



ARTICLES

Behavioural defences against sexually transmitted diseases in primates[☆]

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Sexually transmitted diseases (STDs) are known to exist in wild and domesticated animals, but little is known about behavioural defences that animals use to reduce the risk of acquiring STDs. Using comparative data and a phylogeny of primates, I investigated whether behaviours hypothesized to reduce STD transmission are correlated with measures of STD risk involving mating promiscuity and life-history traits. Comparative tests revealed no support for genital inspection as a means to identify and avoid infected individuals with genital inspection was performed more commonly by males than females and uncorrelated with mating promiscuity. Primate species characterized by increased promiscuity were not more likely to display genital self-grooming following mating. Similarly, males and females of these species were not more likely to urinate immediately after mating, counter to suggestions that urination flushes microorganisms from the urethra and surrounding genital areas. Finally, monogamy was not correlated with a slow life history, which differs from predictions that monogamy is a response to increased STD risk in long-lived animals. Tests involving monogamy remained unsupported after controlling for potentially confounding variables, and all tests yielded similar results in phylogenetic and nonphylogenetic tests. Few results were significant even before controlling statistically for multiple comparisons, but nonsignificance was unlikely due to low statistical power or poor data quality in all tests. Instead, the comparative patterns were consistent with theoretical models showing that precopulatory behavioural defences to STDs, such as mate choice, are unlikely to be fully effective. In addition, many putative behavioural defences to STDs in primates entail substantial fitness costs in terms of reproductive output, offspring quality and infanticide avoidance.

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Sexually transmitted diseases (STDs) are ubiquitous in animal societies. For example, a recent comparative study documented over 200 sexually transmitted parasites among 27 orders of hosts (Lockhart et al. 1996), and chlamydia may be a threat to breeding success of at least one endangered species, the koala, *Phascolarctos cinerus* (Weigler et al. 1988; Canfield et al. 1991). STDs commonly cause sterility, and compared to other infectious diseases, are more likely to result in lifetime infections (Holmes et al. 1994; Lockhart et al. 1996). Hosts possess two potential types of counterstrategies to STDs: immune defence and behavioural defence. Comparative studies of immune defence parameters in nonhuman primates and

carnivores revealed that evolutionary transitions to increased mating promiscuity are correlated with higher baseline leukocyte counts (Nunn et al. 2000, 2003; Nunn 2002), which is consistent with the role of the immune system as a defence against STDs. This interpretation is supported by the presence of high levels of immunoglobulins (particularly IgA) in the mucosal lining of the female reproductive tract (Cohen et al. 1994) and observations that phagocytic leukocytes engulf spermatozoa and seminal fluids within minutes after their deposition in female mammals (Austin 1975; Phillips & Mahler 1977; Pandya & Cohen 1985; Barratt et al. 1990).

In contrast to immune defence mechanisms, behavioural counterstrategies to STDs are virtually unknown. This gap in our understanding of host responses to infectious disease is surprising because of increased interest in STDs following the AIDS epidemic and detailed investigations on behavioural counterstrategies to

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nonsexually transmitted disease (Hart 1990; Møller et al. 1993; Kavaliers et al. 1997; Penn et al. 1998; Kiesecker et al. 1999; Klein et al. 1999). One study found that postcopulatory genital grooming reduces the risk of STD transmission in male rats (Hart et al. 1987), but few studies have investigated genital grooming in other animals. Freeland (1976) speculated that aspects of primate behaviour, including opposition by group members to immigrants, provide benefits in terms of reducing STD risk, while other researchers have suggested that STD risk favours the evolution of monogamy (Immerman 1986; Loehle 1995). The proposal that STDs limit promiscuous behaviour has been investigated theoretically (Thrall et al. 1997, 2000), but empirical evidence for this proposal is lacking. Mate choice in the context of STD infection also has been examined theoretically (Kneil 1999). Studies of milkweed leaf beetles, *Labidomera clivicornis* (Abbot & Dill 2001) and two-spot ladybirds, *Adalia bipunctata* (Webberley et al. 2002) found no evidence for mate choice to avoid sexually transmitted mites, but few other studies have addressed this issue empirically.

The detailed information available on primate sexual behaviour (Dixson 1998) and life history (Harvey & Clutton-Brock 1985; Ross & Jones 1999) offers an opportunity to identify behaviours that reduce STD transmission. In this paper, I use phylogenetic comparative methods to investigate behavioural defences to STDs in primates. A wide diversity of STDs have been documented in free-living and captive populations of nonhuman primates (Lockhart et al. 1996), including simian immunodeficiency virus (SIV: e.g. Galat-Luong et al. 1994; Jolly et al. 1996; Santiago et al. 2002), simian T-lymphotrophic virus (STLV: e.g. Voevodin et al. 1997), papillomavirus (O'Banion et al. 1987), herpesvirus (simian agent 8, Levin et al. 1988) and trichomonas (Soulsby 1982). SIV and STLV have been studied extensively in wild populations of Old World primates, with field studies conducted on over 35 primate species revealing rates of infection as high as 60% for SIV (Jolly et al. 1996) and 47% for STLV (Voevodin et al. 1997). Thus, STDs are widespread in primates.

Based on previous research in animals and behavioural defences reported in humans (Donovan 2000a, b), I tested the following hypotheses.

Hypothesis 1

Individuals benefit from inspecting potential mating partners prior to copulation and avoiding those with symptoms of STD infection. Genital inspection is a partner-specific preventative measure that requires identification of infection status and, in the case of females inspecting males, the ability to reject potential mates that show symptoms of STD infection. This hypothesis predicts that genital inspection by males and females is correlated with mating promiscuity. Mating promiscuity is one of the primary factors thought to increase an individual's exposure to STDs, although this assumption is largely untested outside of humans (Holmes et al. 1994). Genital inspection by males may also function in assessing female reproductive condition (Dixson 1998), but the generally higher transmission rate of STDs from

males to females (Holmes et al. 1994) predicts that females will be more concerned with genital inspection under the STD hypothesis.

Hypothesis 2

Following copulation, self-grooming may function to remove bodily fluids that contain sexually transmitted pathogens, such as seminal fluid, and other types of parasites that are transmitted by close contact. If self-grooming functions in STD prevention, it is predicted to be more common among promiscuous species of primates. I examined comparative patterns involving two types of grooming. Manual self-grooming involves inspection of the genitalia and grooming with the hands to remove bodily fluids left by mating partners. Oral self-grooming may directly kill sexually transmitted parasites through physical washing as well as antipathogen properties of saliva (Hart et al. 1987), including lysozyme and lactoferrin (Baron et al. 2000).

Hypothesis 3

Postcopulatory urination is commonly thought to reduce STD risk in humans (Hooper et al. 1978; Donovan 2000b). Urination may be more effective in preventing STDs in males because the male urethra is a primary site of infection for many sexually transmitted pathogens, whereas the mucosal lining of the female reproductive tract offers a greater surface area for inspection (Holmes et al. 1994). Moreover, urine does not wash out parts of the female anatomy in which sperm and seminal fluids are deposited (vagina, cervix and uterus; Dixson 1998). Thus, postcopulatory urination is predicted to be more common in promiscuous species and practised by males more than females.

Hypothesis 4

Lifetime monogamy reduces the risk of acquiring STDs (Loehle 1995), predicting that species at greatest risk of acquiring STDs should be monogamous. Comparison of traits in promiscuous and monogamous species is not useful in this analysis because mating behaviour is the dependent variable. However, animals with slow life histories probably experience increased risk of acquiring STDs, predicting that a slow life history is correlated with monogamy after controlling for other factors. The association between life history and STD risk occurs partly through allometry, with larger-bodied (and longer-lived) species tending to live at lower densities that make other direct transmission routes less effective (De Leo & Dobson 1996; Thrall et al. 1998). Life history has an additional effect that operates through its connection to mortality because sexually transmitted parasites die when the host dies, making it difficult for STDs to become established in conditions of high host mortality (Thrall et al. 2000). Both factors predict that STD risk increases with lower mortality and a slower life history (see also Thrall et al. 1993; Loehle 1995).

Table 1. Genital inspection, nonphylogenetic and phylogenetic results

	Nonphylogenetic analysis				Phylogenetic analysis		
	Effect	F	df	P	Positive contrasts/ total contrasts	t	P
Genital inspection of males by females, conservative classification							
Relative testes mass	–	0.22	1,27	0.64	1/4	–1.08	0.36
Duration of oestrus	–	0.00	1,36	0.98	3/5	–0.18	0.87
Genital inspection of males by females, liberal classification							
Relative testes mass	+	3.59	1,27	0.069	7/8	2.55	0.038
Duration of oestrus	+	2.41	1,36	0.13	8/13	1.33	0.21
Genital inspection of females by males, conservative classification							
Relative testes mass	+	8.61	1,30	0.0064	5/7	1.25	0.26
Duration of oestrus	+	0.27	1,39	0.61	3/8	0.54	0.61
Genital inspection of females by males, liberal classification							
Relative testes mass	+	0.00	1,30	0.94	*		
Duration of oestrus	+	1.24	1,39	0.27	*		

*Too few contrasts to conduct statistical tests (≤ 1 contrast).

METHODS

Hypotheses 1 to 3

I acquired data on precopulatory genital inspection, postcopulatory genital grooming and postcopulatory urination using a survey sent out to a broad spectrum of primatologists, based on resources available at Primate Information Network (<http://www.primate.wisc.edu/pin/>). The data collected from this survey are presented in the Appendix (www.elsevier.com/locate/anbehav). For genital inspection, I requested information on each of the sexes separately, and for genital self-grooming, I obtained information on the use of hands or mouth. I excluded prosimians from the manual grooming analysis because they are known to use their mouths rather than hands for grooming (Barton 1987), and their inclusion therefore may bias the comparative results. An assumption underlying the analysis of oral genital grooming is that saliva possesses anti-STD properties (Hart et al. 1987). I therefore also requested information on oral grooming of wounds, because this is consistent with the presence of lysozyme, lactoferrin and other defensive proteins in the saliva (Lee-Huang et al. 1999; Baron et al. 2000). I also requested information on the presence of postcopulatory urination by either sex. For postcopulatory behaviours, I did not specify a time period following mating in which the behaviour had to be documented because preliminary surveys revealed that this information was not widely available and would have greatly restricted the taxonomic scope of the analysis.

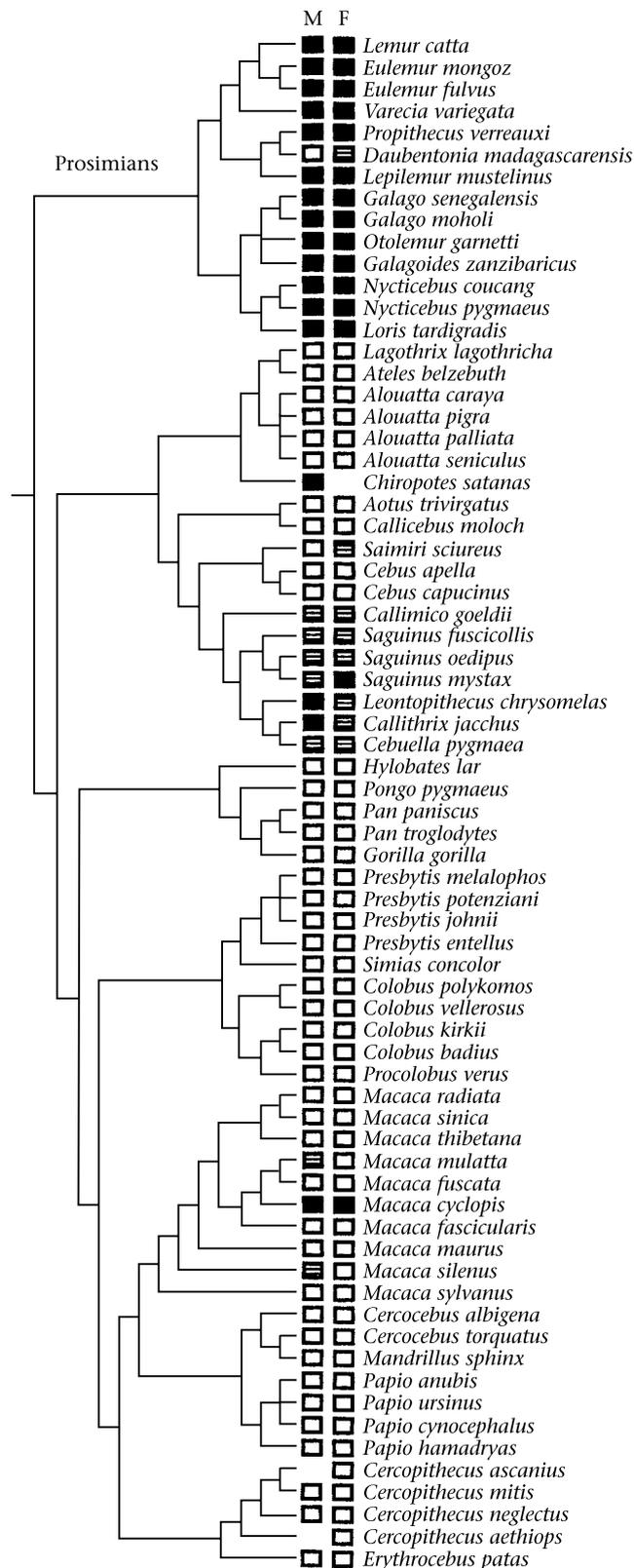
Survey data may be difficult to interpret, particularly when analysing data that are not collected consistently by different researchers. At present, these are the only data available, and one aim of this study is to call greater attention to these questions for future research. For 21 species, however, I received responses from more than one investigator for at least one trait on the survey, thus allowing some assessment of the reliability of responses. The traits that were most variable included female inspection of males (11 of 18 species with multiple answers

showed mixed responses) and manual grooming by males (6 of 19 species) and females (7 of 19 species; the number of species differs here and elsewhere because some respondents were unable to answer all survey questions). The other variables showed conflict in fewer than 15% of species for which multiple answers were provided, although no trait was exempt from variation. I also examined variability between species with multiple responses. Five species showed no variability, and no species showed variable responses for all of the eight behavioural parameters examined here. It is notable, however, that I received multiple responses for three callitrichid species (*Saguinus fuscicollis*, *S. mystax*, *Callicebus jacchus*), and these were among the nine most variable species (33–40% of variables were conflicting). Because callitrichids are known to have variable mating systems (Goldizen 1988), heterogeneity in response may reflect adaptive intraspecific variation in the behavioural traits. Another species providing particularly variable responses (50% of variables) was the Hanuman langur, *Presbytis entellus*, which also shows notable variation in mating behaviour (e.g. Borries et al. 2001). Variability in response among species was unrelated to the number of respondents for that species (Spearman rank correlation: $r_s=0.26$, $N=21$, $P=0.25$, with a maximum of four responses per species).

Variable responses highlight the types of data that need to be collected systematically in the future, but they raise questions about the proper procedure for analysing data in the present. For this study, I flagged conflicting variables for each species and analysed the data assuming that conflicting codes reflect absence of the trait (conservative analysis), and then repeated the analysis assuming that conflicting codes reflect presence of the trait (liberal analysis). I also used this procedure for variables in which respondents reported intermediate levels of the behaviour in question, indicated by qualifiers such as 'sometimes', 'occasionally', or 'rarely'. The analyses therefore capture extreme ends of the spectrum of potential variation.

To test the hypotheses, I used continuous measures of promiscuity involving testes mass (Harcourt et al. 1995) and the duration of oestrus (van Schaik et al. 1999). Testes mass, after correcting for body mass, reflects sperm com-

petition and serves as a continuous measure of mating promiscuity (see Nunn et al. 2000). The duration of oestrus also is correlated with the number of mating partners (van Schaik et al. 1999), thus providing an additional continuous measure of mating promiscuity.



Hypothesis 4

To test Hypothesis 4, I acquired data on life-history characteristics (longevity, interbirth interval, age at first reproduction and weaning age) from Ross & Jones (1999). Animals were classified as monogamous or nonmonogamous based on previous reviews of primate behaviour (Smuts et al. 1987; Rowe 1996) and an unpublished comparative database used in previous studies (Nunn 1999). To ensure that classifications of mating system were most accurate, I conducted the analyses after removing nocturnal species that forage solitarily, because little is known about the dynamics of mating in these species (Bearder 1987). I also removed the callitrichids because their mating systems are known to be extremely flexible (Goldizen 1988). In addition, communal rearing of offspring has the potential to shorten life-history parameters in these species, particularly the interbirth interval. I also excluded humans and I classified *Cercopithecus neglectus* as monogamous in the analyses to generate a contrast to the other guenons, which are less monogamous. In addition to conducting tests with discrete measures of promiscuity, I repeated analyses using relative testes mass and the duration of oestrus, predicting that species with slower life histories should have smaller relative testes mass or a shorter duration of oestrus. All life-history traits were significantly positively related to body mass, although longevity was nonsignificant in some phylogenetic comparative tests. Thus, I controlled for body mass by using residuals from least-squares regression (Harvey & Pagel 1991) of life-history traits on female mass.

An alternative explanation for significant results in Hypothesis 4 involves parental care. Monogamy may be associated with a slow life history if the period of parental care is long and offspring require assistance from both parents to achieve independence. Male care is rare in primates and found to varying degrees in both monogamous and nonmonogamous species (Whitten 1987), but to exclude the possibility that monogamy relates to the need for additional care, I repeated tests using longevity corrected for weaning age rather than body mass. According to some verbal descriptions of the effect of life history on STD risk (e.g. Loehle 1995), it is the number of reproductive events rather than a slow life

Figure 1. Phylogenetic distribution of oral self-grooming in males (M) and females (F) following copulation. ■: Presence of the trait; □: absence of trait; ▨: conflicting responses or intermediate values of the trait (see Methods). Species without these designations indicate that no information was available. Oral self-grooming is concentrated in prosimians and callitrichids, with limited occurrence in macaques, highlighting the primate radiations in which more detailed study is needed. The phylogeny was taken from Purvis (1995).

history that facilitates spread of STDs. I therefore conducted a third and final set of tests using an estimate of lifetime reproductive events, calculated from life-history traits as (longevity – age at first reproduction)/interbirth interval.

Comparative Methods and Statistics

I used phylogenetic comparative methods to test hypotheses (Harvey & Pagel 1991), with all results based on Purvis' (1995) composite estimate of primate phylogeny. I also provide nonphylogenetic results for comparison, because differences in the results may reveal the presence of confounding variables (Purvis & Webster 1999; Nunn & Barton 2000, 2001). Nonphylogenetic results also may be more accurate under an alternative model of trait evolution (Price 1997; Harvey & Rambaut 2000), although the data analysed here generally met the assumptions of independent contrasts after branch length and data transformation (Harvey & Pagel 1991; Garland et al. 1992). I used independent contrasts (Felsenstein 1985) to examine the association between two continuous characters or one continuous and one discrete variable, as implemented in the computer program CAIC (Purvis & Rambaut 1995).

All probabilities reported here are two tailed with a significance criterion of $\alpha=0.05$. With the large number of tests that are performed, the issue of multiple comparisons arises (Sokal & Rohlf 1995). With a maximum of four comparisons (i.e. analysing relative testes mass and the duration of oestrus in conservative and liberal classifications for each behaviour), the Dunn–Sidak method gives a revised $\alpha=0.0127$ for determining statistical significance. This turns out to be not very useful, however, because the vast majority of tests were nonsignificant, raising the alternative issue of low statistical power (Cohen 1988; Thomas & Juanes 1996). I therefore calculated statistical power using the computer program GPOWER (Erdfelder et al. 1996). These results are presented in the Discussion, where issues concerning nonsignificance are raised.

RESULTS

Hypothesis 1: Genital Inspection

Counter to predictions, females were not more likely to inspect male genitalia in more promiscuous species. Inspection by females was a trait that showed extreme variation amongst respondents, and different interpretations of conflicting and intermediate responses influenced the results. Thus, in liberal classification of the data, patterns of response were in the predicted direction and significant in one phylogenetic test, whereas patterns were opposite to predictions and nonsignificant in the more conservative classification (Table 1). Genital inspection of females by males also showed weak associations with promiscuity levels (Table 1), with only one significant result (testes mass under conservative classification). Males of most primate species perform inspection

behaviour, resulting in too few data points to test the predictions under liberal classifications in phylogenetic comparative tests.

For many human STDs, male-to-female transmission is higher than female-to-male transmission (see Holmes et al. 1994). This may be due to the greater surface area of the mucosal lining of the female reproductive tract, the greater potential for trauma to this surface in females than males, and because males deposit potentially infectious bodily fluids in the female. Thus, females are expected to show genital inspection more than males, but this is not the case. In 76–96% of species, males inspected female genitalia ($N=72$ species with data), while only 13–57% of species showed genital inspection by females ($N=68$ species). This sex difference probably represents the role of genital inspection in assessing female reproductive condition (Dixson 1998) rather than checking for STDs. In addition, species in which females inspected more than males were not characterized by increased promiscuity (relative testes mass: positive relationship: $F_{1,27}=0.13$, $P=0.72$, 4 of 4 contrasts in predicted direction, $t_3=2.15$, $P=0.12$; duration of oestrus: positive relationship, $F_{1,36}=0.79$, $P=0.38$, only 2 of 7 contrasts in predicted direction, $t_6=-0.26$, $P=0.80$).

Hypothesis 2: Postcopulatory Genital Grooming

Oral genital grooming following copulation was reported mainly for prosimian primates (Fig. 1). Of 14 prosimians in the database with information on oral genital grooming by males, 13 were reported to perform genital grooming, with only *Daubentonia madagascariensis* males failing to perform the behaviour. *Daubentonia* is nonmonogamous, while some monogamous prosimians (e.g. *Eulemur mongoz*) perform oral genital grooming, thus providing no support for the prediction that oral grooming is more common in promiscuous species.

Expanding the analysis of oral self-grooming to anthropoids, unequivocal male oral grooming was reported in only four anthropoids out of 54 species with information, with an additional seven species performing the behaviour in liberal interpretations of the survey responses (Fig. 1). All of the callitrichids were reported to perform male genital grooming by at least one respondent to the survey. Combining anthropoids and prosimians, oral genital grooming by males was unrelated to measures of mating promiscuity (Table 2), with the only significant results found in the nonphylogenetic analyses and in a direction opposite to predictions. Results were largely the same when the analysis was limited to anthropoids.

Among female anthropoids ($N=55$ species), only two species were reported to show unequivocal oral grooming by females, with an additional seven species reported to show oral grooming at least occasionally (Fig. 1). Thus, in all callitrichids with one sex reported to groom orally, the other sex also groomed at least occasionally, resulting in phylogenetic patterns that were largely the same in both sexes. As with males, female genital grooming was not more common in promiscuous primates (Table 2), with the two significant results in a direction opposite to

Table 2. Postcopulatory oral grooming, nonphylogenetic and phylogenetic results

	Nonphylogenetic analysis				Phylogenetic analysis		
	Effect	<i>F</i>	<i>df</i>	<i>P</i>	Positive contrasts/ total contrasts	<i>t</i>	<i>P</i>
Male oral grooming, conservative classification							
Relative testes mass	+	0.04	1,26	0.84	7/9	2.45	0.04
Duration of oestrus	–	19.9	1,38	<0.0001	5/7	0.29	0.78
Male oral grooming, liberal classification							
Relative testes mass	+	0.05	1,26	0.83	2/5	–0.46	0.67
Duration of oestrus	–	1.66	1,38	0.21	2/4	–0.97	0.41
Female oral grooming, conservative classification							
Relative testes mass	+	0.34	1,28	0.57	*		
Duration of oestrus	–	19.4	1,39	<0.0001	0/2	–2.45	0.25
Female oral grooming, liberal classification							
Relative testes mass	–	0.03	1,28	0.87	3/3	4.28	0.051
Duration of oestrus	–	7.78	1,39	0.008	1/3	–1.01	0.42

*Too few contrasts to conduct statistical tests (≤ 1 contrast).

predictions. Results were largely the same when the analysis was limited to anthropoids.

An assumption underlying this analysis is that saliva possesses anti-STD properties (Hart et al. 1987). I therefore repeated analyses using only species that were reported to also groom wounds orally, but this resulted in the exclusion of only six species and provided largely congruent results.

Among anthropoids, most species were reported to show some form of genital self-inspection and/or manual grooming by males. As mentioned in the Methods, however, the numbers in this case varied depending on interpretation of the survey responses and intermediate codes (Fig. 2). Of 52 species with information, male genital self-inspection was reported in 23–67% species, while female genital self-inspection was reported in 13–65% of species. This variability in response may reflect intraspecific variation, inconsistent behaviour on the part of individual males or females, or error on the part of respondents. In analyses that examine the extremes of this variation, no significant patterns emerged for species that showed manual grooming to be more promiscuous (Table 3).

Hypothesis 3: Postcopulatory Urination

Information on postcopulatory urination by males was available for 53 species, and of these, only one to three species were reported to display the behaviour. For females, information was available for 55 species, and only three to seven species were reported to urinate after mating. Hence, the secondary prediction was rejected: postcopulatory grooming was slightly more common in females than males. The primary prediction, which relates postcopulatory urination to promiscuity levels, also was unsupported for both sexes (Table 4).

Hypothesis 4: Life History and Mating System

In nonphylogenetic analysis of species values, monogamous species were not more likely to show slow life

histories after controlling for body mass or parental investment (i.e. weaning age). Phylogenetic analysis using independent contrasts revealed a mixture of positive and negative associations, but none were significant (Table 5). Analyses using continuous measures of promiscuity (testes mass and the duration of oestrus) also provided no support for the hypothesis, with only one significant result among 24 tests and a mixture of positive and negative slopes (Table 6).

The number of reproductive events may be the key variable explaining variation in STD risk (e.g. Loehle 1995). Counter to predictions, however, monogamous species had fewer potential reproductive events (species values log transformed: 1.16 versus 1.01, $F_{1,50}=2.59$, $P=0.11$; contrasts: 2 of 4 contrasts negative, $t_3=0.54$, $P=0.63$). Analysis of testes mass revealed a significant relationship in contrasts analysis but in a direction opposite to predictions ($b=0.60$, $F_{1,29}=4.94$, $P=0.03$), and this was upheld in nonphylogenetic analysis of species values ($b=1.92$, $F_{1,30}=8.51$, $P=0.007$). The number of reproductive events showed a negative tendency with body mass (species: $b=-0.14$, $F_{1,49}=3.06$, $P=0.09$; contrasts: $b=-0.11$, $F_{1,46}=0.90$, $P=0.35$) and a statistically more discernible relationship with weaning age (species: $b=-0.23$, $F_{1,34}=3.90$, $P=0.06$; contrasts: $b=-0.42$, $F_{1,32}=7.07$, $P=0.012$). Correcting the number of reproductive events for body mass and weaning age, however, failed to provide consistent results in tests of the hypotheses.

DISCUSSION

These analyses failed to reveal strong or consistent support for any of the hypothesized behavioural defences to STDs. Monogamy was inconsistently correlated with life-history traits, and putative behavioural counterstrategies involving genital grooming, inspection of mating partners, and postcopulatory urination were unassociated with increased promiscuity. Negative results are difficult to interpret and may be the result of low statistical power. I therefore calculated the statistical power using the

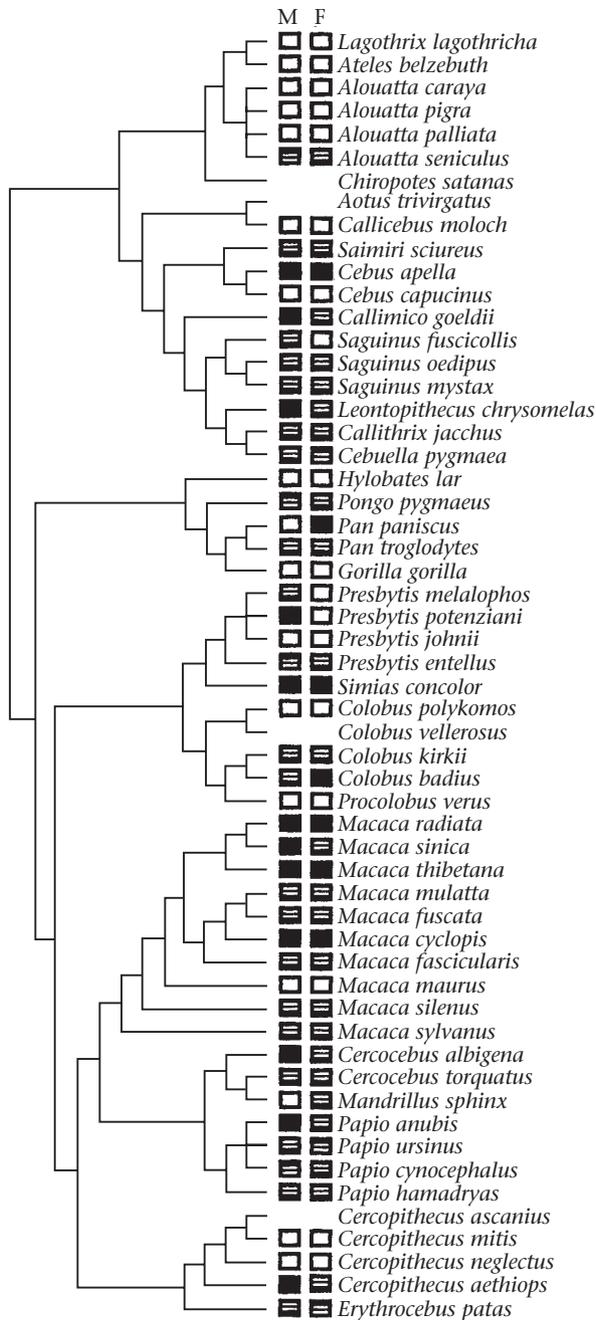


Figure 2. Phylogenetic distribution of manual self-grooming and/or self-inspection in males (M) and females (F) following copulation. ■: Presence of the trait; □: absence of the trait; ▨: conflicting responses or intermediate values of the trait (see Methods). Species without these designations indicate that no information was available. These species were included in the phylogeny to indicate species with missing data, as compared to Fig. 1. Prosimians were eliminated, however, because most species use their mouths for all types of grooming. Manual self-grooming is more flexible than oral grooming, but also is more subjectively defined, leading to a large number of conflicting and intermediate values. The phylogeny was taken from Purvis (1995).

program GPOWER. I based sample size on the minimum (21), median (31) and maximum (63) number of species' data points in nonphylogenetic analyses in Tables 1–6

and assumed a 'medium' effect size (Cohen 1988; Erdfelder et al. 1996) in a two-tailed test with $\alpha=0.05$. Statistical power was moderate, even with the largest sample sizes (Table 7), and lower in phylogenetic tests, where the degrees of freedom commonly were less than 10. In nearly one-third of the tests in Tables 1–6, however, patterns were actually opposite to predictions, indicating that low statistical power cannot account for all nonsignificant results.

Use of surveys, rather than systematically collected and published data, also may weaken data quality in some tests and so may reduce the power to detect underlying patterns. But data quality probably varies among the predictions tested and so also cannot account for all nonsignificant results. For example, trained observers would be likely to notice oral self-grooming if it occurred immediately after mating, as it does in most prosimians (Fig. 1). The phylogenetic patterns that emerge in prosimians and callitrichids therefore are likely to be biologically meaningful. By comparison, collection of data on postcopulatory urination is subject to greater error because it is a common physiological process elicited by a variety of stimuli. Moreover, if urination is performed as a defence against STDs, it may not occur immediately following copulation, making it difficult to associate the behaviour with risk factors for STD transmission.

An additional explanation for the nonsignificant results involves intraspecific variation and highlights the need for further study. The behaviours investigated here may vary intraspecifically according to population-specific STD risk factors, with this variation reducing the strength of cross-species patterns and producing nonsignificant results (Nunn & Barton 2001). In fact, analysis of multiple responses for the same species reveals variation between some primates with variable mating systems (callitrichids, *Presbytis entellus*; see Methods), highlighting the need for detailed intraspecific studies of predictions within these primate radiations.

The results presented here raise the possibility that mammals possess few effective behavioural counterstrategies to STDs. In milkweed leaf beetles and ladybirds, individuals do not avoid mating with infected partners (Abbot & Dill 2001; Webberley et al. 2002), and the same may be true for nonhuman primates. Research on humans also suggests that few behaviours are fully effective against STDs. For example, genital washing (within 1 h) and postcopulatory urination (within 30 min) provide no significant protection against gonorrhoea transmission ($N=527$ men; Hooper et al. 1978). Many human STDs produce few or inconsistent symptoms, including HIV, chlamydia and papillomavirus (e.g. Holmes et al. 1994), making it difficult to avoid mating with infected individuals through precopulatory genital inspection.

Theoretical considerations also suggest that precopulatory behaviours will be less effective against STDs for the simple reason that these behaviours directly impact reproductive success. For example, a reduction in sexual contact, such as monogamy or shorter copulation, reduces the risk of acquiring an STD. For males, this may

Table 3. Postcopulatory manual grooming in anthropoids, nonphylogenetic and phylogenetic results

	Nonphylogenetic analysis				Phylogenetic analysis		
	Effect	<i>F</i>	<i>df</i>	<i>P</i>	Positive contrasts/ total contrasts	<i>t</i>	<i>P</i>
Male manual grooming, conservative classification							
Relative testes mass	+	1.16	1,22	0.29	2/4	0.69	0.54
Duration of oestrus	–	0.00	1,31	0.97	2/6	0.30	0.77
Male manual grooming, liberal classification							
Relative testes mass	+	1.66	1,22	0.21	3/6	0.65	0.54
Duration of oestrus	+	1.66	1,31	0.21	3/8	0.70	0.50
Female manual grooming, conservative classification							
Relative testes mass	+	0.17	1,22	0.68	0/2	–1.17	0.45
Duration of oestrus	+	0.02	1,31	0.90	3/5	–0.15	0.89
Female manual grooming, liberal classification							
Relative testes mass	+	3.00	1,22	0.097	3/5	0.73	0.51
Duration of oestrus	+	2.35	1,31	0.14	5/9	1.30	0.23

Table 4. Postcopulatory urination, nonphylogenetic and phylogenetic results

	Nonphylogenetic analysis				Phylogenetic analysis		
	Effect	<i>F</i>	<i>df</i>	<i>P</i>	Positive contrasts/ total contrasts	<i>t</i>	<i>P</i>
Male urination, conservative classification							
Relative testes mass	+	0.01	1,24	0.91	*		
Duration of oestrus	+	0.22	1,32	0.64	*		
Male urination, liberal classification							
Relative testes mass	+	1.58	1,24	0.22	2/3	0.20	0.86
Duration of oestrus	+	0.08	1,32	0.78	3/3	2.85	0.104
Female urination, conservative classification							
Relative testes mass	–	0.06	1,24	0.80	*		
Duration of oestrus	+	0.12	1,34	0.74	2/2	1.65	0.35
Female urination, liberal classification							
Relative testes mass	+	0.36	1,24	0.56	4/5	1.09	0.34
Duration of oestrus	+	0.76	1,34	0.39	6/6	2.53	0.053

*Too few contrasts to conduct statistical tests (≤ 1 contrast).

Table 5. Life history and monogamy, nonphylogenetic and phylogenetic results

	Nonphylogenetic analysis				Phylogenetic analysis			
	Effect*	<i>F</i>	<i>df</i>	<i>P</i>	Positive contrasts/ total contrasts	<i>t</i>	<i>df</i>	<i>P</i>
Correcting life-history traits for body mass								
Longevity	–	1.17	1,63	0.28	1/6	0.74	5	0.49
Interbirth interval	+	2.35	1,60	0.13	3/6	–0.94	5	0.39
Age first reproduction	+	0.71	1,59	0.40	3/6	0.91	5	0.41
Correcting life-history traits for weaning age								
Longevity	–	1.49	1,37	0.23	1/5	–1.70	4	0.16
Interbirth interval	+	0.81	1,40	0.37	3/4	0.22	3	0.84
Age first reproduction	+	1.57	1,39	0.22	3/5	1.10	4	0.33

*A positive effect indicates that life-history traits are larger in monogamous species, as predicted under Hypothesis 4.

involve missed mating opportunities, resulting in substantially reduced reproductive success, while female primates that mate with only one male may face increased

risk of infanticide from other males (Hrdy 1974; van Schaik & Janson 2000). Likewise, males in polygynous systems that experience the greatest mating success are

Table 6. Life-history and promiscuity measures

	Nonphylogenetic analysis				Phylogenetic analysis			
	Effect*	F	df	P	Effect*	F	df	P
Testes residuals								
Interbirth interval, corrected for mass	–	4.09	1,32	0.052	–	0.47	1,30	0.50
Interbirth interval, corrected for weaning	–	1.30	1,21	0.27	–	0.11	1,19	0.75
Age first reproduction, corrected for mass	–	0.39	1,32	0.54	+	0.36	1,30	0.55
Age first reproduction, corrected for weaning	–	1.16	1,21	0.29	+	0.21	1,20	0.65
Longevity, corrected for mass	+	4.35	1,36	0.044	+	2.47	1,33	0.13
Longevity, corrected for weaning	+	0.36	1,22	0.55	+	1.31	1,21	0.26
Duration of oestrus								
Interbirth interval, corrected for mass	–	0.49	1,35	0.49	+	1.61	1,33	0.21
Interbirth interval, corrected for weaning	–	0.64	1,26	0.43	+	0.09	1,24	0.77
Age first reproduction, corrected for mass	+	3.56	1,36	0.07	+	1.02	1,34	0.32
Age first reproduction, corrected for weaning	+	2.69	1,26	0.11	+	1.66	1,25	0.21
Longevity, corrected for mass	+	2.01	1,34	0.17	+	0.07	1,32	0.79
Longevity, corrected for weaning	+	2.69	1,24	0.11	+	4.36	1,21	0.049

*Effect is the direction of the slope for both nonphylogenetic and phylogenetic analyses. This analysis differs from previous ones by predicting a negative effect (i.e. slower life history should lead to reduced promiscuity). Moreover, these analyses of contrasts use two continuous measures, as compared to discrete variables in previous tests.

more likely to be infected with STDs (Graves & Duvall 1995; Thrall et al. 2000), and females therefore may experience benefits by avoiding these males. These benefits must be weighed by the costs, however, such as the genetic benefits that may make these males successful.

More explicit theoretical approaches also account for why some seemingly plausible precopulatory behavioural defences are uncorrelated with STD risk. Thus, results involving genital inspection of mating partners are in line with theoretical expectations that behavioural counterstrategies to STDs involving mate choice will be rare (Graves & Duvall 1995; Knell 1999). Several factors may lead to low detection of STDs. If choices are made based on infection cues, this is likely to reduce the virulence of the STD and reduce the importance of detection, as examined in a recent theoretical model (Knell 1999). Moreover, infected hosts and parasites will have congruent interests in hiding the infection status of the host: individuals identified as 'infected' would have low reproductive success, as would the pathogen infecting them. Despite these arguments, I included Hypothesis 1 because infections in some individuals may produce symptoms that are detectable by mating partners (Holmes et al. 1994).

Finally, socioecological realities suggest that behavioural counterstrategies will be difficult to implement in mammals. For example, any factors that result in females

living in groups (Wrangham 1979; van Schaik 1989) will make monogamy less likely: in multimale–multifemale primate groups, the risk of infanticide is expected to lead to promiscuous mating by females (van Schaik et al. 1999). Factors that increase male intrasexual competition also are likely to limit female options for choosing mating partners (Smuts & Smuts 1993), and females in one-male groups will have limited options for female choice at the outset. Thus, implementation of STD defences may be more difficult for females than males in mammalian social groups characterized by intense intrasexual competition among males.

As noted above, socioecological factors also may provide better explanations for many of the behaviours examined here. Thus, predominantly male inspection of females is consistent with males monitoring female reproductive condition (Dixon 1998), which was noted by several respondents to the survey. Similarly, urination by females following mating was observed mainly (but not exclusively) among prosimian and New World primates, many of which are known to perform urine washing and other olfactory behaviours (e.g., Robinson 1979; Boinski 1992). Finally, the phylogenetic patterns reported here suggest that body size may be a correlate of oral self-grooming behavior (Fig. 1). Callitrichids and prosimians are among the smallest-bodied primates, and it may be that larger-bodied species experience physical limitations in oral grooming.

In conclusion, I found no support for hypothesized behavioural counterstrategies to STDs to be related to risk factors for STD transmission. Among humans, efforts to control the spread of STDs have proven remarkably difficult (Brandt 1987; Holmes et al. 1994). In the U.S.A., for example, 14% of college women acquire genital papillomavirus infections per year, and more than 65 million adults in the U.S.A. are infected with an incurable STD (Center for Disease Control 2000). An understanding

Table 7. Statistical power analysis

Test	Statistical power
Smallest sample (N=21)	0.19
Median sample (N=31)	0.27
Largest sample (N=63)	0.50

of how nonhuman primates deal with STD risk may provide insights to the human epidemic. In addition, some STDs may be a threat to captive breeding of endangered species (Weigler et al. 1988; Canfield et al. 1991). The comparative analyses presented here provide hypotheses for future investigation of these questions and highlight the kinds of data that are needed for these investigations.

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