Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope

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Several authors have suggested that African antelope (family Bovidae) exemplify coadaptation of ecological, behavioral, and morphological traits. We tested four hypotheses related to the ecology and behavior of 75 species of African antelope using both conventional statistical techniques and techniques that account for the nonindependence of species by considering their phylogenetic relationships. Specifically, we tested the hypotheses that (1) dietary selectivity is correlated negatively with body mass, (2) dietary selectivity is correlated negatively with group size, (3) gregarious species either flee or counterattack when approached by predators, but solitary and pair-living species seek cover to hide, and (4) body mass and group size are correlated positively. Each of these hypotheses was examined for the global data set (family Bovidae) and, when possible, within the two antelope subfamilies (Antilopinae and Bovinae) and within 7 of the 10 antelope tribes. The results of our conventional and phylogenetically corrected analyses supported the hypotheses that group and body size vary predictably with feeding style and that antipredator behavior varies with group size. The hypothesis that body mass and group size are correlated positively was supported by conventional statistics, but these two traits were only weakly related using a phylogenetically corrected analysis. Moreover, qualitative and quantitative comparisons within each of the eight major African antelope tribes generally gave little support for the four hypotheses tested. Thus, although our analyses at the subfamily level provided results that were consistent with prior hypotheses, our analyses at the level of tribes were equivocal. We discuss several possible explanations for these differences. *Key words:* African antelope, antipredator behavior, Bovidae, behavioral ecology, coadaptation, diet, group size, independent contrast, phylogenetic constraint, phylogeny. *[Behav Ecol 11:452–463 (2000)]*

Ecologists have long sought to identify links between ecology, behavior, and morphology using comparisons within groups of related species (e.g., Crook, 1965; Crook and Gartlan, 1966). Tremendous diversity in ecology, body size, and social behavior in the African antelope (Bovidae) has made this group a natural choice for comparative studies (e.g., Estes, 1974; Geist, 1974; Hofmann, 1973, 1989; Leuthold, 1977; Kingdon, 1982; Lundrigan, 1996). In a particularly influential paper, Jarman (1974) compiled information on the social behavior of 75 species and compared qualitatively their body size, diet, group size, habitat preference, and antipredator behavior. He concluded that (1) dietary selectivity was correlated negatively with body mass, (2) dietary selectivity was correlated negatively with group size, (3) gregarious species either fled or counterattacked when approached by predators, but solitary and pair-living species more often sought cover in which to hide, and (4) body mass and group size were related positively. Jarman's (1974) conclusions have subsequently influenced many workers (e.g., Drickamer et al., 1996; Krebs and Davies, 1981; Wilson, 1976), despite the fact that they were not based on the results of statistical analyses.

Here, we reevaluate Jarman's conclusions using phylogenetically based statistical techniques that are now expected of comparative analyses but that were not available in 1974 (Felsenstein, 1985; Garland et al., 1993, 1999). By considering phylogeny in our analyses, we have attempted to account statistically for the degree to which the patterns Jarman observed in African antelope may have reflected shared evolutionary history (simple inheritance from ancestors) rather than adaptive links between behavior and ecology (Harvey and Pagel, 1991; Losos, 1990). Specifically, our analyses aimed to test whether traits considered by Jarman are coadaptive and evolved repeatedly within different clades or whether these traits have been canalized within clades, possibly as a result of phylogenetic constraint or inertia (Blackburn and Evans, 1986; Futuyma, 1998; Ridley, 1996). First, we review briefly Jarman's rationale for identifying five major classes of antelope with regard to body size, diet, and social behavior. Second, we examine Jarman's conclusions using conventional statistical methods. Third, we repeat these analyses while incorporating a composite estimate of the phylogenetic relationships of all 75 species studied (see Figure 1). Last, we consider how information on intraspecific variation in African antelope may relate to Jarman's ideas.

Background

Jarman's (1974) four main conclusions stemmed from a discussion of the morphology and ecology of African antelope. He first divided the 75 antelope species into five classes (a–e) based on feeding style. Species in class a were primarily browsers that selected foods with a high protein-to-fiber ratio, such as flowers, fruits, and seed pods. Species in Jarman's class b fed either on select parts of grasses or on the new leaves of shrubs. Class c species fed selectively on a range of grasses and browse, class d species fed unselectively on grasses, and class e species fed nonselectively on a wide range of grasses and browse. Jarman assigned most small-bodied species to classes a and b, reasoning that their small mouths and narrow muzzles facilitated their specialization on the most nutritious

bovini	Syncerus	caffer(forest)
bovini	Syncerus	caffer(plains)
tragelaphini	Tragelaphus	euryceros
tragelaphini	Tragelaphus	scriptus
tragelaphini	Tragelaphus	spekei
tragelaphini	Tragelaphus	imberbis
tragelaphini	Tragelaphus	angasi
tragelaphini	Tragelaphus	strepsiceros
tragelaphini	Taurotragus	derbianus
tragelaphini	Taurotragus	oryx
tragelaphini	Tragelaphus	buxtoni
neotragini	Oreotragus	oreotragus
neotragini	Madoqua	kirki
neotragini	Madoqua	saltiana
neotragini	Madoqua	guentheri
neotragini	Raphicerus	sharpei
neotragini	Raphicerus	melanotis
neotragini	Raphicerus	campestris
neotragini	Neotragus	pygmaeus
neotragini	Neotragus	batesi
neotragini	Nesotragus	moschatus
neotragini	Dorcatragus	megalotis
neotragini	Ourebia	ourebi
antilopini	Gazella	leptoceros
antilopini	Gazella	granti
antilopini	Gazella	thomsoni
antilopini	Gazella	spekei
antilopini	Gazella	rufifrons
antilopini	Gazella	dorcas
antilopini	Gazella	pelzeni
antilopini	Gazella	soemmeringi
antilopini	Gazella	dama
antilopini	Antidorcas	marsupialis
antilopini	Ammodorcas	clarkei
antilopini	Litocranius	walleri
hippotragini	Oryx	dammah
hippotragini	Oryx	gazella
hippotragini	Oryx	beisa
hippotragini	Addax	nasomaculatus
hippotragini	Hippotragus	niger
hippotragini	Hippotragus	equinas
alcelaphini	Damaliscus	dorcas
alcelaphini	Damaliscus	lunatus
alcelaphini	Damaliscus	korrigum
alcelaphini	Beatragus	hunteri
alcelaphini	Alcelaphus	buselaphus
alcelaphini	Alcelaphus	caama
alcelaphini	Alcelaphus	lichtensteini
alcelaphini	Connochaete	taurinus
alcelaphini	Connochaete	gnou
aepycerotini	Aepyceros	melampus
cephalophini	Sylvicapra	grimmia
cephalophini	Cephalophus	monticola
cephalophini	Cephalophus	natalensis
cephalophini	Cephalophus	nigrifrons
cephalophini	Cephalophus	rufilatus
cephalophini	Cephalophus	zebra
cephalophini	Cephalophus	leucogaster
cephalophini	Cephalophus	jentinki
cephalophini	Cephalophus	dorsalis
cephalophini	Cephalophus	spadix
cephalophini	Cephalophus	silvicultor
cephalophini	Cephalophus	niger
cephalophini	Cephalophus	ogilbyi
cephalophini	Cephalophus	callipygus
peleini	Pelea	capreolus
reduncini	Kobus	megaceros
reduncini	Kobus	leche
reduncini	Kobus	ellipsiprymnus
reduncini	Kobus	defassa
reduncini	Kobus	kob
reduncini	Kobus	vardoni
reduncini	Redunca	fulvorufula
reduncini	Redunca	arundinum
reduncini	Redunca	redunca

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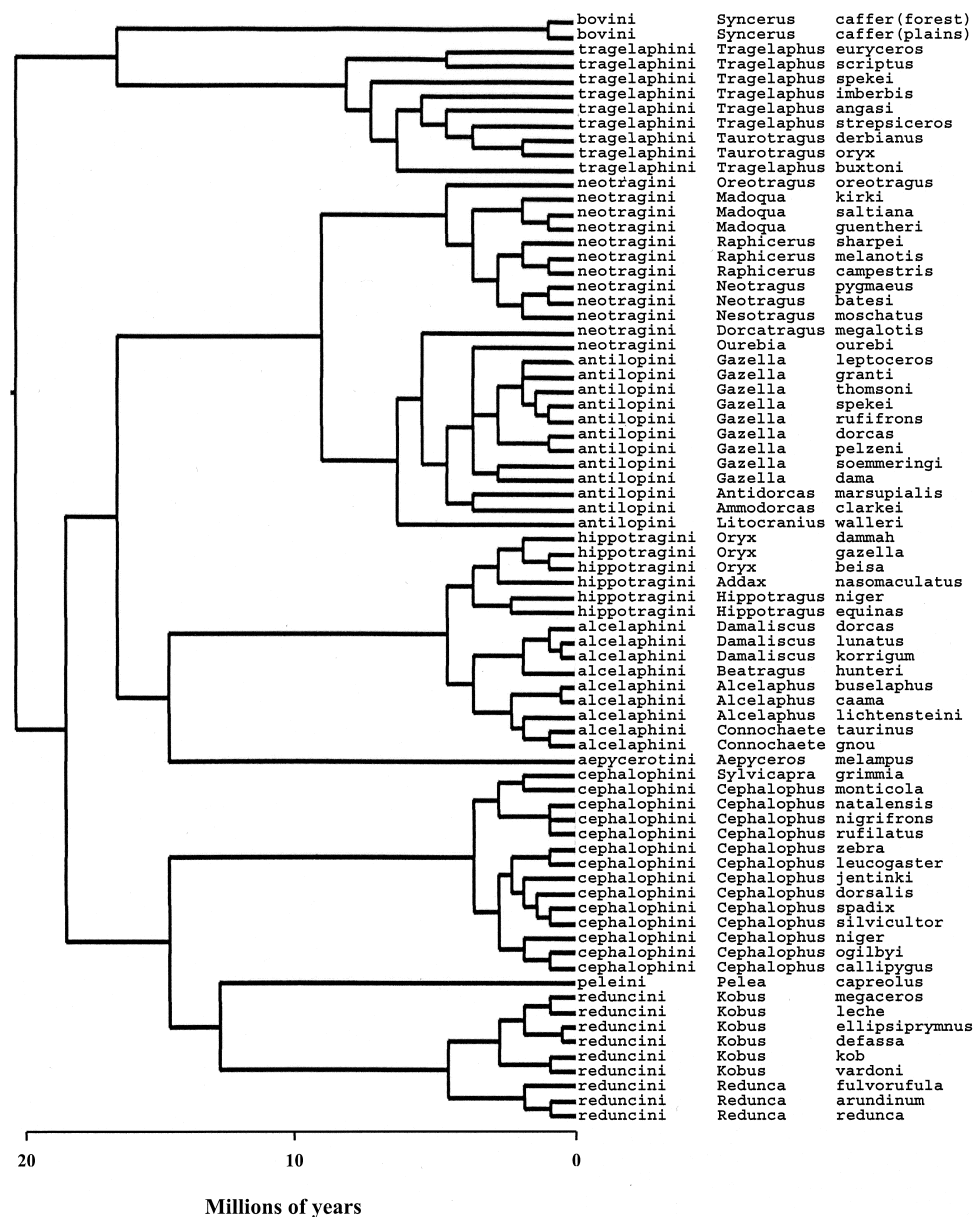
Millions of years

Figure 1
Hypothesized phylogenetic relationships and estimated divergence times of 75 species or subspecies of African antelope studied by Jarman (1974). The branching pattern of the 10 clades is based on Gatesy et al. (1997). Branching patterns within clades and estimates of divergence times are based on molecular, morphological, and paleontological information (see Appendix B).

parts of plants. He characterized large-bodied species as feeding less selectively on coarse grasses (classes d and e), in part because they lack the morphology and dexterity to feed selectively on only newer shoots, leaves, and fruits.

Jarman (1974) reasoned further that the clumped dispersion and limited availability of high-quality plant parts, combined with the greater mass-specific metabolic demands of smaller-bodied antelope, resulted in competition for food and selection for territorial behavior in selective feeders. For roughage feeders, Jarman argued that the widespread supply of coarse grasses resulted in little competition for food and, thus, little selection for spacing behavior. He also suggested that feeding and social behavior were modified by habitat openness and predation risk. Life in open habitats should favor group formation as well as year-round territorial behavior. Furthermore, the low nutritive value and seasonal availability of coarse grasses should require larger, open-country antelope to cover larger areas than small-bodied selective feeders in order to find enough food. Following this rationale, Jarman concluded that selective feeders (classes a and b) typically oc-

cur singly, in monogamous pairs, or in small groups that are territorial year-round, whereas roughage feeders (classes d and e) occur in larger groups and seldom defend access to feeding territories.

Finally, Jarman (1974) hypothesized that the antipredator behavior of antelope was the result of social organization and habitat. Species that feed in large groups in open habitat either take flight upon attack by a predator or stand their ground and counterattack, depending on their group size at the time of attack and their body size relative to that of the predator (category A). By contrast, solitary antelope and those in pairs are found more often in closed habitats and generally adopt behaviors to avoid detection by predators such as hiding or standing motionless when a predator is detected (category B). Overall, and in support of the points outlined above, Jarman concluded that body size and group size are correlated positively, with small antelope typically occurring singly or in small groups, and large antelope typically occurring in large groups.

METHODS

The data

To allow a direct comparison between Jarman's (1974) conclusions and our own results, we based our analyses on the same 75 species that he studied, but we have altered Latin names to reflect current taxonomy. These 75 species include all of the African antelope and all of the African Bovidae except two species of "goat antelope," the Aoudad (*Ammotragus lervia*) and ibex (*Capra ibex*). We obtained data on body mass, group size, diet, and antipredator behavior from Jarman (1974), but we updated these estimates for each species with more recent data where possible (Estes, 1991; Haltenorth, 1988; Kingdon, 1997; Macdonald, 1984; Stuart and Stuart, 1997) (see Appendix A). To update data, we calculated for each species a mean value for continuous traits, or a consensus for categorical traits, by combining Jarman's information with that provided in the references listed above. Body mass and group size were $\log_{10}$-transformed before analysis to satisfy assumptions of normality and homogeneity of variances. Diet and antipredator behavior were treated as categorical variables, with each species placed into one of Jarman's five diet and two antipredator behavior categories.

The phylogenetic organization of the eight antelope clades and the relationships among 34 of all 75 species were based on Gatesy et al. (1997) and reflect a combination of molecular and morphological analyses. We estimated the phylogenetic relationships of the remaining 41 species and divergence times for all species using information provided in 19 references cited in Appendix B. Our objective in assembling this phylogeny was to take a best judgment consensus of available information in an attempt to achieve maximum resolution (e.g., as in Garland et al., 1993). Where little or no phylogenetic information was available for a particular species, it was placed beside congeners, creating a soft polytomy (Purvis and Garland, 1993).

Conventional statistical analyses

Simulation studies have shown that conventional statistical tests have unacceptably high type I error rates when applied to phylogenetically nonindependent data, such as those used in this study (Díaz-Uriarte and Garland, 1996; Grafen, 1989; Harvey and Rambaut, 1998; Martins, 1996; Martins and Garland, 1991; Purvis et al., 1994). We include these tests here for comparison with results of phylogenetically corrected analyses and not as acceptable alternatives. Conventional analyses were done using parametric statistical tests (Sokal and Rohlf, 1981). We used ANOVA to test for relationships between body mass and feeding selectivity and to test for relationships between group size and feeding selectivity. We used ANCOVA to test for a relationship between group size and feeding selectivity, while controlling statistically for relationships with body mass. We also used ANOVA to test the relationship between group size and antipredator behavior and ANCOVA to test the same relationship, but with body mass as a covariate. Body mass was used as a covariate in each of these analyses to account for its strong correlation with each of the traits we considered (e.g., see Calder, 1984; Harvey and Pagel, 1991; Peters, 1983).

We tested the relationship between body mass and group size with ordinary linear regression. Each of Jarman's (1974) conclusions was examined for the global data set (family Bovidae) and, when possible, within the 2 antelope subfamilies (Antilopinae and Bovinae) and within 7 of the 10 antelope tribes (Tragelaphini, Cephalophini, Reduncini, Hippotragini, Alcelaphini, Antilopini, and Neotragini). The Bovini were not included in tribe-level analyses because only two subspecies of

the African buffalo (*Syncerus caffer caffer* and *S. c. nanus*) represent it here. The impala (*Aepyceros melampus*) and rhebok (*Pelea capreolus*) were also not included in tribe-level analyses because each is the sole extant member of its tribe. We also did not conduct within-tribe analyses involving diet or antipredator behavior when these variables were invariant within a tribe (e.g., Cephalophini).

Phylogenetically based statistical analyses

We evaluated Jarman's (1974) four main conclusions using two statistical procedures developed to account for phylogenetic relationships. We used phylogenetically corrected analyses of covariance (Garland et al., 1993) to test his conclusions that body mass is negatively correlated with feeding selectivity, that group size is negatively correlated with feeding selectivity, and that group size is correlated with antipredator behavior. This method uses Monte Carlo simulations of continuous-valued traits along a user-specified phylogenetic tree (PDSIMUL program of Garland et al., 1993) to obtain null distributions of F statistics (PDANOVA) for hypothesis testing. The test statistic is calculated using a standard ANCOVA procedure applied to the real data set (PDSINGLE or any conventional statistical package), but the critical value of the test statistic ($\alpha = 0.05$) is obtained from the 95th percentile of the null distribution of F statistics calculated from simulated data (for empirical examples, see Ferguson et al., 1996; Garland et al., 1993, 1997; Harris and Steudel, 1997; Reynolds, 1997; Reynolds and Lee, 1996).

To evaluate Jarman's (1974) conclusions on a finer scale, we tested the effect of clade (antelope tribe) on body mass and group size using the Monte Carlo simulation procedures (body mass by clade; group size by clade; group size by clade with body mass as a covariate). Our null hypothesis was that the body mass and group size differences observed among the eight antelope tribes would not be greater than could occur by chance under a model of random character evolution along the specified phylogenetic tree (Figure 1).

We performed 1000 simulations under a gradual Brownian motion model (see Felsenstein, 1985, 1988; Martins and Garland, 1991), but with values restricted to biologically realistic ranges for body mass and group size (Garland et al., 1993). We used limits of 1 and 100 for group size. The former is the smallest group size possible; the latter is slightly above the mean group size of the African buffalo (Sinclair, 1977). We used limits of 1 and 2000 kg for body mass. The former is slightly below the size range of the smallest extant bovid, the royal antelope (*Neotragus pygmaeus*); the latter is slightly above the size range of the largest extant bovid, the Asian water buffalo (*Bubalus bubalis*).

For all simulations, we used starting values of 2 for group size and 20 kg for body mass. These estimates reflect the common assertion, based on one of the earliest fossil bovids (*Eotragus*) and molecular data, that the first bovid was similar to extant members of the tribe Neotragini (Allard et al., 1992; Estes, 1991; Gentry, 1978, 1992; Kingdon, 1982). Final values (expected mean of values for the 75 species at the tips of the tree) were set to equal the observed mean values of body mass and group size, 94.1 kg and 9.2, respectively, for the 75 species. Thus, directional trends in the evolution of these two traits were simulated (see Garland et al., 1993). All of the foregoing parameters were transformed by $\log_{10}$ before simulation. Because we were testing the relationship between group size and body mass, we specified zero correlation between these traits.

To test the hypothesis that larger-bodied antelope form larger social groups, we derived correlation coefficients and regressions by use of Felsenstein's (1985) method of phylo-
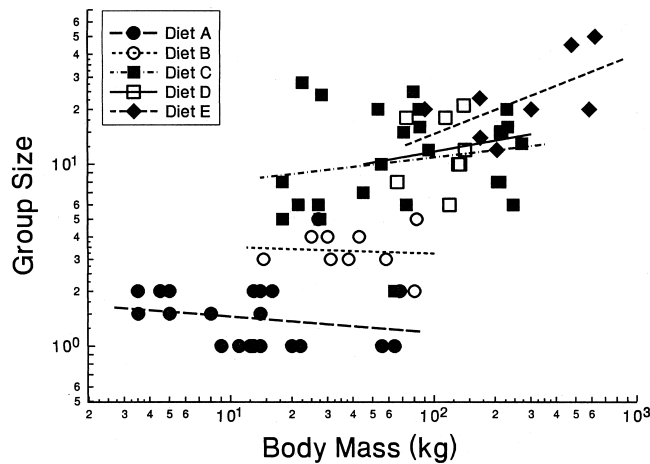
Figure 2
Scatterplot of $\log_{10}$-transformed values of group size and body mass for 75 species or subspecies of African antelope separated by diet class following Jarman (1974; see Introduction). Species in class a are selective browsers, species in class b feed selectively on grasses or browse, class c species feed on a range of grasses and browse, class d species feed unselectively on grasses, and class (e) species feed nonselectively on a wide range of grasses and browse. Lines represent the ordinary least-squares regression for each diet class. Associated statistics provided in Table 1.

genetically independent contrasts (PDSINGLE program of Garland et al., 1999). This method also uses topology and branch length information to correct for the high type I error rates that result when comparative data are analyzed with conventional statistical procedures, but in a way different from the simulation approach described above (review in Garland et al., 1999). In brief, Felsenstein's independent contrasts method computes weighted differences between the trait values of pairs of sister species and then of each successive node, working down the phylogenetic tree from the tips to the root. Each contrast is weighted by the expected variance of phenotypic change, as estimated by the branch lengths leading to the species or nodes being compared. The final result is, in principle, a phylogenetically independent and identically dis-

tributed data set consisting of $N - 1$ standardized contrasts (Felsenstein, 1985; Garland et al., 1992, 1999). Soft polytomies can be accounted for by bounding degrees of freedom (Purvis and Garland, 1993), but we did not do this here because recent simulation studies (Garland and Díaz-Uriarte, 1999) show that this should have little effect for the small number of soft polytomies contained in the phylogeny used for analyses (see Figure 1).

The adequacy of the branch lengths used in calculating a set of independent contrasts can be checked in several ways. The most commonly used method is to check for patterns in a plot of the absolute values of the standardized contrasts against their standard deviations (square roots of sums of branch lengths). A significant correlation between these measures indicates that branch lengths are inadequate and should be transformed (Díaz-Uriarte and Garland, 1996, 1998; Garland and Díaz-Uriarte, 1999; Garland et al., 1992). We found no significant correlation for our independent contrasts of log body mass ($n = 74$, $r = .11$, $p = .37$) or log group size ($n = 74$, $r = .05$, $p = .68$), so no transformations were applied. We also checked whether clades might differ with respect to the mean values of the absolute values of the standardized contrasts, which could indicate differences among clades in average rates of evolution (Garland, 1992), but found no clear evidence for this. All relationships with independent contrasts were computed by regression through the origin (Garland et al., 1992; Grafen, 1989).

RESULTS

Conventional analyses

The results of our conventional analyses of body size and diet, group size and diet, antipredator behavior and group size, and body size and group size supported Jarman's (1974) initial conclusions. Thus, a comparison of body masses across Jarman's five diet classes revealed that selective feeders (classes a and b) were smaller than unselective, roughage feeders (classes d and e; Table 1 and Figure 2), and that intermediate feeders (class c) fell between these extremes. A comparison of mean group size among the five diet classes revealed that selective feeders form smaller groups than unselective feeders (Table 1 and Figure 2). Last, antelope that form small groups

Table 1
Jarman's five diet classes in relation to $\log_{10}$ body mass and $\log_{10}$ group size (see Figure 2)

| Source of variation	Sum of squares	df	Mean square	F	Conventional tabular		Monte Carlo simulation	
					Critical value	p	Critical value	p
log%10 Body mass								
Main effect	15.02	4	3.76	32.17	2.49	<.001	2.16	.005
Error	8.17	70	.12					
Total	23.19	74	.31					
$\log_{10}$ Group size								
Main effect	14.97	4	3.74	79.05	2.49	<.001	18.64	<.001
Error	3.31	70	.05					
Total	18.28	74	.25					
$\log_{10}$ Group size with $\log_{10}$ body mass as a covariate								
Main effect	5.05	4	1.26	26.53	2.50	<.001	18.66	.018
Covariate	.03	1	.03	.63	3.98	.431	34.04	.783
Explained	15.0	5	3.0	63.03	2.35	<.001	19.00	<.001
Error	3.28	69	.05					
Total	18.28	74	.25					
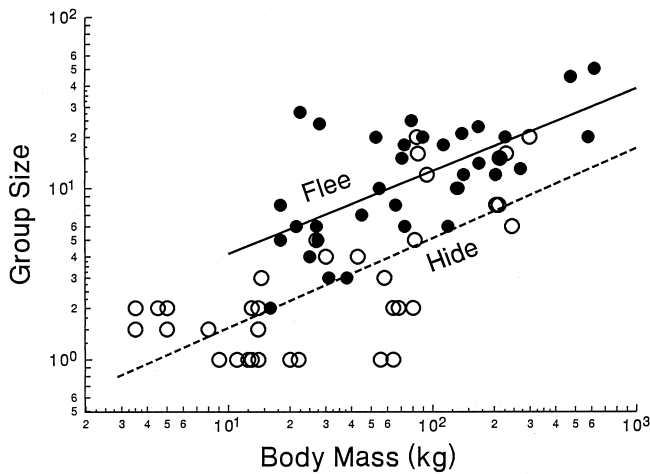
Figure 3
Scatterplot of $\log_{10}$-transformed values of group size and body mass for 75 species or subspecies of African antelope separated by antipredator behavior (see Jarman, 1974). Antipredator behavior is divided into two general categories, antelope that flee to avoid predation (filled circels) and those that hide (open circles). Lines represent the ordinary least-squares regression for each class of antipredator behavior. Associated statistics provided in Table 2.

were more likely to hide from predators, whereas those in larger groups were more likely to flee or to make a defensive stand when attacked (Table 2 and Figure 3).

Considering all 75 species, group size was positively related to body mass using conventional analyses (see Figures 2 and 3 and Tables 3 and 4). This relationship also was significantly positive in each of the two bovid subfamilies, but in only one of seven antelope tribes (Table 4 and Figure 4).

Phylogenetic analyses

Accounting for the phylogenetic relationships of the 75 species of African antelope considered by Jarman (1974) resulted in a significant change in one of the four major results of the conventional analyses. Results of a phylogenetically corrected ANCOVA supported Jarman's conclusions that body mass and

feeding selectivity were negatively correlated (Table 1), that group size and feeding selectivity were negatively correlated (Table 1), and that antelope that flee from predators occur in larger groups than those that hide (Table 2). Critical F values obtained by Monte Carlo simulation were eight to nine times larger than conventional tabular critical values, but were still less than the F values for the real data set (Table 2). Contrary to Jarman's conclusion, body mass did not differ significantly between the two antipredator categories (Table 2).

In contrast to the generally supportive results above, we also found that body mass and group size were only marginally positively correlated when phylogenetic relationships were accounted for using independent contrasts ($p = 0.06$; Table 4 and Figure 4). Moreover, after phylogenetic correction, we found no significant correlation between body mass and group size for species of the subfamily Antilopinae (Table 4 and Figure 4). We did find a positive correlation between body mass and group size for members of the subfamily Bovinae (Table 4), but body mass and group size were unrelated within each of the seven antelope tribes (Table 4). However, because of small samples sizes, our statistical power (see Garland and Adolph, 1994) to detect a range of biologically important effect sizes ($r = .30-.60$) was low to moderate for the tribes Hippotragini, Alcelaphini, Reduncini, and Tragelaphini ($1 - \beta = 0.26-0.72$) (Cohen, 1988). Statistical power was adequate for all other tests ($1 - \beta > 0.80$).

We also found that neither group size nor body mass differed among the eight antelope tribes (clades) more than occurs under the simulations of random character evolution that we used. The F values for the real data were much greater than conventional critical values for the ANOVAs of body mass and of group size by tribe, as well as for the ANCOVA of group size by tribe, but they were well below the 95th percentiles of F values for the simulated data (Table 3).

DISCUSSION

Jarman (1974), Crook (1965), and Crook and Gartlan (1966) all provide vivid examples of how the physiology and morphology of species and the productivity, seasonality, and structure of habitats are linked to interspecific variation in the social behavior of vertebrates. Jarman's work on African antelope, in particular, is one of the most frequently cited exam-

Table 2
Two classes of antipredator behavior in relation to $\log_{10}$ body mass and $\log_{10}$ group size

Source of variation	Sum of squares	df	Mean square	F	Conventional tabular		Monte Carlo simulation	
					Critical value	p	Critical value	p
$\log_{10}$ Body mass								
Main effect	3.71	1	3.71	13.92	3.97	<.001	33.13	.250
Error	19.48	73	.27					
Total	18.28	74	.31					
$\log_{10}$ Group size								
Main effect	7.41	1	7.41	49.73	3.97	<.001	3.36	.010
Error	1.87	73	.15					
Total	18.28	74	.25					
$\log_{10}$ Group size with $\log_{10}$ body mass as a covariate								
Main effect	2.54	1	1.26	31.5	3.97	<.001	28.17	.040
Covariate	5.08	1	5.08	63.03	3.97	<.001	33.66	.004
Explained	12.48	2	6.24	77.51	3.12	<.001	26.34	<.001
Error	5.8	72	.08					
Total	18.28	74	.25					

Table 3

Antelope clade in relation to $\log_{10}$ body mass and $\log_{10}$ group size

Source of variation	Sum of squares	df	Mean square	F	Conventional tabular Critical value	p	Monte Carlo simulation Critical value	p
$\log_{10}$ Body mass								
Main effect	18.67	7	2.67	38.90	2.14	<.001	77.98	.330
Error	4.46	65	.07					
Total	23.12	72[a]	.32					
$\log_{10}$ Group size								
Main effect	13.39	7	1.91	27.45	2.14	<.001	54.35	.350
Error	4.53	65	.07					
Total	17.92	72[a]	.25					
$\log_{10}$ Group size with $\log_{10}$ body mass as a covariate								
Main effect	3.87	7	.55	8.48	2.16	<.001	49.84	.870
Covariate	.36	1	.36	6.00	3.99	.017	8.01	.100
Explained	13.76	8	1.72	26.42	2.09	<.001	48.97	.310
Error	4.17	64	.07					
Total	17.92	72[a]	.25					

[a] Impala (*Aepyceros melampus*) and rhebok (*Pelea capreolus*) were not included because each constitutes its own tribe.

ples of coadaptation in behavioral and ecological traits (e.g., Drickamer et al., 1996; Eisenberg, 1981, Gould, 1982, Lott, 1991; Wilson, 1976). Surprisingly, however, Jarman's (1974) conclusions, which were based on narrative descriptions, have not been examined statistically. In this study, we reanalyzed Jarman's data using conventional statistical techniques as well as methods that account for the potential effects of phylogeny. We first review our results and then speculate briefly on their implications. Last, we discuss intraspecific variation of behavior in African antelope in light of Jarman's hypotheses.

Feeding style and group size, feeding style and body size

Jarman's (1974) conclusion that group size and body size varied predictably with feeding style was supported by both conventional and phylogenetically corrected analyses (Table 1 and Figure 2). With several exceptions, roughage-feeding antelope were larger and occurred in larger groups than did selective feeders. However, these patterns were much clearer when we considered the African bovids as a group than when we considered individual tribes. The correlation between group size, body mass, and feeding style was clear in the Tra-

gelaphini, a group that includes relatively small, solitary, and selectively feeding species, such as bushbuck (*Tragelaphus scriptus*), as well as large, gregarious, and less selective species, such as eland (*Taurotragus oryx*). In contrast, the Cephalophini, Neotragini, and Alcelaphini all include species that vary markedly in body mass, but this variation was not correlated with group size or feeding style. Overall, differences between the critical F values from conventional analyses and those derived from Monte Carlo simulations of body mass and group size on the phylogenetic tree support our observation that the patterns suggested by Jarman are clearer for the Bovidae as a whole than for its individual tribes.

Group size and antipredator behavior

Jarman (1974) suggested that group-living antelope were most likely to occur in open habitats and to use vigilance and flight as primary defenses against predation. In contrast, he suggested that solitary or pair-living antelope were more common in closed habitats and more likely to adopt behaviors that would reduce detection by predators. Both our conventional and phylogenetically corrected analyses support these sugges-

Table 4

Regression of $\log_{10}$ body mass and $\log_{10}$ group size using conventional least squares regression and independent contrasts

| Group	n	Conventional regression L 95% CI	Slope	U 95% CI	r	Independent contrasts L 95% CI	Slope	U 95% CI	r
All species	75	0.515	0.655	0.795	.738	−0.011	0.248	0.507	.218
Subfamily Bovinae	11	0.517	1.080	1.644	.822	0.297	0.883	1.469	.751
Tribe Tragelaphini	9	0.238	0.983	1.729	.763	−0.066	0.709	1.484	.633
Subfamily Antilopinae	64	0.506	0.674	0.841	.714	−0.190	0.101	0.391	.088
Tribe Neotragini	11	−0.515	−0.175	0.164	−.388	−0.437	0.017	0.403	−.033
Tribe Antilopini	13	−0.886	0.069	1.025	.046	−0.965	0.045	1.056	.028
Tribe Hippotragini	6	−1.208	−0.327	0.554	−.458	−1.829	−0.448	0.933	−.410
Tribe Alcelaphini	9	−0.834	0.201	1.235	.171	−1.853	−0.039	1.775	−.002
Tribe Cephalophini	14	−0.343	−0.069	0.205	−.156	−0.331	0.079	0.488	.120
Tribe Reduncini	9	−0.315	0.603	1.520	.506	−1.228	0.005	1.218	.004

L, lower; U, upper.
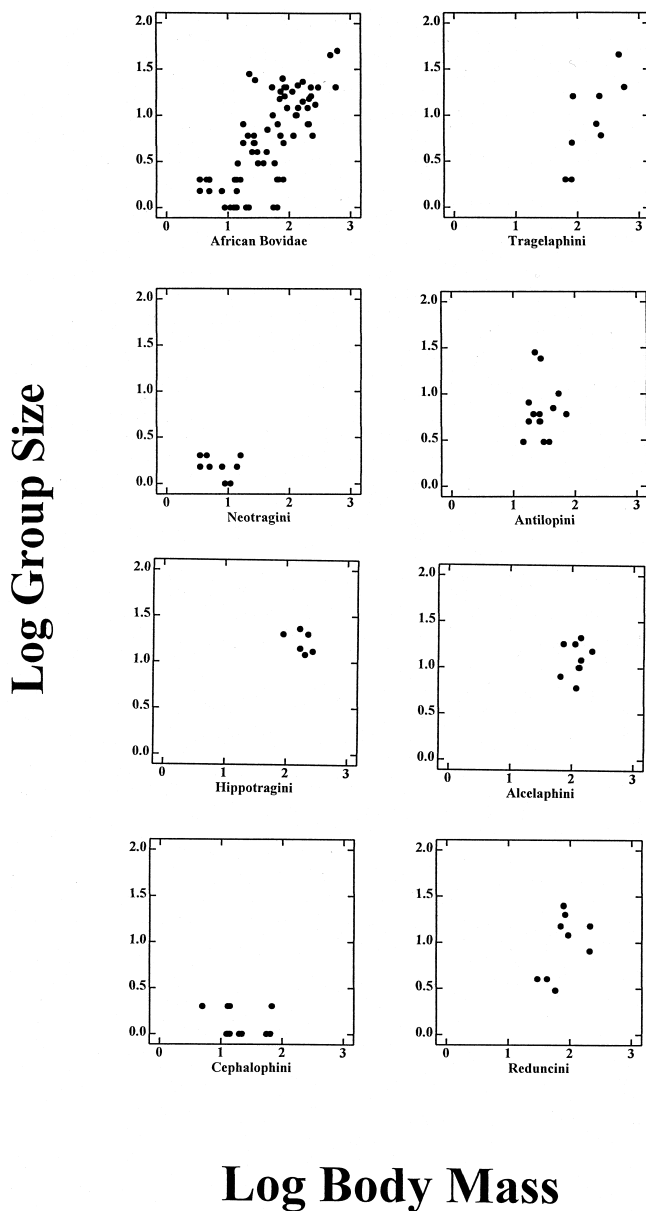
Figure 4
Scatterplot of log$_{10}$-transformed values of group size and body mass for 75 species or subspecies of African antelope and for 7 of 10 antelope tribes. Associated statistics provided in Table 4.

tions. We found that antelope that flee when faced with a predator are more often those that occur in larger groups than those that avoid detection by freezing or hiding, even when body mass was included as a covariate (Figure 3 and Table 2).

Group size and body mass

In contrast to Jarman's (1974) conclusion, we found only weak positive correlations between group size and body mass after the effects of phylogeny were considered (Table 4 and Figures 2 and 3). Moreover, our phylogenetically corrected results suggested that body mass and group size were unrelated within each of seven antelope tribes (Table 4 and Figure 4). Our statistical power was low in four of these tribes because of the small number of species within them (n = 6–9), not

because phylogenetic methods have inherently low power (see Garland and Adolph, 1994; Grafen, 1989; Harvey and Rambaut, 1998; Martins, 1996; Purvis et al., 1994). In contrast to the results of the phylogenetic analysis, a conventional comparison of body mass and group size, both across all 75 species and within the subfamily Antilopinae, revealed a strong positive relationship (Table 4). These results are one of several cases in which including phylogeny in analyses dramatically changed the slope of a regression (e.g., Garland et al., 1993; Pagel, 1998; Promislow, 1991).

Group size and body size among clades

Results from our phylogenetically corrected ANCOVA of body mass and group size suggest that there is no need to invoke special ecological or behavioral explanations for clade attributes because they did not vary more than expected under a random model of gradual, Brownian-motion character evolution (with trends and limits) along the phylogeny shown in Figure 1 (Table 3). A number of previous studies have shown that differences among clades are rarely judged to be statistically significant (but see Garland et al., 1997) when test values are compared to a null distribution derived from simulations along a user-specified phylogenetic tree (Ferguson et al., 1996; Garland et al., 1993; Pagel, 1998; Reynolds, 1997; Reynolds and Lee, 1996).

Phylogenetic constraints versus environmental influences

Implicit in Jarman's (1974) thesis is the idea that common suites of adaptive traits have evolved repeatedly in the African antelope. More recently, authors have pointed out that variation within species is often related to local environmental conditions and that individual animals maximize fitness by responding flexibly to seasonal or geographic variation in the environment (Bradbury and Vehrencamp, 1977; Curry, 1989; Foster and Endler, 1999; Lott, 1991). Thus, one view suggests a more or less unlimited response by species to spatial and temporal variation in the environment, whereas another view suggests a canalization of traits imposed by phylogenetic constraints (Blackburn and Evans, 1986; Futuyma, 1998; Ridley, 1996). Our results suggest that the correlation between body size and group size reported by Jarman is more a result of variation that exists among tribes rather than within them (Figure 4 and Table 4). Because antipredator behavior and diet were treated as categorical variables and were often monotypic within tribes, we were unable to test for correlations among these traits within tribes. Qualitative comparisons showed that relationships of antipredator behavior, diet, body size, and group size were also weak or absent within tribes (Figures 5 and 6). The absence of strong correlations between body size, group size, and behavior among species within clades may indicate that some element of the phylogenetic history of these clades has prevented an otherwise anticipated course of divergence (McKitrick, 1993). Alternatively, a lack of correlated divergence within clades might reflect a loss of plasticity as a result of specialization within a niche, such as that seen in the specialized diet of Cephalophini. Finally, clades in which body size, group size, and behavior appear to be unrelated may have been prevented by competition from occupying new habitats or niches or may have diverged too recently to have undergone substantial radiation.

It is also possible, however, that finer scale analyses of diet and habitat preference will be required to effectively describe patterns of behavioral variation within clades. Kingdon (1982) criticized Jarman (1974) for developing a classification system that was more conceptually attractive than realistic and for characterizing phenotypic traits that appear to vary among
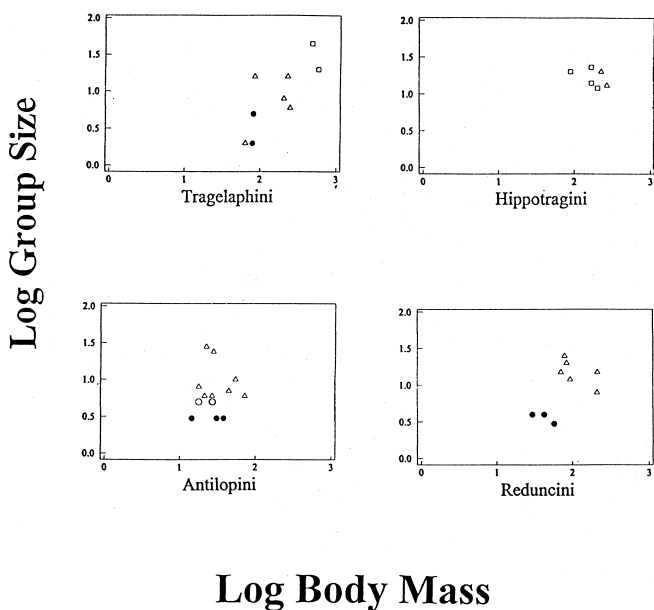
Log Body Mass

Figure 5
Scatterplot of log_{10}-transformed values of group size and body mass for four tribes of African antelope separated by diet class (see Jarman 1974). Species in class a (open circles) are selective browsers, species in class b (filled circles) feed selectively on grasses or browse, class c (open triangles) species feed on a range of grasses and browse, class (d) (filled triangles) species feed nonselectively on grasses, and class e (open squares) species fed unselectively on a wide range of grasses and browse. Tribes not shown were monotypic for a given diet class.

populations within species as fixed traits. Group size, in particular, shows dramatic geographic and seasonal variation among and within populations for nearly half of all species of African antelope (Estes, 1991). Using mean values for group size and other traits may make it more difficult to detect fine-scale responses of populations to environmental variation where these exist within species, and this points to a possible weakness in our analyses. However, even where data on geographic variation in group size exists and thus could be incorporated into analyses in principle, it is uncertain to what degree this variation results simply from seasonal variation within populations as opposed to genetically based differences among populations. With more detailed data on seasonal and geographic variation in group size, future analyses could divide species further into phenotypically distinct populations to minimize the amount of averaging across species.

Intraspecific variation in behavior

Several authors have suggested that the extent to which ecological, morphological, and behavioral traits are coadapted will be measured most accurately by comparing subspecies or closely related species living in different environments (e.g., Foster and Cameron, 1996; Foster and Endler, 1999; Harvey and Pagel, 1991; Lott, 1991). This approach should minimize potential phylogenetic influences relative to those of ecology on social behavior, and it has the potential to test if coadaptation in ecology and behavior occur on micro- as well as macro-evolutionary scales (Garland and Adolph, 1994; Garland et al., 1992, 1999). If, as suggested by Jarman (1974) and others (e.g., Estes, 1974; Geist, 1974; Kingdon, 1982), variation in body size and resource distribution cause variation in the social organization of African antelope, then comparisons of populations or subspecies across ecological gradients may
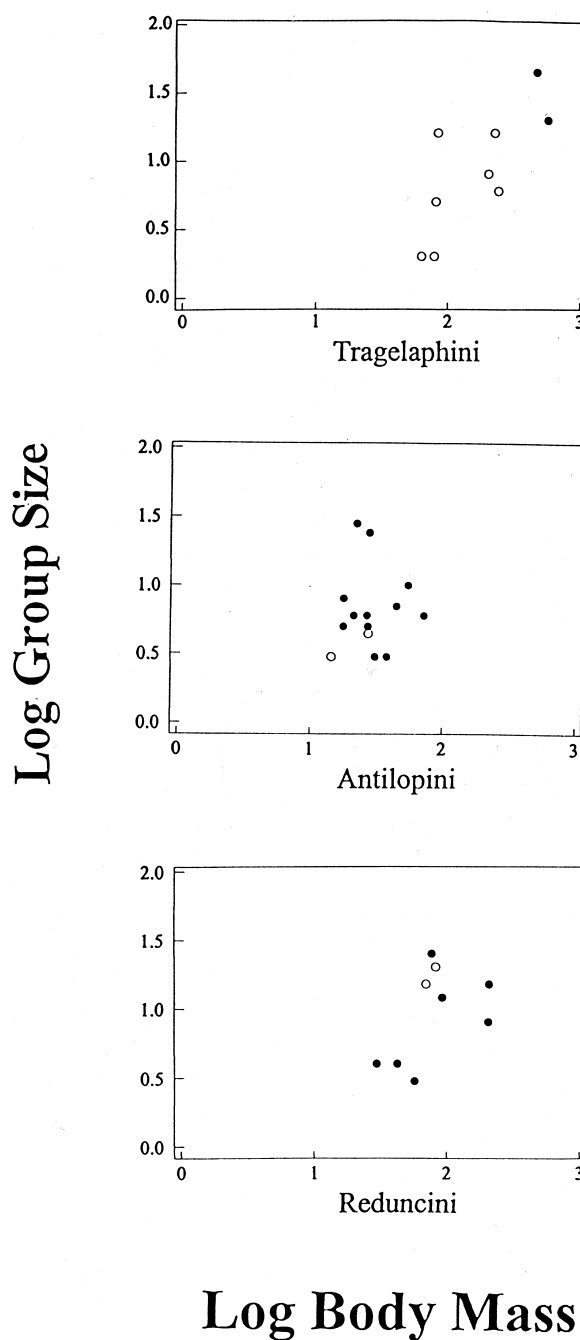

Log Body Mass

Figure 6
Scatterplot of log_{10}-transformed values of group size and body mass for three tribes of African antelope separated by antipredator behavior. Antipredator behavior is divided into two general classes: antelope that flee to avoid predation (filled circles) and those that hide (open circles). Tribes not shown either showed no variation in antipredator behavior or had only one species representing a class.

help determine if behavioral variation is adaptive or only reflective of evolutionary history. At present, insufficient data exist for comprehensive comparisons of this type. Nevertheless, several anecdotal observations suggest that in some antelope, variation in social behavior is a response to variation in habitat and demography. Buffalo, *Syncerus caffer* (Estes, 1991), Grant's gazelle, *Gazella granti* (Walther, 1972), impala, *Aepyceros melampus* (Leuthold, 1970), common reedbuck, *Redunca arundinum* (Jungius, 1971), and oribi, *Ourebia ourebi*

(Arcese P, unpublished results), each form smaller groups in mixed woodland, scrub, or tall grass habitats than they do in short grasslands. Jarman hypothesized that the observation of smaller groups in closed habitats suggests that individuals have switched to a more appropriate predator-avoidance strategy. Alternatively, a shift toward smaller groups in dense habitats may reflect a change in foraging strategy or the practical problems associated with maintaining cohesive groups when moving through thick vegetation.

Variation in breeding behavior has also been related to local demography. Male topi, *Damaliscus lunatus,* defend core areas within large home ranges at low population densities and wooded habitat, but they form leks at high population densities in open grasslands (Duncan, 1975, 1976; Gosling et al., 1987; Monfort-Braham, 1975). Similarly, male lechwe, *Kobus leche,* and kob, *Kobus kob,* occupy leks when in open habitat at high population density, but they defend larger territories or occupy home ranges at low density (Lent, 1969; Leuthold, 1966; Robbel and Child, 1975; Schuster, 1976). These observations are consistent with Jarman's conclusion that territoriality is a proximate response to increased competition for food or mates.

In contrast to these examples of seemingly adaptive behavioral responses are several observations of antelope species that appear fixed in behavior regardless of habitat, population density, or resource distribution. For example, common duiker, *Sylvicapra grimmia,* steinbuck, *Raphicerus campestris,* and

dik-dik, *Madoqua* sp., each occur in closed and open habitats and at varied population densities, and each shows dramatic geographic and seasonal variation in diet. However, each of these species is also reported as being monogamous and territorial throughout their ranges (Estes, 1991). Several authors have proposed that habitat, genetic, and life-history attributes may explain why behavioral flexibility has evolved in some species and not in others (reviews in Foster and Endler, 1999; Lott, 1991), but these hypotheses remain untested for mammals. It is possible that species of antelope that appear inflexible in social behavior simply have not been studied in sufficient detail or in enough localities to document variation where it exists (Arcese et al., 1995; Lott, 1991). In either case, further studies of single species that occur in a wide range of habitats or areas probably offer the fastest route to understand behavioral flexibility and how it relates to coadaptation in the African antelope.

APPENDIX A

Species, body mass, group size, diet, and antipredator behavior classes (see Introduction and Jarman, 1974) used in the analyses

Tribe	Species	Mass (kg)	Group size	Diet class	Antipredator class
Bovini	*Syncerus caffer* (forest)	300[a–f]	20[a,c,d]	e[a–f]	A[a,c,d]
Bovini	*Syncerus caffer* (plains)	620[a–f]	50[a,c,d]	e[a–f]	A[a,c,d]
Tragelaphini	*Tragelaphus euryceros*	245[a–f]	6[a,c,d]	c[a–f]	B[a,c,d]
Tragelaphini	*Tragelaphus scriptus*	64[a–f]	2[a,c,d]	c[a–f]	B[a,c,d]
Tragelaphini	*Tragelaphus spekei*	80[a–f]	2[a,c,d]	b[a–f]	B[a,c,d]
Tragelaphini	*Tragelaphus imberbis*	82[a–f]	5[a,c,d]	b[a–f]	B[a,c,d]
Tragelaphini	*Tragelaphus angasi*	85[a–f]	4[a,c,d]	c[a–f]	B[a,c,d]
Tragelaphini	*Tragelaphus strepsiceros*	230[a–f]	16[a,c,d]	c[a–f]	B[a,c,d]
Tragelaphini	*Taurotragus derbianus*	580[a,b,c,e,f]	20[a]	e[a,b,c,e,f]	A[a,c]
Tragelaphini	*Taurotragus oryx*	475[a–f]	45[a,c,d]	e[a–f]	A[a,c,d]
Tragelaphini	*Tragelaphus buxtoni*	205[a,e,f]	8[a,e]	c[a,e,f]	B[a,c]
Neotragini	*Oreotragus oreotragus*	16[a–f]	2[a,c,d]	a[a–f]	B[a,c,d]
Neotragini	*Madoqua kirki*	5[a–f]	2[a,c,d]	a[a–f]	B[a,c,d]
Neotragini	*Madoqua saltiana*	4[a,b,c,e,f]	2[a]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Madoqua guentheri*	4[a,b,c,e,f]	2[a]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Raphicerus sharpie*	9[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Raphicerus melanotis*	11[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Raphicerus campestris*	14[a–f]	1.5[a,c,d]	a[a–f]	B[a,c,d]
Neotragini	*Neotragus pygmaeus*	4[a,b,c,e,f]	1.5[a,c,d]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Neotragus batesi*	5[a,b,c,e,f]	1.5[a,c,d]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Nesotragus moschatus*	8[a,b,c,e,f]	1.5[a,c,d]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Dorcatragus megalotis*	12[a,b,c,e,f]	5[a,c,d]	a[a,b,c,e,f]	B[a,c]
Neotragini	*Ourebia ourebi*	16[a–f]	3[a,d]	b[a–f]	B[a,c,d]
Antilopini	*Gazella leptoceros*	18[a,b,c,e,f]	6[a,c,d]	c[a,b,c,e,f]	A[a,c]
Antilopini	*Gazella granti*	55[a–f]	10[a,c,d]	c[a–f]	A[a,c,d]
Antilopini	*Gazella thomsoni*	22[a–f]	28[a,c,d]	c[a–f]	A[a,c,d]
Antilopini	*Gazella spekei*	19[a,b,c,e,f]	8[a,c,d]	c[a,b,c,e,f]	A[a,c]
Antilopini	*Gazella rufifrons*	28[a,b,c,d,f]	5[a,c,d]	c[a,d,f]	A[a,d]
Antilopini	*Gazella dorcas*	21[a,b,c,e,f]	17[a,c,d]	c[a,b,c,e,f]	A[a,c]

APPENDIX A, continued

Tribe	Species	Mass (kg)	Group size	Diet class	Antipredator class
Antilopini	*Gazella pelzeni*	18[a]	7[a]	c[a]	A[a]
Antilopini	*Gazella soemmeringi*	42[a,b,c,e,f]	7[a,c,d]	c[a,b,c,e,f]	A[a,c]
Antilopini	*Gazella dama*	70[a,b,c,e,f]	6[a,c,d]	c[a,b,c,e,f]	A[a,c]
Antilopini	*Antidorcas marsupialis*	30[a–f]	24[a,c,d]	c[a–f]	A[a,c,d]
Antilopini	*Ammodorcas clarkei*	30[a,b,c,e,f]	3[a]	b[a,b,c,e,f]	A[a,c]
Antilopini	*Litocranius walleri*	42[a–f]	3[a,c,d]	b[a–f]	A[a,c,d]
Hippotragini	*Oryx dammah*	178[a,d,f]	12[a]	e[a,d,f]	A[a,d]
Hippotragini	*Oryx gazella*	205[a–f]	14[a,c,d]	e[a–f]	A[a,c,d]
Hippotragini	*Oryx beisa*	168[a,b,c,e,f]	23[a,c]	e[a,b,c,e,f]	A[a,c]
Hippotragini	*Addax nasomaculatus*	90[a,b,c,e,f]	20[a,c]	e[a,b,c,e,f]	A[a,c]
Hippotragini	*Hippotragus niger*	228[a–f]	20[a,c,d]	c[a–f]	A[a,c,d]
Hippotragini	*Hippotragus equinas*	270[a–f]	13[a,c,d]	c[a–f]	A[a,c,d]
Alcelaphini	*Damaliscus dorcas*	69[a–f]	8[a,c,d]	d[a–f]	A[a,c,d]
Alcelaphini	*Damaliscus lunatus*	132[a–f]	6[a,c,d]	d[a–f]	A[a,c,d]
Alcelaphini	*Damaliscus korrigum*	114[a]	23[a]	d[a]	A[a]
Alcelaphini	*Beatragus hunteri*	89[a,b,c,e,f]	18[a,c]	d[a,b,c,e,f]	A[a,c]
Alcelaphini	*Alcelaphus buselaphus*	144[a–f]	10[a,c,d]	d[a–f]	A[a,c,d]
Alcelaphini	*Alcelaphus caama*	142[a,b,d]	20[a]	d[a,b,d]	A[a,d]
Alcelaphini	*Alcelaphus lichtensteini*	132[a]	10[a]	d[a]	A[a]
Alcelaphini	*Connochaetes taurinus*	215[a–f]	15[a,c,d]	d[a–f]	A[a,c,d]
Alcelaphini	*Connochaetes gnou*	145[a–f]	21[a,c,d]	d[a–f]	A[a,c,d]
Aepycerotini	*Aepyceros melampus*	53[a–f]	20[a,c,d]	c[a–f]	A[a,c,d]
Cephalophini	*Sylvicapra grimmia*	13[a–f]	2[a,c,d]	a[a–f]	B[a,c,d]
Cephalophini	*Cephalophus monticola*	5[a–f]	2[a,c,d]	a[a–f]	B[a,c,d]
Cephalophini	*Cephalophus natalensis*	14[a,b,c,e,f]	2[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus nigrifrons*	14[a–f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus rufilatus*	13[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus zebra*	17[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus leucogaster*	17[a–f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus jentinki*	66[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus dorsalis*	22[a–f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus spadix*	56[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus silvicultor*	68[a–f]	2[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus niger*	16[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus ogilbyi*	20[a,b,c,e,f]	1[a]	a[a,b,c,e,f]	B[a,c]
Cephalophini	*Cephalophus callipygus*	20[a–f]	1[a]	a[a,b,c,e,f]	B[a,c]
Peleini	*Pelea capreolus*	25[a–f]	4[a,c,d]	b[a–f]	B[a,c,d]
Reduncini	*Kobus megaceros*	84[a,b,c,e,f]	20[a,c]	c[a,b,c,e,f]	B[a,c]
Reduncini	*Kobus leche*	94[a–f]	12[a,c,d]	c[a–f]	B[a,c,d]
Reduncini	*Kobus ellipsiprymnus*	211[a–f]	8[a,c,d]	c[a–f]	B[a,c,d]
Reduncini	*Kobus defassa*	214[a–f]	15[a,c,d]	c[a–f]	B[a,c,d]
Reduncini	*Kobus kob*	79[a–f]	25[a,c,d]	c[a–f]	A[a,c,d]
Reduncini	*Kobus vardoni*	71[a,b,c,e,f]	15[a,c]	c[a,b,c,e,f]	A[a,c]
Reduncini	*Redunca fulvorufula*	30[a,b,c,e,f]	4[a,c]	b[a,b,c,e,f]	B[a,c]
Reduncini	*Redunca arundinum*	58[a–f]	3[a,c,d]	b[a–f]	B[a,c,d]
Reduncini	*Redunca redunca*	43[a–f]	4[a,c,d]	b[a–f]	B[a,c,d]

Measurements of body mass and group size represent a mean value calculated for each species from data provided in six references, indicated by superscripted letters in the table: [a]Jarman (1974), [b]Macdonald (1984), [c]Haltenorth (1988), [d]Estes (1991), [e]Kingdon (1997), [f]Stuart and Stuart (1997). Diet and antipredator behavior designations represent a consensus of these same references.

APPENDIX B

Phylogenetic tree used in the analyses

The information used in constructing the phylogenetic tree used in our analyses is described here. The phylogenetic tree (Figure 1) represents an informal consensus of molecular, morphological, and paleontological information. In general, emphasis was placed on recent molecular or molecular-morphological studies in determining phylogenetic relationships and estimates of divergence times among subfamilies, tribes, species, and subspecies. Where applicable, paleontological data provided confirmation of divergence-time estimates for all taxonomic levels. When conflicts arose among recent molecular studies, we relied on older morphological and paleontological publications. To avoid circularity, we did not in-

clude morphological information that incorporated measurements of attributes that we considered in our analyses (see Felsenstein, 1988). Conflicting or little phylogenetic information was available for *Dorcatragus megalotus, Ourebia ourebi,* and *Oreotragus oreotragus,* and for *Gazella lepticeros* beyond the genus level. The phylogenetic relationship of the sister species *Cephalophus natalensis, C. nigrifrons,* and *C. rufilatus* also were unresolved in the literature. The placement of these species in the cladogram reflects our best judgment and that of our colleagues.

Placement of major clades and estimates of divergence times
Our hypothesized branching patterns of the major antelope clades are based on Gatesy et al. (1997; analysis 18 and consensus of analyses). Additional branching patterns and esti-

mates of divergence times are based on Allard et al. (1992), Gatesy et al. (1992, 1994), Georgiadis et al. (1990), Gentry (1992), and Vrba (1984).

Bovini and Tragelaphini
Our estimates of phylogenetic relationships and divergence times in the Bovini and Tragelaphini are based on published analyses of molecular data (Gatesy et al., 1997; Georgiadis et al., 1990; Matthee and Robinson, 1999) as well as on a study of morphology (Kingdon, 1982).

Antilopini and Neotragini
Gentry (1992) and others (Gatesy et al., 1997; Kingdon, 1982) have challenged previous separations of the tribes Antilopini and Neotragini. We present these tribes here as interdigitated, reflecting a consensus of several publications (Gatesy et al,. 1997; Georgiadis et al., 1990; Gentry, 1992; Matthee and Robinson, 1999; Nowak, 1991; Vassart et al,. 1995).

Cephalophini
Our placement of species in the tribe Cephalophini is based primarily on studies of molecular data (Georgiadis et al., 1990; Robinson et al., 1996, Van Vuren B, personal communication). Other phylogenetic relationships and divergence-time estimates within the Cephalophini were provided by studies of morphology (Groves and Grubb, 1981; Kingdon, 1982, Nowak, 1991).

Hippotragini and Alcelaphini
Our estimates of the phylogenetic relationships and divergence times of the Alcelaphini and Hippotragini are based on Gatesy et al. (1994). Additional information was provided in Georgiadis et al. (1990), Grobler and Van der Bank (1995), Vrba (1979,1984), and Vrba and Gatesy (1994).

Reduncini
Our estimates of the phylogenetic relationships of the Reduncini are based on Gatesy et al. (1997). Additional information and divergence estimates were provided in Georgiadis et al. (1990).

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