus*, have been found contemporaneously with horned ones (Janis, 1982). Nonetheless, females of these lines would also have the genetic ability to develop horns, and would begin to express hornedness at some later stage if this became advantageous in response to some behavioural or ecological selective pressure (Kiltie, 1985). The phylogeny presented in Figs 1 and 2 suggests that horns in females have become expressed independently between eleven and thirteen times within the ruminants. The widely-spread distribution of female hornedness within and across taxa suggests an adaptive explanation for horns rather than purely a correlated genetic response to the development of horns in conspecific males (Lande, 1980), confirming the necessity of a comparative method that controls for inheritance of characters at higher nodes of evolutionary descent.

The only hypothesis under consideration here which predicts some direct relationship between hornedness and body size is the Predator Defence Hypothesis (Table 2; Packer, 1983) although the predicted direction of the relationship was opposite to that found here. However, both the Male Dis-

placement and Female Competition Hypotheses would predict an indirect correlation with body size on the basis that larger species occur in more cohesive groups with higher rates of intraspecific aggressive interactions. While the Andromimicry Hypothesis also might suggest a correlation with body size as larger-bodied, more gregarious species are more likely to have bisexual aggregations, the relationship is likely to be weaker.

The size of groups in which females occur is the most reliable predictor of female hornedness amongst the variables tested here, even when the confounding effects of body size have been removed. Inter-individual distances typically decrease as a function of group size (*e.g.* Risenhoover & Bailey, 1985; Prins, 1989) and can result in higher frequencies of agonistic interactions per individual animal (Marler, 1956; Patterson, 1965; Zucker, 1974; Vestal & Vander-Stoep, 1978; Rutberg, 1983), in which possession of weaponry can ultimately lead to substantial reproductive advantages.

Sensitivity to phylogeny

The exact phylogenetic construction used to generate the series of pairwise contrasts is crucial in an analysis of this kind (Mace & Pagel, 1995). Particularly when the number of contrasts is small, a single change in the phylogeny may produce significantly different results. For this reason, a sensitivity analysis was carried out to discover whether these results held true if Gentry's (1992) phylogeny was modified in such a way as to reposition certain genera whose present position is somewhat controversial. Within the Bovidae, the position of two genera in particular (*Boocerus* and *Aepyceros*) have been subject to much debate.

The first, *Boocerus*, was formerly classified either as a species within *Taurotragus* (Simpson, 1945) or as a subgenus of *Taurotragus* (Haltenorth, 1963). More recently, *Boocerus* has been placed as a subgenus of *Tragelaphus* (Koopman, 1967; Ansell, 1971; Nowak & Paradiso, 1983) or even as a species within *Tragelaphus* (van Gelder, 1977a, b; Corbet & Hill, 1991). Earlier classifications placed *Aepyceros* within the Antilopini (Simpson, 1945; Nowak & Paradiso, 1983), while later workers have tended to view it as an early departure from the alcelaphines and placed it within its own tribe, the *Aepycerotini* (Gentry, 1978, 1990; Vrba, 1979, 1984; Macdonald, 1984; Lowenstein, 1986). Still others have included *Aepyceros* in its own subfamily *Aepycerotinae* (Meester & Setzer, 1971; East *et al.*, 1988).

TABLE 8. Predictive values of variables for female hornedness following revisions of the phylogenetic relationships of *Boocerus* and *Aepyceros*

	Weight	Height	TGS	MGS	Habitat	Food	Groups	Sexual assoc.
Revision 1: <i>Boocerus</i> placed with <i>Taurotragus</i>								
<i>t</i>	1.66	1.98	2.37	2.69				
df	10	11	11	11				
<i>p</i>	0.127	0.073	0.037	0.021				
Fisher's <i>p</i>					0.342	0.300	0.032	0.410
Revision 2: <i>Aepyceros</i> placed in Antilopini								
<i>t</i>	1.72	2.06	3.05	3.09				
df	10	11	11	11				
<i>p</i>	0.117	0.064	0.011	0.010				
Fisher's <i>p</i>					0.360	0.320	0.013	0.410
Revision 3: Both revisions incorporated into phylogeny								
<i>t</i>	1.33	1.74	2.52	2.70				
df	9	10	10	10				
<i>p</i>	0.216	0.113	0.030	0.022				
Fisher's <i>p</i>					0.345	0.341	0.030	0.414

The initial analysis was therefore repeated sequentially with the following modifications: (i) *Boocerus* was removed from *Tragelaphus* and placed closer to *Taurotragus*, (ii) *Aepyceros* was placed within the Antilopini and (iii) both these revisions were incorporated. The reanalysis (Table 8) shows that the original results are robust to adjustments in the interpretation of phylogenetic relationships. Furthermore, the revisions mainly act in such a way as to emphasize and clarify the trends revealed initially: the three measures of group size continue to predict hornedness to within the 95% confidence interval, while the influence of the other variables are unchanged or slightly negated (particularly body weight and shoulder height).

The predictive power of group size is actually improved by Revision 2, where *Aepyceros* is taken from alongside the alcelaphines and placed in the Antilopini, but is reduced by placing *Boocerus* closer to *Taurotragus* than to *Tragelaphus* (Revision 1). These results therefore would support current views on tragelaphine classification but would call into question the position of *Aepyceros* suggested by recent studies using cladistic and

immunological methods (*e.g.* Lowenstein, 1986; Gentry, 1992), supporting rather the traditional viewpoint based mainly on phenotypy (*e.g.* Simpson, 1945; Haltenorth, 1963). The use of behavioural evidence currently receives low priority in construction of phylogenetic paradigms, but these results perhaps call for a more weighted role for behaviour in such tasks.

Aggression rates and hornedness in Oreotragus

While group size predicts hornedness with considerable accuracy in this analysis, it is important to note that it is not group size *per se* which selects for horns, but rather the rate and degree of aggressive interactions per individual female. Unfortunately, data on absolute rates and intensity of aggressive behaviour in females are still somewhat sparse, but will provide a more direct test for hornedness when they become available. However, because aggression rates increase as a function of group size, group size can be used here as a convenient 'handle' on the underlying driving force on horn evolution.

An important test of this assumption, and of the Female Competition Hypothesis itself, would be a comparison between two closely related lineages where differences exist in hornedness but which normally occur in groups of the same size. Table 4 shows that there are two such cases in this analysis: comparisons 4 (*Cephalophus vs Sylvicapra*) and 5 (horned and hornless races of *Oreotragus*). Both pairs of comparisons are comprised of small and sedentary species which are usually monogamous and territorial (Estes, 1974, 1991b; Dunbar & Dunbar, 1980; Gosling, 1986). Group size rarely exceeds three animals, a state which is maintained by enforced dispersal of offspring and repulsion of territorial intruders. When indirect means of territory defence (*e.g.* scent marking, static optic advertising) fail to dissuade potential intruders, resident pairs chase and fight them (Dunbar & Dunbar, 1974; Roberts, 1994), sometimes fatally (Norton, 1980). Aggression by females is almost exclusively intra-sexual and can escalate to severe frontal butting even between hornless animals (Dunbar & Dunbar, 1974; Roberts, 1994).

Female hornedness is more likely to evolve, even when group size remains constant, if the rate of aggressive interactions increases in one lineage or population. This could occur in two ways: either by increasing aggression rates towards female offspring or by increasing territorial en-

counter rates. The rate of aggression by females towards female offspring is unlikely to differ greatly between these two paired contrasts, particularly between populations of the same species (*i.e.* *O. oreotragus*), except where special circumstances prevail. For example, if the cost of dispersal is high (*e.g.* fewer extra-territorial areas of suitable habitat, greater predator density), a juvenile may be more reluctant to leave the natal territory and so will coerce higher levels of aggression from its parents before it is evicted. We would therefore expect hornedness to be more likely when population density and the degree of territory compression are high.

An alternative explanation is that differences in territorial intruder rates may account for the distribution of hornedness in these species. In common with the costs of natal dispersal, intrusion rates (and hence number of aggressive territorial encounters) are inversely related to territory size (Waser, 1976; Hixon, 1980). As territory size decreases, the benefits to females of possessing horns thus increase proportionally to changes in encounter rate. Historically, the benefits gained by successful resource defence at some lower threshold territory size in *Oreotragus* or *Cephalophus* females may have outweighed the energetic costs of producing horns, at which point horns became expressed. Possession of horns by only one female in a pairwise contest creates a substantial asymmetry in fighting ability (Maynard Smith & Parker, 1976; Hammerstein, 1981) and would have led to a rapid spread of hornedness through a population towards an evolutionarily stable strategy (or ESS: Maynard Smith & Price, 1973; Maynard Smith, 1982; Parker, 1984) in which all or nearly all members of the population are horned.

Adequate data to test the hypothesis that population density and territory compression influence horn expression are not yet available within populations of *Cephalophus maxwelli* and *C. monticola* and between *Cephalophus* vs *Sylvicapra*, but do exist for *Oreotragus*.

The incidence of hornedness and territory size in populations of Oreotragus oreotragus

Females of only one klipspringer race, *O. o. schillingsi*, are horned (Roosevelt & Heller, 1915; Kingdon, 1982). This race occurs in Kenya south of Mount Kenya (Roosevelt & Heller, 1915; Kingdon, 1982), in Uganda as far west as the Dodoth Hills, and in Tanzania south to Rukwa (7° 50'S 32° 10'E:

TABLE 9. *The incidence of hornedness and territory size in populations of Oreotragus oreotragus*

Study site	Hornedness	Territory size (ha)	Source
Tsavo, Kenya	Yes	1.4	Dunbar (unpubl.)
Gilgil, Kenya	Yes	2	Dunbar (unpubl.)
Matobo, Zimbabwe	No	5.5	Roberts (1994)
Sankaber, Ethiopia	No	8.1	Dunbar & Dunbar (1974)
Drakensberg, R.S.A.	No	10	Scotcher (1980)
Gamka, R.S.A.	No	15	Norton (1980)
Sentinel, Zimbabwe	No	21.5	Roberts (1994)
Springbok, R.S.A.	No	49	Norton (1980)
Kuiseb, Namibia	No	100	Scotcher (1980)

J. Kingdon, pers. comm.). In this region klipspringers occupy territories of 2 ha or less (Table 9). All other races and populations of *O. oreotragus* (distributed in Ethiopia and throughout southern Africa) have hornless females and occupy larger territories, which range from between 8-15 ha (Dunbar & Dunbar, 1974; Roberts, 1994) to around 100 ha (Scotcher, 1980). This comparison thus lends firm support to the Female Competition Hypothesis despite strict limits on group size, and is a reminder that it is the rate of aggressive contests between females which selects for hornedness, rather than group size itself.

The fact that not all female members of an *O. o. schillingsi* population are horned (Kingdon, 1982) could be explained in a number of ways. Firstly, horn development in females may be a very recent phenomenon such that the ESS has not yet been achieved. Secondly, a reversal to hornlessness may be currently in progress, perhaps as a long-term gradual increase in territory size in response to changing environmental conditions. Thirdly, the ESS might be for a certain proportion of the female population to be normally hornless. Hornlessness may be advantageous at low frequency as energetic costs of horn production are foregone during maturation, perhaps allowing an earlier beginning to the female's breeding career. In support of this, Green & Rothstein (1991) have demonstrated that a trade-off exists between growth and reproduction in female *Bison*, and Altmann (1991) showed that energy budgets during very early life have profound effects on subsequent survival and reproductive success in baboons. However, hornlessness as a strategy cannot invade this ESS because above a certain frequency of hornless females the asymmetry in number of contests won

by horned over hornless females will become so great as to preferentially select for hornedness. Further study should assess the frequency of horned and hornless strategies in this race of *Oreotragus* and attempt to quantify the fitness consequences of each, particularly by establishment of the age at onset of breeding and measuring lifetime breeding success.

Comparison of the Female Competition and Andromimicry Hypotheses

The Female Competition and Andromimicry Hypotheses generate similar predictions regarding hornedness and are perhaps the hardest to separate. Data that can be adduced to support either one can often be interpreted in a way that also supports the other. One of the principal foundations of the Andromimicry Hypothesis is that females 'track' (or mimic) the developmental stage of juvenile offspring only as far as the dispersal stage. Estes (1991a, p. 426-427) demonstrates a correlation between dispersal stage and the stage when female horns no longer resemble those of juvenile males, and suggests that once offspring have been forced to leave the natal group there is no reason for females to track male horn development further. However, it is equally likely that this correlation could reflect the pressures that operate on juvenile males themselves, independent of the function of female horns. Females may thus be horned for reasons of contest competition, while the degree of deviation from parity with male horn length dictates the stage at which despotic aggression is elicited by juvenile horns. The same is true of the onset of horn development: juvenile males of female-horned species may be able to begin horn development earlier than in female-hornless species (Estes, 1991a, p. 425), but this can still occur if horns have developed for reasons of female competition.

Similarly, attribution by the Female Competition Hypothesis of small territory size as a determinant of female hornedness in *O. oreotragus* also has a parallel under the Andromimicry Hypothesis. If the costs of dispersal by juveniles correlate with territory compression, the benefits to females in delaying dispersal by mimicking males may be sufficient to cause hornedness to develop.

While the two hypotheses are qualitatively similar, the results of this analysis favour the Female Competition Hypothesis as a more reliable and universal predictor of hornedness in female ruminants. This does not exclude the possibility that secondary benefits in terms of offspring's delayed

dispersal and earlier horn growth may accrue to females of female-horned species, but does assert that these benefits are not the primary reason for the evolution of horns. However, it is important to note that the Female Competition Hypothesis is concerned only with hornedness; it makes no claim to explain the evolution of non-offensive male characters which may have been mimicked by females in the way proposed by the Andromimicry Hypothesis (Estes, 1991a) or for other reasons (*e.g.* to counter sex-biased predation).

In summary, horn development represents one way in which females may have adapted in the face of competition to increase their fitness. The extent to which females of most taxa compete for resources and how this shapes and defines social behaviour is becoming increasingly recognised in behavioural studies (Ahnesjö *et al.*, 1993; Berglund *et al.*, 1993). As the degree of competition becomes greater, behavioural and structural means of conferring individual dominance are expected to evolve. This analysis suggests that the expression of hornedness is one direct consequence of resource competition and probably evolved in response to increasing levels of aggressive interaction, primarily (but not exclusively) towards other females.

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