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The evolution of parasite-defence grooming in ungulates

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Grooming repertoires are exhibited by all terrestrial mammals, and removal of ectoparasites is an important ancestral and current function. Parasite-defence grooming is regulated both by a central control mechanism (programmed grooming model) and by cutaneous stimulation from bites (stimulus-driven model). To study the evolution of parasite-defence grooming in ungulates, we compared species-typical grooming behaviour with host morphology and habitat to test predictions of the programmed grooming model while taking into account phylogenetic relatedness. We observed grooming in 60 ungulate species at ectoparasite-free zoological parks in which the confound of differential tick exposure was controlled for and stimulus-driven grooming was ruled out. Concentrated-changes tests indicated that sexually dimorphic grooming (in which breeding males groom less than females) has coevolved with sexual body size dimorphism, suggesting that intrasexual selection has favoured reduced grooming that enhances vigilance of males for oestrous females and rival males. Concentrated-changes tests also revealed that the evolution of complex oral grooming (involving alternate use of both teeth and tongue) and adult allogrooming (whereby conspecifics oral groom body regions not accessible by self grooming) was concentrated in lineages inhabiting closed woodland or forest habitat associated with increased tick exposure, with such advanced grooming being most concentrated in Cervidae. Regression analyses of independent contrasts indicated that both host body size and habitat play a role in the evolution of species-typical oral grooming rates, as previously reported. These results indicate that the observed grooming represents centrally driven grooming patterns favoured by natural selection in each lineage. This is the first phylogenetically controlled comparative study to report the evolution of parasite-defence grooming behaviours in response to selection pressures predicted by the programmed grooming hypothesis.

ADDITIONAL KEYWORDS: body size – habitat – parasites – programmed grooming – sexual size dimorphism – ticks – vigilance.

INTRODUCTION

Grooming, broadly defined, involves all forms of body surface care, and is an activity of importance to the survival and wellbeing of animals. Either directed to an individual's own body or to that of a conspecific, grooming is virtually ubiquitous among terrestrial vertebrates. Among the many possible functions of grooming (e.g. maintenance of insulation, thermoregulation, communication, or social relationships; e.g. Muller-Schwarze, 1974; Seyfarth, 1977; Thiessen *et al.*, 1977; McKenna, 1978; Patenaude & Bovet, 1984; Walther, 1984; Schino, 1988, 1998, 2001; Ferkin *et al.*, 2001), parasite-removal is among the most important. Because ticks are the most important ectoparasites of wild animals (Allan, 2001), we focused on tick-removal grooming in this study. However, grooming is effective in removing lice from rodents, birds, and cattle (Lewis, Christensen & Eddy, 1967; Brown, 1974; Murray, 1987), mites from rodents (Wiesbroth, Friedman & Powell, 1974) and ectoparasitic flies from vampire bats (Wilkinson, 1986); grooming may also remove other ectoparasites (e.g. fleas, chiggers). However, for large mammals such as ungulates, the cost of

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The cost of ectoparasites for host animals has been well documented, including tick-associated declines in growth for domestic calves (Little, 1963; Sutherst *et al*., 1983; Kaiser, Sutherst & Bourne, 1991). For example, a moderate tick load on a calf can result in a 10–44 kg reduction in weight gain per year due to blood loss and tick-induced anorexia (Norval *et al*., 1988). A similar loss of reserves in a wild animal would be expected to have fitness-compromising consequences. The efficacy of grooming in removing ectoparasites has been established through experimental studies in which grooming was restricted (Koch, 1981, 1988; Hart, 1990; Mooring, McKenzie & Hart, 1996a; Eckstein & Hart, 2000). For example, impala (*Aepyceros melampus* Sundevall) wearing a neck harness that partially prevented oral self-grooming harboured 20 times more adult female ticks compared with impala wearing control harnesses that permitted grooming (Mooring *et al*., 1996a). Given the costs of ectoparasite infestation, individuals with effective grooming behaviour would be at a selective advantage. However, grooming may incur costs, such as compromised vigilance against predators (Maestripieri, 1993; Cords, 1995; Mooring & Hart, 1995a) and conspecifics (Mooring & Hart, 1995b; Mooring, McKenzie & Hart, 1996b), saliva loss from oral grooming (Ritter & Epstein, 1974), attrition of dental elements in ungulates that use their teeth to groom (McKenzie, 1990), and the thermoregulatory costs of winter hair loss in the northern environment (Mooring & Samuel, 1999). An optimal grooming rate should thus balance the cost of ticks against the costs of grooming.

THE PROGRAMMED GROOMING MODEL

The ‘programmed grooming model’ is a conceptual framework for the neurobiological regulation of parasite-defence grooming (Hart *et al*., 1992; Mooring, 1995). It postulates a type of central programming that periodically evokes a bout of grooming in order to remove ticks before they are able to attach and blood-feed. There is ample evidence for central control of grooming (Roth & Rosenblatt, 1967; Nelson *et al*., 1975; Colbern & Gispen, 1988; Fentress, 1988; Spruijt, Van Hooff & Gispen, 1992). Because engorging ticks are costly, preventive removal before they engorge would be adaptive. This is in contrast to the ‘stimulus-driven grooming model’ (Riek, 1962; Willadsen, 1980; Wikel, 1984), in which grooming is a direct response to cutaneous irritation from tick bites. The two models are not mutually exclusive, and indeed central and peripheral mechanisms are thought to operate concurrently as a complementary system. Previous studies suggest that programmed grooming predominates in the natural environment (Hart *et al*., 1992; Mooring & Hart, 1992, 1993, 1995a, b, 1997a,b; Olubayo *et al*., 1993; Mooring, 1995; Hart, Hart & Wilson, 1996; Mooring *et al*., 1996a,b, 2000, 2002; Mooring & Samuel, 1998a,b; Mooring, Gavazzi & Hart, 1998; but see Mooring & Samuel, 1998c for an exception).

Several predictions emerge from the programmed grooming model. These are not necessarily independent of one another, and interactions between some could occur:

The body size principle

This principle is based on the recognition that smaller animals, with a greater surface area-to-mass ratio, incur higher costs for a given density of tick infestation relative to larger ones (Hart *et al*., 1992). Assuming an equal rate of infestation, small-bodied animals should groom at a higher rate and consequently maintain a lower density of ticks compared with larger animals. Intraspecifically, juveniles have been observed to groom more than adults (Mooring & Hart, 1997a,b; Mooring & Samuel, 1998a,b; Mooring *et al*., 2002) and harbour fewer ticks as a result (Gallivan *et al*., 1995). Vulnerability to ectoparasites would favour the evolution of higher programmed grooming rates in members of small-bodied species, and lower rates in larger-bodied individuals, as observed in earlier studies in which phylogeny was not controlled (Hart *et al*., 1992; Olubayo *et al*., 1993; Mooring *et al*., 2000). After controlling for phylogenetic similarity, there should be a negative relationship between body size and grooming rate, all other things being equal.

The vigilance principle

This predicts that males of polygynous species will groom less than females in the same herd during the breeding season (sexually dimorphic grooming) in order to maintain high levels of vigilance for rival males or oestrous females (Hart *et al*., 1992) . A corollary of the vigilance principle is that such males should carry more ectoparasites. Sexually dimorphic grooming has been observed in a wide range of ungulates (Hart *et al*., 1992; Mooring & Hart, 1995b; Mooring *et al*., 1996b, 1998, 2002; Mooring & Samuel, 1998a), and territorial male impala, rutting male white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) carried many more ticks than females (Drew & Samuel, 1985; Main *et al*., 1981). Because sexual dimorphism in body size has evolved in response to sexual selection for mating success by competing males (e.g. Andersson, 1994; Mitani, Gros-Louis & Richards, 1996; Plavcan & Van Schaik, 1997; Lindenfors & Tullberg, 1998; Owens & Hartley, 1998; Loison *et al*., 1999; Szekely, Reynolds & Figuerola, 2000; Dunn, Whittingham & Pitcher, 2001; Ord, Blumstein & Evans, 2001; Pérez-Barbería, Gordon &

Pagel, 2002), sexually dimorphic grooming is expected to have evolved in those species exhibiting sexually dimorphic body size, but not in sexually monomorphic species. We assume that a monomorphic body plan is indicative of reduced intrasexual selection, and thus a reduced need to maintain vigilance during the breeding season compared with sexually dimorphic species.

The tick challenge principle

This predicts that, within a population, grooming rate will track the intensity of tick challenge (Mooring, 1995). Because tick challenge may vary dramatically over time and space, animals are predicted to adjust grooming rate on either a seasonal or a geographical basis. Because the programmed rate of grooming may be modified according to other needs that would increase its cost, the rate need not be directly proportional to tick density (as predicted by the stimulus driven model). Programmed grooming can be further distinguished from stimulus-driven grooming because it predicts that (1) hosts that groom the most will have the fewest ticks (cf. the stimulus-driven prediction that hosts that have the most ticks will groom the most), and (2) baseline rates of programmed grooming will be non-zero, even in a tick-free environment. The tick challenge prediction has been supported for African and North American ungulates (Mooring, 1995; Mooring & Hart, 1997a, 1997b; Mooring & Samuel, 1998b).

The habitat principle

This is related to the previous category, but in this case the predicted correlation is between grooming and habitat, rather than tick density. Because habitats with a greater density of ectoparasites expose hosts to a higher risk of infestation, animals that inhabit such areas are predicted to groom more frequently than those utilizing habitats of lower parasite density. A broad generalization is that closed habitats, such as woodland and forest, have a greater abundance of ticks than open ones, such as grassland or savanna (Londt & Whitehead, 1972; Semtner & Hair, 1973; Norval, 1977; Barnard, 1986; Garris, Popham & Zimmerman, 1990; Carroll & Schmidtmann, 1996). This is because free-living ticks must maintain water balance, and relatively few tick species have adapted to the aridity and desiccating effects of direct sunlight. Although variation in host density and use of adjacent habitats can complicate the picture, host animals living in more closed habitats should generally be exposed to a greater density of ticks, and natural selection should have favoured relatively higher grooming rates in such species compared with inhabitants of open habitats. This prediction has been supported in African antelope (Hart *et al*., 1992, 1996) and a survey of 25 bovids (Mooring *et al*., 2000). Because of the fitness costs imposed by tick infestation, members of species inhabiting closed, more parasite-dense habitats would be favoured by natural selection to evolve more efficient parasite-defence grooming patterns compared with inhabitants of open, more parasite-sparse habitat. Increased parasite-removal efficiency might be reflected in a greater frequency of grooming, adult allogrooming for removing parasites from parts of the body not accessible to self-grooming, and more complex grooming, such as use of both teeth and tongue in oral grooming.

TESTING THE PREDICTIONS

If a programmed grooming mechanism has shaped the evolution of grooming in mammals, one might predict that the above-mentioned principles will have influenced the patterns of grooming exhibited by extant species after taking into account phylogenetic relatedness. One might also predict that there would be evidence of coevolution between grooming and body size and specific habitat characteristics. We tested these predictions by calculating independent contrasts and using concentrated-changes tests. We applied these formal phylogenetic analyses to the extensive data set of Mooring *et al*. (2000, 2002), which were collected to ask different questions, to explicitly study the evolution of parasite-defence grooming. Support for the predictions would constitute support for the programmed grooming model and its evolutionary assumptions, while falsification would suggest that the observed grooming primarily serves functions other than parasite defence.

In this study we took advantage of a large sample of ungulates in which phylogenetic relationships were hypothesized from molecular analyses, relative tick abundance in the ancestral environment could be inferred from typical habitat, and baseline grooming rates were observed in an ectoparasite-free environment. The absence of ticks allowed us to control for differential tick exposure, which would have been a major confound in wild populations. Because the stimulus-driven grooming model would predict no grooming in the absence of ectoparasite stimulation, stimulus-driven grooming could be ruled out and we assumed all grooming was centrally regulated. We focused on oral grooming (using teeth, tongue, or both) and scratching with the hindleg. For oral grooming, we considered both self-grooming and allogrooming because previous work has indicated that allogrooming (in which one individual delivers oral grooming to a conspecific) may also be under the control of the intrinsic timing mechanism proposed by the programmed grooming model (Mooring & Hart, 1992, 1997b; Mooring, 1995).

Table 1. Regression results from the analyses of phylogenetically independent contrasts when females, males, and the averages of both sexes were studied (significant *P*-values are in bold)

	Grooming measures[a]	R^2 [b]	Full model p[c]	Mass	Habitat max	R[d]	Mass-alone-p[e]	R[d]	Habitat-alone-p[e]
Females	ORBT	0.134	**0.015**	**0.013**	0.160	–0.323	**0.011**	0.189	0.144
Females	OREP	0.157	**0.007**	**0.006**	0.138	–0.352	**0.005**	0.198	0.126
Females	SCRBT	0.029	0.424	0.195	0.935	–0.170	0.189	0.019	0.885
Females	SCREP	0.015	0.640	0.363	0.776	–0.118	0.365	–0.031	0.810
Females	%GRM	0.158	**0.007**	**0.015**	**0.050**	–0.315	**0.013**	0.257	**0.046**
Males	ORBT	0.091	0.108	**0.038**	0.959	–0.301	**0.034**	0.048	0.738
Males	OREP	0.064	0.220	0.098	0.723	–0.248	0.083	0.084	0.566
Males	SCRBT	0.046	0.330	0.401	0.183	–0.095	0.511	–0.177	0.218
Males	SCREP	0.026	0.533	0.474	0.342	–0.086	0.554	–0.125	0.387
Males	%GRM	0.042	0.362	0.163	0.943	–0.205	0.152	0.038	0.791
Overall	ORBT	0.106	**0.039**	**0.029**	0.228	–0.288	**0.024**	0.168	0.195
Overall	OREP	0.136	**0.014**	**0.012**	0.171	–0.328	**0.010**	0.189	0.146
Overall	SCRBT	0.019	0.572	0.345	0.614	–0.120	0.357	–0.059	0.654
Overall	SCREP	0.011	0.721	0.498	0.632	–0.085	0.513	–0.058	0.659
Overall	%GRM	0.091	0.063	0.062	0.178	–0.249	**0.053**	0.185	0.153

[a] ORBT = oral bouts per h; OREP = oral episodes per h; SCRBT = scratch bouts per h; SCREP = scratch episodes per h; %GRM = per cent scans grooming (oral and scratch)

[b] The proportion of variation explained in the multiple regression of contrasts of body mass and habitat max on each dependent variable

[c] The overall significance of these multiple regressions

[d] Bivariate regression coefficients

[e] *P*-values from bivariate regressions

METHODS

Study site and subjects

We conducted observations on 60 species of ungulates at the San Diego Wild Animal Park (SDWAP) and San Diego Zoo (SDZ) during July–August 1998 and May–August 2001. Latin binomials or trinomials, common names (as assigned by the Zoological Society of San Diego), and family taxon are listed in Appendix 1. Details on the study site are available elsewhere (Mooring *et al*., 2000, 2002). Animals at SDWAP and SDZ are free of ectoparasites, insofar as ticks or other ectoparasites have not been detected during drag censusing or examination of animals routinely immobilized by veterinary staff (Mooring & Hart, 1992). Of the species surveyed (Appendix 1), 49 were dimorphic (males larger than females) in body plan, with a polygynous mating system (males mate with >1 female), while 11 species of dwarf antelope and deer were monomorphic and monogamous or weakly polygynous (Mooring *et al*., 2002). We conducted observations on adult females of all species, and adult males of 51 species. With the exception of two species, all animals were individually marked with ear notches and ear tags, or could be identified from natural features. Because markings on Przewalski's horses (*Equus prezewalskii*) and lowland wisent (*Bison bonasus*) were not visible to us, we randomly selected three individuals from the herd to generate three observation sessions per 'individual' (data point) of each sex class (see Observational Procedures). Altogether, we observed 404 females and 133 males, for a total of 351 observation hours.

Observational procedures

Ungulates practised two principal forms of self grooming: (1) oral grooming that was directed to body regions posterior to the head and neck, and (2) scratching with the hindleg directed to the anterior portion of the body, primarily the head and neck. Oral grooming was performed with teeth only, tongue only, or both teeth and tongue. When both teeth and tongue were used in combination, an upward scraping movement of the teeth was often followed by a rapid lick of the tongue on the area just scraped. Presumably, ectoparasites thus dislodged from the pelage with the teeth would subsequently be removed by the tongue and ingested. Because teeth-and-tongue grooming is a more sophisticated pattern of oral grooming compared with pure teeth-scraping or tongue-licking, we consider it to be a more complex grooming pattern. Although we were not always able to see the teeth and/or tongue during oral grooming, all clear observations of complex oral grooming were recorded (Appendix 1). In species that allogroomed, oral grooming was directed to the head, neck, or another anterior region of a conspecific. When allogrooming of this sort occurred between adults (as opposed to maternal grooming between mother and young), we made a note of it (Appendix 1). Like teeth-and-tongue oral grooming, adult allogrooming is a more complex grooming activity that has most likely evolved under more intense selection pressure from ectoparasites in the environment.

We distinguished between grooming 'episodes' and 'bouts'. An episode consisted of each individual grooming motion (i.e. tongue-lick, teeth-scrape, or hindleg-scratch). Although biting insects may cause irritation, insect-repelling movements (e.g. tail switching, head shaking, foot stamping, ear flicking) are readily distinguished from tick-removal oral or scratch grooming (to be conservative, single-episode oral grooming bouts were discarded in case they were directed at insects). Bouts were defined as an uninterrupted sequence of episodes separated from any subsequent bout by an interval of at least 5 s and/or a switch to another body region. Behavioural observations were conducted according to the procedures detailed in Mooring *et al*. (2000, 2002). Briefly, we used spotting scopes and binoculars to conduct focal animal observations (of 10 or 20 min duration) in which grooming episodes and bouts were continuously recorded and instantaneous scans recorded activity budgets (Altmann, 1974). We conducted three observations per individual, each conducted on a different day. Following a period of training, interobserver reliability tests (Caro *et al*., 1979) were conducted among all observers in both years. Observers focused on the same animal at the same time and recorded grooming data. The mean Pearson correlation coefficients were high, ranging from 0.944 to 0.998 during 1998, and from 0.956 to 0.996 during 2001.

For data analysis, we extrapolated the number of oral or scratch grooming bouts and episodes per observation session to hourly grooming rates. We then calculated mean grooming rate for each animal and took the grand mean to compute the mean species grooming rate for females, males, and both sexes combined (Appendix 2). For activity scans, we calculated the mean percentage of time that oral or scratch grooming occurred on a scan out of the total scans recorded during the session (Appendix 2).

MASS AND HABITAT DATA

For each species, we searched the literature for information on mass and habitat use. Reference works consulted were Estes (1991), Grzimek (1968), Gurung & Singh (1996), Haltenorth & Diller (1980), Kingdon (1997), MacDonald (1984), and Nowak (1999). For mass, we used sources that gave separate mass values for males and females when available. We calculated mean mass of females, males, and males and females combined (Appendix 2). Mean mass values were either means or mid-values of the mass range given in the literature. We scored habitat from 1 to 6, ordered from the most open to the most closed (1, no trees/shrubs, including desert, semidesert, grassland, floodplain; 2, bush/scrub savanna; 3, savanna woodland; 4, open woodland; 5, woodland; 6, forest/dense forest). Species scores (Appendix 1) were based on the most closed habitat utilized (habitat max) because closed habitats are reported to harbour higher densities of ticks than more open terrain (see Introduction).

PHYLOGENY CONSTRUCTION

Given the lack of consensus among previously published phylogenetic studies for ungulate species, we developed a composite tree based on the most recent, comprehensive, molecular studies and supplemented these data with taxonomies and studies based on morphological traits. Ambiguities over species placements were resolved by lending more weight toward recent molecular investigations, as these tend to incorporate increasingly more sophisticated analysis techniques and include larger numbers of taxa. It should be noted that composite trees based primarily on morphological or palaeontological data for artiodactyls yield a slightly different topology (e.g. Pérez-Barbería *et al*., 2002), as previously published phylogenetic analyses of this clade frequently are not characterized by a clear consensus.

The general positions of the Probisicidea, Perissodactyla, and Artiodactyla branches were based on Gatesy & Arctander (2000). Rhinocerotidae and Equidae branch positions were based on Berger & Gompper (1999) and Gatesy & Arctander (2000). The positions of the Cervidae, Bovidae, Giraffidae, and Tragulidae were based on cladistic analyses by Gatesy, O'Grady & Baker (1999).

Cervidae branch

The general positions of the Cervinae/*Muntiacus* and *Pudu pudu* were inferred from Cronin *et al*. (1996), Douzery & Randi (1997), Gatesy *et al*. (1999), Randi *et al*. (1998), and Webb (2000). The placement of the *Elaphodus*/*Muntiacus* clade was based on Amato, Egan & Schaller (2000). Resolution within Cervinae/*Axis*/*Dama* was based on Cronin *et al*. (1996), Emerson & Tate (1993), and Randi *et al*. (1998). The placement of *Elaphurus davidianus* was based on Berger & Gompper (1999) and Cronin *et al*. (1996), while that of *Cervus albirostris* was based on the Corbet (1978) taxonomy.

Bovidae branch

All information gained from the simultaneous analysis of data sets in Gatesy & Arctander (2000) was retained in the Bovidae tree. Gatesy & Arctander (2000) was used to infer the basic branches within Bovidae and supplemented with information from the following sources. Resolution within the Bovini/Tragelaphini tribes was based on Schreiber *et al*. (1999) (*Bison*, *Bos*), Gatesy & Arctander (2000) (placement of *Syncerus*), and Mathee & Robinson (1999) (*Tragelaphus*, *Taurotragus*). Resolution within the Antilopini clade was based on Gatesy *et al*. (1999), Mathee & Robinson (1999), and Rebholz & Harley (1999) (general position of *Madoqua*). Resolution within the *Gazella*/*Antilope* clade was taken from Rebholz & Harley's (1999) parsimony cladogram. Within the Alcelaphini, the position of the *Neotragus*/*Aepyceros* clade (Hassanin & Douzery, 1999; Mathee & Robinson, 1999) was based on Gatesy *et al*. (1999). Positions of *Connochaetes* and *Damaliscus* were taken from Gatesy & Arctander (2000). Topographies within the Caprini (*Ovis*, *Capra*) and Hippotragini (*Oryx*, *Hippotragus*) tribes and the general placement of the *Kobus* and *Cephalophus* branches in the Cephalophini tribe were based on Gatesy & Arctander (2000). Relationships within the *Kobus* and *Cephalophus*/*Sylvicapra* clades were derived from additional sources: Brasheres, Garland & Arcese (2000) (*Cephalophus*, *Sylvicapra*), Gatesy *et al*. (1999), Gatesy & Arctander (2000) (*Kobus*), Hassanin & Douzery (1999), and Mathee & Robinson (1999) (placement of *Oreotragus* in clade with *Cephalophus*/*Sylvicapra*).

The concentrated-changes test relies on the topology of a given phylogeny and does not incorporate branch length estimates, as do alternative methods (Pagel, 1994; Read & Nee, 1995; Nee, Read & Harvey, 1996). However, the concentrated-changes test was appropriate for our analyses because of the scarcity of information on branch lengths and divergence times for ungulate taxa (Pérez-Barbería *et al*., 2002; Pérez-Barbería & Gordon, 1999, 2000, 2001), unless arbitrarily assigned (see Pérez-Barbería *et al*., 2002). Concentrated-changes tests can statistically detect correlated changes based on fewer character state changes than other methods (Ridley, 1983; Sillen-Tullberg, 1993; Cooper *et al*., 2002; Cooper, 2002). The concentrated-changes test (but not independent contrasts analyses) requires that polytomies be resolved. Therefore, polytomies were randomly resolved to create a dichotomously branching phylogeny (Figs 1–3), and we used the same tree for all subsequent analyses.

STUDYING THE EVOLUTION OF CATEGORICAL TRAITS

Using the available data and MacClade 4.03 (Maddison & Maddison, 1992, 2001), and assuming parsimony, we reconstructed the evolutionary history of categorical variables. We then used the concentrated-changes test (Maddison & Maddison, 2001), which is designed for testing the association of changes in a binary character with some other binary variable within a clade of interest. It tests whether changes in one (dependent) character are more concentrated than expected by chance on branches having a shared character state for another (independent) character. The significant concentration of dependent changes on certain branches may mean that the state of the independent character enables or selects for gains in the dependent character.

The concentrated-changes test was used to test three specific hypotheses:

(1) Whether the evolution of sexually dimorphic grooming was concentrated in species with sexually dimorphic body plans. This tests the importance of body size dimorphism (and by implication, sexual selection) in explaining the evolution of dimorphic grooming in ungulates.

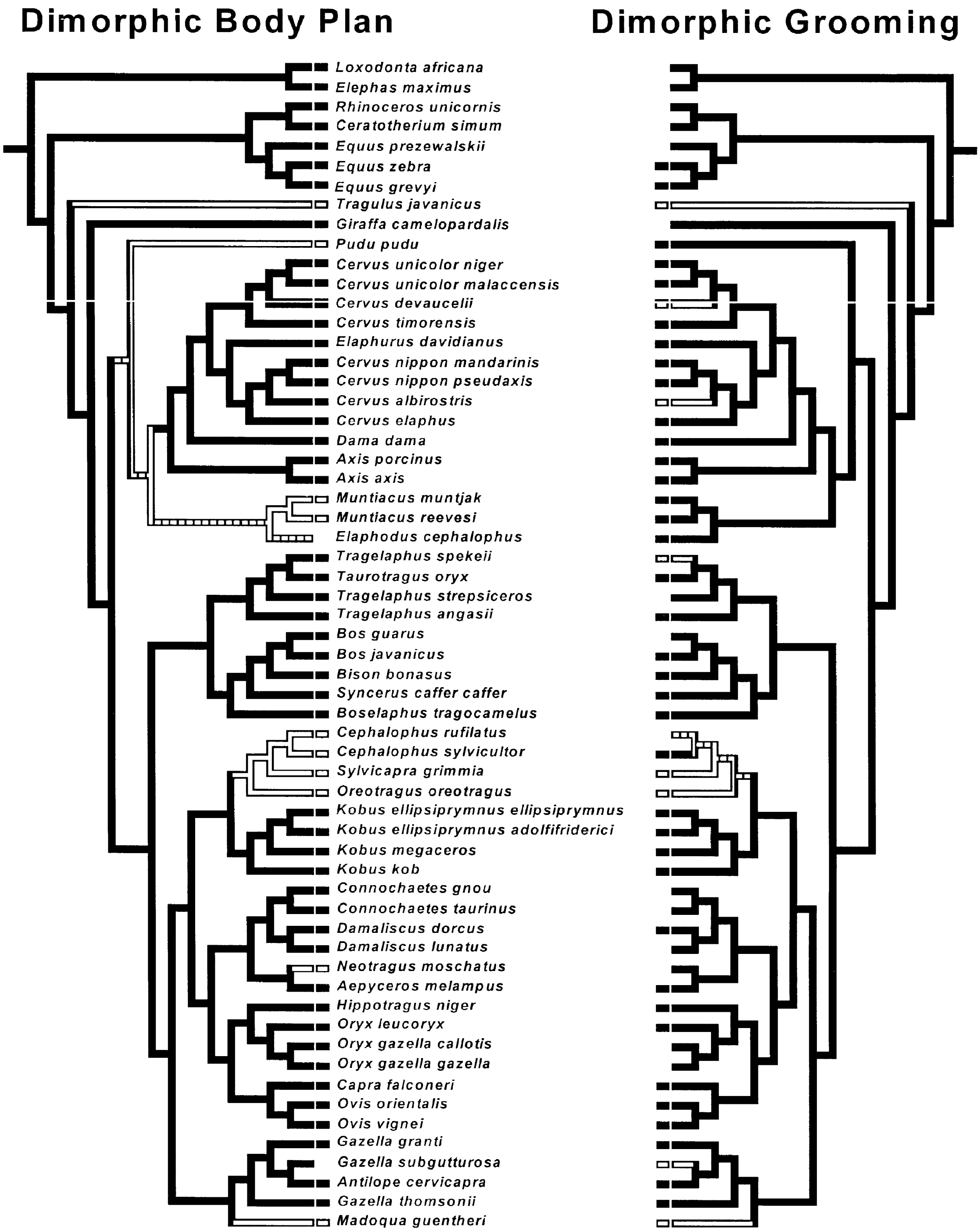
(2) Whether the evolution of complex grooming (employing the teeth and tongue) was concentrated in species found in closed, and therefore tick-infested, habitat. This and the following hypothesis determine the importance of habitat in explaining the evolution of grooming in ungulates.

(3) Whether the evolution of adult allogrooming was concentrated in species found in closed, and therefore tick-infested, habitat.

We calculated the concentrated-changes test when characters were reconstructed three different ways: assuming strict parsimony, after applying an ACCTRAN resolution (which accelerates changes towards the tree's root; i.e. changes among states happen earlier on the tree, thus increasing the number of reversals), and after applying a DELTRAN resolution (which delays changes away from the root; i.e. state changes occur later on the tree, thus increasing independent gains) (Swofford & Maddison, 1987). The large number of species under investigation prevented us from calculating an exact probability; we report P-values calculated using a simulation algorithm (Maddison & Maddison, 1992) with 10 000 replicates. This method has been shown to provide results consistent with those using an exact P-value calculation (Maddison, 1990). Results were similar regardless of resolution (strict parsimony, ACCTRAN, DELTRAN); we illustrate and report the results from the analysis based on strict parsimony.

STUDYING THE EVOLUTION OF CONTINUOUS TRAITS

Using the available data, the phylogeny described above, and Compare 4.4 (Martins, 2001), we calculated phylogenetically independent contrasts (Felsen-



Dimorphic Body Plan

Dimorphic Grooming

Figure 1. Parsimonious reconstruction of sexually dimorphic body plan in ungulates (left) and sexually dimorphic grooming in ungulates (right). In this and the following phylogenetic reconstructions, black fill illustrates the presence of the trait (in this case, sexually dimorphic body plan or grooming), white fill its absence, and a hatched fill illustrates an equivocal reconstruction. The concentrated-changes test revealed that sexual size dimorphism and sexually dimorphic grooming have coevolved ($P < 0.0001$). Families (from Nowak, 1999) are as follows: Proboscidea (*Loxodonta, Elephas*), Rhinocerotidae (*Rhinoceros, Ceratotherium*), Equidae (*Equus*), Tragulidae (*Tragulus*), Giraffidae (*Giraffa*), Cervidae (*Cervus, Elaphurus, Dama, Axis, Muntiacus, Elaphodus*); subfamilies within Bovidae are as follows: Bovinae (*Tragelaphus, Taurotragus, Bos, Bison, Syncerus, Boselaphus*), Cephalophinae (*Cephalophus, Sylvicapra, Oreotragus*), Hippotraginae (*Kobus, Connochaetes, Damaliscus, Hippotragus, Oryx*), Caprinae (*Capra, Ovis*), Antilopinae (*Gazella, Antilope, Madoqua*); the taxonomic placement of *Neotragus* and *Aepyceros* is uncertain.

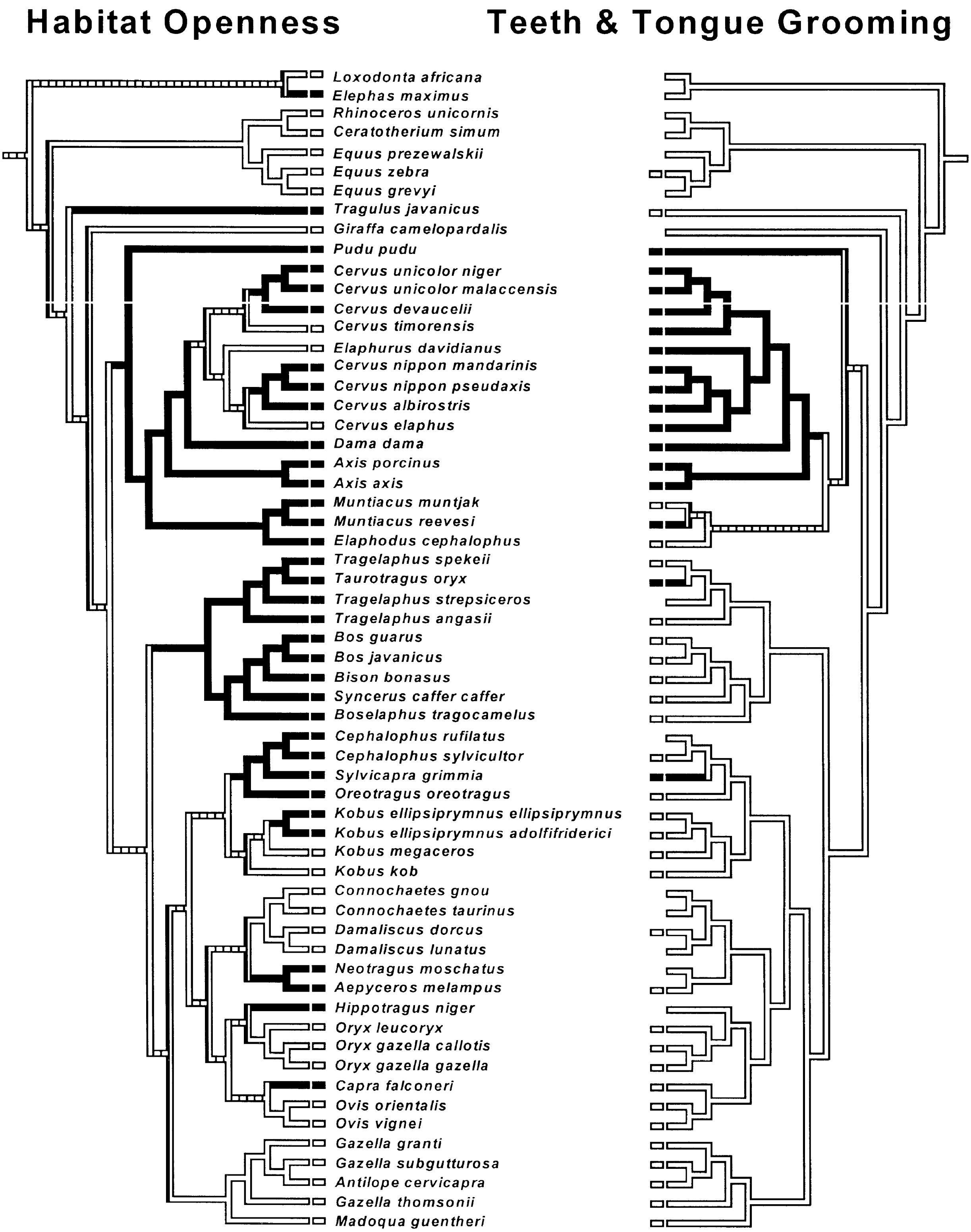


Figure 2. Parsimonious reconstruction of habitat preference (defined as open = white or closed = black) in ungulates (left) and complex grooming utilizing both teeth and tongue in ungulates (right). Families and subfamilies as in Fig. 1. The concentrated-changes test indicated that the evolution of complex grooming was concentrated in species inhabiting closed habitat ($P < 0.0001$), and examination of the parsimonious reconstruction reveals that complex grooming was most common in the Cervidae.

Figure 3. Parsimonious reconstruction of habitat preference (defined as open = white or closed = black) in ungulates (left) and adult allogrooming in ungulates (right). Families and subfamilies as in Fig. 1. The concentrated-changes test indicated that the evolution of adult allogrooming was concentrated in species inhabiting closed habitat ($P < 0.003$), and examination of the parsimonious reconstruction illustrates that adult allogrooming was most common within the Cervidae, Bovinae, and Cephalophinae.

stein, 1985; Harvey & Pagel, 1991) of the continuous variables. As with a variety of phylogenetic techniques to analyse continuous data, independent contrasts aims to 'factor out' similarity among taxa due to common ancestry. The logic of this technique is that, although species themselves are not statistically independent (because they share a phylogenetic history), the differences between them are. Thus, differences in character values between adjacent species creates a 'contrast' as well as a nodal value, which is then used to create additional contrasts. These contrasts are phylogenetically unbiased. We then regressed independent contrasts of body size and habitat openness (independent variables) against the average number of bouts and episodes per hour for oral grooming and scratching, and against total time allocated to all forms of grooming (dependent variables). Body mass was treated as a 'covariate', thus allowing us to study the independent effect of habitat after controlling for variation explained by body mass. We did this for females, males, and the overall average of both. Because we had fewer data for males, 11 species were excluded from the analyses of males alone. In addition to this 2-factor multiple regression, we also conducted bivariate regressions of the contrasts of either body mass or habitat openness against dependent variables. These enabled us to remove non-significant variables in order to better examine the relationships of interest. Regressions were fitted using Statview 5.1 (SAS Institute, 1998) and forced through the origin (Garland, Harvey & Ives, 1992; Purvis & Rambaut, 1995).

RESULTS

ANALYSES OF CATEGORICAL TRAITS

The concentrated-changes test revealed that both sexually dimorphic body plans and sexually dimorphic grooming (Fig. 1) are ancestral in ungulates and have been lost several times. It is extremely unlikely that the relationship between the evolutionary loss of sexual body size dimorphism and the joint evolutionary loss of sexual dimorphism in grooming occurred randomly ($P < 0.0001$). We can thus view these traits as having coevolved.

There are strong phylogenetically based habitat preferences (Figs 2, 3). Most members of Cervidae surveyed (81%) inhabit closed habitat, all members of Equidae and Rhinocerotidae prefer open habitat, and species within Bovidae are found in both open (46%) and closed (54%) environments. Of the bovids, all species belonging to the subfamilies Bovinae (Genera *Tragelaphus*, *Taurotragus*, *Bos*, *Bison*, *Syncerus*, *Boselaphus*) and Cephalophinae (*Cephalophus*, *Sylvicapra*, *Oreotragus*) are found in closed habitats, all members of subfamily Antilopinae (*Gazella*, *Antilope*, *Madoqua*) prefer open environments, and most (73%) members of the subfamilies Hippotraginae (*Kobus*, *Connochaetes*, *Damaliscus*, *Hippotragus*, *Oryx*) and Caprinae (*Capra*, *Ovis*) inhabit open habitats. The taxonomic placement of *Neotragus* and *Aepyceros* is equivocal, and both are found in closed habitat.

Two lines of evidence suggest that tick-infested closed habitats have had an effect on grooming behaviour. First, the evolutionary origin of complex grooming that employed the alternate action of teeth and tongue (Fig. 2) is concentrated in species found in closed habitats ($P = 0.003$). Furthermore, complex grooming appears to be concentrated in the Cervidae, insofar as 88% of cervids sampled practised it, as opposed to only 7% of the Bovidae. Second, the evolutionary origin of adult allogrooming (Fig. 3) was also concentrated in species found in closed habitats ($P < 0.0001$). Adult allogrooming was predominant in Cervidae (80% of cervids surveyed), but was unusual (23%) in Bovidae. With the exception of *Aepyceros*, all bovid allogrooming was observed in the subfamilies Bovinae and Cephalophinae (50% and 75% of species surveyed, respectively).

ANALYSES OF CONTINUOUS TRAITS

Bivariate plots illustrate a negative correlation between body mass and grooming rate by females in analyses of raw data (Fig. 4). Results from the phylogenetically independent contrasts confirmed the importance of body size in explaining variation in grooming by females (Table 1). The multiple regressions of independent contrasts of body mass and habitat against grooming rate revealed a significant effect for bouts and episodes of oral grooming delivered per hour, and percent time grooming (oral bouts: $R = 0.13$, $P = 0.015$; oral episodes: $R = 0.16$, $P = 0.007$; % scans grooming: $R = 0.16$, $P = 0.007$). This means that females of larger-sized species groomed less than smaller-sized species, and females of species that lived in more closed habitats groomed more frequently than species inhabiting more open habitat. Body mass had a greater influence on grooming rate than habitat in the overall model, with habitat significant only for grooming time. For bivariate regressions, independent contrasts of body mass against grooming showed a significant negative relationship between mass and grooming rate (oral bouts: $R = -0.32$, $P = 0.01$; oral episodes: $R = -0.35$, $P = 0.005$; % scans grooming: $R = 0.32$, $P = 0.01$). The regression of habitat against grooming indicated a significant positive relationship between habitat maximum values and grooming time (% scans grooming: $R = 0.26$, $P = 0.05$), suggesting that species found in more tick-dense woodlands and forests tended to groom more. The rate of scratch bouts or episodes

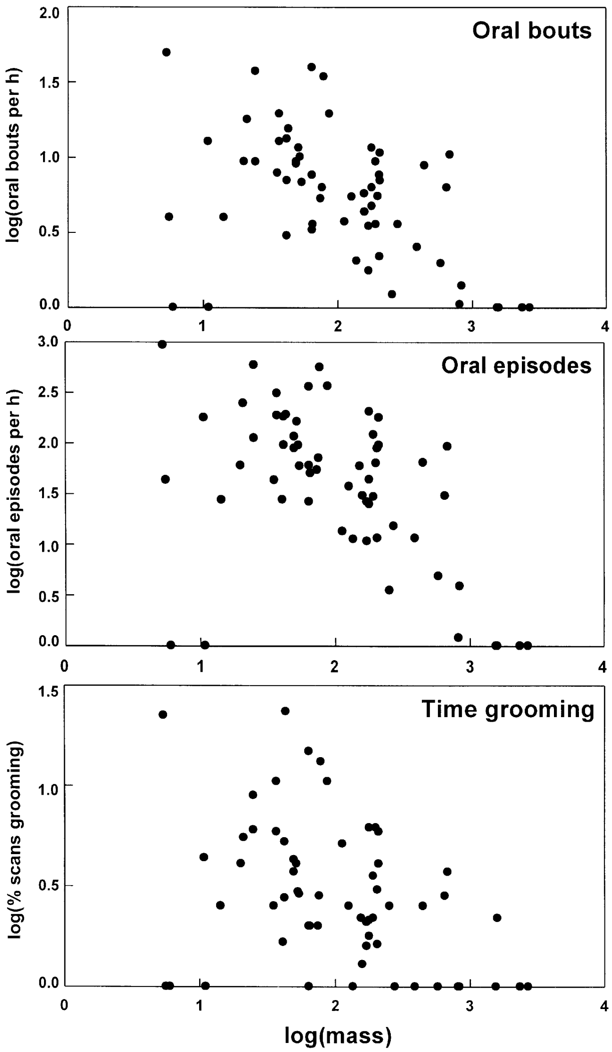


Figure 4. Log-log scatter plots of mean body mass against grooming measures for female ungulates, based on raw data. Results of phylogenetically independent contrasts confirmed the importance of body size in explaining variation in grooming rate by female ungulates (see text).

delivered per hour was not significant for any of the analyses.

Body mass and habitat were not as influential in explaining variation in grooming for the subset of species for which we had data on males (Table 1). None of the multiple regression models were significant for males. However, bivariate regression of independent contrasts of mass against oral bouts per hour revealed a significant negative relationship (oral bouts: R = –0.30, $P = 0.03$). When the data on males and females were combined for the multiple regression (Table 1), we found that body mass, but not habitat, explained significant variation in oral grooming rates (oral bouts: R = 0.11, $P = 0.04$; oral episodes: R = 0.14, $P = 0.01$). As with females, bivariate regression showed a significant negative relationship between body mass and grooming effort (oral bouts: R = –0.29, $P = 0.02$; oral episodes: R = –0.33, $P = 0.01$; % scans grooming: R = –0.25, $P = 0.05$).

DISCUSSION

Repertoires of grooming important to survival are exhibited by all terrestrial mammals and many other vertebrates. Parasite-defence is likely to be an ancestral function in the evolution of grooming. Grooming behaviour is under the influence of multiple genes, including the *Hoxb8* gene, which, when disrupted, leads to excessive self-grooming and allogrooming in mice (Greer & Capecchi, 2002), but other genes that influence this complex behaviour are currently unknown. Attempts to trace the evolution of grooming must at this time rely primarily upon comparative studies of host behaviour, ecology, morphology, and parasite abundance or diversity (e.g. Basibuyuk & Quicke, 1999; Clayton & Walther, 2001). In this study, we compared species-typical aspects of host grooming behaviour (rate, oral grooming technique, adult allogrooming) with host morphology (body size, sexual size dimorphism) and ecology (habitat characteristics influencing tick density) in order to trace the evolution of parasite-defence grooming in ungulates. By conducting our behavioural observations at ectoparasite-free zoological parks, we controlled for the confounding ecological influence of differential tick challenge that would be present in the wild. Thus, our grooming measures reflect only the species-typical, centrally driven grooming rates favoured by natural selection in each lineage.

Results of the concentrated-changes test indicated that sexually dimorphic oral grooming (breeding males groom less than females) has coevolved with sexual dimorphism in body size, meaning that dimorphic grooming was concentrated in those lineages of the tree characterized by high levels of body size dimorphism (males are larger than females). Sexual body size dimorphism in vertebrates is characteristically produced by high male–male competition, which is itself the result of intrasexual selection for mating success in males (e.g. Andersson, 1994; Mitani *et al.*, 1996; Plavcan & Van Schaik, 1997; Lindenfors & Tullberg, 1998; Owens & Hartley, 1998; Loison *et al.*, 1999; Szekely *et al.*, 2000; Dunn *et al.*, 2001; McElligott *et al.*, 2001; Ord *et al.*, 2001). Thus, sexual selection appears to have simultaneously selected for dimorphism in features that directly influence male competitive ability (e.g. body size, strength, weaponry, reproductive behaviour strategies) and features that indirectly influence mating success by improving vigilance for oestrous females and rival males (e.g. reduced grooming and feeding time).

Sexually dimorphic grooming appears to be regulated (directly or indirectly) by androgens insofar as increased testosterone leads to reduced grooming/preening and increased vigilance in some mammals and birds (Fusani *et al.*, 1997; Mooring *et al.*, 1998; Lynn *et al.*, 2000). Castration of male goats resulted in accelerated oral grooming (Mooring *et al.*, 1998), while a decline in oral grooming followed testosterone supplementation of castrated goats (Kahuma *et al.*, 2003). Many recent studies have shown a positive correlation between circulating levels of testosterone and parasite load or suppressed immune function in male birds, reptiles, and mammals (Weatherhead *et al.*, 1993; Saino & Moller, 1994; Saino, Moller & Bolzern, 1995; Zuk, 1996; Moller, Sorci & Erritzoe, 1998; Eens *et al.*, 2000; Olsson *et al.*, 2000; Poiani, Goldsmith & Evans, 2000; Willis & Poulin, 2000; Hughes & Randolph, 2001a, b). The 'immunocompetence handicap hypothesis' (Folstad & Karter, 1992) proposes that, because testosterone has the dualistic effect of stimulating development of secondary sexual characters while suppressing immunocompetence, it acts as a double-edged sword. Males with exaggerated sexually selected characters must trade off increased mating success with increased vulnerability to parasite burden. Thus, the evolution of male hormonal physiology has been influenced by sexual selection for increased mating success and programmed grooming for effective parasite defence. In fact, it is at least theoretically possible that some of the increased ectoparasite burden observed in males with elevated testosterone (e.g. Weatherhead *et al.*, 1993; Saino & Moller, 1994; Eens *et al.*, 2000; Olsson *et al.*, 2000; Poiani *et al.*, 2000; Hughes & Randolph, 2001a, b) is the result of suppressed grooming function rather than (or in addition to) compromised immune function.

The results of additional analyses with the concentrated-changes test indicated that the evolution of both complex oral grooming (in which teeth and tongue alternately scrape and lick through the pelage to efficiently remove ticks) and adult allogrooming (in which conspecifics oral groom those parts of the body not accessible to self-grooming) has been concentrated in regions of the tree associated with closed habitats (woodland and forest). Because more closed habitats are associated with increased tick exposure to hosts, these findings imply that those lineages that were exposed to high levels of tick challenge in their ancestral environments tended to evolve derived grooming characters that are more effective in removing ticks. In essence, 'ticky' habitats favoured the evolution of more advanced grooming techniques. While complex oral grooming and adult allogrooming were mostly concentrated in the Cervidae, suggesting that common ancestry has played a major role in the distribution of advanced grooming modes, the presence of adult allogrooming in eight bovid species (of three different families) found in closed habitats indicates that allogrooming has independently evolved a number of times by convergent evolution.

It should be pointed out that most closed-habitat dwellers are browsers that use complex oral movements to select green leaves and buds (Pérez-Barbería, Gordon & Nores, 2001), suggesting that complex grooming could be partly a product of the greater oral ability of browsers compared with grazers. Closed habitats are associated with both high tick density and hosts of greater oral dexterity. Closed-habitat dwellers may be preadapted for performing complex grooming patterns, which are favoured by natural selection in their tick-dense environment. Habitat type also interacts with host mass and body size dimorphism, with closed-habitat dwellers being smaller and more monomorphic than ungulates of open habitats due to covariance with mating system (Loison *et al.*, 1999; Pérez-Barbería *et al.*, 2002), thus more vulnerable to tick infestation because of both body size and habitat. The interactions among body size, habitat use, feeding technique, and grooming pattern or rate point to the evolutionary complexity of grooming behaviour in the wild.

Results of independent contrasts indicate that both body size and habitat play a role in species-typical oral grooming rates, as well as total time grooming. The multiple regression revealed that, although both mass and habitat influence grooming rates, body size explains more of the variation in grooming than habitat. Bivariate regressions also indicated the greater influence of body mass on grooming rate. Our phylogenetically corrected analyses confirm the correlations previously reported between mass/habitat and grooming rate for 25 bovid species (Mooring *et al.*, 2000). Without controlling for phylogeny, the multiple regression of Mooring *et al.* (2000) indicated that mass and habitat explained 52–64% of the variation in oral grooming, compared with our phylogenetically corrected multiple regression in which mass and habitat only explained 13–16%. Thus, after these morphological and ecological influences have been accounted for, common ancestry explains much of the variation in oral grooming among ungulates.

Scratch grooming measures were not significant for any of our analyses, although they were for the phylogenetically uncorrected analysis by Mooring *et al.* (2000). This suggests that most of the variation can be explained by shared evolutionary history. A number of previous studies have indicated that scratch grooming is less influenced by a central grooming control mechanism than is oral grooming (Hart *et al.*, 1992;

Mooring, 1995; Mooring *et al*., 1996b; Mooring & Hart, 1997a).

Given the important influence of habitat on advanced grooming techniques shown in the concentrated-changes test, it appears counter-intuitive that habitat had such a weak role in the independent contrasts analysis. This makes more sense when it is recalled that environmental tick density is seasonal, and programmed grooming sets a baseline rate of grooming appropriate for the low-tick season. Most of the influence of habitat on grooming rate would be seen during the high-tick season, when the peripheral irritation of tick bites would entrain the rate of programmed grooming to the increased level required. Because our behavioural observations were deliberately conducted in a tick-free setting (in order to remove the tick challenge effect), most variation in oral grooming was associated with body mass, not habitat. However, the significant influence of habitat on total grooming time in the multiple and bivariate regressions indicates that baseline levels of programmed grooming have evolved to species-typical rates appropriate to the tick density of the ancestral habitat.

The weak relationship between body size and oral grooming rate of males indicates that the body size effect in our results is driven by the female data. Two reasons for this come to mind. First, the smaller sample size of males (both individuals and species) decreases statistical power and increases the possibility of sampling error. Second, sexually dimorphic grooming by males produced variation in male grooming independent of mass, thus obscuring the body size relationship. Our previous work has indicated that males display sexually dimorphic grooming in 85% of species exhibiting body-size dimorphism (Mooring *et al*., 2002); however, it should be pointed out that in that study it was not possible to always know which males were reproductively active, probably resulting in the pooling of some breeding and non-breeding males. This would have the effect of introducing random increases or decreases in grooming rate independent of body size, thus masking the body-size effect.

The logic of the programmed grooming model and its attendant predictions (the body size, habitat, vigilance, and tick challenge principles) is firmly rooted in the presupposition that centrally regulated, parasite-defence grooming has evolved in lineages in response to the costs of fitness-compromising ectoparasites. These costs may vary for individuals depending upon body size, reproductive status, and ecological conditions, but it is taken as a given that selection pressures have resulted in historical changes in the frequency of genes coding for grooming behaviour. This is the first study to support the evolutionary presumption of the programmed grooming model. Parasite-defence grooming patterns and rates cannot be explained merely in terms of current ecology without reference to the historical relatedness and common ancestry of lineages. Although this study has focused on ungulates, it is likely that similar evolutionary relationships in grooming patterns are present in other mammalian species that are exposed to ectoparasites and engage in frequent grooming (e.g. rodents, felids, primates), and perhaps birds and other terrestrial vertebrates.

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APPENDIX 1

Species observed at SDWAP and SDZ: binomial or trinomial designation, common name, family, whether the species exhibits sexually dimorphic body size (SDB), sexually dimorphic grooming (SDG), complex oral grooming (teeth and tongue) (COG), adult allogrooming (AA) and habitat maximum (HM) score ('?' indicates that the presence or absence of the trait is uncertain).

Species	Common name	Family	SDB	SDG	COG	AA	HM[a]
Aepyceros melampus rendilis	Kenyan impala	Bovidae	Yes	Yes	No	Yes	5
Antilope cervicapra	Blackbuck	Bovidae	Yes	Yes	No	No	4
Axis axis axis	Indian axis deer	Cervidae	Yes	Yes	Yes	Yes	6
Axis porcinus porcinus	Indian hog deer	Cervidae	Yes	Yes	Yes	Yes	6
Bison bonasus bonasus	Lowland wisent	Bovidae	Yes	Yes	No	No	5
Bos gaurus gaurus	Indian gaur	Bovidae	Yes	?	No	No	6
Bos javanicus javanicus	Javan banteng	Bovidae	Yes	Yes	No	Yes	6
Boselaphus tragocamelus	Nilgai	Bovidae	Yes	Yes	No	Yes	6
Capra falconeri heptneri	Turkomen markhor	Bovidae	Yes	Yes	No	No	5
Cephalophus rufilatus rufilatus	Western red-flanked duiker	Bovidae	No	?	?	?	5
Cephalophus silvicultor silvicultor	Eastern yellow-backed duiker	Bovidae	No	Yes	No	Yes	6
Ceratotherium simum	White rhinoceros	Rhinocerotidae	Yes	?	?	?	4
Cervus albirostris	White-lipped deer	Cervidae	Yes	No	Yes	?	5
Cervus duvauceli duvauceli	Barasingha	Cervidae	Yes	Yes	Yes	Yes	1
Cervus elaphus sibiricus	Altai wapiti	Cervidae	Yes	Yes	Yes	Yes	4
Cervus nippon mandarinus	Mandarin sika	Cervidae	Yes	Yes	Yes	Yes	6
Cervus nippon pseudaxis	Indochinese sika	Cervidae	Yes	Yes	Yes	No	6
Cervus timorensis russa	Javan rusa	Cervidae	Yes	No	Yes	Yes	6
Cervus unicolor malaccensis	Malayan sambar	Cervidae	Yes	Yes	Yes	Yes	6
Cervus unicolor niger	Indian sambar	Cervidae	Yes	Yes	Yes	Yes	6
Connochaetes gnou	White-tailed gnu	Bovidae	Yes	?	?	?	2
Connochaetes taurinus albojubatus	Eastern white-bearded gnu	Bovidae	Yes	?	?	?	3
Dama dama	European fallow deer	Cervidae	Yes	Yes	Yes	Yes	6
Damaliscus dorcas phillipsi	Blesbok	Bovidae	Yes	Yes	No	No	3
Damaliscus lunatus jimela	Jimela topi	Bovidae	Yes	?	?	No	3
Elaphodus cephalophus cephalophus	Western tufted deer	Cervidae	No	Yes	No	Yes	6
Elaphurus davidianus	Pere David's deer	Cervidae	Yes	Yes	Yes	No	1
Elephas maximus	Indian elephant	Elephantidae	Yes	No	No	No	6
Equus grevyi	Grevy's zebra	Equidae	Yes	Yes	?	No	2
Equus prezewalskii	Prezwalski's horse	Equidae	Yes	?	?	?	1
Equus zebra hartmannae	Hartmann's mountain zebra	Equidae	Yes	Yes	No	No	2
Gazella granti roosevelti	Roosevelt's gazelle	Bovidae	Yes	Yes	No	No	3
Gazella subgutterosa subgutterosa	Persian goitered gazelle	Bovidae	Yes	No	No	No	1
Gazella thomsonii thomsonii	Thomson's gazelle	Bovidae	Yes	Yes	No	No	2
Giraffa camelopardalis	Giraffe	Giraffidae	Yes	?	?	?	3
Hippotragus niger niger	South African sable antelope	Bovidae	Yes	Yes	?	No	5
Kobus ellipsiprymnus adolfifriderici	Lake Victoria defassa waterbuck	Bovidae	Yes	Yes	No	No	5
Kobus ellipsiprymnus ellipsiprymnus	Ellipsen waterbuck	Bovidae	Yes	Yes	No	No	5
Kobus kob thomasi	Uganda kob	Bovidae	Yes	Yes	No	No	3
Kobus megaceros	Nile lechwe	Bovidae	Yes	Yes	No	No	1
Loxodonta africana	African elephant	Elephantidae	Yes	No	No	No	4
Madoqua guentheri smithi	Kenyan Guenther's dik-dik	Bovidae	No	No	No	No	2
Muntiacus muntjak vaginalis	North Indian muntjac	Cervidae	No	Yes	No	?	6
Muntiacus reevesi micrurus	Formosan Reeve's muntjac	Cervidae	No	Yes	Yes	Yes	6
Neotragus moschatus zuluensis	Zulu suni	Bovidae	No	?	?	?	6
Oreotragus oreotragus stevensoni	Zimbabwean klipspringer	Bovidae	No	No	No	No	5
Oryx gazella callotis	Fringe-eared oryx	Bovidae	Yes	?	No	No	2
Oryx gazella gazella	Gemsbok	Bovidae	Yes	?	No	No	2
Oryx leucoryx	Arabian oryx	Bovidae	Yes	Yes	No	No	1
Ovis orientalis gmelini	Armenian mouflon	Bovidae	Yes	Yes	No	No	1

APPENDIX 1 *Continued*

Species	Common name	Family	SDB	SDG	COG	AA	HM[a]
Ovis vignei arkal	Transcaspian urial	Bovidae	Yes	Yes	No	No	1
Pudu puda	Southern pudu	Cervidae	No	Yes	Yes	Yes	6
Rhinoceros unicornis	Indian rhinoceros	Rhinocerotidae	Yes	?	?	?	1
Sylvicapra grimmia caffra	South-eastern crowned duiker	Bovidae	No	No	Yes	Yes	5
Syncerus caffer caffer	Cape buffalo	Bovidae	Yes	Yes	No	No	6
Taurotragus oryx pattersonianus	East African eland	Bovidae	Yes	Yes	Yes	No	5
Tragelaphus angasi	Lowland nyala	Bovidae	Yes	Yes	No	Yes	5
Tragelaphus spekei spekei	East African sitatunga	Bovidae	Yes	No	No	Yes	6
Tragelaphus strepsiceros	Greater kudu	Bovidae	Yes	?	?	?	5
Tragulus javanicus ravus	Malayan lesser chevrotain	Tragulidae	No	No	No	No	6

[a] Habitat score: 1 = no trees/shrubs, including desert, semidesert, grassland, floodplain; 2 = bush/scrub savanna; 3 = savanna woodland; 4 = open woodland; 5 = woodland; 6 = forest/dense forest; 'Habitat maximum' is the most closed habitat utilized by the species.

APPENDIX 2

Species observed at SDWAP and SDZ: sample size of females and males, mean mass, rates of oral and scratch grooming, and percentage of activity scans grooming.

Species	Sex[a]	N[b]	Mass (kg)	ORBT[c]	OREP	SCRBT	SCREP	%GRM
Aepyceros melampus rendilis	F	9	50.0	10.39	160.7	3.06	52.7	3.0
	M	5	62.5	4.60	30.6	1.60	54.4	1.2
Antilope cervicapra	F	10	35.0	18.60	309.6	8.00	162.4	9.7
	M	3	35.0	2.33	24.8	8.00	197.3	2.0
Axis axis axis	F	10	86.0	18.50	365.2	2.95	45.8	9.5
	M	6	86.0	5.00	50.4	1.92	40.4	2.4
Axis porcinus porcinus	F	10	40.5	12.30	179.4	2.00	30.8	4.2
	M	4	40.5	6.50	80.2	1.13	13.9	1.1
Bison bonasus bonasus	F	10	675.0	9.40	88.6	0.20	0.4	2.7
	M	4	675.0	1.50	7.0	0.00	0.0	0.0
Bos gaurus gaurus	F	26	825.0	0.04	0.4	0.03	0.2	0.8
Bos javanicus javanicus	F	10	650.0	5.24	29.1	0.70	5.4	0.9
	M	5	650.0	2.30	7.3	0.40	2.0	0.6
Boselaphus tragocamelus	F	7	169.0	2.57	25.6	1.07	15.1	1.1
	M	4	241.0	0.00	0.0	0.38	1.5	0.0
Capra falconeri heptneri	F	10	41.0	6.16	95.1	4.41	45.4	1.7
	M	4	95.0	1.98	16.9	2.75	25.2	0.3
Cephalophus rufilatus rufilatus	F	3	10.0	0.00	0.0	0.00	0.0	0.0
	M	2	10.0	0.00	0.0	0.00	0.0	0.0
Cephalophus silvicultor silvicultor	F	3	62.5	6.67	60.0	3.33	48.7	1.0
	M	3	62.5	4.33	16.0	3.00	23.7	1.0
Ceratotherium simum	F	10	1550.0	0.00	0.0	0.00	0.0	0.0
Cervus albirostris	F	4	125.0	4.50	36.0	1.00	10.5	1.5
	M	1	204.0	4.50	49.5	1.50	6.0	0.0
Cervus duvauceli duvauceli	F	10	177.0	10.60	204.2	2.00	30.8	5.4
	M	5	177.0	6.80	103.0	3.20	37.0	3.3
Cervus elaphus sibiricus	F	8	207.5	9.63	177.1	2.75	38.0	4.6
	M	5	207.5	1.60	26.0	2.80	45.2	3.6
Cervus nippon mandarinus	F	10	48.0	8.58	89.5	1.55	17.1	1.7
	M	3	48.0	1.73	14.5	0.50	2.5	0.8
Cervus nippon pseudaxis	F	9	48.0	8.06	112.0	1.00	12.0	3.3
	M	4	48.0	4.50	105.5	3.00	45.5	2.3

APPENDIX 2 *Continued*

Species	Sex[a]	N[b]	Mass (kg)	ORBT[c]	OREP	SCRBT	SCREP	%GRM
Cervus timorensis russa	F	8	53.0	5.94	58.2	2.50	23.0	2.3
	M	3	73.0	8.00	144.7	1.33	32.0	4.0
Cervus unicolor malaccensis	F	9	190.5	2.61	28.6	1.28	11.5	1.1
	M	6	190.5	0.33	6.7	0.33	3.7	0.0
Cervus unicolor niger	F	10	190.5	8.55	118.9	0.60	5.8	2.6
	M	2	190.5	3.00	47.0	1.00	6.0	1.5
Connochaetes gnou	F	7	135.0	1.11	10.2	0.67	6.0	0.0
Connochaetes taurinus albojubatus	F	6	200.0	4.57	61.6	3.32	45.4	2.1
Dama dama	F	10	42.0	14.51	190.7	2.69	42.3	4.3
	M	2	83.0	7.20	115.1	0.60	4.8	2.6
Damaliscus dorcas phillipsi	F	5	62.5	38.40	366.4	21.40	451.0	14.6
	M	1	72.5	22.00	300.0	32.00	924.0	6.1
Damaliscus lunatus jimela	F	2	112.5	2.75	12.8	7.50	85.5	4.2
	M	1	140.0	2.00	16.0	4.00	48.0	0.0
Elaphodus cephalophus cephalophus	F	4	33.5	7.00	40.5	3.00	39.0	1.6
	M	1	33.5	2.00	12.0	2.00	32.0	3.0
Elaphurus davidianus	F	10	159.0	3.40	28.9	0.35	1.7	0.3
	M	2	214.0	0.00	0.0	2.00	14.0	0.0
Elephas maximus	F	5	2720.0	0.00	0.0	0.00	0.0	0.0
Equus grevyi	F	2	385.0	1.50	10.5	0.00	0.0	0.0
	M	2	430.0	0.00	0.0	0.00	0.0	0.0
Equus prezewalskii	F	6	250.0	0.22	2.6	0.06	0.9	1.5
Equus zebra hartmannae	F	3	275.0	2.67	14.0	0.00	0.0	0.0
	M	1	300.0	0.00	0.0	0.00	0.0	0.0
Gazella granti roosevelti	F	10	51.0	9.00	96.5	3.20	40.5	1.4
	M	1	68.0	6.00	42.0	4.00	84.0	0.0
Gazella subgutterosa subgutterosa	F	8	35.5	11.88	186.6	3.88	60.1	4.7
	M	2	35.5	21.75	334.5	7.75	227.0	14.4
Gazella thomsonii thomsonii	F	10	20.0	16.95	238.2	5.60	124.6	5.2
	M	4	27.5	17.13	349.9	4.13	105.1	6.1
Giraffa camelopardalis	F	7	815.0	0.05	0.2	0.00	0.0	0.0
Hippotragus niger niger	F	3	210.0	6.00	96.0	1.33	15.3	3.0
	M	1	235.0	2.00	46.0	0.00	0.0	0.0
Kobus ellipsiprymnus adolfifriderici	F	8	175.0	3.75	24.8	1.00	12.3	0.8
	M	2	235.0	1.00	12.0	0.00	0.0	0.0
Kobus ellipsiprymnus ellipsiprymnus	F	8	175.0	5.25	43.8	0.50	4.5	1.2
	M	2	235.0	1.00	14.0	0.00	0.0	0.0
Kobus kob thomasi	F	9	63.5	2.67	48.9	2.00	43.6	1.0
	M	1	93.0	0.00	0.0	0.00	0.0	0.0
Kobus megaceros	F	9	75.0	5.33	69.4	9.89	197.3	3.7
	M	2	105.0	0.00	0.0	8.00	104.0	3.0
Loxodonta africana	F	2	2350.0	0.00	0.0	0.00	0.0	0.0
Madoqua guentheri smithi	F	1	4.6	3.00	40.5	1.50	25.5	0.0
	M	1	4.6	4.50	48.0	0.00	0.0	0.0
Muntiacus muntjak vaginalis	F	3	23.5	8.33	114.5	0.50	4.0	5.1
	M	2	23.5	6.40	55.0	2.60	37.8	2.1
Muntiacus reevesi micrurus	F	3	23.5	36.33	582.3	10.67	198.0	7.8
	M	2	23.5	18.00	207.0	2.00	23.0	4.5
Neotragus moschatus zuluensis	F	1	5.0	0.00	0.0	0.00	0.0	0.0
	M	1	5.0	0.00	0.0	0.00	0.0	0.0
Oreotragus oreotragus stevensoni	F	2	13.2	3.00	27.0	1.00	11.0	1.5
	M	1	10.6	6.00	58.0	0.00	0.0	3.0
Oryx gazella callotis	F	10	202.5	1.20	10.6	1.50	18.6	1.5
	M	3	210.0	1.67	9.7	0.00	0.0	0.0

APPENDIX 2 *Continued*

Species	Sex[a]	N[b]	Mass (kg)	ORBT[c]	OREP	SCRBT	SCREP	%GRM
Oryx gazella gazella	F	9	202.5	6.56	90.1	2.22	21.3	2.0
	M	1	210.0	8.00	58.0	0.00	0.0	0.0
Oryx leucoryx	F	10	155.0	4.80	58.0	1.80	26.6	1.2
	M	1	155.0	2.00	38.0	4.00	54.0	0.0
Ovis orientalis gmelini	F	9	40.0	2.00	26.7	1.56	15.6	0.7
	M	8	40.0	1.38	11.2	2.00	19.7	1.2
Ovis vignei arkal	F	6	61.5	2.33	25.2	1.17	17.3	0.0
	M	4	61.5	0.00	0.0	1.25	11.8	0.0
Pudu puda	F	2	9.6	12.00	177.8	3.75	63.0	3.4
	M	1	9.6	0.00	0.0	4.00	48.0	0.0
Rhinoceros unicornis	F	5	1600.0	0.00	0.0	0.00	0.0	0.0
Sylvicapra grimmia caffra	F	4	18.8	8.50	60.5	5.00	94.5	3.1
	M	3	16.3	24.67	396.7	8.00	159.3	12.1
Syncerus caffer caffer	F	3	576.0	1.00	4.0	0.00	0.0	0.0
	M	2	686.0	0.00	0.0	0.00	0.0	0.0
Taurotragus oryx pattersonianus	F	4	450.0	8.00	64.5	0.00	0.0	1.5
	M	4	700.0	3.50	25.5	0.00	0.0	0.8
Tragelaphus angasi	F	5	76.0	33.60	557.6	7.60	126.4	12.1
	M	1	120.0	24.00	204.0	2.00	58.0	9.1
Tragelaphus spekei spekei	F	6	72.5	4.33	52.3	2.00	29.0	1.0
	M	1	100.0	10.00	74.0	0.00	0.0	0.0
Tragelaphus strepsiceros	F	10	167.5	0.77	9.8	0.17	2.5	0.6
Tragulus javanicus ravus	F	1	4.4	48.00	956.0	4.00	38.0	21.2
	M	1	4.4	58.00	1444.0	0.00	0.0	18.2

[a] F = females; M = males

[b] Number of individuals observed for grooming rates

[c] ORBT = oral bouts per h; OREP = oral episodes per h; SCRBT = scratch bouts per h; SCREP = scratch episodes per h; %GRM = per cent scans grooming (oral and scratch)