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Patterns of MHC selection in African mole-rats, family Bathyergidae: the effects of sociality and habitat

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African mole-rats are a family of rodents exhibiting an eclectic range of social behaviour and occupying a variety of habitat types. These differences are likely to impact upon the risk of parasite transmission and virulence, with increasing sociality predicted to correspond to an increased risk of transmission. We investigate these factors by analysing the major histocompatibility complex (MHC), a set of genes responsible for encoding highly variable intermediaries of the vertebrate adaptive immune response. To this end we assessed selection at exons 2 and 3 of the MHC class II *DQα1* gene of four African mole-rat species representing a range of social behaviours. We demonstrate that: (i) the overall pattern of selection at these exons differentiates according to the predicted function of different regions, with the presence of positive selection indicating the likely influence of host–parasite coevolution; and (ii) contrary to the often observed and predicted positive correspondence between sociality and the risk of parasite transmission, two highly social African mole-rat species in fact appear to have comparatively weak positive selection, suggesting diminished host immunity and thus a low overall risk of parasite transmission.

Keywords: African mole-rats; Bathyergidae; major histocompatibility complex genes; natural selection; sociality

1. INTRODUCTION

African mole-rats are a family of subterranean Hystricomorph rodents occurring in multifarious habitats throughout sub-Saharan Africa. Their range in social and breeding strategies, from solitary living, to small social groups, to large eusocial colonies, is unusual among mammals (reviewed in Bennett & Faulkes 2000). These differences in social strategies are of particular interest with reference to differences in host–parasite dynamics and its effects on the evolution of the major histocompatibility complex (MHC) genes, whose products are highly variable intermediaries of the vertebrate adaptive immune response (Klein 1986).

Animals living gregariously may suffer from both increased risks of horizontal transmission of parasites and multiple infections when compared to solitary-living behaviour (Alexander 1974). Intraspecific studies have indeed demonstrated a positive correlation between the degree of sociality and the intensity of parasitism (e.g. Davies & Dye 1991; Côté & Poulin 1995). Higher levels of parasitic transmission promote the evolution of virulence, in turn giving rise to selection for increased disease resistance in the host species (Bull 1994; Frank 1996; Møller *et al.* 2001). Host genes involved in immunity may therefore be conjectured to be under stronger selection in social species relative to solitary living ones.

MHC molecules present an antigenic peptide, bound to a domain known as the antigen recognition site (ARS), to circulating T lymphocytes, eliciting an immune response if the antigen is recognizd as non-self (Roitt *et al.* 1996). Two distinct classes occur: class I molecules present endogenously derived antigen to cytotoxic T lymphocytes, whereas class II molecules present exogenously derived antigen to helper T lymphocytes (Roitt *et al.* 1996). MHC polymorphism is largely concentrated at codons encoding residues forming 'pocket regions' of the ARS, which bind to the side chains of antigenic peptide (Bjorkman *et al.* 1987; Fremont *et al.* 1992; Brown *et al.* 1993). These regions provide different MHC molecules, encoded by different alleles, with their specific binding properties. Studies of these sites in a number of MHC genes from a variety of species indicate that variability is maintained by pathogen-driven positive selection (e.g. Hughes & Nei 1988, 1989; Potts & Slev 1995; Paterson 1998; Binz *et al.* 2001). Positive selection is said to occur when the ratio of the non-synonymous to synonymous substitution rates exceeds unity (Nei & Gojobori 1986). By contrast, purifying selection, which has been shown to act on codons encoding residues outside the pocket regions (for example see the aforementioned studies), is characterized by a ratio of less than unity.

We attempt to answer two questions: (i) Is the pattern of selection at the African mole-rat MHC consistent with that observed in previous studies of these genes in other species? (ii) Does the pattern of selection at the MHC of different African mole-rats offer any insight into the effects of social behaviour with specific reference to host–parasite dynamics? We examine patterns of selection at exons 2 and 3 of the MHC class II *DQα1* gene, in humans known to respectively encode part of the ARS (both pocket and non-pocket residues) and a conserved transmembrane region known as the IG-like domain, in four species of African mole-rat with distinct life histories. The solitary living silvery mole-rat, *Heliophobius argenteocinereus*, inhabits comparatively mesic habitats with subterranean food resources that are evenly distributed (Jarvis *et al.* 1994; Bennett & Faulkes 2000). The common mole-rat, *Cryptomys hottentotus hottentotus*, occurs in both mesic and xeric environments (Skinner & Smithers 1991; Faulkes *et al.* 1997). Colonies comprise cooperatively breeding

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mole-rats that may number up to 14, with reproduction monopolized by a single breeding pair (Bennett 1989; Bennett & Faulkes 2000). Colonies of the Damaraland and naked mole-rat (*Cryptomys damarensis* and *Heterocephalus glaber*, respectively), also exhibit a reproductive division of labour together with cooperative care of the young and overlapping generations, and thus represent two eusocial, but evolutionarily divergent, species of African mole-rat (Michener 1969; Wilson 1971: Jarvis 1981; Jarvis & Bennett 1993). With up to 41 and 295 Damaraland and naked mole-rats, respectively, reported in colonies, group sizes can be large (Bennett & Faulkes 2000). Both species occur in xeric habitats with a sporadic food distribution, particularly the naked mole-rat, resulting in comparatively higher constraints to dispersal than for the common and silvery mole-rats.

We predict that sites in exon 2 that encode pocket residues will be under the influence of positive selection, with all other sites affected by purifying selection. Moreover, we expect that the intensity of selection will be tempered by the extent of population substructure. Subdivision of a population into demes (social groups in this context) results in the random effects of genetic drift becoming more important than natural selection (Wright 1931). We predict that these effects will be most evident at exon 3, where sites are expected to be primarily governed by purifying selection. However, the intensity of positive selection, which we expect to occur at some sites in exon 2, may be influenced by the effects of parasite transmission, as well as population substructure.

2. MATERIAL AND METHODS

(a) *Sampling and DNA extraction*

Using standard techniques (e.g. Faulkes *et al.* 1997), DNA was extracted from the skin biopsies of the following samples: 10 common mole-rats (colonies '600' and '1000' in Steinkopf, South Africa (29°17′ S, 17°45′ E) and colonies 'Z/X6000', 'A2000', 'CS400', 'BX', 'P' and 'W8000' in Somerset West, South Africa (34°4′ S, 18°50′ E)); 14 Damaraland mole-rats ('Oddballs camp colony 1' and 'Royal island colony 1' in the Okavango region, Botswana (19°32′ S, 23°11′ E), colonies '30' and '31' in Hotazel, South Africa (27°17′ S, 23°0′ E), 'Colony 1' in Bulawayo, Zimbabwe (20°9′ S, 28°38′ E) and colony 'New 2000' in Dordabis, Namibia (22°58′ S, 17°41′ E)); 10 naked mole-rats (colonies '1' to '4' in Lerata, Kenya (0°37′ N, 37°39′ E), colonies 'K' and 'MAd 2' in Mtito Andei, Kenya (2°41′ S, 38°9′ E) and colony 'Ethiopia 1' in Diredawa, Ethiopia (9°35′ N, 41°49′ E)); and 12 silvery mole-rats (Athi plains, Kenya (1°43′ S, 37°0′ E), and Dakawa, (6°26′ S, 37°34′ E), Mbete (6°52′ S, 37°41′ E), Mlali (6°57′ S, 37°41′ E), and Morogoro (6°50′ S, 37°39′ E), all in Tanzania).

(b) *PCR and sequencing*

Primers D1 and D2 from Slade *et al.* (1993) were used to isolate exons 2 and 3 (and the intermediate intron) of the MHC class II *DQα1* gene (hereafter referred to as *BLA-DQα1*, where BLA stands for bathyergid leucocyte antigen). The 25 µl PCR volumes, containing 1 µl of template DNA, 2.5 µl of NH_4 (10×), 2 µl of dNTPs (2.5 mM), 0.3 µl of each primer (25 pmol μl^{-1}), 0.75 µl of $MgCl_2$ (50 mM) and 0.1 µl of *Taq* polymerase (5 u μl^{-1}), were run through the following conditions: 94 °C for 3 min followed by 30 cycles of 30 s at 94 °C, 45 s at 57 °C, and 45 s at 72 °C, and a final 10 min at 72 °C. Amplification using these primers yielded a product of *ca*. 850 bp. PCR products, having been purified using the Wizard PCR Preps DNA Purification System (Promega Corp., Madison), were cloned using the pGEM-T Easy Vector System (Promega Corp., Madison). Clones from 10 common, 13 Damaraland, 10 naked and 10 silvery mole-rat animals were sequenced using BigDye v2 terminator reactions from Applied Biosystems run on an ABI 3700.

(c) *Likelihood-ratio analysis*

Analyses of selection were performed using the program CodeML, which is contained in the PAML 3.11 program suite (Yang 2001), and is based on the likelihood-ratio method of Goldman & Yang (1994). The models implemented in this study, M0, M1, M2, M3, M7 and M8, which are based upon different statistical distributions of a parameter known as the ω ratio, were formally set out in Yang *et al.* (2000); note that the ω ratio represents the type and intensity of selection and is equivalent to the d_N/d_S selection parameter of Nei & Gojobori (1986) (Yang *et al.* 2000). The one-ratio model, M0, assumes a single ω ratio for all codon sites. The neutral model, M1, estimates the proportion, p_n, of sites falling into each of two classes: p_0, sites under purifying selection, i.e. $\omega_0 = 0$, and p_1, those that are selectively neutral, i.e. $\omega_1 = 1$. The selection model, M2, adds another site class to those contained in M1, ω_2. Both ω_2 and the proportion of sites that fall into this class, p_2, are estimated from the data, thus allowing for the possibility of positively selected sites (indicated if $\omega_2 > 1$). The discrete model, M3, estimates three site classes from the data: ω_0, ω_1 and ω_2, and their corresponding proportions, p_0, p_1 and p_2. The β model, M7, is based on the β distribution and allows the ω ratio to take values of between zero and unity. Finally, model M8 has an extra site class, a free ω-ratio, over M7. The likelihood-ratio test statistics for comparing nested models are calculated as follows: $2(L_b - L_a)$ is compared with a χ^2-distribution with $P_b - P_a$ degrees of freedom, where L_a and L_b are log-likelihood values and P_a and P_b are the number of parameters for each of the models being compared. Models M0, M1, M2 and M3 are nested as are M7 and M8. Non-rooted phylogenetic trees, used as part of the likelihood-ratio analysis, were drawn under a HKY85 model using maximum-likelihood analysis in PAUP 4.0 b10 (Swofford 2002).

3. RESULTS

In all, eight exon 2 and five exon 3 common mole-rat alleles, 13 exon 2 and five exon 3 Damaraland mole-rat alleles, nine exon 2 and four exon 3 naked mole-rat alleles and 10 exon 2 and six exon 3 silvery mole-rat alleles were identified (sequences have been submitted to GenBank, accession numbers AY395908–AY395960 and AY395962–AY395981). Table 1 shows the results of the likelihood-ratio analyses of exons 2 and 3 of the *BLA-DQα1* gene in each of the four species. Table 2 provides a summary of the test statistics. For exon 2 in all species except the naked mole-rat, likelihood values for those models that allow for the inclusion of positive selection, i.e. M2, M3 and M8, were found to fit the data significantly better than the other models (M0, M1 and M7). Although only one of these comparisons for the naked mole-rat is significant, models M2, M3 and M8 were still found to fit the data better. Based on model M3, which usually had the highest likelihood scores, all four mole-rat

Table 1. Results of likelihood-ratio tests of, respectively, (*a*) exon 2 and (*b*) exon 3 of the BLA-DQα1 gene in each of four species of African mole-rat.
(P is the number of parameters, L is the log-likelihood value, κ is the estimated transition/transversion rate ratio, ω is the selection parameter and p_n is the proportion of sites that fall into the ω_n site class. For models M7 and M8, p and q are the shape parameters of the β function.)

species	model	P	L	parameter estimates
(*a*)				
naked mole-rat	M0	17	−551.927	$\omega = 0.925$, $\kappa = 1.325$
	M1	17	−546.184	$p_0 = 0.480$, $p_1 = 0.520$, $\kappa = 1.126$
	M2	19	−543.568	$p_0 = 0.508$, $p_1 = 0.206$, $p_2 = 0.286$, $\omega_2 = 2.954$, $\kappa = 1.432$
	M3	21	−543.543	$p_0 = 0.095$, $p_1 = 0.552$, $p_2 = 0.353$, $\omega_0 = 0.117$, $\omega_1 = 0.117$, $\omega_2 = 2.746$, $\kappa = 1.428$
	M7	18	−546.431	$p = 0.050$, $q = 0.050$, $\kappa = 1.115$
	M8	20	−543.543	$p_0 = 0.647$, $p_1 = 0.353$, $p = 13.293$, $q = 99.000$, $\omega = 2.747$, $\kappa = 1.428$
Damaraland mole-rat	M0	21	−612.123	$\omega = 1.122$, $\kappa = 1.603$
	M1	21	−608.753	$p_0 = 0.347$, $p_1 = 0.653$, $\kappa = 1.372$
	M2	23	−600.888	$p_0 = 0.170$, $p_1 = 0.732$, $p_2 = 0.097$, $\omega_2 = 7.980$, $\kappa = 1.647$
	M3	25	−600.460	$p_0 = 0.663$, $p_1 = 0.213$, $p_2 = 0.125$, $\omega_0 = 0.602$, $\omega_1 = 0.602$, $\omega_2 = 6.289$, $\kappa = 1.577$
	M7	22	−608.803	$p = 0.121$, $q = 0.076$, $\kappa = 1.350$
	M8	24	−600.462	$p_0 = 0.875$, $p_1 = 0.125$, $p = 99.000$, $q = 64.821$, $\omega = 6.307$, $\kappa = 1.578$
common mole-rat	M0	13	−491.728	$\omega = 1.502$, $\kappa = 2.045$
	M1	13	−468.102	$p_0 = 0.791$, $p_1 = 0.210$, $\kappa = 0.987$
	M2	15	−441.456	$p_0 = 0.832$, $p_1 = 0$, $p_2 = 0.168$, $\omega_2 = 20.872$, $\kappa = 1.071$
	M3	17	−441.456	$p_0 = 0.797$, $p_1 = 0.035$, $p_2 = 0.168$, $\omega_0 = 0$, $\omega_1 = 0$, $\omega_2 = 20.872$, $\kappa = 1.510$
	M7	14	−469.773	$p = 0.05$, $q = 0.144$, $\kappa = 1.611$
	M8	16	−441.460	$p_0 = 0.832$, $p_1 = 0.168$, $p = 0.05$, $q = 99.000$, $\omega = 20.894$
silvery mole-rat	M0	20	−381.670	$\omega = 0.674$
	M1	20	−377.970	$p_0 = 0.695$, $p_1 = 0.305$, $\kappa = 0.832$
	M2	22	−373.244	$p_0 = 0.574$, $p_1 = 0.389$, $p_2 = 0.37$, $\omega_2 = 17.250$, $\kappa = 1.232$
	M3	24	−372.910	$p_0 = 0.186$, $p_1 = 0.776$, $p_2 = 0.038$, $\omega_0 = 0.317$, $\omega_1 = 0.317$, $\omega_2 = 15.289$, $\kappa = 1.172$
	M7	21	−378.006	$p = 0.050$, $q = 0.137$
	M8	23	−372.912	$p_0 = 0.962$, $p_1 = 0.038$, $p = 46.034$, $q = 99.000$, $\omega = 15.306$, $\kappa = 1.173$
(*b*)				
naked mole-rat	M0	8	−434.818	$\omega = 0.859$, $\kappa = 1.718$
	M1	8	−434.700	$p_0 = 0.247$, $p_1 = 0.753$, $\kappa = 1.687$
	M2	10	−433.367	$p_0 = 0$, $p_1 = 0.982$, $p_2 = 0.018$, $\omega_2 = 71.451$, $\kappa = 1.243$
	M3	12	−433.366	$p_0 = 0.017$, $p_1 = 0.965$, $p_2 = 0.018$, $\omega_0 = 0.960$, $\omega_1 = 0.960$, $\omega_2 = 68.931$, $\kappa = 1.239$
	M7	9	−434.717	$p = 0.144$, $q = 0.05$, $\kappa = 1.667$
	M8	11	−433.366	$p_0 = 0.982$, $p_1 = 0.018$, $p = 99.000$, 4.123, $\omega = 68.981$, $\kappa = 1.239$
Damaraland mole-rat	M0	9	−454.319	$\omega = 0.464$, $\kappa = 2.963$
	M1	9	−454.250	$p_0 = 0.494$, $p_1 = 0.506$, $\kappa = 3.032$
	M2	11	−454.210	$p_0 = 0.375$, $p_1 = 0$, $p_2 = 0.625$, $\omega_2 = 0.752$, $\kappa = 2.980$
	M3	13	−454.210	$p_0 = 0.375$, $p_1 = 0.312$, $p_2 = 0.313$, $\omega_0 = 0.0001$, $\omega_1 = 0.752$, $\omega_2 = 0.752$, $\kappa = 2.980$
	M7	10	−454.214	$p = 0.358$, $q = 0.401$, $\kappa = 2.982$
	M8	12	−454.210	$p_0 = 0.376$, $p_1 = 0.624$, $p = 0.050$, $q = 99.000$, $\omega = 0.752$, $\kappa = 2.980$

(*Continued.*)

Table 1. (*Continued.*)

species	model	*P*	*L*	parameter estimates
common mole-rat	M0	9	−450.893	$\omega = 0.580$, $\kappa = 4.742$
	M1	9	−451.300	$p_0 = 0.226$, $p_1 = 0.774$, $\kappa = 5.041$
	M2	11	−450.893	$p_0 = 0$, $p_1 = 0$, $p_2 = 1$, $\omega_2 = 0.580$, $\kappa = 4.742$
	M3	13	−450.893	$p_0 = 0.333$, $p_1 = 0.333$, $p_2 = 0.333$, $\omega_0 = 0.580$, $\omega_1 = 0.580$, $\omega_2 = 0.580$, $\kappa = 4.742$
	M7	10	−450.896	$p = 99.000$, $q = 71.526$, $\kappa = 4.743$
	M8	12	−450.893	$p_0 = 0$, $p_1 = 1$, $p = 0.404$, $q = 2.587$, $\omega = 0.580$, $\kappa = 4.742$
silvery mole-rat	M0	12	−412.505	$\omega = 0.214$, $\kappa = 2.142$
	M1	12	−407.870	$p_0 = 0.908$, $p_1 = 0.092$, $\kappa = 1.799$
	M2	14	−400.730	$p_0 = 0.915$, $p_1 = 0.074$, $p_2 = 0.012$, $\omega_2 = 56.384$, $\kappa = 2.489$
	M3	16	−400.623	$p_0 = 0$, $p_1 = 0.988$, $p_2 = 0.012$, $\omega_0 = 0.00001$, $\omega_1 = 0.066$, $\omega_2 = 54.876$, $\kappa = 2.463$
	M7	13	−408.431	$p = 0.050$, $q = 0.352$, $\kappa = 1.896$
	M8	15	−400.624	$p_0 = 0.988$, $p_1 = 0.012$, $p = 7.030$, $q = 99.000$, $\omega = 54.888$, $\kappa = 2.463$

species possess at least some sites under positive selection. The p_n values indicate that the proportion of sites under positive selection never exceeded 35%. The intensity of this selection, represented in this case by ω_2, is weakest in the naked mole-rat (2.746), followed by the Damaraland (6.289), silvery (15.289), and lastly the common mole-rat (20.782).

By contrast, for exon 3, models M2, M3 and M8 either failed to detect any positive selection and/or did not have significantly higher likelihood scores than models M0, M1 and M7 for any of the species. Additionally, the p_n values indicate that purifying selection influences a high proportion of sites. Based on the results from model M3, allowing comparison with the exon 2 analysis, purifying selection is weakest in the naked mole-rat (ω_0 and ω_1 are 0.96 and represent 98.2% of sites in exon 3), followed by the Damaraland (ω_1 and ω_2 are 0.752, representing 62.5% of sites), common (ω_0, ω_1 and ω_2 are 0.58, representing 100% of sites), and finally the silvery mole-rat in which it is the strongest (ω_1 is 0.066, representing 98.8% of sites).

4. DISCUSSION

The results demonstrate that the pattern of selection at exon 2 of the *BLA-DQα1* gene appears to be quite different from that affecting exon 3 and is consistent with that of MHC class II genes. Purifying selection, influencing between 98.2% and 100% of sites (see model M3, table 1*b*), appears to be the pre-eminent factor in the evolution of codons in exon 3. This corresponds with that expected for this region, given that it encodes residues forming the conserved IG-like domain of the MHC glycoprotein. By contrast, a proportion of codons in exon 2 do consistently appear to be under the influence of positive selection and are likely to encode residues forming the highly variable pocket regions of the ARS.

As predicted, the rank order in the strength of purifying selection at sites in exon 3 corresponds with the apparent extent of population substructure, i.e. strongest in the comparatively panmictic silvery mole-rat and becoming progressively weaker in the common, Damaraland and finally naked mole-rat. Though the extent of population substructure (arising from alternative social strategies and habitat types), with its effects on drift and selection, may also directly affect exon 2, the presence of positive selection may indicate the additional influence of parasitic transmission and virulence. Consistent with a study by Hambuch & Lacey (2002), in which positive selection at an MHC class II locus was shown to be stronger in a species of social tuco-tuco than a solitary living one, positive selection at the MHC of the social common mole-rat is stronger than that of the solitary living silvery mole-rat. However, by stark contrast in the Damaraland and naked mole-rat, two species exhibiting eusociality, the most extreme form of social behaviour, positive selection is much weaker than in the silvery mole-rat. We therefore suggest that purely equating increasing parasite transmission/virulence and host immunity to increasing host sociality is something of an oversimplification and that the effects of social strategy on host–parasite dynamics are dependent upon a balance between two factors: the risks of intra- and intercolonial parasite transmission. For the social common mole-rat opportunities for dispersal are

Table 2. Summary of test statistics for the likelihood-ratio analyses of exon 2 and 3 of the *BLA-DQα1* gene. (n.s., not significant.)

species	region	models compared	test statistic	degrees of freedom	significance
common mole-rat	exon 2	M2 versus M1	53.292	2	0.1%
		M3 versus M0	100.544	4	0.1%
		M1	53.292	4	0.1%
		M2	0	2	n.s.
		M8 versus M7	56.626	2	0.1%
	exon 3	M2 versus M1	0.814	2	n.s.
		M3 versus M0	0	4	n.s.
		M1	0.814	4	n.s.
		M2	0	2	n.s.
		M8 versus M7	0.006	2	n.s.
Damaraland mole-rat	exon 2	M2 versus M1	15.730	2	0.1%
		M3 versus M0	23.326	4	0.1%
		M1	16.586	4	1%
		M2	0.856	2	n.s.
		M8 versus M7	16.682	2	0.1%
	exon 3	M2 versus M1	0.080	2	n.s.
		M3 versus M0	0.218	4	n.s.
		M1	0.080	4	n.s.
		M2	0	2	n.s.
		M8 versus M7	0.008	2	n.s.
naked mole-rat	exon 2	M2 versus M1	5.232	2	n.s.
		M3 versus M0	16.768	4	1%
		M1	5.282	4	n.s.
		M2	0.050	2	n.s.
		M8 versus M7	5.776	2	n.s.
	exon 3	M2 versus M1	2.666	2	n.s.
		M3 versus M0	2.904	4	n.s.
		M1	2.668	4	n.s.
		M2	0.002	2	n.s.
		M8 versus M7	2.702	2	n.s.
silvery mole-rat	exon 2	M2 versus M1	9.452	2	1%
		M3 versus M0	17.520	4	1%
		M1	10.120	4	5%
		M2	0.668	2	n.s.
		M8 versus M7	10.188	2	1%
	exon 3	M2 versus M1	14.280	2	0.1%
		M3 versus M0	23.764	4	0.1%
		M1	14.345	4	1%
		M2	0.214	2	n.s.
		M8 versus M7	15.614	2	0.1%

relatively high (Spinks *et al.* 2000) and these two factors are likely to act in an additive fashion giving rise to a high net risk of parasite transmission, strong selection for parasite virulence and for host immunity (manifested as strong positive selection at the MHC). However, the habitat-induced constraints on dispersal in the two eusocial species are comparatively high, particularly so for the naked mole-rat (Faulkes *et al.* 1997). Consequently, the risk of intercolonial parasite transmission is likely to be low, offsetting the high risk of intracolonial transmission predicted to occur owing to the large group sizes, and giving rise to a low net risk of parasite transmission.

5. CONCLUDING REMARKS

Previous studies looking at host–parasite interactions with respect to host sociality have tended to focus on aspects of parasite transmission. However, we have shown that the evolution of the host's immune system can, in itself, yield valuable insight into the effects that alternative social strategies have on the coevolution of the host and its parasites. Though earlier studies identified gregarious behaviour as a factor in increasing parasite load and immune investment, this study, along with other recently published work (Wilson *et al.* 2003), shows that while this may be true in some cases, the effects of migration and habitat cannot be ignored, and that these may even act to reverse the apparently 'disadvantageous' effects of sociality.

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