Immune Defense and Host Sociality: A Comparative Study of Swallows and Martins

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ABSTRACT: Sociality is associated with increased risks of parasitism, predation, and social competition, which may interact because social stress can reduce immunity, and parasitized individuals are more likely to fall prey to a predator. A mechanism allowing evolution of sociality in spite of high costs of parasitism is increased investment in antiparasite defenses. Here we show that the impact of parasites on host reproductive success was positively associated with the degree of sociality in the bird family Hirundinidae. However, the cost of parasitism in highly colonial species was countered by high levels of T- and B-cell immune responses. Investment in immune function among colonial species was particularly strong in nestlings, and among social species, this investment was associated with a relatively prolonged period of development, thereby leading to extended exposure to parasites. Thus, highly social species such as certain species of swallows and martins may cope with strong natural selection arising from parasites by heavy investment in immune function at the cost of a long exposure to nest parasites.

Keywords: coevolution, coloniality, Hirundinidae, parasitism, swallows, virulence.

Parasites impose strong selection pressures on their hosts by reducing their reproductive success and increasing their mortality rate. Numerous observational and experimental studies have provided evidence of such effects (reviews in Lehmann 1993; Møller 1997). Freeland (1976, 1979) originally suggested that parasites may have played an important role in the evolution of host sociality by imposing strong selection pressures on their hosts. Subsequent intraspecific studies of the relationship between host sociality and degree of parasitism have often found positive relationships (e.g., Davies and Dye 1991; Davies et al. 1991; Poulin 1991; Wcislo 1996; Schmid-Hempel 1998; reviews in Møller et al. 1993; Côté and Poulin 1995), although that is not always the case (Poiani 1992; reviews in Møller et al. 1993; Côté and Poulin 1995). A meta-analysis by Côté and Poulin (1995) showed that the degree of parasitism increases with the degree of sociality in intraspecific studies. Thus, fitness costs of parasitism have been hypothesized to be particularly important in highly social hosts (Rothschild and Clay 1952; Alexander 1974; Møller et al. 1993; Møller and Erritzøe 1996; Møller 1997), although the mechanisms involved remain unresolved: Highly social hosts may either suffer from the presence of more virulent parasites or simply from the attack of larger numbers of parasites.

The evolution of virulence has been the subject of intense theoretical investigation in recent decades. The relative rate of horizontal parasite transmission (Anderson and May 1982; Ewald 1983) and the frequency of multiple infections of hosts (Bremerman and Pickering 1983; Bull 1994; Frank 1996) have been hypothesized to select for increased virulence. Interestingly, host sociality promotes both these factors that are supposed to increase parasite virulence. A high degree of sociality will increase the rate of horizontal transmission of parasites due to frequent contacts among host individuals. Similarly, frequent contacts among hosts will increase the frequency of multiple infections with different genetic strains of parasites. Highly social hosts may have evolved a number of mechanisms to cope with increased parasite virulence. For example, Sherman et al. (1988) hypothesized that social insects may have adjusted their degree of polyandry to parasite selection pressures as a means of increasing parasite resistance. Alternatively, highly social hosts may invest more in immune function than solitary

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hosts. In accordance with this latter suggestion, Møller and Erritzøe (1996) found that highly social species of birds consistently had larger immune defense organs than solitary species when comparing pairs of closely related species that differed in their degree of sociality. Here it is useful to distinguish between proximate and ultimate explanations of host-parasite interactions. At the proximate level, we should expect that better defended host individuals suffered less from the negative effects of parasites than poorly defended hosts. In accordance with this prediction, several recent field studies of birds have demonstrated that surviving individuals have stronger immune responses than nonsurvivors (Saino et al. 1997*a*, 1997*b*; Christe et al. 1998, 2001; González et al. 1999; Hörak et al. 1999; Soler et al. 1999). At the ultimate level, a stronger impact of parasites on hosts should select for a greater investment in antiparasite defense. Thus, we should expect a positive correlation between fitness cost of parasitism and investment in antiparasite defense among species. Moreover, an increased investment in defense at the proximate and the ultimate levels should give rise to a trade-off with life-history traits (such as growth, survival and reproduction). Thus, we predict a cost for increased investment in defense in highly social species (Merino et al. 1998, 2000).

If the evolutionary scenario of costs of parasitism selecting for greater investment in immune function is important, we predict a positive association between strength of immune response and host sociality. To test this prediction, we used a comparative analysis based on host-parasite interactions in the bird family of swallows and martins, Hirundinidae. This family of 86 species has a wide range of nest aggregations ranging from completely solitary to highly colonial species with breeding aggregations of several thousand pairs (Turner and Rose 1989). Increased numbers of breeding pairs in a locale are associated with increased synchrony of behavior and reproduction, reduced interneighbor distance, increased frequency of social foraging and social antipredator behavior, and a number of other phenotypic changes in social behavior (Turner and Rose 1989; Brown and Brown 1996). Hence, sociality in this bird family is not only a question of differences in the numbers of nests in a particular site but also a reflection of clear differences in social behavior. Here we report on the relationship between these variables (cost of parasitism, host immune defense, and the cost of host immune defense) and sociality based on extensive field studies of 13 species from three different continents.

Material and Methods

Literature Data

We performed an extensive literature search of studies in which reproductive success had been compared between parasitized and unparasitized nests in order to obtain information on parasite effects on host reproductive success. These studies compared samples of nests sprayed with a pesticide to samples of nests receiving a control treatment, with the exception of a study on the tree swallow *Tachycineta bicolor*, which compared the reproductive success rates of parasitized and naturally parasite-free nests (Rogers et al. 1991). These parasite treatments eliminated not only ectoparasites like fleas, lice, mites, and hippoboscid flies but also the effect of these parasites as vectors and producers of skin wounds that may become infected with virus and bacteria. Parasite impact on host reproductive success was expressed as the percentage reduction in seasonal production of fledglings in control nests relative to pesticide treated nests. If estimates were available for more than a single sample, overall estimates were weighted by sample size. Exactly the same populations for which we had obtained information on immune response were used for these calculations. In highly colonial hosts, it is known that ectoparasites subsequently immigrate to sprayed nests because of the close proximity of neighboring nests, while that is rarely the case in solitary species (A. P. Møller, unpublished data; C. R. Brown and M. B. Brown, unpublished data). Thus, the negative effects of parasites on host reproductive success reported here are likely to be minimum estimates.

The degree of sociality was estimated as the largest colony size reported in the literature, since a very large proportion of adults of a given species will breed in large as compared to small colonies (see Jarman 1982). Hence, large colonies represent the social context to which most individuals are exposed and thus the most common selective environment. The correlation coefficient between $\log_{10}$-transformed mean and maximum colony size was $r = 0.98$, $N = 13$ species, $P < .0001$. However, we present the results for both mean and maximum colony size, although the conclusions are qualitatively similar.

Experimental Protocol

We studied 13 different species of swallows and martins from 1996–1998 and tested both nestlings and adults for immune responses. If they had evolved strong immune responses, hosts could defend themselves against more intense selection by parasites. Standard components of immunocompetence include T-lymphocyte response to challenge with phytohaemagglutinin (PHA) and B- and T-lymphocyte response to challenge with sheep red blood cells (SRBC; National Research Council 1992), and intraspecific studies have shown that stronger responses are associated with increased survival in birds (Saino et al. 1997*a*, 1997*b*; Christe et al. 1998, 2001; González et al. 1999; Hörak et al. 1999; Soler et al. 1999; Merino et al.

2000). The PHA response is associated with an increase in heterophils involved in binding microorganisms: heterophils internalize the microorganisms and subsequently kill them by producing reactive oxygen and nitrogen intermediates and catabolic enzymes (McCorkle et al. 1980; Lochmiller et al. 1993; Roitt et al. 1996). The SRBC response is a measure of immune function relevant for responses toward a range of endoparasites (Roitt et al. 1996). We estimated the response to these two different antigens in both nestlings and adults when possible. Response to PHA was used to obtain an in vivo response of T-cells because PHA stimulates T-lymphocyte proliferation. We assessed T-lymphocyte immune responsiveness using injection with PHA, which is a standard method to assess cell-mediated immunity in poultry (Cheng and Lamont 1988). The thickness of the left and right wing webs (patagium) of nestlings and adults at premarked sites was measured with a pressure-sensitive caliper, a so-called spessimeter (Alpa S.p.A., Milano, cod. SM112), to the nearest 0.01 mm. To avoid damaging the skin of the birds, we removed the spring from the pressure-sensitive caliper and replaced it with a 16-g weight that we placed on top of the instrument. Nestlings may respond to injections with antigens depending on their developmental stage, and this was standardized in the field by testing nestlings of different species that had reached an age of two-thirds of their average nestling period. This was done to control for differences in developmental rate among species. Extensive studies of barn swallow *Hirundo rustica* and the house martin *Delichon urbica* nestlings do not provide any evidence to suggest that PHA response depends on absolute age in the range 10–16 d (A. P. Møller, unpublished data). The right wing web was injected with 0.2 mg of PHA (Sigma, L-8754) in 0.04 mL of phosphate buffered saline (PBS). The left wing web was only injected with 0.04 mL PBS. Twenty-four hours later, we remeasured the thickness of wing webs at the injection sites. The measure of immune response is the difference in wing web thickness between day 2 and day 1 for the PHA-inoculated wing minus the difference in wing web thickness, hereafter "wing web swelling," between day 2 and day 1 for the PBS-inoculated wing (see Saino et al. 1997*b* for details of the methods used here). Measurements of skin thickness and the difference in skin thickness during repeat measurements of the same individual are highly repeatable with values exceeding 0.98. Thus, the measurements are reliable.

Response to immunization with SRBC was used as an in vivo measure of B- and T-cell activity (Roitt et al. 1996). Both nestlings and adults were injected, but nestlings generally responded weakly or not at all. The data are only for adults. Humoral immunity was assessed from antibody response to a single injection with heterologous erythrocytes. Birds were injected intraperitoneally with 0.1 mL of a 5% solution of SRBC after the first blood samples had been taken. A second blood sample was obtained after 7 d, the capillaries were centrifuged, and the plasma was separated from the red blood cells. Hemagglutinating antibody titers were estimated by the microhemagglutination assay (Wegman and Smithies 1966); all tests were performed by the same technician. This method consists of serial twofold dilutions of heat-inactivated serum (56°C for 30 min) in PBS mixed with an equal volume of a 1% SRBC solution (in PBS) and incubated at 40°C for 1 h. These estimates are highly repeatable with values exceeding 0.98 for multiple tests of the same individual. Titers are expressed as the $\log_2$ of the reciprocal of the highest dilution of serum showing positive hemagglutination. None of the preinjection plasma samples showed a positive response in the hemagglutination test.

The duration of the nestling period of different species was obtained from the literature. The entire data set can be found in the appendix.

Comparative Methods

Since data for species cannot be considered to be statistically independent observations because of similarity due to common ancestry, we tested the predictions using statistically independent linear contrasts (Purvis and Rambaut 1995). This comparative method calculates standardized differences in variables of interest at the tips and the nodes of a phylogeny (Felsenstein 1985). Contrasts were calculated using the software package CAIC (Purvis and Rambaut 1995). We assumed that branch lengths were proportional to the number of species in a clade; thus, we assumed a gradual mode of evolution (Purvis and Rambaut 1995). However, the results were very similar when branch lengths were set to the same value, assuming a punctuated mode of evolution (Purvis and Rambaut 1995). Since all variables were continuous, we used the "Crunch" procedure in Purvis and Rambaut's (1995) software package to calculate the contrasts.

For the comparative analyses, we used a phylogeny of the family Hirundinidae based on DNA-DNA hybridization (Sheldon and Winkler 1993; D. Winkler, personal communication). This phylogeny is robust since Sibley and Ahlquist (1990), who also used DNA-DNA hybridization, found a similar topology for some of the species included here. Furthermore, A. P. Møller (unpublished data) found a similar topology of a phylogeny based on morphological characters and nest structure. Thus, the phylogeny can be considered to be robust. The phylogeny can be found in figure 1. Even when using a standard taxonomy of the family Hirundinidae (Turner and Rose 1989) for the comparative analyses, we still reached qualitatively similar conclusions (results not shown).

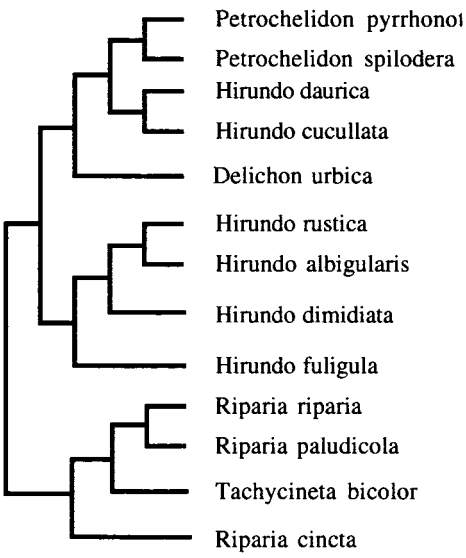

Figure 1: A phylogenetic hypothesis of the 13 species of the family Hirundinidae considered in this study (based on Sheldon and Winkler 1993; D. Winkler, personal communication; and A. P. Møller, unpublished data [phylogeny based on morphological and nest characters]). The phylogeny only illustrates the branching pattern, while the length of branches is arbitrary.

All variables were $\log_{10}$ transformed to achieve normal distributions before calculations, except for parasite-induced mortality, which was square root–arcsine transformed. The relationship between two variables was estimated using linear regression through the origin (Purvis and Rambaut 1995). Since the PHA immune response and duration of the nestling period increases with body size, we controlled for any effect of allometry by calculating residuals from a regression of the dependent variable on body mass, and these residuals were subsequently used for the analyses.

Results

We investigated whether the reduction in reproductive success of hosts caused by ectoparasites increased with degree of host sociality. This was the case since parasite impact on host reproduction increased significantly with colony size (fig. 2). The relationship based on standardized linear contrasts was significantly positive (linear regression for maximum colony size: $F = 93.51$, df $= 1, 4$, $r^2 = 0.96$, $P = .0006$, 0.165 ± 0.017 [slope $\pm$ SE]; mean colony size: $F = 195.62$, df $= 1, 4$, $r^2 = 0.98$, $P = .0002$, 0.238 ± 0.017). Hence, parasites had greater impact on the reproductive success of hosts as colony size increased across hirundine species.

Mean wing web swelling of nestlings increased with the level of parasite-induced mortality across species (linear regression based on standardized contrasts: $F = 9.97$, df $= 1, 4$, $r^2 = 0.71$, $P = .034$, 0.594 ± 0.188). Similarly, wing web swelling of both nestlings and adults increased with colony size (fig. 3). The relationship based on standardized linear contrasts was significantly positive (linear regression for adults: maximum colony size: $F = 8.33$, df $= 1, 10$, $r^2 = 0.45$, $P = .016$, 0.079 ± 0.028; mean colony size: $F = 5.35$, df $= 1, 10$, $r^2 = 0.35$, $P = .043$, 0.109 ± 0.047; nestlings: maximum colony size: $F = 13.98$, df $= 1, 11$, $r^2 = 0.56$, $P = .0033$, 0.118 ± 0.032; mean colony size: $F = 9.42$, df $= 1, 11$, $r^2 = 0.46$, $P = .011$, 0.167 ± 0.054; we corrected PHA responses for any effects of allometry by using body mass as a covariate in the analyses).

There was also a positive relationship between SRBC response of adults and colony size (linear regression based on standardized contrasts: maximum colony size: $F = 23.07$, df $= 1, 4$, $r^2 = 0.85$, $P = .0086$, 0.348 ± 0.073; mean colony size: $F = 30.05$, df $= 1, 4$, $r^2 = 0.88$, $P = .0054$, 0.488 ± 0.089). The correlation between SRBC and

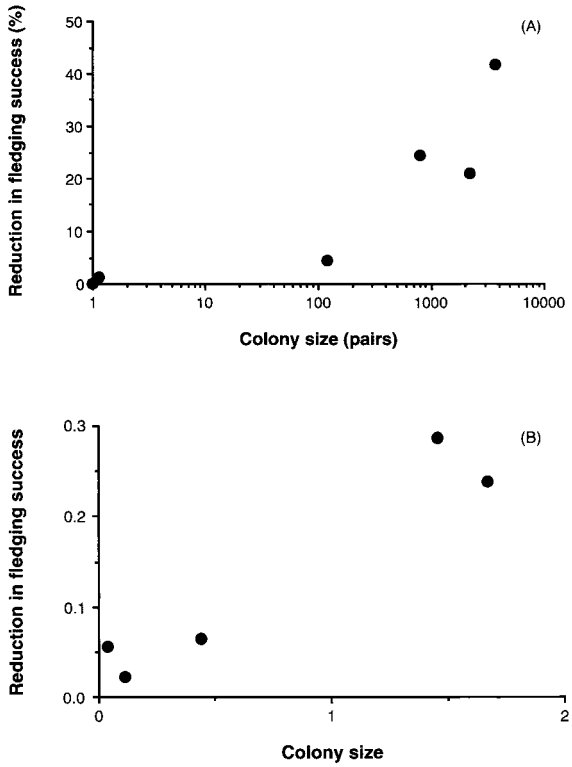

Figure 2: Parasite-induced reduction in host reproductive success in relation to colony size for different species of swallows and martins. The reduction in reproductive success was estimated as the percentage difference in mean number of fledglings between nests treated with a pesticide and control nests. *A*, Species. *B*, Contrasts.

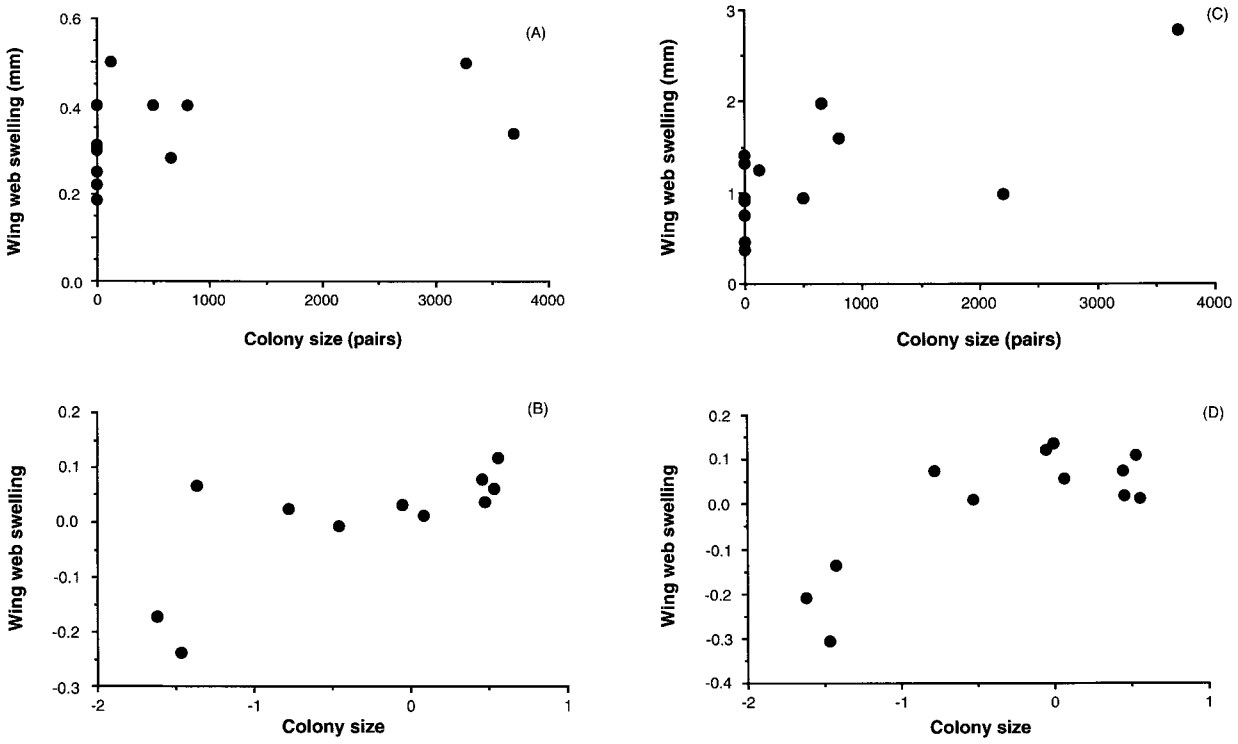

Figure 3: Wing web swelling (mm; response to a challenge with phytohemagglutinin) of different species of swallows and martins in relation to colony size for adults (*A*, species; *B*, contrasts) and nestlings (*C*, species; *D*, contrasts).

PHA response of adults was positive and significant (linear regression based on standardized contrasts: $F = 206.65$, $df = 1, 4$, $r^2 = 0.98$, $P < .0001$, 3.694 ± 0.257). Thus, when host species were colonial, they produced more T- and B-cell responses than when they were solitary.

There was a strongly positive association between nestling and adult immune response across taxa (linear regression based on standardized contrasts: $F = 21.75$, $df = 1, 10$, $r^2 = 0.69$, $P = .0009$, 1.039 ± 0.233). The slope of this relationship did not deviate from isometry ($t = 0.16$, $df = 9$, NS). Nestlings, thus, had a PHA response proportional to that of adults. However, nestling responses were almost three times as large as adult responses (paired *t*-test, $t = 8.63$, $df = 11$, $P < .001$; nestlings: 1.23 ± 0.19 mm; adults: 0.34 ± 0.03 mm).

Swallow and martin species with a strong nestling T-cell immune response had a significantly longer relative nestling period than species with a weak response (fig. 4). The relationship based on standardized linear contrasts was significantly positive (linear regression: $F = 5.86$, $df = 1, 11$, $r^2 = 0.31$, $P = .049$, 0.101 ± 0.046; we corrected both the duration of the nestling period and the PHA response for any effects of allometry by using body mass as a covariate in the analyses). Thus, nestlings of species with strong immune responses tended to have a longer exposure to ectoparasites in the nest than nestlings of species with weak responses.

Discussion

Sociality has been hypothesized to be associated with increased risks of parasitism, predation, and social competition (Alexander 1974). Such effects may interact because social stress can reduce immunity (Apanius 1998) and because parasitized individuals are more likely to fall prey to predators (Temple 1986; Møller and Erritzøe 1996). Social hosts have frequently been hypothesized to suffer greater fitness costs from the negative impact of parasites than less social hosts (Rothschild and Clay 1952; Alexander 1974; Møller et al. 1993; Brown and Brown 1996; Møller and Erritzøe 1996; Møller 1997). We have shown here that at the interspecific level, which describes evolutionary, ultimate patterns, social hosts do indeed suffer more from the negative effects of parasitism than less social hosts (fig. 2). There are at least two explanations for this pattern: the first, parasites of social hosts are more virulent than parasites of solitary hosts; and the second, parasites of social hosts are more abundant

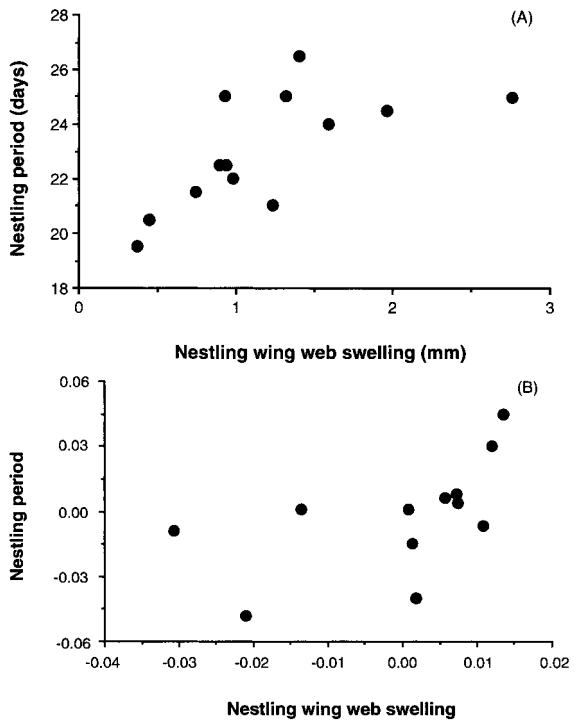

Figure 4: Duration of the nestling period (d) in relation to wing web swelling (mm; response to a challenge with phytohemagglutinin) in nestlings of different species of swallows and martins. *A*, Species. *B*, Contrasts.

than parasites of solitary hosts. These solutions are not mutually exclusive, and we cannot readily distinguish between them experimentally. However, ectoparasites are very common and reach thousands of individuals in the nests of both solitary and social host species of the swallow and martin family (e.g., Burtt et al. 1991; Rogers et el. 1991; Møller 1994; Brown and Brown 1996). Hence, it seems unlikely that the weak effect of parasites on host reproductive success in solitary host species is caused by a general absence of parasites.

Social hosts have been hypothesized to invest differentially in immune function because of the supposedly greater impact of parasites on their fitness than on the fitness of more solitary hosts (Møller and Erritzøe 1996) and was originally tested by determining whether colonial species of birds had larger immune defense organs than closely related solitary species. Indeed, the mass of both the bursa of Fabricius and the spleen was consistently larger in the more social host species (Møller and Erritzøe 1996). Since the bursa of Fabricius is the site of initial B-cell synthesis in nestling birds, the study by Møller and Erritzøe (1996) suggested that parasites selected for greater investment in immune function at a very early stage of development. This study supports this conclusion by showing that both T- and B-cell responses were consistently stronger in more social species of martins and swallows. Some species were tested at an older absolute age than others, which may account for the observed patterns, if the strength of immune responses increases with age of nestlings. However, we have not found a positive relationship between PHA response and age of nestlings in *Hirundo rustica* in the range 10–15 d (A. P. Møller, unpublished data) or in *Petrochelidon pyrrhonota* in the range 10–18 d (A. P. Møller and C. R. Brown, unpublished data). Thus, this alternative explanation can be rejected. We have shown repeatedly that PHA responses are no stronger in parasitized nests than in fumigated ones (see Christe et al. [1998, 2001] for *Oeciacus hirundinis* infesting *Delichon urbica*, Szép and Møller [1999] for *Ixodes lividus* infesting *Riparia riparia*, and A. P. Møller [unpublished data] for *Ornithonyssus bursa* infesting *H. rustica* and *Oeciacus vicarius* and *Ceratophyllus celsus* infesting *P. pyrrhonota*), which implies that differences in parasite exposure do not contribute in a significant way to differences in measures of PHA response. This also seems unlikely to be a general explanation at the interspecific level. Even the solitary species have prevalences and intensities of infestation with ectoparasites (e.g., Burtt et al. 1991) as high as those of the highly colonial species (e.g., Brown and Brown 1996). Thus, we can conclude that coloniality indeed seems to have selected for increased immunocompetence. Furthermore, the PHA response was significantly larger in nestlings than in adults breeding in the same nests, although exposure to ectoparasites should be similar in the two age classes. This difference suggests that nestlings do indeed invest more than adults in immune function in highly social host species because nestlings experience a particularly intense selection pressure from ectoparasites.

Investment in immune function has at the proximate level been shown to be efficient since survivors generally have stronger responses than nonsurvivors, even in several of the species investigated in this study (see Saino et al. [1997*a*, 1997*b*] and Merino et al. [2000] for *H. rustica*, Christe et al. [1998, 2001] for *D. urbica*, Soler et al. [1999] for *Oenanthe leucura*, González et al. [1999] for *Passer domesticus*, Hörak et al. [1999] for *Parus major*, and A. P. Møller [unpublished data] for *H. rustica*). While the direct effects of parasites may be involved in generating this selection differential, parasite-mediated predation may also play an important role (Temple 1986; Møller and Erritzøe 2000). At the ultimate, evolutionary level, stronger immune responses may be more efficient, although this effect may be masked by coevolutionary responses of parasites to selection pressures imposed by hosts. This interpretation is supported by a comparative analysis of parasite-mediated nestling mortality and PHA response across bird species, which shows a highly significant positive relationship

(Martin et al. 2001). Thus, while nestlings and adults of social hosts have stronger immune responses than individuals of solitary hosts, social hosts still suffer more in terms of fitness costs from the effects of parasites than solitary hosts (fig. 2).

Nestling birds are exposed to parasites in their nests, while adults may avoid some the deleterious effects of parasites by spending time away from their nests. If the cost of parasitism is greater in colonial species than in solitary ones, there should be selection for early fledging within species since nestlings thereby could evade their parasites. This proximate mechanism has actually been shown for the barn swallow *H. rustica* and the sand martin *R. riparia* (Møller 1990; Szép and Møller 1999). However, at the ultimate level, nestling birds may experience difficulties of evolving a short developmental period. For example, Ricklefs (1992) hypothesized that a trade-off exists between embryonic development and the ontogeny of an efficient immune system. Since nestling hirundines with a strong immune response have a relatively long developmental period, they may pay a developmental cost by being able to produce a strong immune response. This causes an increase in the duration of exposure to parasites relative to that experienced by nestlings of species that develop a weaker immune response. Highly social species may invest differentially in immune function to counter the detrimental impact of parasites; this, in turn, selects for increased virulence in parasites (van Baalen 1998), which, in turn, selects for even greater immune responses. If immune responses are costly in terms of duration of ontogeny, the offspring of highly social host species may end up being exposed to the detrimental effects of virulent parasites for a longer time than the offspring of solitary host species. This situation could be considered to be a coevolutionary tragedy of the commons caused by the coevolutionary interactions between hosts and parasites. At a proximate level, this relationship may be reflected in a trade-off between investment in immunity and growth as shown in intraspecific studies (Merino et al. 1998, 2000; Fair et al. 1999). However, this benefit is achieved at an ultimate, evolutionary cost in terms of relatively longer duration of development.

Could the results be caused by ecological factors that both affect colony size and host immune response? Coloniality has been hypothesized to evolve when food is unpredictably distributed in space and time and, hence, undefendable (Lack 1968; Brown and Brown 2001). Thus, we might expect that unpredictable, superabundant food exploited by colonial species also allows the production of strong immune responses. We suggest that this is an unlikely evolutionary scenario. In particular, highly colonial species often suffer from partial or complete reproductive failure (Turner and Rose 1989; Brown and Brown 1996), while that is rarely the case for less colonial or solitary species of swallows and martins (Turner and Rose 1989; Møller 1994). Since highly colonial species of swallows and martins suffer from greater costs of ectoparasitism (fig. 1), we suggest that a long coevolutionary history of interactions between hosts and parasites has given rise to the evolution of strong immune responses in colonial species.

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APPENDIX

Table A1: Summary information on maximum and mean colony size, duration of nestling period, body mass, parasite-induced nestling mortality, wing web swelling of nestlings and adults, and sheep red blood cell (SRBC) response of adults

Species	Maximum colony size (pairs)[a]	Mean colony size (pairs)[b]	Nestling period (d)[c]	Body mass (g)[d]	Parasite-induced mortality (%)[e]	Wing web swelling nestlings (mean [SE]; mm)[f]	*N*[g]	Wing web swelling adults (mean [SE]; mm)[h]	*N*	SRBC response adults (mean [SE])[i]	*N*
Delichon urbica	800	78	24.0	18.3	24.3	1.59 (.06)	43	.40 (.07)	28	…	…
Hirundo albigularis	1	1	20.5	21.3	…	.45 (.08)	5	.22 (.05)	7	.37 (.11)	4
Hirundo cucullata	1	1	26.5	27.1	…	1.41 (.13)	6	.40 (.06)	2	…	…
Hirundo daurica	1	1	22.5	19.1	.0	.94 (.05)	23	…		…	…
Hirundo dimidiata	1	1	21.5	11.0	…	.75 (.08)	4	.25 (.02)	3	.11 (.01)	2
Hirundo fuligula	3	2	25.0	22.4	…	1.32 (.09)	4	.30 (.08)	5	…	…
Hirundo rustica	120	8	21.0	18.9	4.4	1.24 (.03)	113	.50 (.07)	37	…	…
Petrochelidon pyrrhonota	3,700	394	25.0	21.6	41.6	2.78 (.07)	193	.34 (.09)	34	3.18 (.05)	22
Petrochelidon spilodera	650	70	24.5	20.6	…	1.97 (.06)	22	.28 (.03)	24	1.22 (.12)	8
Riparia cincta	1	1	22.5	21.5	…	.90 (.09)	3	.31 (.05)	12	…	…
Riparia paludicola	500	18	25.0	13.1	…	.93 (.06)	5	.40 (.08)	8	…	…
Riparia riparia	3,179	198	22.0	13.5	21.0	.99 (.06)	78	.51 (.09)	12	2.12 (.14)	10
Tachycineta bicolor	1	1	19.5	20.1	.0	.37 (.03)	74	.18 (.02)	41	.17 (.04)	36

[a] Maximum colony size for exactly the same study populations as those with information on parasitism and host immune responses was obtained from Glutz von Blotzheim (1985), Turner and Rose (1989), Keith et al. (1992), and Brown and Brown (1996).

[b] Mean colony size for exactly the same study populations as those with information on parasitism and host immune responses was from our own field observations with the exception of *P. pyrrhonota*, which was from Brown and Brown (1996), and *R. riparia*, which was from Szép (1999).

[c] Duration of the nestling period was from de Lope (1981), Turner and Rose (1989), Keith et al. (1992), Møller (1994), C. Brown, unpublished data, and A. P. Møller and S. Merino, unpublished data.

[d] Adult body mass was from Turner and Rose (1989) and Keith et al. (1992).

[e] Parasite impact for exactly the same study populations as those with information on host immune responses was calculated from data in Brown and Brown (1986), Møller (1990), Rogers et al. (1991), de Lope et al. (1993), Szép and Møller (1999), and S. Merino and A. P. Møller, unpublished data.

[f] Data recorded in this study.

[g] The number of colonies sampled for the colonial species were three for *D. urbica*, one for *H. fuligula*, three for *H. rustica*, six for *P. pyrrhonota*, three for *P. spilodera*, three for *R. paludicola*, and one for *R. riparia*.

[h] Data recorded in this study.

[i] Data recorded in this study.

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