

Losing the last feather: feather loss as an antipredator adaptation in birds

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Birds often lose feathers during predation attempts, and this ability has evolved as a means of escape. Because predators are more likely to grab feathers on the rump and the back than on the ventral side of an escaping bird, we predicted that the former feathers would have evolved to be relatively loosely attached as an antipredator strategy in species that frequently die from predation. We estimated the force required to remove feathers from the rump, back, and breast by pulling feathers with a spring balance from a range of European bird species in an attempt to investigate ecological factors associated with ease of feather loss during predation attempts. The force required to loosen a feather from the rump was less than that required to loosen a feather from back, which in turn was less than that required to loosen a feather from the breast. The relative force needed to loosen rump feathers compared with feathers from the back and the breast was smaller for prey species preferred by the most common predator of small passerine birds, the sparrowhawk *Accipiter nisus*. Likewise, the relative force was also smaller in species with a high frequency of complete tail loss among free-living birds, which we used as an index of the frequency of failed predation attempts. The relative force required to remove feathers from the rump was smaller in species with a high frequency of fear screams, another measure of the relative importance of predation as a cause of death. Feather loss required particularly little force among solitary breeding bird species that suffer the highest degree of predation. Antipredator defense in terms of force required to remove feathers from the rump was larger in species with a strong antiparasite defense in terms of T-cell-mediated immune response. These findings are consistent with the hypothesis that different defenses are antagonistic and that they are traded off against each other. *Key words:* alternative defense strategies, antagonistic defenses, immune defense, sociality. [*Behav Ecol*]

Predation is one of the most common causes of death in animals, and there is thus a high premium on efficient antipredator defenses that can reduce the risk of predation. Numerous antipredator defenses that include vigilance, warning calls, fear screams, camouflage, and warning coloration have all been shown to reduce the risk of predation for an individual (review in Curio 1976). Such successful antipredator behavior selects for the evolution of predators that can circumvent such defense mechanisms. Evolutionary analyses of predation and antipredator adaptations have revealed clear evidence of escalation in this arms race between predator and prey (Vermeij 1987).

A unique kind of antipredator defense is the shedding of parts of the body (autotomy) as a means of escape. Autotomy is common in mollusks, polychetes, arthropods, and lizards (Edmunds 1974; Vitt et al. 1977). Cooper et al. (2004) showed across lizards that differences in the ease of tail loss were positively correlated with the risk of predation. The tail is generally lost because that is the part of the body that is closest to the predator, and also because its loss does not entirely doom the survival of an individual. Similarly, fright molt of feathers from rump, back, and tail in birds may allow avian prey to escape a predator when already caught or about to be caught because the predator loses its grip (Dathe 1955; Mester and Pünthe 1959; Tautenhahn 1959; Berger 1960; Höglund 1964). Alternatively, fright molt can be used to confuse a predator in pursuit in the same way as the ink of an octopus may

confuse a predator (Lindström and Nilsson 1988). Although descriptions of such defenses have been published, there is very little information about intra- and interspecific variation in this behavior and whether it provides individuals with a selective advantage. Likewise, there has been no attempt to make stringent predictions about the nature of these antipredator defenses and thereby make more crucial tests of this presumed adaptation.

If the loss of feathers during a predation attempt was an adaptation to terminate an initiated predation event to the advantage of the prey, we could make 6 predictions. First, we would expect differences in the force needed to loosen a feather between feather tracts, with feathers being easier to remove on the rump than elsewhere on the body (the rump is the body part of a fleeing prey individual that is the closest to an attacking predator). Second, we would predict that species of birds that commonly fall prey to predators have relatively looser feathers on the rump than species that are less preferred prey. Third, we would expect a standardized measure of ease of feather loss to be significantly positively correlated with the frequency of predation attempts because frequent attack would have selected for greater ease of feather loss. More specifically, we would expect the ease of feather loss from the rump to correlate positively with the frequency of individuals in wild populations that have completely lost their tail (or any other measure of the ability to successfully escape an attack by a predator). Fourth, we would predict that the ease of feather loss should be positively correlated with the frequency of fear screams that we assume have evolved to attract other predators that may disrupt an ongoing predation event (Högstedt 1983). Fifth, if species that differ in ecology suffer from different degrees of predation, we would predict species with low predation rates to have less ease of feather loss than

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species with high rates of predation. For example, colonially breeding species of birds may suffer less from predation than solitary species because the presence of a large number of individuals in a single site allows early detection of an approaching predator (e.g., Møller 1987; Danchin and Wagner 1997). In addition, colonial breeding also results in a dilution effect due to the superabundance of prey relative to the number of predators (Burger et al. 1980; Danchin and Wagner 1997).

Sixth, antipredator or antiparasite defenses are generally considered to be costly to develop and maintain, an assumption for which there is experimental evidence (antiparasite defenses: e.g., Moret and Schmid-Hempel 2000; Møller et al. 2001; Bonneaud et al. 2003; antipredator defenses: Wilson 1992). Defenses are presumed to have evolved due to selection pressures from antagonists such as predators and parasites. Offense by such heterospecifics typically acts at a specific stage in the life cycle, reducing the intensity of later selection pressures for other kinds of defenses. Therefore, different hierarchical levels of host defense should be negatively related because the defense that acts the earliest should have priority due to its greater effect on fitness. Antiparasite defense should be relatively less important, but certainly not unimportant in species with high predation risk, because investment in antipredator defense would have greater positive impact on fitness than antiparasite defense. Conversely, in species with little risk of predation, antiparasite defenses should play a more important role than in species with a high risk of predation because any improvement in defense against parasites would differentially increase fitness compared with an increment in antipredator defense. Previous studies of host defense against parasites have either analyzed avoidance or evasion behavior (Fineblum and Rausher 1995; Mauricio et al. 1997; Sokolowski et al. 1997; Soler et al. 1999). Here we extend this approach by investigating the potential trade-off between antiparasite and antipredation defenses. We do this by analyzing the relationship between ease of feather loss from the rump, relative to loss from other feather tracts that are not predicted to be subject to the same selection pressure, and a component of the immune system that acts as an antiparasite defense, T-cell-mediated immune response. If there is a trade-off between antipredation and antiparasite defenses, we should expect a positive correlation between intensity of T-cell response and the force required to remove feathers from the tail.

In summary, we tested the hypothesis that relative ease of feather loss from the rump and back of birds has evolved as an antipredator defense. This was done by testing a number of critical assumptions and predictions derived from this hypothesis, using extensive field data on the ease of feather loss collected from 70 different species of birds during a period of 5 years.

METHODS

Data and general methods

One of us (A.P.M.) recorded all accidental loss of feathers from birds captured in mist nets for bird banding during the years 1990–2005. Feather loss was recorded as being from the rump, back, tail, or other parts of the body. Among individuals captured, all individuals that had lost part or all the tail previously were carefully checked for lost feathers from the rump and the back by inspecting these feather tracts for naked patches of skin with lacking feathers.

Force needed to remove feathers in relation to body position

The ease of feather loss was estimated by recording the force needed to remove feathers from a dead bird. Birds were de-

livered to J.E., and they were all freshly dead. Any bird that had been damaged after being hit by a car was discarded from the analysis, as were all individuals in molt in any part of the body. We recorded the force needed to remove a feather, using a spring balance for pulling the feather. The reading was made at the moment when the feather was pulled out. Feathers were selected in the following ways: rump feathers were selected from the second or third penultimate row just above the tail toward the middle of the rump. Back feathers were selected from the middle at the border between the back and the mantle. Breast feathers were selected from the middle as close to the sternum as possible. To record repeatability of the estimate of this force, we pulled out 2 feathers from a subsample of individuals and found a high degree of consistency estimated as the repeatability (Becker 1984) (rump: $F = 34.44$, $df = 81,82$, $P < 0.0001$, R (standard error [SE]) = 0.94 (0.01); back: $F = 24.96$, $df = 83,84$, $P < 0.0001$, R (SE) = 0.92 (0.01); breast: $F = 21.03$, $df = 80,81$, $P < 0.0001$, R (SE) = 0.94 (0.01)). The total sample consisted of 260 individuals of 70 different species. The force needed to remove feathers was \log_{10} transformed.

We estimated ease of feather loss from dead individuals of all bird species for ethical reasons. However, this procedure required validation for a sample of species on both live and dead individuals. We captured live birds in Spain and Ukraine and removed single feathers from the rump, back, and breast, using the procedure described above. A single person held the bird with one hand while pulling the spring balance gently with the other hand until the feather was pulled out. In no case did the bird show any evidence of distress such as producing an alarm call or fear scream. The relative ease of feather loss after adjusting for body mass was positively correlated between live and dead birds for all 3 feather tracts for a sample of 27 live individuals of 15 species (Table 1). In addition, the relative ease of feather loss from the rump, after adjusting for ease of feather loss from the back and the breast, was also strongly positively correlated between live and dead birds (Table 1). These findings justify the use of data from dead birds in the subsequent analyses.

Ethical note

We captured live birds in Spain and Ukraine to test whether ease of feather removal from live and dead individuals of the same species were positively correlated. We inquired about

Table 1

Linear regressions between residual force needed to remove a feather from the rump, back, and breast of a live bird, after adjusting for effects of body mass, and residual force needed to remove a feather from the rump, back, and breast of a dead bird of the same species, after adjusting for effects of body mass

Variable	<i>F</i>	<i>df</i>	<i>r</i> ²	<i>P</i>	Slope (SE)
Residual rump	8.58	1,13	0.40	0.012	0.504 (0.172)
Residual back	5.66	1,13	0.30	0.033	0.515 (0.216)
Residual breast	6.50	1,13	0.33	0.024	0.578 (0.227)
Residual rump over back and breast	9.78	1,13	0.43	0.008	0.803 (0.257)

The final analysis of residual rump over back and breast investigates the relationship between residual force needed to remove a feather from the rump of a live bird, after adjusting for the force needed to remove a feather from the back and the rump, and residual force needed to remove a feather from the rump of a dead bird, after adjusting for the force needed to remove a feather from the back and the rump. The analyses were based on 15 species. See Methods for further details.

official permission to measure the strength required to remove feathers but were told that no permission was required. We deliberately reduced the sample size to the minimum possible to reduce the level of any suffering while still maintaining a high probability of making a rigorous test of whether the ease of removing feathers from live and dead birds were positively correlated.

Predation risk and feather looseness

We estimated the risk of predation by sparrowhawks based on a total of 31 745 prey items of 64 species of birds, whereas 3178 other prey items were excluded because they were mammals, cage birds, or migrants. These data derived from a study by Nielsen (2004) of European sparrowhawks lasting for 21 years in an area of 2417 km² in Northern Denmark. Prey remains of the European sparrowhawk were systematically collected near 1709 nests during April–September 1977–1997 (Nielsen 2004; Møller and Nielsen 2006), with only prey judged to be less than 1 month old being included. All nest sites were visited a similar number of times during each breeding season, and sampling effort can therefore be considered to be similar across sites. Here we calculated the expected number of prey by using information on abundance as prey relative to the breeding density of birds (Grell 1998). Grell (1998) provides maps of the density of breeding birds based on systematic point counts of breeding birds carried out by hundreds of amateurs, allowing estimates of the mean density of breeding prey species in the study areas of Nielsen (2004). Such point counts provide reliable estimates of breeding bird density (see summary in Grell 1998).

We estimated a logarithmic index of prey vulnerability as the observed log₁₀ transformed number of prey minus the log₁₀ transformed expected number of prey. The expected number of prey according to abundance was estimated as the proportion of prey individuals of each species according to the abundance based on point counts multiplied by the total number of prey individuals.

Predation risk and tail loss in wild birds

We recorded the frequency of complete loss of tail feathers from birds as an estimate of successful escape from a predation event during 1998–2005 in Denmark and France. Every time a bird was seen, we recorded whether it had or did not have a tail, and this was recorded until a minimum sample had been obtained. For blue tit *Parus caeruleus*, house martin *Delichon urbica*, and sand martin *Riparia riparia*, C. Biard, A. Marzal, and T. Szép kindly provided information from their population studies. The frequency of tail loss was square-root arcsine transformed.

Ease of feather loss and frequency of fear screams

We recorded the frequency of screams from birds captured in mist nests during 1990–2005 in Denmark, France, and Ukraine. This measure reflects attempts by birds to attract a second predator on being captured by a predator (Högstedt 1983). Every time an individual was removed from a mist net after capture, we recorded whether it emitted a scream or not (see Högstedt 1983 for details). Sample sizes for different species ranged from 12 to over 5000. The frequency of screaming was square-root arcsine transformed.

Feather looseness, coloniality, and sexual dichromatism

We classified the species as being solitary or colonial breeders using information obtained from the social organization sec-

tions in Cramp and Perrins (1977–1994) and Møller et al. (2001). Basically, species with large, multipurpose breeding territories that contained nest site, food, and shelter were classified as solitary, whereas species with small, aggregated territories that only contained nest sites were classified as colonial. We recorded body mass to the nearest 0.1 g for all specimens studied.

We classified species as being sexually monochromatic or dichromatic depending on whether males and females could be distinguished from each other based on external coloration, according to descriptions of plumage and soft parts in Cramp and Perrins (1977–1994) and other sources.

Antipredator versus antiparasite defenses

We recorded responses to phytohemagglutinin during the breeding seasons 2000–2005 in nestlings and adults. T-cell-mediated immune response to a challenge with phytohemagglutinin is a standard estimate for the ability of an individual to produce a T-cell-mediated immune response (Goto et al. 1978; McCorkle et al. 1980; Parmentier et al. 1993; Dietert et al. 1996). We tested all nestlings in nest found and all adults captured in mist nets. Injection with phytohemagglutinin results in local activation and proliferation of T-cells, followed by local recruitment of inflammatory cells and increased expression of major histocompatibility complex molecules (Goto et al. 1978; Abbas et al. 1994; Parmentier et al. 1998). Before injection, we removed the feathers from a small spot of skin on the wing web (patagium) of the right and the left wings and marked the sites of injection with a permanent, water-resistant color marker. We then measured the thickness of the skin to the nearest 0.01 mm with a pressure-sensitive caliper (Teclock SM112). For each wing web, we made 3 measurements to quantify measurement error, and measurements had repeatabilities above 0.95 (SE = 0.03).

Subsequently, we injected 0.2 mg phytohemagglutinin dissolved in 0.04 ml physiological water in one wing web and 0.04 ml physiological water in the other wing web. Nestlings were injected at a standard relative age during their ontogeny (when they were two-thirds through their normal nestling period) rather than at a similar absolute age. Approximately, 24 h later, we remeasured the thickness of the skin at the 2 sites of injection, as described above. In adult birds, we made the second measurement after 6 h in captivity. Previous intraspecific and interspecific studies of this immune response have shown that this interval is sufficient for obtaining a maximum response of a magnitude similar to that obtained after 24 h (Navarro et al. 2003; Møller et al. 2003). The index of cell-mediated immune response was calculated as the thickness of the wing web injected with phytohemagglutinin at the second measurement minus that just before injection minus the difference in thickness of the wing web injected with physiological water, expressed in mm. All sample sizes are reported in the Appendix. T-cell response was log₁₀ transformed. The entire data set is presented in the Appendix 1.

Comparative analyses

We analyzed relationships among variables using 2 different approaches: first, by analyzing species-specific data and, second, after accounting for similarity among species due to common phylogenetic descent, using standardized linear contrasts (Felsenstein 1985) as implemented in the computer program CAIC (Purvis and Rambaut 1995). Although we present analyses based on both approaches in line with numerous other comparative analyses published in recent years, we consider the results of analyses based on contrasts to be the statistically most rigorous. The reason is that many characters

have a nonrandom distribution with clear evidence of clumping. For example, colonial breeding is clumped in a few families such as corvids, hirundines, and sparrows, with similarity among taxa being caused by common descent rather than independent evolution. Hence, reliance on analyses based on species-specific data will provide biased correlations between characters, whereas analyses of contrasts will not. We calculated contrasts using a gradual model of evolution with branch length being proportional to the number of species within a clade (Purvis and Rambaut 1995), although a second series of analyses based on equal branch lengths (Purvis and Rambaut 1995) provided similar results. Hence, we only report the first series of analyses. All regressions were forced through the origin because the dependent variable is not expected to have evolved when there has been no evolutionary change in the independent variable (Garland et al. 1992). We tested some of the underlying assumptions of contrast analyses in the following ways. Standardization of contrast values was checked by examination of absolute values of standardized contrasts against their standard deviations (Garland et al. 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that the transformations made the variables suitable for regression analyses. In cases where extreme residuals were recorded, we tested for the robustness of the findings by excluding contrasts with studentized residuals greater than 1.96 (Jones and Purvis 1997). Likewise, we ranked the independent variable to test if the conclusions remained unchanged after using ranks rather than absolute values of the contrasts in the regressions, and in no case did this procedure give rise to conclusions different from those obtained with the contrast values.

We used stepwise linear regression (with probability to enter set to 0.25 and a probability to leave of 0.10) to find the best-fit model using predictor variables, using the software JMP (2000). None of the final models differed when comparing forward and backward elimination models, suggesting that the conclusions were robust. The number of species differed for the variables, but we consistently used the largest number of species once the best model had been identified. There was no evidence of collinearity between variables because the maximum correlation between any 2 variables was Pearson $r = 0.50$. Green (1979) suggested that any correlation less than 0.70 will eliminate serious problems of collinearity.

The phylogenetic hypothesis used was based mainly on information from Sibley and Ahlquist (1990) combined with information from other sources (Sheldon et al. 1992; Blondel et al. 1996; Badyaev 1997; Leisler et al. 1997; Cibois and Pasquet 1999; Barker et al. 2001; Donne-Goussé et al. 2002; Yuri and Mindel 2002; Barker et al. 2004; Cibois and Cracraft 2004) (Appendix 2).

RESULTS

Of 16 827 birds captured, 4348 had lost one or more feathers. Among these, 72.2% lost feathers from the rump, 29.2% from the back, 2.3% from the tail, and 7.3% from other feather tracts (some individuals lost feathers from more than one feather tract and were counted as such). 62 birds were captured which had some or all their tail feathers missing. Of these, 38 had lost large parts of the feathers on the rump, and 3 had lost large parts of feathers on the back.

The ease of losing feathers differed significantly among the 3 feather tracts across all species (Figure 1; Table 1). Feathers were more easily lost from the rump than from the back and than from the breast (repeated-measures ANOVA: $F = 32.44$, $df = 2, 68$, $P < 0.0001$).

There was a significant difference in ease of feather loss from the rump, back, and tail among species after using body

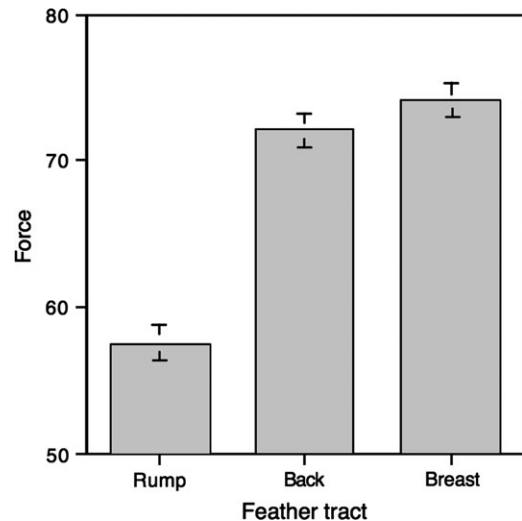


Figure 1
Mean (SE) force needed to remove feathers from the rump, back, and breast of 70 different bird species.

mass as a covariate (rump: $F = 3.30$, $df = 65, 192$, $P < 0.0001$, repeatability R (SE) = 0.37 (0.02); back: $F = 3.50$, $df = 65, 192$, $P < 0.0001$; R (SE) = 0.39 (0.02); breast: $F = 2.69$, $df = 65, 192$, $P < 0.0001$, R (SE) = 0.30 (0.03)). Likewise, there was a significant difference in relative ease of losing a feather from the rump after using the ease of losing feathers from the back and the breast as covariates ($F = 1.47$, $df = 65, 192$, $P = 0.022$, R (SE) = 0.11 (0.03)).

Prey preference by the sparrowhawk significantly predicted the force required to remove feathers from the rump relative to the back and the breast (Figure 2; Table 2a). Species of birds that were preferred prey by the sparrowhawk lost feathers more easily from the rump than less preferred prey (Table 2a). In addition, ease of feather loss was predicted by coloniality (Table 2a). The effects of body mass, body mass squared, and sexual dichromatism did not reach statistical significance. An analysis of contrasts provided similar conclusions (Table 2a).

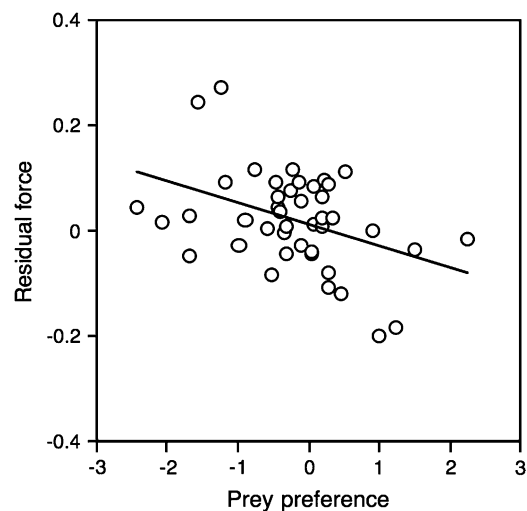


Figure 2
Relative force needed to remove feathers from the rump relative to the back in relation to prey preference by the sparrowhawk. The line is the linear regression line.

Table 2

Stepwise regression analyses of ease of feather loss in relation to (a) prey selection by the sparrowhawk (ease of feather loss from the rump the dependent variable), (b) tail loss (dependent variable), (c) screaming by captured birds (dependent variable), (d) coloniality (ease of feather loss from the rump the dependent variable), and (e) T-cell response (ease of feather loss from the rump the dependent variable) for models based on species-specific data and statistically independent linear contrasts

Variable	<i>F</i>	df	<i>r</i> ²	<i>P</i>	Slope (SE)
(a) Prey selection					
Species	142.01	4,38	0.94	<0.0001	
Prey selection	9.01	1,38		0.005	-0.05 (0.02)
Back feathers	5.42	1,38		0.025	0.31 (0.13)
Breast feathers	21.26	1,38		<0.0001	0.67 (0.14)
Coloniality	7.36	1,38		0.010	0.09 (0.03)
Contrasts	40.02	4,38	0.81	<0.0001	
Prey selection	7.31	1,38		0.010	-0.04 (0.01)
Back feathers	7.43	1,38		0.001	0.34 (0.12)
Breast feathers	17.93	1,38		0.0001	0.52 (0.12)
Coloniality	7.29	1,38		0.010	0.11 (0.04)
(b) Tail loss					
Species	6.50	2,20	0.38	0.0064	
Rump feathers	28.40	1,20		<0.0001	-0.17 (0.03)
Breast feathers	5.25	1,20		0.033	0.08 (0.03)
Contrasts	7.13	2,20	0.42	0.0046	
Rump feathers	10.68	1,20		0.0039	-0.10 (0.03)
Breast feathers	3.43	1,20		0.079	0.06 (0.03)
(c) Screaming					
Species	14.84	2,45	0.40	<0.0001	
Rump feathers	25.00	1,45		<0.0001	-1.67 (0.33)
Breast feathers	29.46	1,45		<0.0001	1.94 (0.36)
Contrasts	9.35	2,44	0.30	<0.0001	
Rump feathers	17.99	1,44		<0.0001	-1.83 (0.43)
Breast feathers	8.84	1,44		0.0048	1.22 (0.41)
(d) Coloniality					
Species	284.41	3,65	0.93	<0.0001	
Back feathers	12.34	1,65		0.0008	0.43 (0.12)
Breast feathers	21.24	1,65		<0.0001	0.58 (0.13)
Coloniality	4.71	1,65		0.34	0.08 (0.04)
Contrasts	30.03	3,64	0.59	<0.0001	
Back feathers	9.39	1,64		0.0032	0.36 (0.12)
Breast feathers	10.25	1,64		0.0021	0.33 (0.12)
Coloniality	11.34	1,64		0.0013	0.05 (0.02)
(e) T-cell response					
Species	104.43	3,29	0.92	<0.0001	
Breast feathers	73.66	1,29		<0.0001	0.82 (0.10)
Nestling T-cell response	7.02	1,29		0.013	0.21 (0.08)
Adult T-cell response	4.80	1,29		0.037	0.18 (0.08)
Contrasts	13.16	3,29	0.58	<0.0001	
Breast feathers	8.79	1,29		0.006	0.39 (0.13)
Nestling T-cell response	5.42	1,29		0.027	0.22 (0.10)
Adult T-cell response	10.81	1,29		0.0027	0.23 (0.07)

All models initially included force needed to remove feathers from the rump, back, and tail; body mass; and the additional variables listed in the table. The final models are reported in the table.

The frequency of tail loss ranged from 0.000 to 0.005 among 24 species with a mean (SE) of 0.0017 (0.0003). There was a negative relationship between the frequency of tail loss and the force required to remove feathers from the rump but a positive relationship for breast feathers (Figure 3; Table 2b). A similar conclusion was reached when the analysis was based on contrasts (Table 2b). Therefore, tail loss predicted relative ease of feather loss from the rump.

Estimated frequency of fear screams in this study was strongly positively correlated with estimates reported by Högstedt (1983) ($r = 0.99$, $t = 44.59$, $df = 20$, $P < 0.0001$), and did not differ significantly in a paired *t*-test ($t = -1.23$, $df = 21$, $P = 0.23$). The frequency of screaming by captured birds was negatively related to the force required to remove feathers from the rump (Figure 4; Table 2c). An analysis of contrasts showed a similar result (Table 2c). Weighting

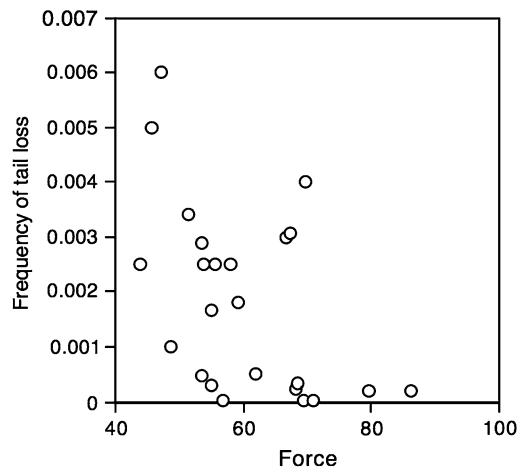


Figure 3
Frequency of complete tail loss in relation to force needed to remove feathers from the rump relative to the breast in 24 bird species.

the statistical analyses by sample size did not change any of the findings.

The force required for removing feathers from the rump relative to other feather tracts differed between colonial and solitary breeding bird species. It was more difficult to remove feathers from the rump in colonial than in solitary species (Figure 5; Table 2d), although only in an analysis of contrasts (Table 2d).

We found highly significant, consistent differences in cell-mediated immune response in nestlings and adults among species when testing these differences with 1-way ANOVAs (see Møller et al. 2001; Møller et al. 2003; Møller et al. 2005 for details). This demonstrates that this measure of immune response is species specific. Relative force required for removing feathers from the rump was significantly predicted by the ease of removal of feathers from the breast and by T-cell-mediated immune response of nestlings (Figure 6A) and adults (Figure 6B; Table 2e). An analysis of contrasts revealed a similar conclusion, with species with stronger immune re-

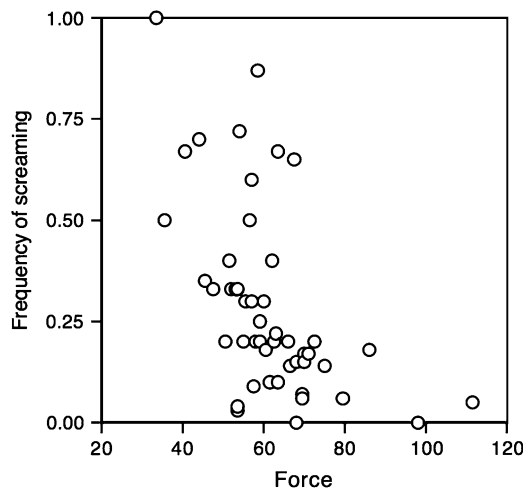


Figure 4
Frequency of fear screams in relation to force needed to remove feathers from the rump relative to the breast in 48 bird species.

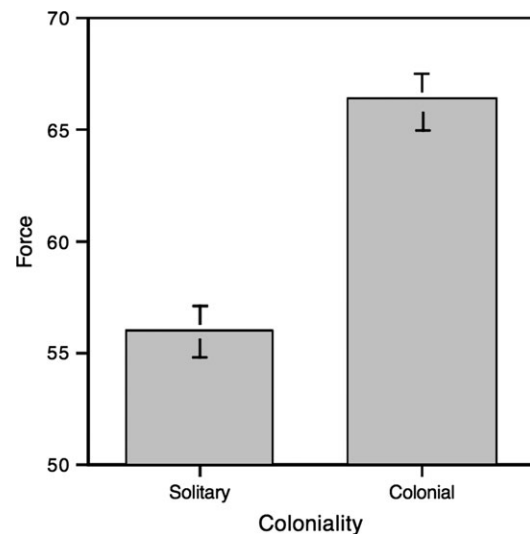


Figure 5
Relative force (\pm SE) needed to remove feathers from the rump relative to the back in relation to breeding sociality of different bird species.

sponses in both nestlings and adults also having rump feathers that were more difficult to remove (Table 2e). The potentially confounding effects of body mass, ease of feather removal from the back, sampling effort, or coloniality did not enter as significant predictors in any of these statistical analyses. If we weighted the statistical analyses by sample size, this did not change any of the results.

DISCUSSION

Birds lost feathers to a different degree as shown by the force required to remove feathers from the rump, back, and breast, and our comparative analyses revealed highly consistent differences among feather tracts and species. Rump feathers were relatively loose compared with feathers from the back and the breast. In addition, the relative ease of losing rump feathers was correlated with preference of prey by the most common avian predator (the sparrowhawk), the frequency of complete tail loss of tails in live birds recorded in the field, and the frequency of fear screams by captured birds. The relative ease of feather loss was greater in solitary than in colonial species. Finally, species with strong T-cell mediated immune responses in both nestlings and adults had greater difficulty losing feathers than species with weak immune responses, even when the analysis was controlled for degree of coloniality. These findings are consistent with the hypothesis that predation has affected the evolution of relative ease of feather loss in birds as an antipredator adaptation.

An underlying assumption of this study of the ease of feather loss is that this measure reliably reflects a history of predation-mediated selection. We tested this assumption in 3 different ways, and all tests were consistent with the assumption. First, we directly tested whether the ease of feather loss was related to prey preference by the most common predator of small passerine birds, the sparrowhawk. This test revealed that preferred prey species lost feathers from the rump relatively more easily than less preferred species. This result was independent of a number of potentially confounding variables that previously have been shown to predict prey preference in this predator such as sexual

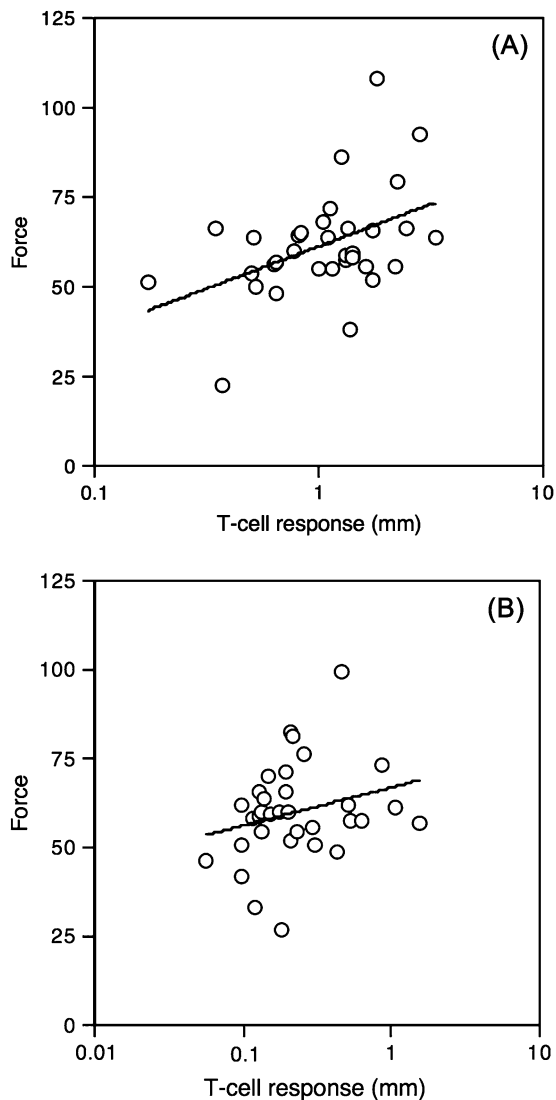


Figure 6
Relative force needed to remove feathers from the rump relative to the back in relation to T-cell-mediated immune response of (A) nestlings and (B) adults in different bird species. The lines are the linear regression lines.

dichromatism (Huhta et al. 2003; Møller and Nielsen 2006) and relative body size of the prey (Selås 1993; Götmark and Post 1996; Huhta et al. 2003; Møller and Nielsen 2006). Second, the frequency of tail loss in free-living birds was correlated with the relative ease of feather loss from the rump. Individuals that had completely lost their tails were assumed to have survived a predation attempt, whereas individuals captured by the tail by a predator but failed to lose their tail by definition died in the predation attempt. Given the negative relationship between frequency of tail loss and the force required to remove feathers from the rump, we can deduce that the survival value of loose feathers increased with the ease of feather loss. Third, the frequency of screams emitted by captured birds, which has been interpreted as fear screams that can elicit an attack by a second predator that might provide an opportunity for escape by the otherwise doomed prey individual (Högstedt 1983), was strongly negatively correlated with the force needed to remove feath-

ers from the rump. Therefore, we can interpret interspecific variation in the ease of feather loss as reflecting variation in predation risk. Similarly, Cooper et al. (2004) found that intraspecific variation in risk of predation affected the ease of costly tail loss in lizards.

Predation risk has been thought to vary with ecological conditions in a predictable manner. Coloniality, which arises from the spatial aggregation of breeding pairs, may have evolved due to the foraging and antipredation benefits associated with the presence of many conspecifics in a single site (Burger et al. 1980; Danchin and Wagner 1997). Predation risk may be reduced in colonial species because the presence of many eyes makes the detection of a predator more rapid and predictable (Møller 1987; Danchin and Wagner 1997) and because of the dilution effect of coloniality (Burger et al. 1980; Danchin and Wagner 1997). In addition, colonial species also tend to be gregarious outside the breeding season, providing similar antipredator advantages of sociality even when individuals are not reproducing (Lack 1968). If these mechanisms were at work, we should expect colonial bird species to be attacked or killed less often by predators than solitary species. Consistent with this expectation, the relative ease of feather loss from the rump differed considerably between colonial and solitary species of birds, with solitary species losing feathers more readily than colonial species. This suggests that differences in the intensity of natural selection caused by predators is related to degree of sociality by their prey and that these differences have affected the relative ease of feather loss in these 2 groups of species.

Antipredator and antiparasite defenses are likely to be costly to develop and maintain (e.g., Moret and Schmid-Hempel 2000; Møller et al. 2001; Bonneaud et al. 2003), and because antiparasite defense should be relatively less important in species with high predation risk, we should expect a negative relationship between antiparasite and antipredation defenses (Fineblum and Rausher 1995; Mauricio et al. 1997; Sokolowski et al. 1997; Soler et al. 1999). Indeed, we found for T-cell-mediated immune response of both nestlings and adults a significant and independent positive relationship between force required to remove feathers from the rump and immune response. This finding was as we had predicted a priori. Previous comparative studies of age-specific immune responses have suggested that age-specific selection pressures due to parasitism have affected life history traits in age-specific ways (Martin et al. 2001). Here, we have shown significant positive relationships between immune response and relative ease of feather loss both for nestlings and adults, although the association was strongest for adults. Consistency in the relationship for the 2 age classes suggests that the selection pressures on ease of feather loss are independent of age.

The findings concerning interspecific variation in the relative ease of feather loss from the rump are consistent with the suggestion of “adaptation unto death” (Högstedt 1983). A number of additional predictions can be made concerning this antipredation adaptation. More specifically, we should expect feathers to be lost in predation-rich environments such as the tropics more readily. In contrast, there should have been little or no selection for ease of feather loss in birds in predation-free environments such as oceanic islands. Given that predation can have important implications for the evolution of life histories (Roff 1992), we can also predict that the ease of feather loss should covary with life history traits. Ease of feather loss equates with a high risk of mortality among adults, selecting for a fast life history such as an early age at first reproduction, small egg size, large clutch size, and a large number of clutches per year.

APPENDIX 1

Information on T-cell-mediated immune response (mm) (SE, N) in nestlings and adults, tail loss (fraction of individuals without a tail), screaming (fraction of birds handled that emitted a scream), coloniality (0: solitary; 1: 2–10 pairs; 2: 11–100; 3: 101–1000; 4: above 1000 pairs), sexual dichromatism (0: monochromatic; 1: dichromatic), force needed to pull a feather from the rump, back, and breast, prey preference by the sparrowhawk, body mass (g), and sample size for feather data. See Methods for further details

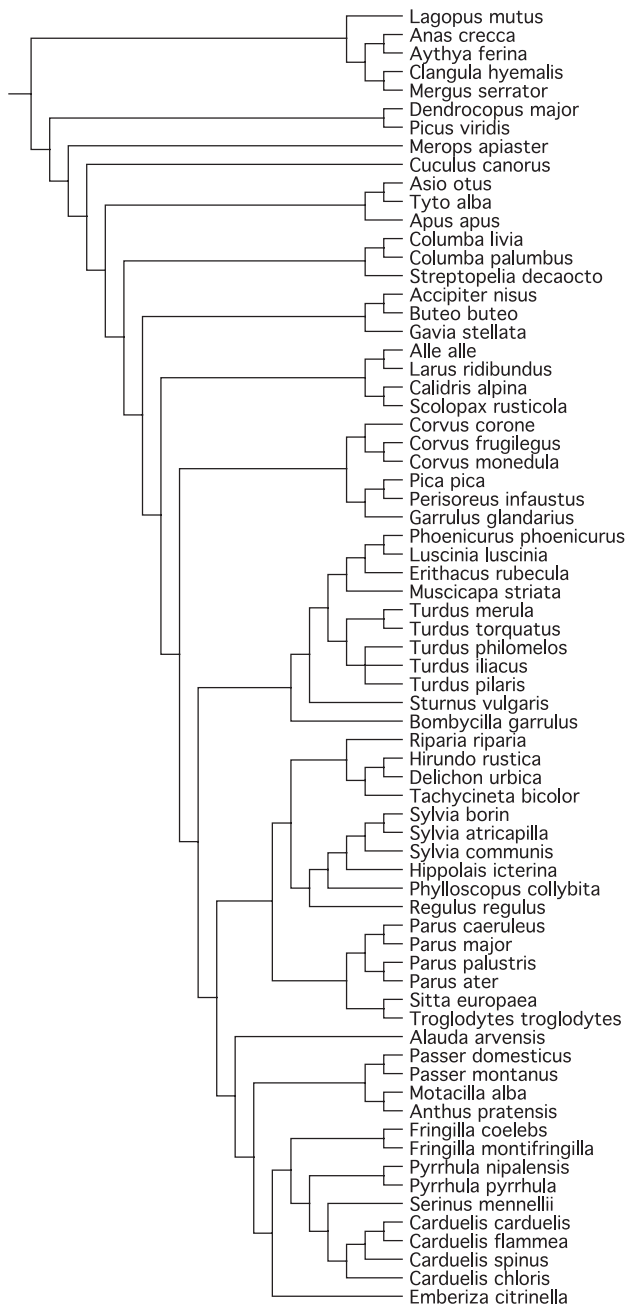
Species	Nestling T-cell response (mm) (SE) N	Adult T-cell response (mm) (SE) N	Tail loss (N)	Screaming	Coloniality	Sexual dichromatism	Rump feathers (SE)	Back feathers (SE)	Breast feathers (SE)	Prey preference	Body mass (g)	N
<i>Accipiter nisus</i>	1.69 (0.17) 2	—	0.00100 (500)	—	0	1	243.19 (32.78)	277.76 (62.84)	437.89 (76.29)	—	200.00	4
<i>Alauda arvensis</i>	0.40 (0.04) 3	—	—	0.10	0	0	81.18 (—)	95.51 (—)	93.01 (—)	−0.14	34.60	1
<i>Alle alle</i>	—	—	—	—	4	0	88.51 (22.5)	121.26 (8.75)	98.14 (—)	—	147.00	2
<i>Anas crecca</i>	—	—	—	—	0	1	142.01 (16.5)	199.26 (7.75)	196.01 (—)	—	286.50	2
<i>Anthus pratensis</i>	—	—	—	0.30	0	0	23.51 (—)	29.01 (—)	30.01 (—)	0.18	19.25	1
<i>Apus apus</i>	1.80 (0.01) 3	0.46 (0.16) 3	—	0.05	3	0	130.84 (—)	85.01 (—)	88.01 (—)	−1.55	30.20	1
<i>Asio otus</i>	—	—	—	—	0	0	126.01 (—)	224.51 (—)	260.01 (—)	—	255.50	1
<i>Aythya ferina</i>	—	—	—	—	0	1	185.51 (—)	344.01 (—)	350.51 (—)	—	669.50	1
<i>Bombycilla garrulus</i>	—	—	—	0.30	0	1	62.51 (8.26)	70.01 (8.04)	90.68 (7.54)	—	61.10	3
<i>Buteo buteo</i>	2.03 (0.37) 3	—	—	—	0	0	717.51 (—)	512.51 (—)	617.51 (—)	—	761.00	1
<i>Calidris alpina</i>	—	—	—	—	0	0	37.84 (—)	40.51 (—)	30.51 (—)	—	43.05	1
<i>Carduelis carduelis</i>	—	0.07 (—) 1	—	0.15	0	1	21.01 (—)	24.51 (—)	22.51 (—)	−0.26	15.60	1
<i>Carduelis chloris</i>	0.83 (0.08) 4	0.14 (0.01) 15	0.00300 (1000)	0.14	0	1	24.56 (2.66)	26.20 (3.00)	29.03 (2.33)	0.18	27.65	11
<i>Carduelis flammaea</i>	—	0.06 (0.01) 7	—	0.18	0	1	17.51 (0.76)	22.18 (1.45)	21.68 (2.49)	−0.90	13.05	3
<i>Carduelis spinus</i>	—	—	0.00290 (384)	0.04	0	1	16.02 (6.47)	19.31 (8.20)	25.61 (6.20)	1.49	13.80	3
<i>Clangula hyemalis</i>	—	—	—	—	0	1	275.84 (52.04)	400.68 (26.86)	332.94 (22.26)	—	722.50	3
<i>Columba livia</i>	3.29 (0.30) 4	1.57 (0.24) 7	—	0.17	2	0	180.26 (8.75)	181.76 (26.25)	192.01 (14.00)	—	261.00	2
<i>Columba palumbus</i>	2.26 (0.32) 3	0.85 (0.05) 3	—	0.15	0	0	210.18 (—)	259.01 (—)	190.01 (—)	−1.16	494.50	1
<i>Corvus corone</i>	1.68 (0.05) 8	—	0.00167 (3000)	—	0	0	192.51 (94.50)	220.76 (19.25)	282.01 (89.50)	—	544.50	2
<i>Corvus frugilegus</i>	2.69 (0.15) 3	—	0.00000 (10 000)	—	4	0	349.76 (10.75)	341.84 (78.33)	366.51 (24.00)	—	453.50	2
<i>Corvus monedula</i>	1.57 (0.09) 7	—	0.00033 (9000)	—	2	0	194.51 (16.00)	211.26 (2.25)	202.01 (3.00)	−2.08	249.00	2
<i>Cuculus canorus</i>	1.13 (—) 1	—	—	0.00	0	0	154.01 (19.25)	120.98 (8.79)	111.18 (9.19)	−1.23	82.60	6
<i>Delichon urbica</i>	2.19 (0.08) 16	0.44 (0.04) 31	0.00048 (2100)	0.03	4	0	42.01 (—)	64.84 (—)	53.84 (—)	−0.53	19.55	1
<i>Dendrocopus major</i>	—	—	—	1.00	0	1	43.34 (1.86)	101.01 (—)	92.09 (14.32)	1.00	73.40	3
<i>Emberiza citrinella</i>	0.65 (0.02) 2	0.12 (0.01) 7	0.00250 (400)	0.30	0	1	39.36 (2.39)	49.12 (6.66)	55.90 (9.99)	0.06	26.75	8
<i>Erithacus rubecula</i>	1.00 (—) 1	0.30 (0.02) 11	0.00250 (1200)	0.20	0	0	21.42 (1.83)	27.59 (2.01)	27.85 (1.69)	0.18	16.35	13
<i>Fringilla coelebs</i>	0.82 (0.08) 3	0.20 (0.02) 13	0.00400 (500)	0.06	0	1	24.80 (10.3)	24.65 (3.85)	28.66 (4.09)	0.06	24.20	4
<i>Fringilla montifringilla</i>	—	0.07 (0.01) 12	—	0.10	0	1	33.76 (1.58)	39.26 (2.60)	42.77 (2.90)	—	22.65	6
<i>Garrulus glandarius</i>	—	0.61 (—) 1	—	0.67	0	0	91.68 (18.71)	179.34 (23.32)	155.90 (12.75)	0.46	161.70	3
<i>Gavia stellata</i>	—	—	—	—	0	0	269.01 (—)	337.51 (—)	332.51 (—)	—	1603.00	1
<i>Hippolais icterina</i>	0.27 (—) 1	0.21 (0.01) 5	—	0.87	0	0	26.00 (2.50)	39.51 (2.60)	29.00 (2.60)	−1.68	13.30	2
<i>Hirundo rustica</i>	1.27 (0.01) 425	0.22 (0.01) 102	0.00021 (9350)	0.06	3	1	26.63 (7.65)	29.51 (7.25)	22.29 (5.22)	−0.11	19.10	3
<i>Lagopus mutus</i>	—	—	—	—	0	1	203.21 (—)	332.01 (—)	152.51 (—)	—	457.48	1
<i>Larus ridibundus</i>	—	—	—	—	4	0	212.26 (0.25)	215.01 (8.50)	279.26 (29.75)	—	228.00	2
<i>Luscinia luscinia</i>	—	0.34 (—) 1	—	0.67	0	0	34.00 (—)	25.00 (—)	58.00 (—)	—	25.00	1
<i>Mergus serrator</i>	—	—	—	—	0	1	255.51 (—)	278.51 (—)	289.51 (—)	—	930.00	1

Appendix 1, Continued

Species	Nestling T-cell response (mm) (SE) <i>N</i>	Adult T-cell response (mm) (SE) <i>N</i>	Tail loss (<i>N</i>)	Screaming	Coloniality	Sexual dichromatism	Rump feathers (SE)	Back feathers (SE)	Breast feathers (SE)	Prey preference	Body mass (g)	<i>N</i>
<i>Merops apiaster</i>	—	1.60 (0.04) 12	—	—	3	0	46.41 (3.77)	75.01 (4.45)	73.15 (4.45)	—	55.10	5
<i>Motacilla alba</i>	1.05 (0.10) 6	0.09 (0.07) 3	0.00022 (2000)	0.00	0	1	33.00 (—)	33.00 (—)	39.00 (—)	0.27	20.75	1
<i>Muscicapa striata</i>	0.41 (0.02) 3	0.10 (—) 1	—	0.33	0	0	23.51 (—)	37.01 (—)	31.51 (—)	−0.11	15.50	1
<i>Parus ater</i>	1.10 (0.13) 8	0.15 (0.00) 2	—	0.22	0	0	21.26 (7.75)	26.01 (4.00)	25.16 (3.35)	−0.44	9.25	2
<i>Parus caeruleus</i>	0.52 (0.08) 21	0.13 (0.02) 9	0.00341 (880)	0.40	0	1	17.34 (1.83)	24.01 (0.50)	26.51 (7.00)	0.03	11.75	3
<i>Parus major</i>	0.63 (0.09) 16	0.18 (0.02) 9	0.00180 (1094)	0.25	0	1	26.89 (3.44)	31.51 (2.72)	36.39 (3.17)	0.32	18.50	4
<i>Parus palustris</i>	1.73 (0.13) 2	0.10 (0.01) 2	—	0.20	0	0	24.51 (—)	21.51 (—)	38.01 (—)	−0.42	11.90	1
<i>Passer domesticus</i>	1.33 (0.12) 10	0.23 (0.03) 13	0.00030 (10,000)	0.20	3	1	39.07 (5.39)	56.86 (6.26)	50.01 (5.35)	0.26	30.35	21
<i>Passer montanus</i>	1.81 (0.34) 6	0.19 (0.02) 10	0.00020 (5000)	0.18	2	0	56.92 (16.11)	52.11 (3.52)	47.05 (6.54)	0.51	21.70	8
<i>Perisoreus infaustus</i>	—	—	—	—	0	0	113.01 (—)	—	—	—	84.70	1
<i>Phoenicurus phoenicurus</i>	1.13 (0.06) 2	0.13 (0.01) 3	—	0.17	0	1	21.51 (—)	23.01 (—)	22.84 (—)	−0.48	15.90	1
<i>Phylloscopus collybita</i>	1.14 (0.17) 2	0.06 (0.02) 2	—	0.09	0	0	22.01 (5.50)	23.68 (2.17)	33.76 (5.92)	−0.59	8.10	2
<i>Pica pica</i>	1.41 (0.10) 13	0.64 (0.15) 5	0.00300 (1000)	0.33	0	0	138.76 (20.75)	269.76 (14.25)	176.51 (13.00)	−1.68	228.00	2
<i>Picus viridis</i>	—	—	—	0.33	0	1	112.51 (—)	142.51 (—)	164.01 (—)	—	193.50	1
<i>Pyrrhula nipalensis</i>	—	—	—	—	0	1	16.09 (4.72)	46.66 (4.15)	20.73 (5.38)	—	30.83	2
<i>Pyrrhula pyrrhula</i>	—	0.14 (0.01) 3	0.00500 (1000)	0.35	0	1	16.91 (1.65)	21.22 (1.19)	34.69 (3.63)	−.26	31.05	32
<i>Regulus regulus</i>	0.64 (—) 1	0.21 (0.01) 2	—	0.20	0	1	21.84 (4.00)	31.01 (2.17)	33.85 (9.66)	−.034	5.60	2
<i>Riparia riparia</i>	1.74 (0.18) 6	0.51 (0.02) 25	0.00001 (80,000)	0.07	4	0	30.68 (0.73)	34.68 (2.09)	32.01 (9.78)	−0.33	13.15	3
<i>Scolopax rusticola</i>	—	—	—	—	0	0	57.01 (—)	113.01 (—)	127.84 (—)	—	441.00	1
<i>Serinus mennellii</i>	—	—	—	—	0	1	16.41 (—)	23.31 (—)	31.71 (—)	—	15.00	1
<i>Sitta europaea</i>	1.38 (—) 1	0.12 (—) 1	—	0.50	0	1	22.51 (—)	47.51 (—)	47.51 (—)	1.22	23.90	1
<i>Streptopelia decaocto</i>	2.46 (0.12) 3	1.07 (—) 1	—	0.20	0	0	132.84 (—)	128.01 (—)	138.51 (—)	−0.78	201.50	1
<i>Sturnus vulgaris</i>	1.32 (0.12) 9	0.53 (0.08) 3	0.00000 (15,000)	0.60	2	1	122.51 (16.36)	155.76 (12.02)	158.26 (9.39)	0.04	80.50	4
<i>Sylvia atricapilla</i>	0.77 (0.04) 4	0.13 (0.02) 10	—	0.20	0	1	24.61 (3.91)	23.87 (2.53)	31.84 (3.68)	−0.44	18.85	4
<i>Sylvia borin</i>	0.17 (—) 1	0.26 (0.04) 3	—	0.50	0	0	23.39 (1.88)	28.89 (2.73)	33.22 (4.34)	−0.35	19.05	4
<i>Sylvia communis</i>	0.51 (0.04) 2	0.15 (0.01) 6	—	0.14	0	1	25.01 (—)	20.01 (—)	30.01 (—)	−0.23	14.50	1
<i>Tachycineta bicolor</i>	0.37 (0.03) 74	0.18 (0.02) 41	—	—	0	0	12.00 (—)	45.00 (—)	41.00 (—)	—	20.10	2
<i>Troglodytes troglodytes</i>	0.50 (0.06) 2	0.13 (—) 1	—	0.33	0	0	20.51 (—)	28.76 (5.75)	29.51 (2.50)	−0.99	8.90	2
<i>Turdus iliacus</i>	—	—	0.00250 (400)	0.70	0	0	63.85 (8.96)	109.62 (36.45)	104.73 (18.05)	—	62.85	7
<i>Turdus merula</i>	1.35 (0.02) 9	0.20 (0.02) 20	0.00305 (3600)	0.65	0	1	88.14 (9.23)	85.15 (6.42)	106.25 (9.03)	0.21	95.85	17
<i>Turdus philomelos</i>	—	—	0.00250 (400)	0.72	0	0	61.37 (6.53)	82.01 (9.27)	85.96 (8.17)	0.90	70.50	12
<i>Turdus pilaris</i>	1.61 (0.16) 3	0.31 (0.01) 3	0.00050 (2000)	0.40	2	1	121.51 (—)	114.51 (—)	171.01 (—)	2.24	92.10	1
<i>Turdus torquatus</i>	—	—	—	0.20	0	1	116.34 (11.29)	162.51 (15.88)	132.01 (9.17)	—	117.00	3
<i>Tyto alba</i>	1.05 (0.25) 2	—	—	—	0	0	195.18 (40.33)	190.01 (—)	130.01 (—)	—	308.00	2

APPENDIX 2

Phylogenetic relationships between bird species analyzed for feather loss. See Methods for sources.



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REFERENCES

- Abbas AK, Lichtman AH, Pober JS. 1994. Cellular and molecular immunology. Philadelphia, PA: Saunders.
- Badyaev AV. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behav Ecol* 8:675–90.
- Barker FK, Barrowclough GF, Groth JG. 2001. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc R Soc Lond B Biol Sci* 269:295–308.
- Barker FK, Cibois A, Schikler C, Feinstein J, Cracraft J. 2004. Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci USA* 101:11040–5.
- Becker WA. 1984. Manual of quantitative genetics. Pullman, WA: Academic Enterprises.
- Berger G. 1960. Schreckmauser bei der Grosstrappe (*Otis tarda* L.). *Beitr Vogelkde* 7:126–29.
- Blondel J, Catzeflis F, Perret P. 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *J Evol Biol* 9:871–91.
- Bonneaud C, Mazuc J, González G, Haussy C, Chastel O, Faivre B, Sorci G. 2003. Assessing the cost of mounting an immune response. *Am Nat* 161:367–79.
- Burger J, Olla BL, Winn HE. 1980. Marine birds: behavior of marine animals. Volume 4. New York: Plenum.
- Cibois A, Cracraft J. 2004. Assessing the passerine “Tapestry”: phylogenetic relationships of the Muscicapoidea inferred from nuclear DNA sequences. *Mol Phylogenet Evol* 32:264–73.
- Cibois A, Pasquet E. 1999. Molecular analysis of the phylogeny of 11 genera of the Corvidae. *Ibis* 141:297–306.
- Cooper WE, Perez-Mellado V, Vitt LJ. 2004. Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. *J Zool* 262:243–55.
- Cramp S, Perrins CM, editor. 1977–1994. The birds of the Western Palearctic. Volumes 1–9. Oxford: Oxford University Press.
- Curio E. 1976. The ethology of predation. Berlin, Germany: Springer.
- Danchin E, Wagner RH. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends Ecol Evol* 12:342–47.
- Dathe H. 1955. Über die Schreckmauser. *J Ornithol* 96:5–14.
- Dieter RR, Golemboski KA, Kwak, H, R, Miller TE. 1996. Environment-immunity interactions. In: Davison TF, Morris TR, Payne LN, editors. Poultry immunology. Abingdon, UK: Carfax. p 343–56.
- Donne-Goussé C, Laudet V, Hänni C. 2002. A molecular phylogeny of anseriformes based on mitochondrial DNA analysis. *Mol Phylogenet Evol* 23:339–56.
- Edmunds M. 1974. Defence in animals. Harlow, UK: Longman.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Fineblum WL, Rausher MD. 1995. Trade-off between resistance and tolerance to herbivore damage in a morning glory. *Nature* 377: 517–20.
- Garland Jr T, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 41:18–32.
- Götmark F, Post P. 1996. Prey selection by sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. *Philos Trans R Soc Lond B Biol Sci* 351:1559–77.
- Goto N, Kodama H, Okada K, Fujimoto Y. 1978. Suppression of phytohaemagglutinin skin response in thymectomized chickens. *Poult Sci* 57:246–50.
- Green R. 1979. Sampling design and statistical methods for environmental biologists. New York: Wiley.
- Grell MB. 1998. Fuglenes Danmark. Copenhagen, Denmark: Gad.
- Höglund NH. 1964. Fright moult in Tetraonids. *Viltrevy* 2:419–22.
- Högstedt G. 1983. Adaptation unto death—function of fear screams. *Am Nat* 121:562–70.
- Huhta E, Rytönen S, Solonen T. 2003. Plumage brightness of prey increases predation risk: an among-species comparison. *Ecology* 84:1793–9.
- JMP. 2000. JMP. Cary, NC: SAS Institute Inc.
- Jones KE, Purvis A. 1997. An optimum body size for mammals? Comparative evidence from bats. *Funct Ecol* 11:751–6.
- Lack D. 1968. Ecological adaptations for breeding in birds. London: Methuen.
- Leisler B, Heidrich P, Schulze-Hagen K, Wink M. 1997. Taxonomy and phylogeny of reed warblers (genus *Acrocephalus*) based on mtDNA sequences and morphology. *J Ornithol* 138:469–96.
- Lindström A, Nilsson J-Å. 1988. Birds doing it the octopus way: fright moulting and distraction of predators. *Ornis Scand* 19:165–6.
- Martin TE, Møller AP, Merino S, Clobert J. 2001. Does clutch size evolve in response to parasites and immunocompetence? *Proc Natl Acad Sci USA* 98:2071–6.

- Mauricio R, Rausher MD, Burdick DS. 1997. Variation in the defense strategies of plants: are resistance and tolerance mutually exclusive? *Ecology* 78:1301–11.
- McCorkle Jr F, Olah I, Glick B. 1980. The morphology of the phytohemagglutinin-induced cell response in the chicken's wattle. *Poult Sci* 59:616–23.
- Mester H, Pünte W. 1959. Bemerkungen über die Schreckmauser. *Vogelwelt* 80:179–80.
- Møller AP. 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. *Anim Behav* 35:819–32.
- Møller AP, Christe P, Garamszegi LZ. 2005. Coevolutionary arms races: increased host immune defense promotes specialization by avian fleas. *J Evol Biol* 18:46–59.
- Møller AP, Erritzøe J, Saino N. 2003. Seasonal changes in immune response and parasite impact on hosts. *Am Nat* 161:657–71.
- Møller AP, Merino S, Brown CR, Robertson RJ. 2001. Immune defense and host sociality: a comparative study of swallows and martins. *Am Nat* 158:136–45.
- Møller AP, Nielsen JT. 2006. Prey vulnerability in relation to sexual coloration of prey. *Behav Ecol Sociobiol* 60:227–33.
- Moret Y, Schmid-Hempel P. 2000. Survival for immunity: the price of immune system activation for bumblebee workers. *Science* 290:1166–8.
- Navarro C, Marzal A, de Lope F, Møller AP. 2003. Dynamics of an immune response in house sparrows *Passer domesticus* in relation to time of day, body condition and blood parasite infection. *Oikos* 101:291–8.
- Nielsen JT. 2004. Prey selection of sparrowhawks in Vendsyssel, Denmark [Danish, with English summary]. *Dansk Orn Foren Tidsskr* 98:164–73.
- Parmentier HK, de Vries Reilingh G, Nieuwland MGB. 1998. Kinetic immunohistochemical characteristic of mitogen-induced cutaneous hypersensitivity responses in chickens divergently selected for antibody responsiveness. *Vet Immunol Immunopathol* 66:367–76.
- Parmentier HK, Scharma JW, Meijer F, Nieuwland MGB. 1993. Cutaneous hypersensitivity responses in chickens divergently selected for antibody responses to sheep red blood cells. *Poult Sci* 72:1679–92.
- Purvis A, Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC). *Comput Appl Biosci* 11:247–51.
- Roff DA. 1992. The evolution of life histories. New York: Chapman and Hall.
- Selås V. 1993. Selection of avian prey by breeding sparrowhawks *Accipiter nisus* in southern Norway: the importance of size and foraging behaviour of prey. *Ornis Fenn* 70:144–54.
- Sheldon FH, Slikas B, Kinnarney M, Gill FB, Zhao E, Silverin B. 1992. DNA-DNA hybridization evidence of phylogenetic relationships among major lineages of *Parus*. *Auk* 109:173–85.
- Sibley CG, Ahlquist JE. 1990. Phylogeny and classification of birds, a study in molecular evolution. New Haven, CT: Yale University Press.
- Sokolowski MB, Pereira HS, Hughes K. 1997. Evolution of foraging behavior in *Drosophila* by density-dependent selection. *Proc Natl Acad Sci USA* 94:7373–7.
- Soler JJ, Soler M, Pérez-Contreras T, Aragon S, Møller AP. 1999. Antagonistic anti-parasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. *Behav Ecol* 10:707–13.
- Tautenhahn W. 1959. Schreckmauser bei Amsel. *Vogelwelt* 80:122.
- Vermeij GJ. 1987. Evolution and escalation. Princeton, NJ: Princeton University Press.
- Vitt LJ, Congdon JD, Dickson NA. 1977. Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* 58:326–37.
- Wilson BS. 1992. Tail injuries increase the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia* 92:145–52.
- Yuri T, Mindell DP. 2002. Molecular phylogenetic analysis of Fringillidae, “New World nine-primaried oscines” (Aves: Passeriformes). *Mol Phylogenet Evol* 23:229–43.