

Spleen size, disease risk and sexual selection: a comparative study in primates

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ABSTRACT

If individuals of different species vary in their risk of acquiring infectious disease, this variation is expected to result in systematic differences in immune defence structures across species. I used phylogenetic comparative methods to examine the correlates of spleen mass in primates, based on *a priori* hypotheses involving disease risk, sexual selection and correlations among organ systems. All comparative tests controlled for body mass. Contrary to predictions that more social species experience greater risk of acquiring infectious disease and should therefore exhibit increased immune defence, spleen mass was not associated with measures of sociality. Species with slower life histories had larger spleens, as expected if such species come into contact with a greater number of parasites throughout life. However, spleen mass was unrelated to use of the ground or increased mating promiscuity, both of which are thought to increase transmission of parasites. In contrast to patterns documented in previous research on birds, primate spleen mass showed no association with sexual selection involving male–male competition. The comparative tests found only one correlation among the spleen and other organs, involving the liver, which has some immune defence functions early in life. Several factors may explain the general absence of support for patterns in primates, as compared to patterns documented previously in birds, including differences in the expression of sexual selection and the involvement of the mammalian spleen in bodily functions unrelated to immune defence. These analyses suggest that spleen mass is not a useful predictor of disease risk in primates, which is important for future comparative research on the correlates of parasitism in mammals.

Keywords: comparative study, disease risk, immune system, phylogeny, primates, sexual selection, spleen.

INTRODUCTION

Little is known about how ecological processes involving hosts and their parasites influence differences across host species. If the risk of acquiring infectious disease differs among species and covaries with host features such as social and mating system, then lineages characterized by increased risk of infectious disease should show greater immune defence (Harvey *et al.*, 1991). In tests of mammals, for example, more promiscuous species of

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primates and carnivores exhibit higher baseline leukocyte counts (Nunn *et al.*, 2000; Nunn, in press; C.L. Nunn, J.L. Gittleman and J. Antonovics, unpublished data), suggesting that risk of sexually transmitted disease has influenced patterns of immune defence across species.

Similar tests can be conducted with immune defence organs, such as the spleen. Across species of birds, spleen size correlates with prevalence (John, 1995) and species richness (Morand and Poulin, 2000) of nematodes. Spleen mass is likely to reflect immune defence capabilities in mammals because the spleen is involved in maturation of lymphocytes and as a site for identifying and filtering antigens (Harvey *et al.*, 1991; Roitt *et al.*, 1998). Moreover, parasites may result in increased spleen size in infected individuals through the immune response; hence, differences in infection rates by a broad array of parasites can be detected among species using comparative methods.

I used phylogenetic comparative methods to test whether spleen mass correlates with social, ecological and life-history variables thought to influence the risk of acquiring infectious disease in primates. I also examined potential correlates of spleen mass involving sexual selection, body mass and other organ systems. These tests focused on primates because the quantitative data and phylogenetic information needed to test the key hypotheses are readily available. The following list summarizes the predictions tested, the basis for these predictions and previous research on relevant patterns in primates.

1. Animals living in larger social groups or at higher population densities are predicted to have larger spleens because sociality is thought to increase the spread of many parasites (Møller *et al.*, 1993). Previous research on parasite abundance has revealed an association between prevalence and group size in primates (Davies *et al.*, 1991; see also Côté and Poulin, 1995), but comparative studies of primate immune defence parameters have found no association with group size (Nunn *et al.*, 2000; Nunn, in press; S. Semple, G. Cowlshaw and P.M. Bennett, unpublished data).
2. Primates that use the ground for locomotion are expected to have larger spleens than arboreal primates because terrestrial species may be exposed to more parasites in the soil (e.g. Hausfater and Meade, 1982). Previous research has found ambiguous evidence for an effect of terrestriality using leukocyte counts (Nunn *et al.*, 2000; Nunn, in press). Data on the spleen may therefore clarify the relationship between terrestrial substrate use and immune defence in primates.
3. More promiscuous primate species are expected to have relatively larger spleens if this organ plays a role in defending the body from sexually transmitted diseases (STDs). The spleen is involved in detecting blood-borne pathogens (Roitt *et al.*, 1998), some of which are sexually transmitted (Holmes *et al.*, 1994); previous research on leukocyte counts has revealed support for this prediction (Nunn *et al.*, 2000, unpublished).
4. Immune system parameters are predicted to show relationships with life-history traits because species with slow life histories will tend to come into contact with a greater number of parasites throughout life and may therefore harbour a more diverse parasite community (Poulin, 1995). Moreover, species with a slow life history may require increased immunological protection to achieve maximum longevity (see also Møller, 1997b). In carnivores and primates, numbers of phagocytic leukocytes, such as neutrophils, correlate with body mass and some life-history traits (Nunn *et al.*, 2000, unpublished; Nunn, in press).
5. Parasite-mediated sexual selection (Hamilton and Zuk, 1982) is predicted to lead to an association between spleen mass and sexual selection. This effect may operate through

female choice, if females choose males that are resistant to parasites (Møller, 1997a), or sexual selection may influence immune defence organs through male intra-sexual competition, if such competition leads to injury and thus mechanisms that reduce the risk of infection (P.M. Bennett, I.P.F. Owens and A.P. Møller, unpublished data). I focused on male intra-sexual competition, including canine and body mass dimorphism, because female choice is less well documented for mammals than for birds (e.g. Table 6A in Andersson, 1994) and cannot yet be examined comparatively for primates. A previous comparative study of leukocyte counts revealed no correlation with sexual dimorphism in primates (Nunn, in press).

6. The immune response is costly (Sheldon and Verhulst, 1996; Moret and Schmid-Hempel, 2000), suggesting that maintenance of the immune system itself is costly. I tested for trade-offs (negative correlations) among the spleen and other organs, including the brain, lungs, liver and heart. Aiello and Wheeler (1995) made a similar prediction for trade-offs between the brain and digestive system in primates, but their 'expensive tissue' hypothesis has not been tested definitively. For some organ systems, an equally valid alternative to this predicted negative correlation is a positive one. Thus, between two organs with identical bodily functions, selection on one organ may lead to correlated selection on the other, producing a positive association across species.

In addition to the results reviewed above for primates and carnivores, previous research on birds has revealed support for many of these predictions, with sexual selection leading to larger spleens and higher leukocyte counts (Møller, 1997a; Møller *et al.*, 1998b; P.M. Bennett *et al.*, unpublished data) and sociality influencing the immune response (Møller *et al.*, 2001). Moreover, the relationship between spleen mass and testes mass is negative in birds (Morand and Poulin, 2000), suggesting a trade-off between reproductive and immune systems.

MATERIALS AND METHODS

Comparative data

Data on spleen mass of adults were compiled from the literature for 30 species (Table 1). In all cases, data were used only when the source provided a corresponding estimate of body mass. Because sexual selection may generate differences in immune defence between the sexes (Folstad and Karter, 1992; Møller *et al.*, 1998b), I used data on female spleen mass and body mass when data were available for both sexes. Data on thymus mass were available for some species, but the sample sizes were small ($n = 9$). Moreover, the thymus tends to degenerate in adult animals and becomes inter-digitated with fat (e.g. Kennard and Willner, 1941b; Larson, 1982), making it difficult to measure accurately.

Information on other organ systems was compiled from the same sources as spleen mass. I collated data on heart, liver, lungs, testes and brain mass, as these organs were likely to be measured consistently by different researchers (see Larson, 1982); data were available for more than 15 species per organ. However, some uncertainties arose that should be considered when interpreting the results. It sometimes was impossible to determine from publications if liver mass included the mass of the gall bladder. Similarly, sources often were unclear about whether lung mass was for a single lung or paired lungs, although the latter is most likely and, therefore, assumed here. Despite these uncertainties, all organ masses were

Table 1. Organ data used in the comparative tests

Species	Spleen (g)	Body mass (g)	Alternative spleen mass? ^a	Reference for primary data
<i>Alouatta caraya</i>	9.24	4 983		Stahl <i>et al.</i> (1968)
<i>Alouatta palliata</i>	45.68	6 174		Crile and Quiring (1940)
<i>Aotus trivirgatus</i>	1.94	739		Baer (1994)
<i>Ateles geoffroyi</i>	40.8	7 630		Crile and Quiring (1940)
<i>Callithrix jacchus</i>	0.423	307.7		Wadsworth <i>et al.</i> (1981)
<i>Cebus apella</i>	2.37	2 160		Schwartz <i>et al.</i> (1974)
<i>Cebus capucinus</i>	11.3	3 101		Crile and Quiring (1940)
<i>Cercocebus galeritus</i>	5.35	6 000		Kennard and Willner (1941c)
<i>Cercocebus torquatus</i>	9.0	6 100		Kennard and Willner (1941c)
<i>Cercopithecus aethiops</i>	3.0	1 422	yes	Sauer and Fegley (1960)
<i>Cercopithecus mitis</i>	85.16	4 937		Crile and Quiring (1940)
<i>Galago garnettii</i>	2.17	800		Makita <i>et al.</i> (1989)
<i>Gorilla gorilla</i>	192.8	65 000		Kennard and Willner (1941a)
<i>Homo sapiens</i>	168.0	56 000	yes	Spector (1956)
<i>Hylobates lar</i>	14.0	5 700		Kennard and Willner (1941a)
<i>Macaca arctoides</i>	9.77	6 200	yes	Larson (1982)
<i>Macaca cyclopis</i>	8.0	10 300		Makita <i>et al.</i> (1984)
<i>Macaca fascicularis</i>	7.19	3 300	yes	Larson (1982)
<i>Macaca fuscata</i>	4.57	5 825		Makita <i>et al.</i> (1984, 1985)
<i>Macaca mulatta</i>	4.31	5 210	yes	Larson (1982)
<i>Macaca nemestrina</i>	10.13	5 150		Larson (1982)
<i>Macaca radiata</i>	7.65	4 530		Larson (1982)
<i>Pan troglodytes</i>	95.0	30 100		Kennard and Willner (1941a)
<i>Papio anubis</i>	16.9	12 700	yes	Gest and Siegel (1983)
<i>Papio cynocephalus</i>	17.79	12 970	yes	Larson (1982)
<i>Papio ursinus</i>	18.4	14 500		McConnell <i>et al.</i> (1974)
<i>Saguinus oedipus</i>	1.65	793		Crile and Quiring (1940)
<i>Saimiri oerstedii</i>	0.9	607		Crile and Quiring (1940)
<i>Saimiri sciureus</i>	0.95	662	yes	Middleton and Rosal (1972)
<i>Tarsius spectrum</i>	0.031	168		Kennard and Willner (1941c)

^a Yes: secondary estimates of spleen mass were available in other references.

highly correlated with body mass (Table 2), as expected if signal in the data exceeds these potential sources of error. Spleen mass also showed a strong relationship with body mass (Fig. 1), as found in other studies of mammals (Stahl, 1965) and birds (Harvey *et al.*, 1991; John, 1995; Møller, 1997a; Møller *et al.*, 1998b; Morand and Poulin, 2000).

For group size, population density and the percentage of time spent in terrestrial locomotion, I used information from an unpublished comparative database (unpublished data used here are available at: <http://faculty.virginia.edu/charliennunn> or <http://www.evolutionary-ecology.com/data/1372dataset.html>). In addition to using the percentage of time spent in terrestrial locomotion, substrate use was examined as a ranked discrete variable, with arboreal species = 1, terrestrial species in a wooded environment = 2 and terrestrial species

Table 2. Relationships between organ mass and body mass^a

	Phylogenetic analysis			Non-phylogenetic analysis		
	$N_{\text{contrasts}}$	Slope	F -statistic	N_{species}	Slope	F -statistic
Spleen	26	1.07	66.7***	30	1.17	134.0***
Heart	26	1.02	352.4***	30	0.97	1026.0***
Liver	26	0.79	189.6***	29	0.88	793.4***
Lungs	24	0.90	95.5***	27	0.92	371.0***
Testes	15	0.68	55.6***	17	0.75	30.8***
Brain	17	0.79	142.4***	18	0.80	285.5***

*** All results significant at $P < 0.001$ in two-tailed tests.

^a Numbers differ in analysis of contrasts and species values due to polytomies in the primate tree (Purvis and Rambaut, 1995).

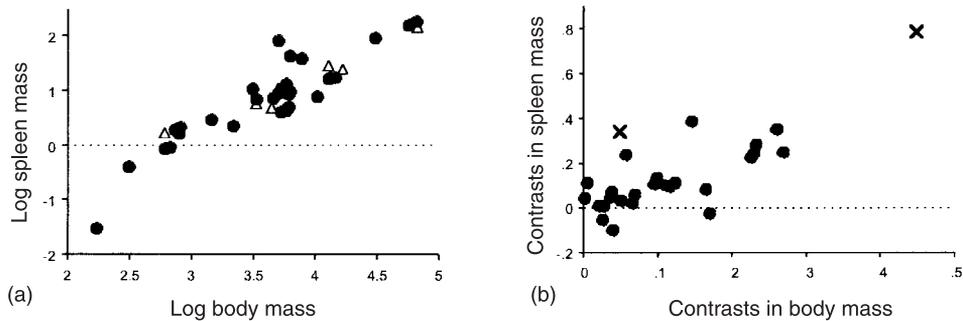


Fig. 1. Allometry of spleen mass in primates. Axes show spleen mass and body mass for species values (a) and independent contrasts (b). Triangles in (a) represent alternative values for eight species used to re-test hypotheses that were significant with the primary dataset. Crosses in (B) represent outliers, which may exert undue leverage on the statistical tests. Analyses were repeated with and without these outliers, but the results were largely the same.

in an open (savanna) environment = 3 (Nunn and van Schaik, 2001). Information on activity period (diurnal vs nocturnal) was taken from Nunn and van Schaik (2001). Data on age at first reproduction, longevity, weaning age and the interbirth interval were taken mainly from Ross and Jones (1999). Diet codes were acquired from Nunn and van Schaik (2001) and percentages of specific dietary components (leaves, fruit) were obtained from the literature. Grooming is commonly thought to have both hygienic and social functions in primates, but hygienic benefits are likely to be restricted to removal of ectoparasites and this behaviour may actually spread directly transmitted diseases, such as those with fecal–oral transmission. I therefore tested for an association between spleen mass and grooming frequency, with grooming data taken from Dunbar (1991). For analysis of mating partner number, species were classified following van Schaik *et al.* (1999), with females having a single mate per oestrous cycle, variation between single and multiple mates per cycle (1+ mates) and many mates. The duration of oestrus was taken from van Schaik *et al.* (1999). Sexual dimorphism in body mass was calculated from data in Smith and Jungers

(1997), while estimates of canine dimorphism were obtained from Plavcan and van Schaik (1992; GDCI measures based on principal components analysis of six canine dimensions).

Life-history variables are highly correlated with body mass in primates (Harvey and Clutton-Brock, 1985). I controlled for body mass in analyses of organs and life-history traits by using residuals from the regression of the trait of interest on body mass (Harvey and Pagel, 1991). When the same body mass estimates are used for X and Y variables, however, the 'Economos problem' arises: a body mass estimate measured with error will tend to bias estimates of residuals for both X and Y traits in a similar direction, creating potentially spurious correlations (Barton and Dunbar, 1997). This problem was avoided by using different estimates of body mass when controlling for the X and Y variables, although to analyse trade-offs among some organs this solution was not available, as the data on body mass came from the same samples. For tests of hypotheses involving life-history variables, I also examined patterns without controlling for mass, because a recent life-history model (Kozłowski and Weiner, 1997) suggests that body mass is a consequence, rather than a cause, of life-history evolution (for an excellent review, see Harvey and Purvis, 1999).

Comparative methods

In testing the above hypotheses and identifying confounding variables, I based my conclusions on results from phylogenetically independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991). In calculating contrasts, I used the computer program CAIC (Purvis and Rambaut, 1995), with the phylogeny and branch lengths from Purvis (1995). All statistical tests reported in this paper are one-tailed when testing directional hypotheses, but two-tailed if specific directional predictions were not possible (for correlations among organs) or when exploring comparative patterns using multivariate methods.

The method of independent contrasts makes several statistical and evolutionary assumptions (Purvis and Rambaut, 1995). Violation of these assumptions has been shown to alter the statistical properties (Type I and II error rates) of tests that use independent contrasts (Purvis *et al.*, 1994; Díaz-Uriarte and Garland, 1996, 1998). To ensure that the contrasts were properly standardized using branch length information, I tested for an association between the absolute value of contrasts and their standard deviations (Garland *et al.*, 1992; Purvis and Rambaut, 1995; Nunn and Barton, 2001). I also examined the association between contrasts and estimates of nodal values (Purvis and Rambaut, 1995; Freckleton, 2000). These tests revealed that log-transformed data and equal branch lengths best met the assumptions of independent contrasts for most tests. After appropriate data and branch length transformations, the assumptions were generally upheld, but some contrasts were identified as outliers. I therefore conducted analyses with and without these outliers. The results were generally the same, but removal of outliers is likely to give conservative results and so these results are presented here.

Another assumption is that the phylogeny used in the tests accurately reflects the evolutionary history of the species being compared. The Purvis (1995) tree is the only phylogeny available for all living primates with information on branch lengths, which are needed to standardize contrasts (Felsenstein, 1985). I based my conclusions on phylogenetic analyses, but I also conducted non-phylogenetic tests. Comparison of phylogenetic and non-phylogenetic results often can reveal the presence of confounding variables shared

through common descent (Purvis and Webster 1999; Nunn and Barton, 2001), and non-phylogenetic tests provide more reliable results under an alternative model of trait evolution (Price, 1997; Harvey and Rambaut, 2000).

Comparative results may be sensitive to the data set used, especially when dealing with variables that are difficult to quantify such as mating promiscuity or life-history traits. Although spleen data are fairly limited, in eight species I was able to find an additional estimate of spleen mass; I used these alternative estimates in a second set of tests. Thus, I used the best estimates of spleen mass for my primary analyses, with precedence for one reference source over another based on the number of spleens analysed, the availability of data on other organs and clear specification of age–sex categories. For significant results, I then repeated the tests using the alternative estimates. I also repeated some tests with alternative measures for brain size (Harvey *et al.*, 1987; Barton, 1999) and testes mass (Harcourt *et al.*, 1995).

Confounding variables and multivariate analyses

Prior to testing the hypotheses, I examined several potential confounding variables. Activity period is a major factor influencing primate socio-ecology, with nocturnal species living in smaller groups and using arboreal substrates (Nunn and van Schaik, 2001). Only two contrasts were available for assessing the effect of activity period on relative spleen mass, giving a non-significant result, but non-phylogenetic analysis revealed no clear pattern ($F_{1,28} = 0.14$). Diet is another factor thought to influence key socio-ecological parameters in primates (e.g. Clutton-Brock and Harvey, 1977; Janson and Goldsmith, 1995), but I found no significant dietary correlates of relative spleen mass.

I performed two types of multivariate analyses to assess the relative roles of variables used in the bivariate tests. First, I used forward and backward stepwise regression to analyse contrasts in the main predictor variables. When more than one variable was available for testing a hypothesis, such as the life-history hypothesis, I chose variables so as to maximize the number of contrasts. Thus, I included as predictor variables group size, substrate use (discrete), mating promiscuity (discrete), residual interbirth interval, body mass dimorphism and body mass (from spleen references), with spleen mass as the response variable. Variables were entered in forward inclusion or removed in backward elimination if the significance probability was greater than 0.25. I also repeated the analyses with an alternative life-history variable that was significant in bivariate tests (age of weaning) and using species data (i.e. non-phylogenetic analysis).

Second, I performed principal components analysis (PCA) on contrasts and species values to determine how suites of variables influence patterns of variation in spleen mass. I investigated the comparative patterns by calculating PCA scores, assessing the influence (loadings) of predictor variables on these scores and then testing whether PCA scores explain significant variation in spleen mass. In initial tests using the predictor variables from the stepwise model, I found that body mass was the primary variable influencing PCA scores. Because body mass was also the best predictor of spleen mass in bivariate tests (Table 2), these PCA scores tended to explain significant variation in spleen mass, but it was difficult to assess the relative roles of the other parameters, such as group size or life-history variables. I therefore repeated the analyses using spleen mass corrected for body mass as the response variable, eliminating body mass as a variable in the PCA.

RESULTS

Hypotheses for disease risk and sexual selection

Neither group size nor population density explained significant variation in relative spleen mass using independent contrasts (group size: $b = 0.048$, $F_{1,25} = 0.08$, $P = 0.39$; population density: $b = -0.18$, $F_{1,23} = 2.67$, $P = 0.94$). The results remained non-significant when using species values in non-phylogenetic tests. Grooming frequency was also unrelated to relative spleen mass in an analysis of independent contrasts ($b = 0.11$, $F_{1,12} = 0.20$, $P = 0.32$) and when using species values.

Contrary to predictions, spleen mass tended to decline with increasing percentage of time on the ground ($b = -0.10$, $F_{1,11} = 4.74$). In exploring further this pattern using species values, the results were significant in a two-tailed test ($b = -0.26$, $F_{1,12} = 14.4$, $P = 0.003$). Use of discrete classes of substrate use revealed that relative spleen mass declined in four of six transitions to terrestrial substrate use ($t_5 = 1.79$).

Spleen mass was unrelated to discrete classifications of mating promiscuity (only three of six contrasts were positive: $t_5 = 0.05$, $P = 0.48$). I also used quantitative data on mating promiscuity involving relative testes mass (a measure of sperm competition) and the duration of oestrus (a longer duration of oestrus is correlated with increased mating promiscuity; van Schaik *et al.*, 1999). After correcting testes mass for body mass, the results were non-significant ($b = 0.08$, $F_{1,14} = 0.06$), including analyses with the data set on testes from Harcourt *et al.* (1995; $b = 0.02$, $F_{1,18} = 0.01$) and in non-phylogenetic tests. The duration of oestrus also failed to explain significant variation in relative spleen mass using contrasts ($b = 0.08$, $F_{1,22} = 0.25$, n.s.) and species values.

Several life-history variables showed significant relationships with relative spleen mass (Table 3). Residual interbirth interval increased with relative spleen mass in contrasts analysis ($b = 0.90$, $F_{1,21} = 3.29$, $P = 0.042$), but this relationship was driven by two outliers and became non-significant when these outliers were excluded (Table 3). Use of species data revealed similar patterns but with some scatter (Fig. 2) and the results were not consistent for all life-history variables (Table 3). Congruent results were obtained when using the alternative estimates of spleen mass and with life-history variables uncorrected for body mass.

Relative spleen mass was unrelated to dimorphism in canine size ($b = -0.17$, $F_{1,16} = 0.12$, $P = 0.63$) or body mass ($b = 0.29$, $F_{1,25} = 1.36$, $P = 0.13$). Non-phylogenetic tests provided similar results.

Correlations and trade-offs among organ systems

In analysing associations among organ systems, the statistical results were mixed in two-tailed tests. Liver mass was related to spleen mass after controlling both variables for body mass ($b = 1.43$, $F_{1,23} = 9.31$, $P = 0.006$). However, this positive relationship became a non-significant trend when outliers were included ($b = 0.72$, $F_{1,26} = 1.50$, $P = 0.23$), with the alternative spleen data set ($b = 0.80$, $F_{1,23} = 1.96$, $P = 0.18$) and in non-phylogenetic tests ($b = 0.77$, $F_{1,27} = 1.60$, $P = 0.22$). It has been proposed that brain mass is negatively correlated with the digestive system in primates (Aiello and Wheeler, 1995), but for the immune system there was no significant relationship between brain mass and spleen mass after correcting both variables for body mass ($b = -0.63$, $F_{1,16} = 1.07$, $P = 0.32$). The

Table 3. Life-history variables and spleen mass, correcting both for body mass using residuals

	Phylogenetic analysis			Non-phylogenetic analysis		
	$N_{\text{contrasts}}$	Slope	F -statistic	N_{species}	Slope	F -statistic
Interbirth interval	20	0.0063	0.00 ^a	23	1.31	13.1***
Longevity	23	-0.061	0.03	25	-0.31	0.31
Age at first reproduction	24	-0.43	0.88	26	0.52	0.82
Weaning age	17	0.53	3.37*	19	0.87	4.37*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^a Results significant when two outliers are included. See text for details.

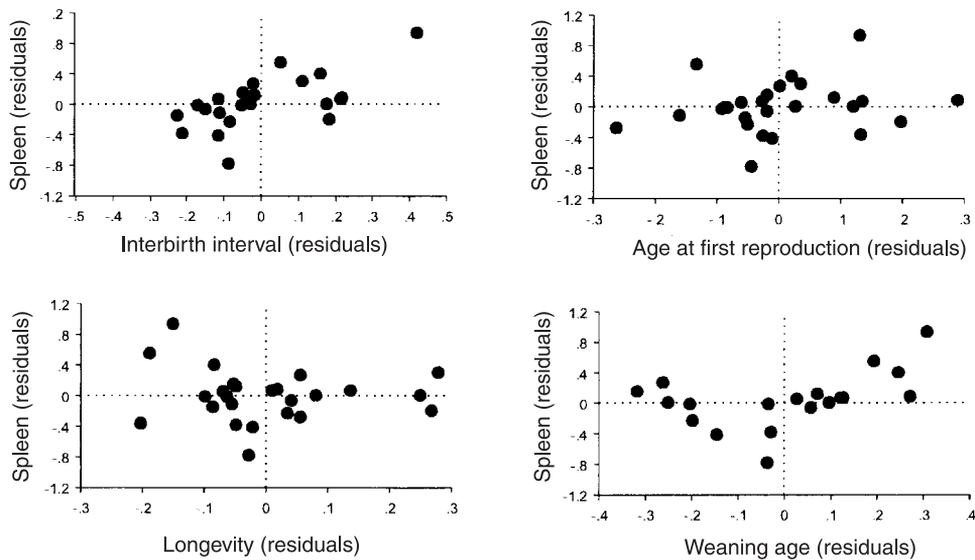


Fig. 2. Associations among life-history variables and spleen mass. All variables are corrected for body mass, using different body mass estimates to control for the ‘Economos’ problem (see Methods). These plots show species values (non-phylogenetic analysis). Statistical results for contrasts and species values are presented in Table 3.

results also were non-significant in non-phylogenetic tests and when using alternative data on brain mass ($b = -0.38$, $F_{1,23} = 0.37$, $P = 0.55$). Finally, as noted above, there was no significant association between spleen mass and testes mass, with F -statistics less than 1. Thus, I found no support for trade-offs among organ systems and the spleen.

Multivariate analyses

In multivariate analysis of contrasts, only two variables were entered in the stepwise model and both were significant in two-tailed tests: spleen mass increased with body mass and declined with shifts to terrestrial substrate use (Table 4). In non-phylogenetic tests, however, substrate use was replaced by residual interbirth interval in the stepwise model ($b = 1.30$, $F_{1,20} = 12.7$, $P = 0.002$), with body mass remaining significant. I also repeated analyses after excluding nocturnal species from the analysis, on the basis that activity period influenced leukocyte counts in primates (Nunn, in press), but this provided qualitatively similar results. Use of weaning age rather than interbirth interval conformed with this pattern: weaning age explained significant variation in non-phylogenetic analysis, but not when using independent contrasts.

In PCA of contrasts, PCA-1 explained 41.3% of the variance among the predictor variables; PCA-2 explained an additional 24.3% of the variance. For PCA-1, the largest loadings (in absolute magnitude) were for group size and terrestriality (Table 5), with their identical signs reflecting the well-known correlation among these traits in previous comparative studies (Clutton-Brock and Harvey, 1977; Nunn and Barton, 2000, 2001). For PCA-2, the largest loadings were for residual interbirth interval and sexual dimorphism, which had opposite signs. Neither of these PCA scores explained significant variation in residual spleen mass (PCA-1: $b = 0.016$, $F_{1,19} = 2.67$, $P = 0.12$; PCA-2: $b = 0.021$, $F_{1,19} = 2.86$, $P = 0.11$). After factor rotation, however, one factor had positive coefficients for residual interbirth interval and negative coefficients for terrestriality (Table 5); this factor explained

Table 4. Multivariate analysis of contrasts for key hypotheses ($n = 22$)

Variable	Slope estimate	<i>F</i> -statistic
Log body mass	1.45	142.7***
Terrestriality codes	-0.21	5.65*
Sexual dimorphism	-0.091	1.08
Group size	0.071	0.71
Mating promiscuity	-0.058	0.81
Residual interbirth interval	0.20	0.49

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, all two-tailed tests in multiple regression through the origin.

Table 5. Factor loadings from PCA analysis of contrasts

	Sexual dimorphism	Interbirth interval	Group size	Mating partner number	Terrestriality
PCA-1	0.28	0.22	-0.41	0.12	-0.43
PCA-2	-0.36	0.53	0.18	-0.16	-0.19
Rotated factor 2	-0.04	0.91	-0.34	-0.02	-0.80

significant variation in relative spleen mass ($b = 0.046$, $F_{1,19} = 6.44$, $P = 0.02$). PCA-3 and PCA-4 increased the variance explained among the predictor variables to 96%, but neither of these PCA scores accounted for significant variation in relative spleen mass.

Further exploration of independent contrasts using PCA failed to reveal additional patterns of interest. In non-phylogenetic analysis, however, PCA-1 explained 45.7% of the variance in the predictor variables, with PCA-2 explaining an additional 19.1%. The largest weighting for PCA-2 was for residual interbirth interval ($= 0.68$; all but mating partner number were positive) and PCA-2 explained significant variation in relative spleen mass ($b = 0.17$, $F_{1,21} = 6.75$, $P = 0.02$).

DISCUSSION

This study used data on primate spleen mass to examine the correlates of immune defence structures. Even after controlling for potentially confounding variables, most predictions went unsupported. An important exception involved life history: spleen mass, after controlling for body mass, showed a significant association with life-history variables. Not all life-history traits showed a significant relationship, however, which is similar to the results for life-history traits in analyses of primate and carnivore leukocyte counts (Nunn, in press; C.L. Nunn *et al.*, unpublished). In primates, for example, neutrophils increased with age at first reproduction and lymphocytes increased with the interbirth interval (unpublished results), while in carnivores, neutrophils increased with age at sexual maturity and gestation length (C.L. Nunn *et al.*, unpublished). Because the life-history hypothesis for disease risk focuses on the importance of a long lifespan, it is striking that longevity was not significant in any of these tests and had a negative slope in analyses involving the spleen.

Only one significant result was found in tests of correlations among organ systems. After controlling for body mass, animals with larger spleens have larger livers, although the results were not significant in all tests. This association might be expected because the liver is the site of development of some B-cells, especially in the fetus (Roitt *et al.*, 1998); however, adult organ masses were analysed here.

Comparison with other taxa

These comparative results contrast sharply with comparative patterns found in analyses of the avian spleen. For example, Møller (1997a) documented an association between spleen mass and sexual dichromatism, which is a surrogate measure of sexual selection. Other immune defence parameters also correlate with sexual selection in birds, including leukocyte counts, thymus mass and the bursa of Fabricius, using measures of sexual selection that involve body mass dimorphism, extra-pair copulation frequency and sexual dichromatism (e.g. Møller, 1997a; Møller *et al.*, 1998a; P.M. Bennett *et al.*, unpublished data). The results from birds can be interpreted in terms of female choice or male–male competition. Møller (1997a) argued that the association between spleen mass and immune system structures is based on female choice (see also Møller *et al.*, 1998a). By comparison, Bennett *et al.* (unpublished data) suggest that a positive association between leukocytes and avian body size dimorphism reflects risks of infection associated with male intra-sexual competition. These relationships are not mutually exclusive because inter-sexual selection and intra-sexual competition are often correlated (Berglund *et al.*, 1996).

Another pattern found in birds, but not in primates, involves an association with sociality. Colonially nesting birds were found to have larger spleens and bursa of Fabricius (Møller and Erritzoe, 1996), while comparative study of the immune response revealed a significant effect of sociality among swallows and martins (Møller *et al.*, 2001). Although not directly related to spleen mass, these studies suggest that sociality can influence immune system parameters. Within primates, a comparative study of the prevalence of malaria revealed that animals living in larger groups experience greater risk of acquiring parasites (Davies *et al.*, 1991). Malaria is vector-transmitted, and animals living in larger groups have been proposed to reduce vector-transmitted parasites through a 'selfish herd' effect (Freeland, 1977; see also Côté and Poulin, 1995), although Davies *et al.* (1991) noted that larger groups may also attract more actively searching insect vectors.

A final difference between primates and birds involves organ trade-offs. Morand and Poulin (2000) found a negative association between relative spleen mass and relative testes mass, suggesting that this pattern reflects a trade-off between these two organ systems. No such relationship was found in primates. Another trade-off proposed for primates is the 'expensive tissue hypothesis', which states that the metabolic requirements of a relatively larger brain are offset by a reduction in gut tissue (Aiello and Wheeler, 1995). Other metabolically costly organ systems, such as the immune system, may therefore be expected to show trade-offs with the brain, but I found no such trade-off with the spleen.

Comparative tests of spleen mass

There are several reasons why most factors were non-significant in the present study. First, these comparative tests may have low statistical power. I therefore calculated statistical power assuming a medium effect size (Cohen, 1988; Erdfelder *et al.*, 1996) and under the following sample sizes: the smallest number of data points used in the bivariate tests ($n = 12$), the largest number of data points ($n = 30$) and the midpoint of these values ($n = 21$). Using the program G*Power and these parameters, I found that the statistical power of two-tailed tests ranged from 0.23 to 0.54, with a value of 0.39 for the intermediate sample size typical of many of the comparative tests conducted here. Thus, statistical power was generally low to moderate, although use of one-tailed tests for *a priori* predictions increased the statistical power of many tests (Cohen, 1988).

Second, the mammalian spleen functions in both immune defence and production and storage of red blood cells, whereas the avian spleen is less involved with red blood cells (e.g. Harvey *et al.*, 1991). Thus, the patterns found in birds (Morand and Poulin, 2000) may be less striking in mammals (Harvey *et al.*, 1991), especially in tests with only moderate statistical power.

Third, birds and mammals exhibit important differences in factors leading to, and thus the expression of, sexual selection. Sexual selection in birds is commonly thought to involve striking plumage modification, which has been linked to factors involving female choice, parasites and immune defence (Hamilton and Zuk, 1982; Folstad and Karter, 1992; Møller *et al.*, 1999). By comparison, primate sexual selection is reflected most directly in size dimorphism (Clutton-Brock *et al.*, 1977; Plavcan and van Schaik, 1992, 1997; Mitani *et al.*, 1996) and genital anatomy (Harcourt *et al.*, 1995; Harcourt, 1996; Dixson, 1998), with few links yet established to male ornamentation within or across species (Smuts, 1987). Hence, these fundamental differences in the expression of sexual selection may explain the different comparative patterns in immune defence structures in birds and primates.

Finally, variability in the size of the spleen within species may conceal differences across species. This is a valid concern when examining immune defence parameters because values may vary substantially among individuals or within an individual over time (i.e. due to the immune response; Roitt *et al.*, 1998). This issue is heightened in the present case because most of the data are from captive animals that may be exposed to novel parasites and antibiotics to control infections. Counter to this argument, spleen mass was highly correlated with body mass (Table 2, Fig. 1; $r^2 = 0.83$ in the species analysis), suggesting that the sample sizes were large enough to detect meaningful patterns despite intraspecific variability in organ mass. Nonetheless, other organ systems listed in Table 2 gave consistently higher r^2 values (>0.90 using species values), and if spleen mass is largely a facultative response to current conditions, then correlations that exist among spleen size, ecology and sociality are likely to be obscured when using captive animals.

The results suggest that data on spleen mass from the literature are not useful for assessing immune defence and disease risk in mammals. This is important information for future research because it is unlikely that investigators will be able to obtain spleen mass estimates from free-ranging wild primates of known health status. In addition, there were trends for certain life-history traits to increase with spleen mass, but these patterns did not involve the expected relationship with longevity. Although longevity may be measured with greater error than other life-history traits, producing non-significant tests, these comparative results suggest that lifespan is not the variable that underlies the broader patterns of immune defence involving life history. A fuller understanding of the interaction between life history and immune defence, therefore, requires additional theoretical and comparative research.

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