

CONVERGENT MATERNAL CARE STRATEGIES IN UNGULATES AND MACROPODS

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Abstract.—Mammals show extensive interspecific variation in the form of maternal care. Among ungulates, there is a dichotomy between species in which offspring follow the mother (“following” strategy) versus species in which offspring remain concealed (“hiding” strategy). Here we reveal that the same dichotomy exists among macropods (kangaroos, wallabies and allies). We test three traditional adaptive explanations and one new life history hypothesis, and find very similar patterns among both ungulates and macropods. The three traditional explanations that we tested were that a “following” strategy is associated with (1) open habitat, (2) large mothers, and (3) gregariousness. Our new life-history hypothesis is that a “following strategy” is associated with delayed weaning, and thus with the “slow” end of the slow-fast mammalian life-history continuum, because offspring devote resources to locomotion rather than rapid growth. Our comparative test strongly supports the habitat structure hypothesis and provides some support for this new delayed weaning hypothesis for both ungulates and macropods. We propose that sedentary young in closed habitats benefit energetically by having milk brought to them. In open habitats, predation pressure will select against hiding. Followers will suffer slower growth to independence. Taken together, therefore, our results provide the first quantitative evidence that macropods and ungulates are convergent with respect to interspecific variation in maternal care strategy. In both clades, differences between species in the form of parental care are due to a similar interaction between habitat, social behavior, and life history.

Key words.—Antipredator behavior, body size, comparative analysis, mammals, maternal investment, parental care.

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Macropods (kangaroos, wallabies and allies) are herbivorous marsupials whose natural distribution is restricted to Australia and Papua New Guinea. Ungulates occupy a similar range of ecological niches to macropods, but are distributed widely across Eurasia, Africa, North and South America. Although macropods are ecologically, behaviorally, and morphologically conservative in comparison with ungulates (Lee and Cockburn 1985), macropods and ungulates are often considered to be convergent because of similarities in both group's relationships between diet, body size, sexual dimorphism, and social organization (Jarman 1983; Jarman and Kruuk 1996). The overall aim of this study is to explore whether this idea of convergence between macropods and ungulates can be extended to parental care. Specifically, we test whether interspecific variation in the way mothers care for their offspring in ungulates and macropods is associated with the same ecological, social, and life history factors in both groups.

In ungulates, maternal care and infant behavior have been classified dichotomously as either “hiding” or “following” (Lent 1974; Walther 1965). Young of following species follow their mothers constantly from soon after birth, whereas young of hiding species do not follow their mothers during the initial period after birth, but lie concealed in vegetation. In hiding species, mothers typically spend most of their time at least 100 m away from their offspring's hiding place, returning intermittently to suckle their young. In contrast, interspecific variation in maternal care strategies has not been thoroughly studied among macropods. Although the well-

studied, large, plains-dwelling macropods have following young and this strategy is usually assumed to be typical of macropods, hiding behavior has been described in detail in one species of wallaby (the red-necked wallaby *Macropus rufogriseus*), and reported to occur in several other species of macropods (Johnson 1987). It is plausible, therefore, that macropods and ungulates may, in fact, share a convergent diversity of maternal care types.

Adaptive explanations for the dichotomy in maternal care strategies in ungulates have usually been based on the mode of protecting offspring from predators, assuming a causal link between the ecology of predation and evolution of behavior. Alternatively, it has been suggested that differences in foraging efficiency between mothers and young in open versus closed habitats may have played a role (Green 1992; Langman 1977), or breeding synchrony selects for following young because it results in increased juvenile survival through predator-swamping, which is less effective if young hide (Estes and Estes 1979; Rutberg 1987). Here we will deal with three traditional explanations based on antipredator adaptations. Hypothesis 1: Open habitat selects for precocial juveniles that follow their mothers from birth because hiding infants suffer greater predation or more harassment from conspecifics in areas lacking cover (Lent 1974). Hypothesis 2: Following is favored in the young of large-bodied species because juvenile survival is increased by more effective maternal defense in these species (Jarman 1974; Lent 1991). Hypothesis 3: Following is adaptive in the young of more gregarious species because group vigilance increases juvenile survival (Estes and Estes 1979; Ralls et al. 1986).

To date, these three traditional explanations for interspecific variation in maternal care strategy have not been tested quantitatively in either ungulates or macropods. In ungulates, the traditional hypotheses are based on descriptive compar-

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isons of body size, group size, habitat, and behavior across species (Jarman 1974; Lent 1974), and from autecological studies showing that vegetation cover reduces predation rates on hiding species, whereas large group size reduces predation rates on followers (Estes and Estes 1979; Barrett 1984; Nelson and Woolf 1987; Fitzgibbon 1990; Aanes and Anderson 1996). Previous authors have not attempted to test predictions that could differentiate between competing hypotheses, but have tended to treat them as an "adaptive suite" without removing the common effect of body size on the other factors (Jarman 1974; Lent 1974). Brashares et al. (2000) have recently shown quantitatively that body size is positively correlated with group size and antipredator behavior (vigilance and flight) of adult antelopes, and that when phylogenetic relationships are taken into account, body size and group size tend to be related, although antipredator behavior remains significantly positively related to group size even after the effects of body size are statistically removed. Group size is likewise positively correlated with body size when phylogenetic methods are used in macropods (Fisher and Owens 2000). In macropods, published information on maternal care has not been synthesized before this study, and information on a possible hider-follower dichotomy in macropods is rudimentary (Jarman 1991; Johnson 1987). As a result, hypotheses that explain variation in maternal care behavior have never been tested in this group, although Johnson (1987) commented that hiding was known or suspected only in small, solitary, forest dwelling wallabies. Finally, no previous studies have explicitly taken account of phylogenetic history in analyzing maternal care strategies among either macropods or ungulates, despite the fact that closely related species often share the same strategy (e.g., all caprines but one are followers; Rutberg 1987).

In this paper, we begin by collating information on the extent of hiding versus following behavior in macropods. We then use this macropod database and a parallel one on ungulates, to test predictions arising from the three antipredator explanations described above. We also propose and test a new life-history hypothesis, Hypothesis 4: that hiding and following are life-history traits linked to the slow and fast end of the life history continuum in ungulates and macropods. The slow-fast continuum describes how slower growth, later weaning and maturity, and longer life span are positively correlated with body size and with each other after body size has been taken into account, but negatively correlated with reproductive rate (Harvey et al. 1989; Saether and Gordon 1994). We suggest that a hiding strategy allows offspring to maximize their growth rate and minimize their age at weaning, because mothers bring milk to the sedentary offspring so that the energetic cost of early infant growth is largely born by the mother rather than the offspring. Conversely, a following strategy puts more of the energetic burden of early growth on the offspring, so that weaning may be delayed as a consequence of following infants being forced to expend more of the energy gained from milk on movement rather than on growth. If this is true, then the following strategy is expected to be associated with "slower" life histories. These associations may arise because maternal care behavior influences life-history evolution or vice versa. All of our tests are based on comparative analyses across species, and we use

both nonphylogenetic and phylogenetic approaches to deal with the fact that some species in the datasets were more closely related than others (see Harvey and Pagel 1991; Martins 2000).

METHODS

We tested Hypothesis 1 (open habitat selects for following because hiding is ineffective in areas lacking dense cover) by determining if habitat openness is associated with following in both macropods and ungulates. We tested Hypothesis 2 (following is favored by maternal size) by examining if species with larger mothers are more likely to have following young. Hypothesis 3 (following is favored in more gregarious species due to benefits of group vigilance) was tested by determining if group size is positively correlated with following and if this effect persists after body size is taken into account. Finally, we investigated our new life-history hypothesis (Hypothesis 4) by testing if following behavior in macropods and ungulates is associated with delayed weaning after effects of body size had been taken into account.

We collated a database on the 27 species of Macropodidae and 138 species of ungulates for which information on the maternal care strategy was available. Variables included maternal care strategy; body weight (g) of adult females; mean group size; habitat openness (ranked 1, closed or dense forest; 2, open forest, woodland, or swamp; 3, open/arid woodland or partly vegetated rocky slopes; 4, treeless plains, tundra, or treeless rocky plateaux); duration of hiding phase; and age at weaning (days). In ungulates, we used two measures of maternal care type. First, we used the dichotomous categories of hiding and following. Previous studies (Lent 1974 and subsequent authors) have used this approach to investigate maternal care in ungulates, thus categorical data are widely available in the literature. There is, however, large variation between species in how long infants hide, ranging from one day to the entire period of nutritional dependence, and there is disagreement about how to categorize species such as goats, which hide for only a short period (O'Brien 1983; Ralls et al. 1986). This suggests that maternal care behavior can also be described on a continuous scale. Because of this, we also considered a measure of the strength of hiding behavior (the proportion of the time between birth and weaning that young ungulates spent in hiding). There were not enough data on hiding macropods to calculate a continuous measure for them. Because ungulate group sizes often change seasonally, we ranked mean group sizes of ungulates in categories from one to ten for analysis. We excluded species that share a nest or burrow with their young (Potoroidae: bettongs and potoroos, and Suidae: pigs and warthogs), arboreal species (*Dendrolagus* spp.: tree kangaroos), and amphibious species (Hippopotamidae). We considered that these groups fall under alternative categories of maternal care, that differ from both hiding and following in terms of their implications for predation risk to the young, maternal investment patterns, and potential for maternal vigilance to affect infant survival. Data were collected from the primary literature, management reports, theses, and unpublished studies (see Table 1 for macropods. Our datasets for both macropods and ungulates are available from the authors on request). If data from more

TABLE 1. Known maternal care in terrestrial macropodidae. Female mass is from Strahan (1995) and Flannery (1990). Care type: H, hiders; F, followers. Habitat type: A, rainforest; B, forest; C, forest ecotone and pasture; D, woodland; E, rock outcrop; F, arid grassland; G, other grassland; H, rainforest ecotone and pasture; I, semiarid shrubland. Evidence (of maternal care type): 1, young rest apart from mothers in captivity; 2, detailed field study; 3, young out of the pouch not seen until half-grown; 4, young usually seen alone, very rarely with mothers; 5, lactating mothers often captured alone; 6, large pouch young but no young-at-foot seen with mothers, adult females rest alone; 7, young left alone on rock outcrops when mother feeds; 8, young hide alone in undergrowth; 9, young rest with mothers in captivity, often seen with mothers in the wild, day and night.

Species	Mass (kg)	Care type	Habitat type	Evidence	Sources of data
<i>Dorcopsis luctuosa</i>	3.58	H	A	1	Bourke 1989
<i>D. muelleri</i>	5.0	H	A	3	pers. com., T. Flannery 1999
<i>Lagorchestes conspicillatus</i>	3.0	F	G/D	9	pers. com., P. Johnson 1999; McCosker 1998
<i>L. hirsutus</i>	1.3	F	F	9	Lundie-Jenkins 1993
<i>Macropus agilis</i>	11.0	F	G/D	9	Bolton et al. 1985
<i>M. antilopinus</i>	17.5	F	G/D	2	Croft 1982
<i>M. dorsalis</i>	6.5	H	B	4, 5	Unpub. obs., D. Fisher; Hoolihan 1994
<i>M. eugenii</i>	5.5	H	C	1	Jarman 1991
<i>M. fuliginosus</i>	16	F	G/D	2	Poole 1995c
<i>M. giganteus</i>	17.8	F	G/D	2	Poole 1995a
<i>M. parma</i>	3.6	H	C	1	pers. com., P. Piggott 1999
<i>M. parryi</i>	11.0	F	G/D	2	Kaufmann 1974, 1975
<i>M. robustus</i>	15.6	F	E in D	2	Poole 1995b
<i>M. rufogriseus</i>	13.8	H	C	2	Johnson 1987; Higginbottom 1991
<i>M. rufus</i>	26.5	F	G	2	Newsome 1995
<i>Onychogalea fraenata</i>	3.4	H	D	2	Fisher 2001
<i>O. unguifera</i>	5.8	H	E in D	6	pers. com., S. Ingleby 1999
<i>Peradorcas concinna</i>	1.4	H	E in D	4, 7	Sanson and Fell 1985
<i>Petrogale assimilis</i>	4.3	H	E in D	7	Horsup 1996
<i>P. inornata</i>	4.2	H	E in D	1	pers. com., P. Johnson 1999
<i>P. lateralis</i>	4.2	H	E in F	1	Hornsby 1978
<i>P. penicillata</i>	6.3	H	E in B	7	Jarman and Bayne 1997
<i>P. persephone</i>	5.2	H	E in A	1	pers. com., P. Johnson 1999
<i>P. xanthopus</i>	7.0	H	E in D	1, 7	Hornsby 1978, Sharp 1997
<i>Setonix brachyurus</i>	2.9	F	I	9	pers. com., E. Sinclair; Shield 1968
<i>Thylgale thetis</i>	3.8	H	H	4, 5, 8	Johnson 1977; Jarman 1991
<i>Wallabia bicolor</i>	13	H	B	8	Johnson 1987

than one study were available, we used the arithmetic mean value.

We performed our comparative analyses in two stages. First, we conducted a series of nonphylogenetic analyses using species as independent data points, and second, we conducted a series of phylogenetic analyses based on "independent contrasts" and randomized phylogenies.

Nonphylogenetic methods assume that traits evolve independently in each species, enabling species to be treated as independent trials in tests of statistical significance. It has recently been suggested that such an approach may be most suitable when studying rapid adaptive radiations (see Price 1997; Harvey and Rambaut 2000; Martins 2000). Phylogenetic methods, on the other hand, take account of statistical nonindependence that arises from closely related species sharing traits of their common ancestor and seek to identify phylogenetically independent changes with respect to the traits in question (Felsenstein 1985; Ridley 1989, Harvey and Pagel 1991). Indeed, it has been suggested that phylogenetic methods should be used even in cases where the traits under study are labile (Ridley 1989). This is because potentially confounding variables may still be distributed nonrandomly with respect to phylogeny. However, the results of phylogenetic methods may depend on the particular phylogeny and type of comparative method used (see Rohlf et al 1990; Price 1997; Harvey and Rambaut 2000; Martins 2000). In the face of this ongoing debate, we used both nonphylogenetic and phylogenetic methods to maximize the chances that any bi-

ological conclusions reached were robust to the exact form of evolution assumed by different comparative models.

For the phylogenetic comparative analyses, we used the program Fels-Rand (Blomberg 2000), which is based on the approach suggested by Losos (Losos 1994; Stamps et al. 1997). This method deals with incompletely known phylogenies by incorporating all phylogenetic knowledge that is available and randomizes only those parts of the tree where phylogenetic data is lacking. Using Fels-Rand, we generated large numbers of "random trees" (or "equiprobable trees"; Maddison 1991) that were topologically concordant with the known parts of the phylogeny, but had each polytomy arbitrarily (randomly) resolved. We then used Felsenstein's (1985) independent comparisons technique to look for associations between phylogenetically independent contrasts (i.e., changes in behavior vs. changes in the explanatory variables) for each of these trees. To incorporate categorical variables (hiding and following behavior) into the contrast analyses, we created a dummy variable and set it equal to zero (hiding) or one (following) and calculated the phylogenetically independent contrasts using Felsenstein's (1985) method. We then tested the significance of the dummy variable in the subsequent regression analyses, as a test for the significant effect of offspring behavior on the dependent variables. Finally, we tested whether, across all equiprobable trees, there was a significant relationship between the contrasts (see Blomberg 2000; Losos 1994; Martins 1994). We controlled for body size by taking the residuals of each con-

trast from the relationship between each variable and the contrasts of body size. For all tests, ungulates and macropods were analyzed separately.

Because there were no branch lengths associated with many of the phylogenies, we set all branch lengths equal. This corresponds to a ‘‘speciational’’ model of evolution (Rohlf et al. 1990; Martins and Garland 1991). Although this model is unlikely to be correct in the details for either ungulates or the macropods, it performs better than other evolutionary models in simulations, as well as performing better than nonphylogenetic approaches (Purvis and Rambaut 1995). For macropods, we based analyses on the phylogeny from Fisher and Owens (2000), and for ungulates, we used a composite molecular phylogeny composed from molecular phylogenies in Groves and Shields (1996), Janecek et al. (1996), Gatesy et al. (1997), Hassanin et al. (1998), Oakenfull and Clegg (1998), Matthee and Robinson (1999), Pérez-Barbería and Gordon (1999), and Rebholtz and Harley (1999). Ancestral character states were inferred using MacClade, following the technique of Swofford and Maddison (1987). We analyzed the data using analysis of variance, Spearman-rank correlations, and linear regression performed in SAS (SAS Institute 1989). Maternal mass, age at weaning, and group size were log-transformed prior to analysis and the proportion of the dependence period spent hiding was arcsin-transformed.

RESULTS

In our datasets, the proportion of macropods and ungulates in each category of maternal care was virtually identical. Thirty-eight percent of ungulate species and 37% of macropod species (Table 1) had following young (Figs. 1a,b).

Antipredator Hypotheses

Hypothesis 1. Habitat cover

The hypothesis that deficiency of concealing cover is positively related to evolution of following behavior was strongly supported. Habitat structure was very strongly related to maternal care strategies in both ungulates and macropods.

Using species values, species with following young occurred in significantly more open habitats in both groups (macropods: mean rank 2.1 ± 0.2 hidiers, 3.2 ± 0.3 followers; ungulates: mean rank 2.1 ± 0.1 hidiers, 3.6 ± 0.1 followers; Table 2). Following ungulates were also found in significantly more open habitats after body size was taken into account. Habitat openness rank was marginally but not significantly higher in following than in hiding macropods ($P = 0.05$) after body size was taken into account (macropods: mean rank -0.33 ± 0.25 hidiers, 0.39 ± 0.23 followers; ungulates: mean rank -0.53 ± 0.12 hidiers, 0.88 ± 0.12 followers; Table 2). The proportion of the dependence period spent hiding (the continuous measure of maternal care type in ungulates) was also inversely related to habitat openness (Spearman rank test; $\rho = -0.37$, $P = 0.006$).

This pattern persisted after controlling for phylogenetic non-independence. In both ungulates and macropods, changes in following behavior were associated with changes in habitat, with increased following being associated with more

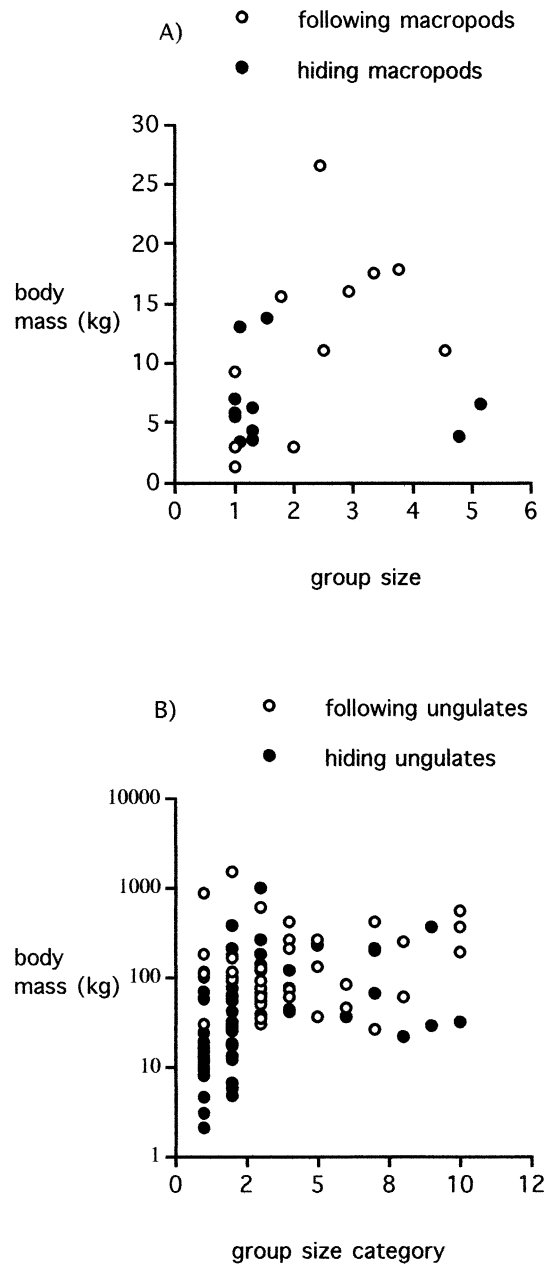


FIG. 1. (A) Body size versus gregariousness (mean group size) in macropods with respect to maternal care strategy, using species as independent data points. (B) Body size versus gregariousness (ranked group size categories) in ungulates with respect to maternal care strategy, using species as independent data points.

open habitats (Table 3). In ungulates, contrasts in the proportion of the dependence period spent hiding were also inversely related to contrasts in habitat openness (mean $r = -0.33$, $P < 0.01$).

Hypothesis 2. Size of mother

Large-bodied ungulate species were more likely to be followers when species data were considered (Table 2, Fig. 1b). However, body size was not related to maternal care in the same way in ungulates and macropods. The proportion of

TABLE 2. Associations between maternal care strategy and explanatory variables, based on analyses using species values as independent data points. H is hypothesis number (1, habitat openness; 2, size of mothers; 3, gregariousness; 4, life history), *F*-value is *F*-ratio associated with ANOVA tests, *P*-value is the two-tailed probability associated with respective *F*-values. Residual values are residuals on body mass.

H	Explanatory variable	Ungulates		Macropods	
		<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value
1	Habitat rank	$F_{1,123} = 67.9$	<0.0001	$F_{1,18} = 10.37$	<0.005
2	Body size	$F_{1,120} = 33.2$	<0.0001	$F_{1,31} = 5.9$	<0.05
3	Group size	$F_{1,112} = 12.7$	<0.0005	$F_{1,23} = 1.22$	0.28
4	Weaning age	$F_{1,85} = 10.3$	<0.01	$F_{1,21} = 5.6$	<0.05
1	Residual habitat rank	$F_{1,123} = 59.2$	<0.0001	$F_{1,18} = 4.4$	0.05
3	Residual group size	$F_{1,112} = 8.5$	<0.005	$F_{1,23} = 1.2$	0.29
4	Residual weaning age	$F_{1,85} = 9.4$	<0.005	$F_{1,21} = 1.3$	0.28

dependence time spent hiding was negatively related to body mass in ungulates ($F_{1,72} = 14.0, P = 0.0004, r^2 = 0.16$). No ungulate species under 25 kg had following young, but several very large species were hidiers (Fig. 1b).

After controlling for nonindependence due to phylogeny, body size was no longer related to maternal care category in ungulates (Table 3), but the proportion of the dependence period spent hiding remained significantly negatively related to body mass (mean regression coefficient = $-0.4337, P < 0.01$).

Following species of macropods were also larger than hiding species (Table 2, Fig. 1a). Medium-sized species (4–9 kg) were exclusively hidiers, and both very large (>15 kg) and very small (<3 kg) species were exclusively followers. Maternal care strategies of macropods are not known in enough detail for a statistical comparison of hiding duration, although red-necked wallabies, which are large for hiding macropods (13.8 kg), hide for 33% of the time between leaving the pouch and weaning, and bridled nailtail wallabies, which are small (3.4 kg), hide for 100% of the time until weaning (Johnson 1987; Fisher and Goldizen 2001).

As in ungulates, contrasts in body size were not related to contrasts in maternal care category in macropods (Table 3).

Hypothesis 3. Gregariousness

The hypothesis that gregarious species are more likely to have evolved following behavior received some support in ungulates but no support in macropods. Ungulate species with hiding young included the entire range of group sizes in the clade (Fig. 1b). Following ungulates did form larger herds than hiding species (Table 2, Fig. 1b). The residual of group size on maternal body mass differed between hiding and fol-

lowing categories of ungulates (-0.45 ± 0.25 for hidiers, 0.88 ± 0.43 for followers; Table 2). Group size in macropods was not associated with maternal care category for species data whether or not body size was taken into account (Table 2, Fig. 1a).

Nor was change in group size of macropods associated with change in following behavior using phylogenetically independent contrasts (Table 3). Changes in group size were not associated with changes in the proportion of dependence spent hiding in ungulates (mean $r = -0.279, ns$).

Hypothesis 4. Life history

There was some support for our new hypothesis, that the following style of maternal care is associated with the evolution of delayed weaning and therefore a slower life-history strategy in both ungulates and macropods. Ungulates with hiding young had significantly younger ages at weaning than those with following young ($F_{1,85} = 15.4, P = 0.0002$), and also had significantly younger residual ages at weaning after maternal mass was taken into account (Table 2).

However, when phylogenetic methods were used, changes in following behavior were not associated with changes in age at weaning (Table 3), and changes in the proportion of the dependence period spent hiding were not related to changes in residual age at weaning in ungulates ($r = 0.012, ns$).

Macropods with hiding young had significantly younger ages at weaning than those with following young (Table 2), and older age at weaning was marginally but not significantly associated with following behavior when phylogenetic contrasts were used (Table 3).

Relationships among the Potential Explanatory Variables

In ungulates, group size was strongly positively associated with habitat openness and body weight, and body weight was positively correlated with age at weaning. Age at weaning was marginally, but not significantly positively associated with group size ($P = 0.08$) and habitat openness ($P = 0.07$) (Table 4). However, the strong association between open habitats and following was not due to a common association with group size in ungulates. The negative relationship between habitat openness and the proportion of the dependence period spent hiding in ungulates persisted after the effect of group size was statistically removed by taking residuals (Spearman rank test, $\rho = -0.31, P = 0.007$). Age at weaning and maternal body mass were strongly positively correlated in ma-

TABLE 3. Associations between maternal care category and explanatory variables, based on analyses using phylogenetically independent contrasts. H is hypothesis number (1, habitat openness; 2, size of mothers; 3, gregariousness; 4, life history), *r* is the mean correlation coefficient derived from randomization, the *P*-value is the two-tailed probability associated with the test statistic.

H	Explanatory variable	Ungulates		Macropods	
		mean <i>r</i>	<i>P</i> -value	mean <i>r</i>	<i>P</i> -value
1	Habitat rank	0.34	<0.01	0.50	<0.01
2	Body size	0.17	ns	0.07	ns
3	Group size	0.28	<0.01	0.26	ns
4	Weaning age	0.10	ns	0.41	<0.1

TABLE 4. Associations among the potential explanatory variables for ungulates, based on raw data and analyses using evolutionarily independent contrasts. Mean r is the mean (Pearson) correlation coefficient derived from randomization, ρ is the Spearman correlation on the raw data, and P -value is the two-tailed probability associated with the test statistic.

	Group size		Habitat rank		Body weight (log)	
Group size	—		—		—	
Habitat rank	$\rho = 0.67$	$P < 0.0001$	—		—	
Body weight (log)	$F_{1,113} = 19.9$	$P < 0.0001$	$\rho = 0.40$	$P < 0.0001$	—	
Age at weaning (log)	$F_{1,85} = 3.1$	$P = 0.08$	$\rho = 0.19$	$P = 0.07$	$F_{1,92} = 76.7$	$P < 0.0001$
	Group size contrast		Habitat rank contrast		Body weight contrast	
Habitat rank contrast	mean $r = 0.2142$	$P < 0.05$	—		—	
Body weight contrast	mean $r = 0.22961$	$P < 0.05$	mean $r = 0.1861$	$P < 0.05$	—	
Age at weaning contrast	mean $r = 0.09414$	ns	mean $r = 0.0882$	ns	mean $r = 0.4197$	$P < 0.01$

crocods, and group size and body mass were marginally but not significantly positively correlated when species values were considered ($P = 0.08$). The other explanatory variables were not correlated (Table 5). Because habitat openness was not correlated with group size in macropods, the strong relationship between habitat and maternal care strategy was not due to a common association with group size.

There was a slight, nonsignificant positive association between age at weaning in macropods and both group size and habitat openness when species-specific data were analyzed, but not when phylogenetic methods were used (Table 5); and none of the explanatory variables were positively correlated with each other, except for age at weaning and maternal body weight (Table 5).

DISCUSSION

Our analyses reveal striking agreements in the ecological and life history correlates of maternal care strategies in ungulates and macropods. Hiding is apparently an ancient trait in both macropods and ungulates (Figs. 2a, b). It appears that ungulates and macropods have evolved following and hiding behavior as solutions to the same challenges on different continents, that is, maternal care strategies in the two clades are convergent.

The Influence of Predation Risk on Maternal Care

Overall, our results strongly supported the first of the three traditional hypotheses that we tested and provided some support for the other two hypotheses in the case of ungulates.

Therefore, these results provide the first quantitative evidence in favor of the traditional view that hiding and following strategies have evolved as alternative tactics of predator avoidance. The first traditional explanation that we tested (Hypothesis 1) was that hiding infants suffer greater predation or harassment in areas lacking cover, so a historical change to more open habitat in some species favored abandonment of the hiding response and the evolution of following behavior (Lent 1974). Hiding has also evolved in clades consisting mainly of followers among species that now inhabit closed habitats (Fig. 2b). Our results reinforce this popular explanation for ungulates based on a much larger dataset than previously, and confirm that the result is robust even when nonindependence due to common ancestry is taken into account. We have also found that, as originally suggested by Johnson (1987) based on a small number of species, following behavior is similarly strongly associated with low-cover habitats in macropods. As for ungulates, this result persisted when we used phylogenetically independent contrasts. Maternal care strategies were related to habitat independently of body weight and group size in both macropods and ungulates.

The second explanation tested (Hypothesis 2) was that following is favored in the young of large-bodied species, possibly because adults are better at physically repelling predators. In this case, maternal defense would increase juvenile survival in these species if they stay close to their mothers (Jarman 1974; Lent 1991). Our results show that body size is indeed related to maternal care in the predicted direction in ungulates and macropods. However, body size may cor-

TABLE 5. Associations among the potential explanatory variables for macropods, based on raw data and analyses using evolutionary independent contrasts. Mean r is the mean (Pearson) correlation coefficient derived from randomization, ρ is the Spearman correlation on the raw data, and the P -value is the two-tailed probability associated with the test statistic.

	Group size		Habitat rank		Body weight (log)	
Group size	—		—		—	
Habitat rank	$\rho = 0.10$	$P = 0.66$	—		—	
Body weight (log)	$F_{1,20} = 3.24$	$P = 0.08$	$\rho = -0.18$	$P = 0.35$	—	
Age at weaning (log)	$F_{1,18} = 1.7$	$P = 0.22$	$\rho = -0.27$	$P = 0.20$	$F_{1,21} = 18.8$	$P < 0.0003$
	Group size contrast		Habitat rank contrast		Body weight contrast	
Group size contrast	—		—		—	
Habitat rank contrast	mean $r = 0.06$	ns	—		—	
Body weight contrast	mean $r = 0.26$	ns	mean $r = 0.17$	ns	—	
Age at weaning contrast	mean $r = 0.26$	ns	mean $r = 0.26$	ns	mean $r = 0.58$	$P < 0.01$

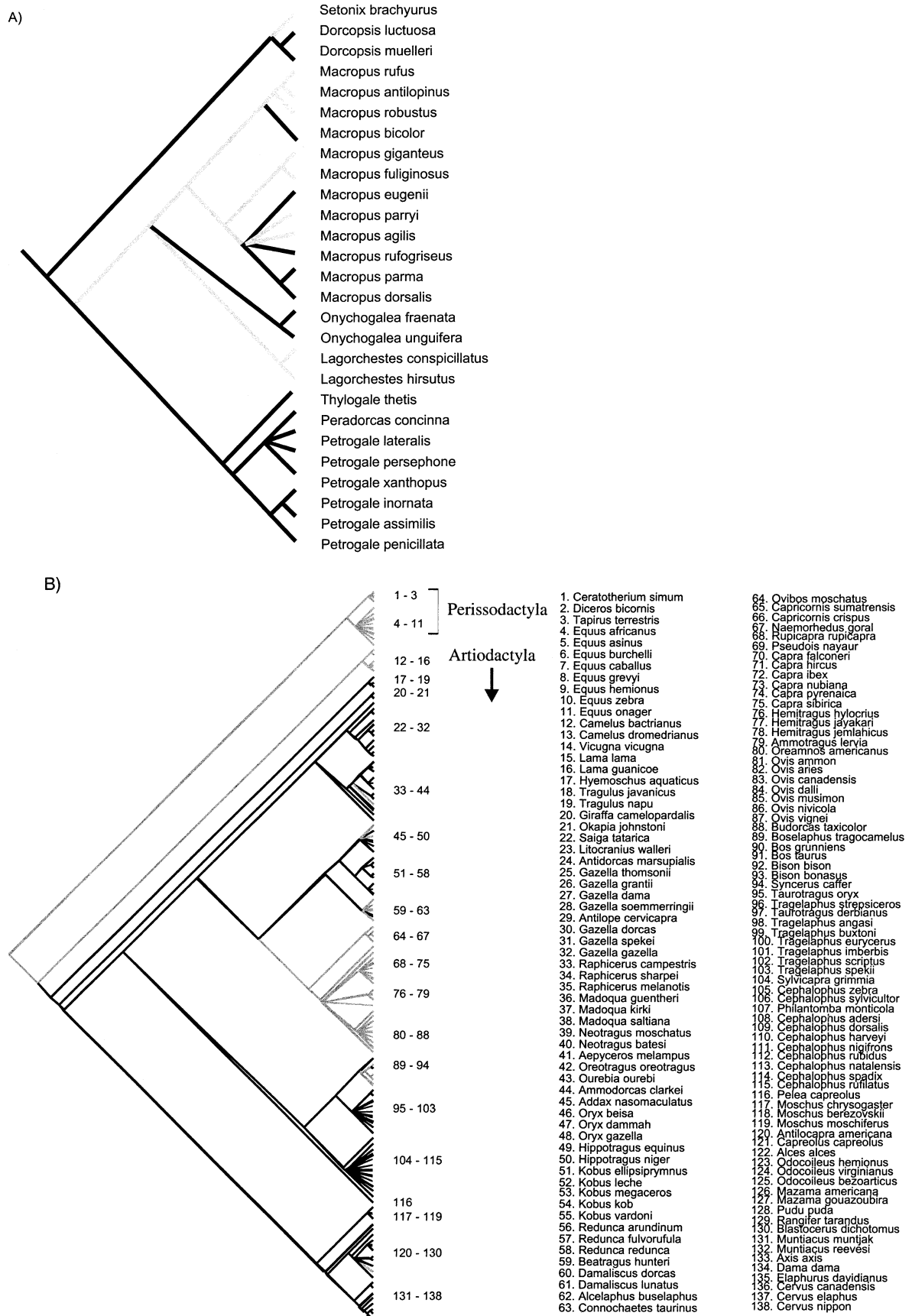


FIG. 2. (A) Maternal care strategies with respect to phylogenetic relationships among species of Macropodidae. (B) Maternal care strategies with respect to phylogenetic relationships among ungulates. Gray represents following and black represents hiding strategies.

relate with infant following because it is correlated with a third important variable, such as age at weaning (see below, Table 4), habitat preferences (Jarman 1974; Jarman 1991), or a tendency to flee from predators (Brashares et al. 2000, and see below), rather than with maternal defense capability. Body size was not related to maternal care tactics after phylogenetic relationships were taken into account.

The final traditional explanation tested (Hypothesis 3) was that young of gregarious species have improved survival if they stay with adults because they benefit from enhanced group vigilance (Estes and Estes 1979; Ralls et al. 1986). This hypothesis received some support from our analyses of ungulates, but not macropods. Gregariousness was related to infant following behavior in ungulates after body size had been taken into account, and this relationship was not explained by common associations with habitat. Brashares et al. (2000) found that vigilance and flight rather than crypsis are adult antipredator tactics associated with large group size in antelopes, but that contrasts in antipredator behavior were not related to contrasts in body size. Studies of individual behavior have also shown that group size is related to vigilance and juvenile survival in following ungulates for example, in wildebeest (*Connochaetes taurinus*) and bighorn sheep (*Ovis canadensis*) (Berger 1978; Estes and Estes 1979). However, group size was not related to maternal care type in ungulates when phylogenetic methods were used. Although group size is related to vigilance in adults of following macropods such as eastern grey kangaroos and red kangaroos (*Macropus giganteus* and *M. rufus*) (Colagross and Cockburn 1993; Watson and Dawson 1993), it was not related to maternal care type among species of macropods (Tables 2 and 3).

Life History and Maternal Care Strategy

Our new life history hypothesis (Hypothesis 4) predicts that the following strategy is associated with the slow end of the mammalian slow-fast continuum, and should therefore be associated with slow growth and long periods of dependence. This is because a hiding strategy allows offspring to conserve energy by being sedentary, which maximizes their growth rate and reduces age at weaning. In these species, mothers endure the energy cost of bringing milk to the offspring. Conversely, following young expend less energy per day on growth and more on movement, so that weaning is delayed. If this is true, then the following strategy is expected to be associated with "slower" life histories, because age at weaning is strongly related to other life history traits in ungulates and macropods (Saether and Gordon 1994; Fisher et al. 2001). Consistent with this hypothesis, age at weaning was higher in followers than in hidiers after body mass was taken into account, and this relationship was marginally non-significant in macropods when phylogenetic contrasts were used (Table 3). Furthermore, the continuous measure of maternal care strategy in ungulates behaves as a typical mammalian life-history variable in scaling allometrically with maternal body mass (Harvey et al. 1989). However, contrasts in age at weaning were not related to contrasts in maternal care strategies in ungulates.

Taken together, these results suggest that predator avoid-

ance is indeed a major explanation for the evolution of the hider-follower dichotomy in both ungulates and macropods, although not all the previous explanations given by Lent (1974) and others are supported by our analyses. It is thought that past species diversification into more open habitats to take advantage of new resources (particularly grass) was accompanied by increasing body size in macropods (Jarman 1974; Hume et al. 1989). This was in turn accompanied by increased gregariousness, which is an effective antipredator strategy in open habitats for adult herbivores (Jarman 1974; Jarman 1991). We propose that, in both macropods and ungulates, high mortality of hiding infants in cover-deficient habitat selected for following behavior in juveniles. In ungulates, improved ability of more gregarious mothers to detect predators in the open may also have played a role. Contrary to suggestions by Jarman (1974) and Lent (1991), the relationship between large body size and following behavior does not imply that maternal defense ability played an important role in either group. Female ungulates regularly chase and attack predators approaching their young, regardless of whether they are hidiers or followers. Even small species such as pudu (*Pudu puda*, 9 kg), dikdik (*Sylvicapra grimmia*, 17 kg), and gazelles (e.g., *Gazella thomsoni*, 20 kg) are reported to attack potential predators (Hick 1969; Kingdon 1982). Group-living macropods rely on flight to avoid predators and no maternal defense of offspring has been observed in macropods of any size (Coulson 1996).

Juvenile followers are weaned later than hidiers of the same body size. Delayed weaning may be a consequence of these infants being forced to expend more of the energy gained from milk on movement rather than on growth. This idea is supported by a study of lactation, metabolism, and growth in two similar-sized ungulates with contrasting strategies in the same habitat. Although two-species comparisons are not conclusive evidence (Garland and Adolph 1994), the hider (mule deer, *Odocoileus hemionus*) did grow faster than the follower (mountain goat, *Oreamnus americanus*) and maternal energy expenditure was greater in the follower (Carl and Robbins 1988). The observation that hiding young take longer after birth to stand and walk than following young (Lent 1974) is also consistent with this idea, as hidiers are expected to conserve energy through sedentary behavior. However, because of predation risk, this option is only available to young of species living in closed habitats. Infant following could also lead to higher total maternal investment in followers than in hidiers due to effects of maternal vigilance on foraging (see Green 1992). Because species that changed from a diet of browse and herbs to a relatively energy-poor diet of grass concurrently invaded more open habitats where grass is available, late weaning may alternatively be a consequence of dietary constraints (Saether and Gordon 1994), and following may be an associated mechanism by which the cost of lactation to mothers is spread over a longer period of time. Conversely, species in predominantly following clades that evolved hiding when they invaded forest habitats and began eating browse may have been released from such constraints.

Another explanation for the relationship between age at weaning and maternal care strategy in ungulates is that late weaning in followers is a byproduct of the benefit of maternal

vigilance in open habitats. Weaning could be delayed simply because it's safer for followers to stay with mothers for longer. However, this argument does not apply to macropods, in which group size is not related to maternal care, and does not explain why ungulate mothers should continue to suckle these young. Weaning is not synonymous with independence, particularly in the many matrilineal macropods and ungulates in which weaned females form extended associations with their mothers (e.g., Jarman 1991).

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