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Predators and microorganisms of prey: goshawks prefer prey with small uropygial glands

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Summary

1. The uropygial gland of birds produces chemical substances with antimicrobial properties that have been shown to reduce the abundance of feather degrading bacteria and other microorganisms. These microorganisms would affect the flight capabilities of birds and, consequently, a relationship between size of uropygial glands and probability of capture by aerial predators should exist.

2. We tested this hypothesis by estimating the susceptibility of 56 species of prey of the goshawk *Accipiter gentilis* Linnaeus to predation as the observed abundance of prey relative to the expected abundance from mean population density.

3. In a comparative analysis of the relationship between relative size of the uropygial gland and susceptibility to predation we found a strong negative relationship accounting for 16% of the variance. This relationship was present in analyses that accounted for similarity due to common phylogenetic descent, the fact that prey of intermediate size were preferred, and that larger prey species have larger uropygial glands.

4. These observations are consistent with uropygial glands being under strong selection from aerial predators that are likely mediated by the effect of uropygial glands on feather degrading bacteria and therefore on flight capabilities of birds.

Key-words: *Accipiter gentilis,* antimicrobial defences, predator-prey interactions

Introduction

Predators survive and reproduce by capturing prey, imposing important selection pressures on prey populations. Any potential prey individual able to escape will survive and potentially produce descendants with superior ability to cope with predation pressure. Hence, it is phenotypic traits associated with predator detection and prey escape capacity that a priori will account for who is going to die. What are the characteristics of preferred relative to available prey?

Sick prey with heavy loads of parasites are eaten disproportionately often, apparently because sick individuals in poor condition are less able to escape than healthy conspecifics (Hudson 1986; Temple 1986; Murray, Cary & Keith 1997; Møller & Erritzøe 2000). A number of studies have shown that prey individuals are more often sick than non-prey (review in Møller 2008).

The uropygial gland is an exocrine gland on the dorsal side of the rump that produces secretions with a negative effect on bacterial and fungal infections of feathers and the skin (Jacob & Ziswiler 1982; Bandyopadhyay & Bhattacharyya 1996, 1999; Shawkey, Pillai & Hill 2003). Previous studies have shown that large uropygial glands produce more waxes than small glands (Elder 1954; Oka & Okuyama 2000; Sandilands, Savory & Powell 2004; Møller, Erritzøe & Rózsa 2009b). Gland size is related to habitat (Kennedy 1971; Jacob & Ziswiler 1982; Johnston 1988; Montalti & Salibián 2000), and aquatic bird species often have larger glands than terrestrial species (Johnston 1988; Galván *et al.* 2008). Jacob & Ziswiler (1982) reviewed old gland removal experiments, showing increased levels of fungi and feather-degrading bacteria such as *Bacillus licheniformis* on feathers, and higher levels of feather degradation, although not in all studies. Several recent studies have suggested that secretions from the uropygial gland may act as a cosmetic that increases plumage brightness and hence improves sexual attractiveness (Andersson & Amundsen 1996; Blanco, Seoane & de la Puente 1999; Figuerola & Senar 2005; Galván & Sanz 2006). Møller, Heeb & Czirjak (2009a) showed for the barn swallow *Hirundo rustica* Linnaeus that the abundance of feather-degrading bacteria decreased with increasing size of the uropygial gland, and that individual hosts living in larger colonies had more feather-degrading bacteria. Møller, Erritzøe & Rózsa (2009b) showed that bird species with larger uropygial glands had

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higher hatching success, indicating that there are fitness costs associated with reduced antimicrobial defence.

The objective of this study was to investigate the function of the uropygial gland in different species of birds by relating the size of the gland to the risk of predation by a common avian predator of many northern temperate areas, the goshawk *Accipiter gentilis* Linnaeus. The goshawk is an avian predator with a preference for prey of intermediate size, with small and large prey being avoided (Møller & Nielsen 2007). Therefore, we included body mass and body mass squared as additional variables in the analyses. Common prey species are usually considered to be more vulnerable than rare prey (Holling 1965; Allen 1988; Endler 1991; Crawley 1992). Two comparative analyses of the uropygial gland showed that species in aquatic habitats had larger glands than species in terrestrial habitats, either to waterproof the plumage or to prevent rapid bacterial and fungal growth under humid conditions (Galván *et al*. 2008; Møller, Heeb & Czirjak 2009a). Thus, we included prey abundance and aquatic habitat as additional variables in the analyses. Finally, the size of uropygial glands was related to migration habits in one study (Galván *et al*. 2008), but not in another (Møller, Heeb & Czirjak 2009a). Migration may potentially also affect the estimation of susceptibility to predation. Hence, we also included migration distance as an additional variable in the analyses.

Materials and methods

PREY PREFERENCES

We calculated an index of prey vulnerability as observed $\log_{10}$-transformed number of prey minus $\log_{10}$-transformed expected number of prey, where a value of zero implies that prey were consumed relative to their abundance, a value of $+1$ implies that prey were consumed ten times more frequently than expected from their abundance, and a value of -1 implies consumption ten times less frequently than expected. The expected number of prey was estimated from the combined breeding density of all species, the total number of prey items, and the proportion of prey items of each species (see below and Møller & Nielsen (2006) for details).

Nielsen & Drachman (1999) studied goshawks during 1977–2004 in an area of 2417 km^2 in Northern Jutland, Denmark. Prey remains were systematically collected near nest sites during April-September, mainly May-June. Only prey remains judged to be less than 1 month old from the condition of feathers was included in the study, because we wanted to be sure that only prey brought by the nest owner was included in the analyses. A total of 21 818 prey items of 82 species was available, with each prey item representing an individual, although this sample was reduced to 54 species because information on uropygial glands was only available for these species. All nest sites were visited a similar number of times during the breeding season, and sampling effort can therefore be considered to be similar across sites.

We calculated the expected number of prey by using information on density of breeding birds obtained from systematic point counts at randomly located sites in each 5 km × 5 km square throughout Denmark (Grell 1998). Maps of the density of breeding birds are reproduced in Grell (1998) based on systematic point counts of breeding birds carried out by hundreds of amateurs, and the mean density of breeding birds in the study areas of Nielsen & Drachman (1999) was extracted from these maps. We could only estimate susceptibility indices for species that were breeding locally and hence had estimated breeding densities.

UROPYGIAL GLANDS

We extracted information on the mass of the uropygial gland from Jacob & Ziswiler (1982), and our own information recorded by JE for all birds brought to a taxidermist from southern Jutland, assuring that prey preferences and uropygial glands were derived from the same populations. JE carefully dissected the glands and weighed the glands on a precision balance to the nearest 0·001 g. For a sample of specimens we had information on both body mass, mass of the uropygial gland and time since death. There was no significant relationship between mass of the uropygial gland and time since death ($F = 0{\cdot}86$, d.f. $= 1{,}109$, $P = 0{\cdot}84$). Estimates of the mass of the uropygial gland were highly repeatable when comparing ten common species from our data set and that of Jacob & Ziswiler (1982)[$F = 10{\cdot}95$, d.f. $= 9{,}10$, $r^2 = 0{\cdot}91$, $P = 0{\cdot}0004$, repeatability R (SE) $= 0{\cdot}83$ (0·14)]. This provides evidence of consistency in estimates across sources. In total, we had information on prey preferences and the size of the uropygial gland for 54 species.

BODY MASS

We recorded body mass on a balance directly from the specimens delivered to JE that were the basis of this study. None of the specimens used was damaged, and there was thus no reason for expecting body mass to be biased.

HABITAT

We classified species as terrestrial (0; not commonly encountering water), partly aquatic (1; spending at least part of the time in water or wet habitats), or completely aquatic (2; spending most or all of the time in water) based on habitat descriptions in Cramp & Perrins (1977–1994) and del Hoyo, Elliott & Sagartal (1992–2008). This classification was fully consistent with our own experience from the field in Northern Denmark.

MIGRATION DISTANCE

We recorded the northernmost and southernmost breeding and wintering latitude to the nearest 0·1 degrees latitude based on the distribution maps in Cramp & Perrins (1977–1994). Migration distance was simply the difference in the mean of the two breeding latitudes and the mean of the two wintering latitudes.

The entire data set is reported in electronic Appendix S1.

STATISTICAL ANALYSES

We tested whether the distribution of continuous variables deviated from normality, and appropriate transformations were made to meet requirements for parametric statistical tests. Body mass was $\log_{10}$-transformed. Aquatic habitat was treated as a dummy variable in the analyses, being similar to using a dichotomous variable as a dummy variable in standard regression analyses (Sokal & Rohlf 1995). This procedure can be justified because intermediate states of the variable are possible and represent biologically meaningful conditions.

COMPARATIVE ANALYSES

Closely related species have similar phenotypes than species that are more distantly related, simply because similarity among closely related species is likely to be due to such pairs of species sharing a recent common ancestor. We controlled for similarity in phenotype among species due to common ancestry by calculating standardized independent linear contrasts (Felsenstein 1985), using the program CAIC (Purvis & Rambaut 1995). We tested the statistical and evolutionary assumptions of the continuous comparative procedure (Garland, Harvey & Ives 1992) by regressing absolute standardized contrasts against their standard deviations. In order to reduce the consequent problem of heterogeneity of variance, (i) outliers (contrasts with Studentized residuals > 3) were excluded from subsequent analyses (Jones & Purvis 1997), and (ii) analyses were repeated with the independent variable expressed in ranks. In neither case did these new analyses change any of the conclusions.

The composite phylogeny used in the analyses was mainly based on Sibley & Ahlquist (1990), combined with information from more recent sources taking priority over Sibley & Ahlquist (Hackett *et al.* 2008; Jønsson & Fjeldså 2006; Fig. 1). Because information for the composite phylogeny came from different studies using different methods, consistent estimates of branch lengths were unavailable. Therefore, branch lengths were transformed assuming a gradual model of evolution with branch lengths being proportional to the number of species contained within a clade. Results based on these branch lengths were compared to those obtained using constant branch lengths (a punctuated model of evolution). Nowhere were results qualitatively different.

We used multiple regression to find best-fit models with the predictor variables, using JMP (2000). Regressions based on contrasts were forced through the origin since the comparative analyses assume that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis & Rambaut 1995).

We assessed relationships based on effect sizes according to the criteria listed by Cohen (1988) for small (Pearson $r = 0{\cdot}10$, explaining 1% of the variance), intermediate (9% of the variance) or large effects (25% of the variance).

Results

Prey preference by the goshawk varied from $+2{\cdot}38$ to $-2{\cdot}26$, mean (SE) $= -0{\cdot}21$ (0·15), $N = 54$ species. Uropygial glands varied from 0·018 g in the bullfinch *Pyrrhula pyrrhula* Linnaeus to 5·79 g in the eider *Somateria mollissima* Linnaeus. Species with relatively large uropygial glands for their body size (with positive residuals from a regression of uropygial gland size on body mass) were unevenly distributed across the phylogeny (Fig. 1). This shows that gland size does not have a strong phylogenetic signal. Body mass of prey varied from 13·1 g in the sand martin *Riparia riparia* Linnaeus to 2067 g for the eider *Somateria mollissima* Linnaeus.

The best fit model explained 71% of the variance in prey preference (Table 1). There was a significant partial effect of mass of the uropygial gland, accounting for an intermediate to large effect size of 20% of the variance (Table 1, Fig. 2). This implies that bird species with large glands were less preferred as prey. In addition, goshawks preferred prey of intermediate body size as shown by the quadratic effect of body mass (Table 1). Finally, there was a preference for less common prey species (Table 1). The partial effect of water habitat was not included in the model ($F = 0{\cdot}62$, d.f. = 1, 48, $P = 0{\cdot}43$), nor was the partial effect of migration distance ($F = 1{\cdot}75$, d.f. = 1, 48, $P = 0{\cdot}19$).

An analysis of contrasts provided qualitatively similar conclusions, with the mass of the uropygial gland accounting for 15% of the variance (Table 1).

Discussion

This comparative study revealed a negative association between the relative size of the uropygial gland and prey preferences by the goshawk. Because of the known antimicrobial properties of secretions, this result may suggest a role of microorganisms explaining predator-prey interactions. We will briefly consider these effects, the effects of confounding variables, possible causal relationships, and the potential role of microorganisms in predator-prey interactions.

The relative size of the uropygial gland accounted for a significant amount of variation in prey preference, with a large to intermediate effect size (sensu Cohen 1988) of 20% in the analysis of species-specific data and 15% in the analysis of contrasts. This finding was independent of all known potentially confounding variables, but also of similarity among species due to common phylogenetic descent. The function of the uropygial gland is partly as an exocrine gland producing waxes that affect the abundance of microorganisms (e. g. Galván *et al.* 2008; Møller, Heeb & Czirjak 2009a; Shawkey, Pillai & Hill 2003), but it may also affect waterproofing of the plumage (Jacob & Ziswiler 1982; Johnston 1988; Galván *et al.* 2008) and the unpalatability of potential prey as suggested for red-billed woodhoopoes *Phoeniculus purpureus* and hoopoes *Upupa epops* Linnaeus (Law-Brown & Meyers 2003; Martín-Vivaldi *et al.* 2009). Here we tested for an effect of water habitat, but found no evidence of this variable predicting the relationship between susceptibility to prey and size of glands. We also tested for the possibility that migratory habits affected the size of uropygial glands, but also susceptibility to predation. However, there was no empirical evidence consistent with that expectation.

Comparative analyses do not readily allow for analysis of causation, so we will entertain both options. First, a large gland may reduce the risk of predation by reducing the abundance of microorganisms that degrade feathers or otherwise reduce the probability of escape from a predator. Second, a high risk of predation may cause a reduction in the size of the uropygial gland. This functional hypothesis rests on the assumption that there is a reduced advantage of suppressing the abundance of microorganisms when hosts anyway have a high probability of being depredated. We cannot readily distinguish between these two hypotheses, although an intraspecific test is possible. If the first hypothesis is correct, we should expect prey to have more microorganisms on their plumage (as a consequence of small gland size) than conspecifics that manage to escape the predator. If the second hypothesis is correct, we should expect the production and maintenance of

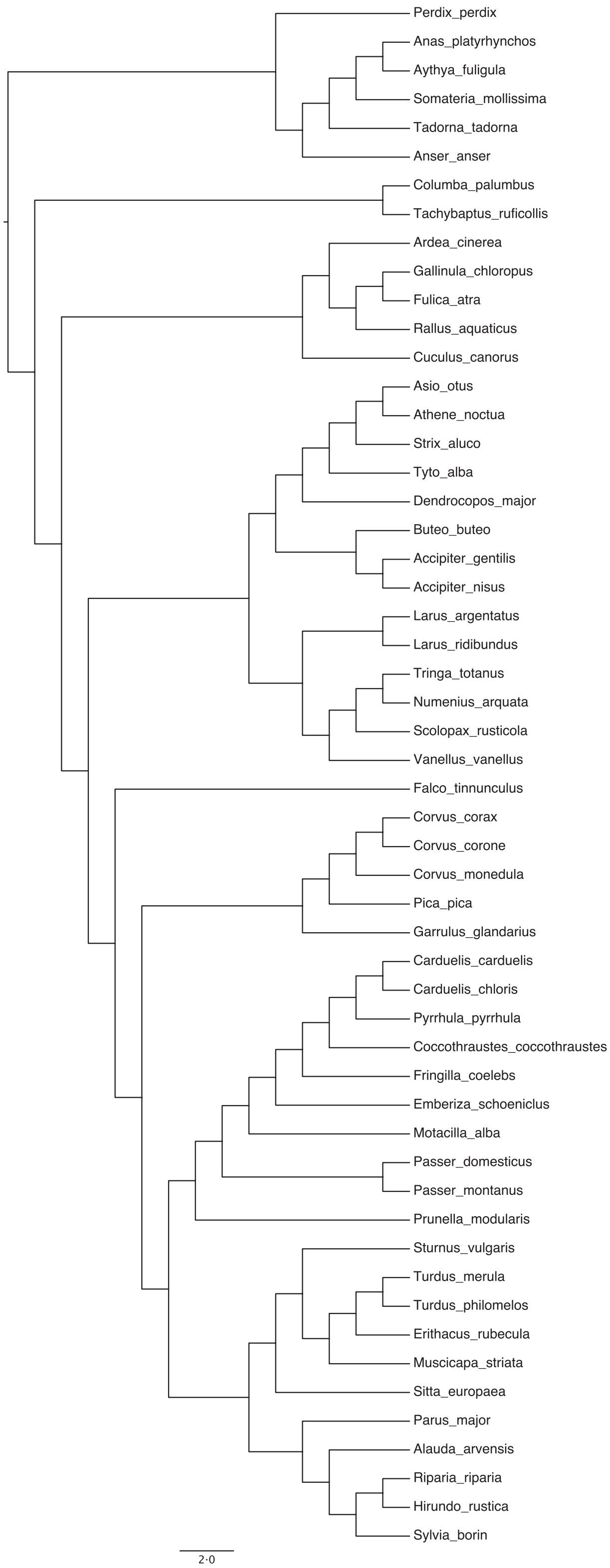

Fig. 1. Phylogenetic relationships between the 54 prey species of the goshawk. Species with relatively large uropygial glands for their body size are indicated with dark branches, species with small glands with white branches, and equivocal cases with hatched branches.

glands to be costly, and an experimental reduction in the abundance of predators should increase the size of the uropygial gland.

Table 1. Prey preference by goshawks in relation to body mass, mass of uropygial gland and population density of different species of prey. The two models had the statistics $F = 29{\cdot}98$, d.f. $= 4{,}49$, $r^2 = 0{\cdot}71$, $P < 0{\cdot}0001$ and $F = 11{\cdot}47$, d.f. $= 4, 49$, $r^2 = 0{\cdot}19$, $P < 0{\cdot}0001$

Factor	Sum of squares	d.f.	*F*	*P*	Slope (SE)
Species					
Body mass	8·56	1	22·92	< 0·0001	1·46 (0·31)
Body mass squared	14·78	1	39·54	< 0·0001	−1·33 (0·21)
Uropygial mass	4·58	1	12·26	0·0010	−1·13 (0·32)
Population density	8·24	1	22·06	< 0·0001	−0·40 (0·09)
Error	18·31	49			
Contrasts					
Body mass	3·73	1	41·63	< 0·0001	7·47 (1·16)
Body mass squared	3·16	1	35·28	< 0·0001	−1·38 (0·23)
Uropygial mass	0·77	1	8·56	0·0052	−1·02 (0·35)
Population density	1·11	1	12·35	0·0010	−0·32 (0·09)
Error	4·39	49			

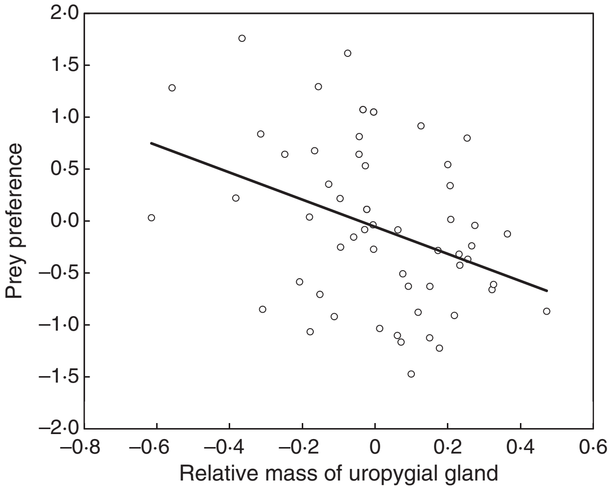

Fig. 2. Prey preference of goshawks for different species of prey in relation to relative size of the uropygial gland (adjusted for body mass). The line is the linear regression line.

The negative relationship between relative size of the uropygial gland and susceptibility to predation by the goshawk raises the question why should there be a negative rather than a positive relationship. Why are not all individuals of prey species producing lots of secretions to reduce the risk of predation? The fact that there is considerable interspecific variation in size of the uropygial gland provides indirect evidence consistent with costs of production and maintenance of uropygial glands and hence costs of production of gland secretions. Furthermore, gland size varies seasonally (Martín-Vivaldi *et al.* 2009) and between the sexes (Martín-Vivaldi *et al.* 2009; Møller, Erritzøe & Rózsa 2009b), and is related to the abundance of ectoparasites and microorganisms (Galván & Sanz 2006; Møller, Erritzøe & Rózsa 2009b). The latter result for parasites and microorganisms suggests that secretions are mainly produced when there is an anti-parasite and antimicrobial advantage to be gained. These correlations are also consistent with costs of gland production and maintenance.

Body size predicted risk of predation as shown in previous studies of the goshawk (Møller & Nielsen 2007) and the sparrowhawk *Accipiter nisus* Linnaeus (Selås 1993; Götmark & Post 1996; Huhta, Rytkönen & Solonen 2003; Møller & Nielsen 2006). Independent of the effects of the uropygial gland and body size, we also found that more common prey were less susceptible to predation than less common prey, as we have reported previously for the goshawk (Møller & Nielsen 2007) and the sparrowhawk (Møller & Nielsen 2006). We have been unable to find any phenotypic characteristic of prey that could account for this finding.

In conclusion, we have shown that avian prey species with larger size of their uropygial glands fell prey to the goshawk less frequently than prey species with small uropygial glands. This finding was independent of similarity due to common phylogenetic descent and a number of potentially confounding variables. The association between relative size of the uropygial gland and prey preference suggests that micro-organisms may play a hitherto neglected role in predator-prey interactions, and that intraspecific studies of this relationship may improve our understanding of this effect.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Appendix S1. Summary statistics for information on prey.

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