Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit

Theunis Piersma1,2,*, Luisa Mendes3, Jasper Hennekens1, Sandra Ratiarison4,5, Stefan Groenewold1 and Joop Jukema6

1Netherlands Institute for Sea Research (NIOZ), The Netherlands
2Centre for Ecological and Evolutionary Studies, University of Groningen, The Netherlands
3Departamento de Zoologia, Faculdade de Ciências, Universidade de Lisboa, Portugal
4Department of Veterinary Pathology, University of Utrecht, The Netherlands
5present address: Laboratoire d’Ecologie Générale, Brunoy, France
6Oosterbierum, Friesland, The Netherlands

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Summary

The indicator mechanism for sexual selection proposed by Hamilton and Zuk (i.e. that sexually selected ornaments signal parasite resistance) has received rather little observational support, and none in the case of long-distance migrant birds. Here we present a test by examining the association between helminth infestations and breeding plumage quality in bar-tailed godwits Limosa lapponica taymyrensis during their spring staging period in the Wadden Sea, The Netherlands. After a non-stop flight from West Africa, these shorebirds refuel in the Wadden Sea in preparation for a second flight to the central Siberian Arctic breeding grounds. Earlier studies have shown that only relatively heavy and well ornamented birds carry out a “top-up” moult during stopover, in which part of the contour feathers recently grown in West Africa are replaced by even fresher ones. Active body moult was therefore taken as the primary indicator of ornament quality. Of 78 birds collected between 1992 and 1997, 42% carried helminths, including four species of digenean trematodes (flukes), three species of cestodes (tapeworms) and an acanthocephalan (spiny-headed worm). Faecal samples examined for helminth eggs in another 92 birds in 1998 and 2000 showed similar rates of infestation. Actively moulting bar-tailed godwits were confirmed to be heavier and to show more extensive breeding plumage than non-moulting birds. In females, but not in males, active moult was associated with fewer cestodes and acanthocephalans. Also, breeding plumage and presence of cestodes were negatively associated in females. We argue that the quality of the breeding plumage reliably indicates parasite resistance in female godwits. The repeatability of plumage scores of females between years is consistent with such resistance having a heritable component. In contrast, male ornaments may demonstrate other qualities, e.g. an ability to combine adequate fuelling and flight performances with moult during the time-stress of migration.

Key words: honest signalling; sexual selection; migration; Hamilton-Zuk hypothesis; parasite resistance; cestodes

Introduction

The evolution of costly secondary sexual traits, such as the feather ornaments carried by birds during the reproductive season, can quite easily be understood if the traits reliably indicate “good genes” (Andersson, 1994). Such genes may, for example, be implicated in the resistance to pathogens and (macro-) parasites (Hamilton and Zuk, 1982). Many empirical studies have now been carried out to test the hypothesis that sexually selected ornaments signal disease resistance (reviews by Andersson, 1994; Møller, 1994; Clayton and Moore, 1997). On the basis of a meta-analysis, Hamilton and Poulin (1997) concluded that “as a whole intraspecific correlations between parasite load and male showiness provide very little support for the hypothesis, with only the effects of...
parasites on fish morphology matching the Hamilton and Zuk prediction” (the positive exception being Wedekind, 1992). Using a larger dataset that included experimental studies with strong effects, Möller et al. (1999) were able to confirm the predicted negative relationship between parasite load and expression of secondary sexual characters. In a new experimental study plumage coloration could be linked with infections by intestinal coccidians (McGraw and Hill, 2000). Whether the Hamilton-Zuk mechanism applies to avian migrants has remained unresolved. Based on a comparative analysis of temperate breeding migratory bird species, Fitzpatrick (1994) proposed that sexually selected traits may honestly signal an ability to cope with the fluctuating selection pressures caused by changing environments rather than involving genetic variation for parasite and disease resistance. Avian migrants would be particularly prone to encounter such fluctuating environments.

Here we provide an observational test of the parasite resistance indicator mechanism of Hamilton and Zuk based on the large natural variation in the feather ornament of a long-distance migrant shorebird species, the bar-tailed godwit (Limosa lapponica, Scolopacidae). We examine whether the presence of actively moulting body feathers and the expression of breeding plumage in godwits are correlated with the likelihood of infestation with intestinal parasites (helminths) of various kinds.

The bar-tailed godwits were studied during the spring stopover in the Wadden Sea, i.e. just before their arrival, territory establishment and mate acquisition on the tundra breeding grounds. These godwits arrive in the Wadden Sea after a 4,000–5,000 km non-stop flight from the West African wintering areas in the last days of April and the first days of May (Piersma et al., 1990). They leave the Wadden Sea in the last days of May and the first of June (average 1 June) for a direct flight of similar length to the arctic breeding grounds on the Taimyr Peninsula, Russia (Piersma and Jukema, 1990). This particular population has recently been assigned separate subspecific status (L. l. taymyrensis; Englemoer and Roselaar, 1998).

Bar-tailed godwits are socially monogamous (Byrkjedal et al., 1989; Yéou et al., 1992; McCaffery and Gill, in press) and during the breeding season both sexes carry a rusty-red plumage (Jukema and Piersma, 2000), that is probably melanin based (Fox, 1976). Males have brighter breeding plumage but they are noticeably smaller in size than females. Before departure from West Africa, godwits begin a partial contour feather moult towards a breeding plumage which is often complete, but which can still be upgraded on the Wadden Sea staging site (Zwarts et al., 1990; Piersma and Jukema, 1993). The extent of breeding plumage of both males and females upon arrival in the Wadden Sea is condition dependent (Piersma and Jukema, 1993). Even more striking, only the heaviest individuals (those with the highest plumage scores) upgrade their plumage by a supplementary partial moult of body feathers. This suggests that only birds in top physical condition are capable of moulting, of making additional investments in the quality of what could be regarded as an ornament (Piersma and Jukema, 1993). That plumage quality is indeed used during mate assessment is likely, but awaits confirmation in the field.

Material and Methods

Bar-tailed godwits were captured during daytime on the grasslands of Texel, the westernmost Frisian island in the Dutch part of the Wadden Sea (53° 03’ N, 04° 48’ E), in the months of May 1992–2000, in almost all cases during the morning (9.30–13.30 hr local time). Birds were captured with a large pull-net (Koopman and Hulscher, 1979). Only fully adult individuals (two or more years of age) are considered here.

Upon capture the birds were weighed by a Pesola spring balance to the nearest g. The extent of breeding plumage was assessed on a scale of 1–7, where 1 = full winter plumage, 2 = trace of breeding plumage, 3 = quarter breeding plumage, 4 = half breeding plumage, 5 = three-quarter breeding plumage, 6 = trace of winter plumage and 7 = full breeding plumage. We also recorded presence or absence of active body moult by searching for growing contour feathers on breast and belly. All measurements were made by a single observer (JJ).

Blood parasites appear to be absent in staging bar-tailed godwits (unpubl. data), which is why we focused on helminths. Catching casualties obtained in 1992 (n = 1), 1993 (n = 9), 1994 (n = 10), 1995 (n = 21), 1996 (n = 22) and 1997 (n =15) were stored frozen at –20°C and later compositionally analysed (see Piersma, 1998 for general methods). Upon dissection the intestinal tract of these birds was removed and carefully opened along the whole length. The contents were scraped from the intestine so that any helminths attached to the intestinal lining would also be collected. All material was conserved in 4% formaldehyde for a few days, stored for some weeks in a solution of 70% ethanol, 5% glycerol and 25% water, and then examined under a binocular microscope. All parasites other than nematodes (which we found in one adult bird only) were collected, measured and sent to taxonomic specialists for identification. Using live birds only, in 1998 (n_{bud} = 45) and 2000 (n_{bud} = 47) we assayed for the presence or absence of helminths (including nematodes) by looking for their eggs in godwit-faeces collected between capture and...
release. The method allows for the accurate detection of the helminth eggs in a non-invasive manner but has the disadvantage that only the presence of egg-producing worms can be detected. Captured birds were placed in individual boxes lined with clean plastic. After birds had defecated, faeces were collected off the plastic and stored in large centrifuge-tubes at 7 °C. All samples were examined within four days of collection. We tested for parasites by identifying and counting parasite eggs in each sample. To increase the chances of detecting eggs we used the flotation technique (for details see Thienpont et al., 1986). We added a 1.3 times normal density solution to each sample to cause eggs to float, using a saturated solution of natriumnitrate (500 g/880.3 ml of distilled water) in 1998 and a sugar solution (640 g glucose and 9.5 ml 40%-formaldehyde in 500 ml mineral water) in 2000. The eggs were attached to a coverslip by touching it to the surface of the solution. After 30 min of drying, a slide was made with the coverslip that was scanned under a light microscope at 100 times magnification. Eggs were identified to class level according to Mehlhorn et al. (1986) under a light microscope using 250 times magnification.

The main part of the data analysis was carried out in a hierarchical way as follows. After describing the intestinal parasite fauna, we examined the degree of helminth infestation in relation to presence or absence of active body moult. Recall that this partial moult will yield the freshest possible, and presumably the highest quality, plumage ornament upon arrival on the breeding grounds. It can be regarded as a measure of the instantaneous body condition. To investigate the predictive value of the extent of breeding plumage (which may reflect the past history of body condition), we then analysed the relationship between the breeding plumage score and presence or absence helminth parasites. All these analyses were carried out for the sexes combined and separately. Where we tested for associations between time periods, sexes and incidences of helminth infestations, we relied on Chi-square statistics. To investigate time-related patterns we used correlation and analyses of (co-)variance. As the plumage score is a ranked variable, the significance of differences in extent of breeding plumage between groups was tested with nonparametric statistics (Mann-Whitney U test). To investigate the predictive

Table 1. Occurrence of helminth parasites in the intestinal tracts of adult male and female bar-tailed godwits collected on the staging grounds in The Netherlands during northward migration.

<table>
<thead>
<tr>
<th>Parasite species</th>
<th>Males (n = 39)</th>
<th>Females (n = 39)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family name, Group name</td>
<td>Fraction of birds infected</td>
<td>Average number of helminths per bird</td>
</tr>
<tr>
<td>Himasthla militaris</td>
<td>0.18</td>
<td>7.2</td>
</tr>
<tr>
<td>(Echinostomatidae, Digenea)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microphallus similis</td>
<td>0.13</td>
<td>2.4</td>
</tr>
<tr>
<td>(Microphallidae, Digenea)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maritrema subdolum</td>
<td>0.10</td>
<td>5.6</td>
</tr>
<tr>
<td>(Microphallidae, Digenea)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trematode spec.</td>
<td>0.00</td>
<td>0.0</td>
</tr>
<tr>
<td>(Digenea)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ophryocotyle proteus</td>
<td>0.20</td>
<td>8.7</td>
</tr>
<tr>
<td>(Davaineidae, Cyclophyllidea, Cestoda)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capsulata edenensis</td>
<td>0.05</td>
<td>0.9</td>
</tr>
<tr>
<td>(Dilepididae, Cyclophyllidea, Cestoda)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Debloria etaplesensis</td>
<td>0.05</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>(Hymenolepididae, Cyclophyllidea, Cestoda)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spiny-headed worm spec</td>
<td>0.00</td>
<td>0.0</td>
</tr>
<tr>
<td>(Acanthocephala)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Any helminth parasite</td>
<td>0.43</td>
<td>24.9</td>
</tr>
</tbody>
</table>

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value of the extent of breeding plumage (which may reflect the past history of body condition), we also analysed the relationship between the breeding plumage score and presence or absence helminth parasites using logistic regression.

Results

The guts of 43% of the male, and 41% of the female bar-tailed godwits were infested with helminths other than nematodes. Parasite numbers varied from 0 to 330 (Table 1). Four species of flukes (trematodes, Digenea), three species of tapeworm (Cestoda) and one species of spiny-headed worm (Acanthocephala) were identified. The trematodes Himasthla militaris, Microphallus similis and Maritrema subdolum and the cestode Ophryocotyle proteus occurred most frequently and were also the most numerous in infested individuals (Table 1). The cestode Capsulata edenensis was not as common as the previous species, but with individuals many centimetres in length it was certainly the most striking helminth that we found. In three birds dissected outside the context of this study, a fifth species of fluke of the genus Cyclocoelum (Cyclocoeliidae) was found throughout the body cavity, especially in the airsacs. One of these birds, a light-weight male without a trace of breeding plumage, additionally carried more than 20 C. edenensis.

There were no obvious sex differences in either the incidence of helminth infestations or the numbers of helminths in the sample of dissected birds (Table 1). The incidence of digenean trematodes was somewhat higher in birds sampled for intestinal content in 1992–1997 (37%) than in birds from which faeces were collected in 1998 (22%) and in 2000 (9%). This variation was significant ($\chi^2 = 13.062, n = 170, p = 0.001$). However, for neither of the helminth groups that will be shown below to be of interest, the variation among years was noteworthy (for cestodes: $\chi^2 = 0.736, p = 0.692$; for acanthocephalans: $\chi^2 = 0.029, p = 0.099$). In the combined dataset the lack of sex differences in the incidences of infestation was confirmed for nematodes ($\chi^2 = 0.987, n = 92, p = 0.320$), digenean trematodes ($\chi^2 = 0.364, n = 170, p = 0.546$), cestodes ($\chi^2 = 9.293, n = 170, p = 0.002$) and acanthocephalans ($\chi^2 = 2.867, n = 170, p = 0.090$). Except for a tendency of cestodes and acanthocephalans to co-occur ($\chi^2 = 6.280, n = 170, p = 0.012$), there were no statistically significant associations between the presence of different helminth groups. For none of the helminth groups was there evidence for an increase in burden with time spent on the Wadden Sea refuelling site (correlation coefficients smaller than 0.1, $p > 0.05$).
Full breeding plumage indicates lack of gut parasites

Actively moulting males (Fig. 1 top) and females (Fig. 1 bottom) were heavier than non-moulting birds (analysis of covariance with day as covariate: for 83 males, F-ratio = 88.5, p < 0.0001, for the covariate day F-ratio = 18.9, p < 0.0001, rate = 3.7 g/d; for 87 females, F-ratio = 37.2, p < 0.0001, for the covariate day F-ratio = 16.1, p < 0.0001, rate = 4.0 g/d; for neither sex were there significant interactions). Moulting males were on average 30 g heavier than non-moulting males (representing 10% of overall average body mass), and moulting females were on average 31 g (9%) heavier than non-moulting females.

No active moult occurred in birds that were captured before 13 May. Therefore, in the analyses of the associations between the presence of body moult and different kinds of helminths (Table 2), only birds sampled on or after 13 May are included. There was a strong positive association between the presence of moult and the absence of cestodes. The association was weaker for acanthocephalans, and no associations were found for nematodes and digenean trematodes. Further analysis revealed that the association between presence of moult and lack of cestodes only occurred in females (χ² = 7.799, n = 75, p = 0.005). Despite a trend in the same direction, the association was not significant in males (χ² = 2.058, n = 77, p = 0.151). Finally, confirming the findings of Piersma and Jukema (1993), actively moulting godwits carried the brighter plumages (Fig. 2; Mann-Whitney U tests, for males: U = 386.0, p < 0.0001, and for females: U = 303.5, p < 0.0001).

In males the extent of breeding plumage was rather similar for birds with and without cestodes (Fig. 3 top; Mann-Whitney U test statistic = 641.5, p = 0.348). However, for females the individuals without cestodes were clearly more ornamented (Fig. 3 bottom; Mann-Whitney U test statistic = 991.0, p = 0.006). To see whether the quality of the ornament (plumage score) directly predicts the likelihood of helminth infestation, we applied a logistic regression. Females with higher plumage scores were less likely to be infected with cestodes than birds with lower plumage scores (difference in log likelihoods of models without and with plumage is 8.565, d.f. = 1, χ²-test: p = 0.003). The plumage effect was not statistically significant for males (difference in log likelihoods is 0.739, p = 0.390).

Discussion

We found that female bar-tailed godwits in active moult and with higher breeding plumage scores have a lower incidence of cestodes. To the best of our knowledge,
this is the first study to demonstrate a relationship between quality of the ornament and parasite burden in a long-distance migrant bird species. Such relationships have been searched for, but not found in the comparative studies of Zuk (1991) and Fitzpatrick (1994). The alternative hypothesis of Fitzpatrick (1994), that sexually selected traits of avian migrants reflect genetic ability to cope with rapidly changing wintering environments, requires assumptions on the variability of wintering habitat quality that seem difficult to fulfill. In the light of the ornament-parasites relationship shown in godwits, at least for females of a coastal shorebird species like the bar-tailed godwit, her specific hypothesis needs no further consideration at this point. Balmford and Read (1991) made the point that hosts can only develop heritable resistance to parasites of which the genotypes are shared by successive generations. Inspired by this, Fitzpatrick (1994) suggested that parasites with long generation times like tapeworms may be best suited to coevolve with a long-distance migrant. Somewhat on the contrary, Zuk (1991) suggested that there may be rather less potential for host-parasite co-evolution in migrant than in resident birds. This is only true to the degree that the parasites encountered by the migratory host are specific to each of the many sites visited in the course of the year. On the tundra breeding grounds the molluscan and crustacean intermediate hosts of the many helminths encountered in this study are absent and bar-tailed godwits run little risk of infestation (see Piersma, 1997). However, digenean genera like Himasthla, Microphallis and Maritrema are common in western Europe (Lauckner, 1990; H. Cremers, pers. comm.). The two common cestodes Ophyryocotyle proteus and Capsulata edenensis apparently have a world-wide distribution and were earlier recorded in bar-tailed godwits wintering in New Zealand (Schmidt and Allison, 1989). In the absence of relevant studies in the West African wintering quarters, it is impossible to conclude whether the godwits encounter these helminths in the Wadden Sea only, or whether they conclude whether the godwits encounter these helminths in the West African wintering quarters, it is impossible to conclude whether the godwits encounter these helminths in the Wadden Sea only, or whether they would be better equipped with a different class of parasites. The two commonly occurring helminths occurring in non-moult ing poorly ornamented females were cestodes and acanthocephalans. These helminths spend relatively long periods in the intestine of the final host and they also share the trait of competing (with the host) for the ‘digested’ nutrients which are taken up through the intestinal wall, rather than being independent of the host’s digestive physiology (Crompton, 1973; Rausch, 1983). Helminths such as these tapeworms and spiny-headed worms thus may be particularly costly to carry (see Connors and Nickol, 1991). The host sex that bears the cost of egg production during a time of potential nutritional stress, such as after arrival on the still snow-covered tundra, might thus incur the highest relative cost of hosting cestodes and acanthocephalans. If this reasoning is correct, males should try harder to select ‘clean’ females. To explain why females do not usually get as rufous as the males, we may bear in mind that growing feathers as well as developing eggs require specific rare nutrients that need storing in advance (e.g. Selman and Houston, 1996). Thus, there may be a fecundity cost of the plumage ornament which limits the expression in females (Fitzpatrick et al., 1995).

Whether a lack of tapeworms implies a specific resistance to their infestation is still a matter of conjecture. Most of the breeding plumage moult occurs in West Africa. A bar-tailed godwit heavily burdened with parasites may find it rather difficult to combine molting and fuelling in West Africa and cestodes would be the direct cause of lack of ornamentation. However, if the parasites that we found were the result of fresh infestations in The Netherlands, they could not have influenced plumage score and more likely indicate inherent resistance. But wherever and whenever infection occurred, greater parasite resistance would decrease the likelihood of such an infestation. McNeil and Díaz (1999) claim that greater yellowlegs Tringa melanoleuca develop some degree of immunity to reinfestation by trematodes. Variation in degree of immunity may have a genetic basis. In this respect it is intriguing that plumage scores of recaptured bar-tailed godwits are repeatable between years in females (based on individuals recaptured with intervals of 1–4 years on Texel in 1992–2000, and scored by a single observer that had no awareness of previous scores nor any expectations, $r = 0.845$, $n = 5$, $p = 0.04$), but not in males ($r = 0.300$, $n = 7$, $p > 0.1$). Such repeatability of plumage scores between years in females only, is consistent with the idea that parasite resistance of females has a heritable component.

The two classes of helminths occurring in non-moult ing poorly ornamented females were cestodes and acanthocephalans. These helminths spend relatively long periods in the intestine of the final host and they also share the trait of competing (with the host) for the ‘digested’ nutrients which are taken up through the intestinal wall, rather than being independent of the host’s digestive physiology (Crompton, 1973; Rausch, 1983). Helminths such as these tapeworms and spiny-headed worms thus may be particularly costly to carry (see Connors and Nickol, 1991). The host sex that bears the cost of egg production during a time of potential nutritional stress, such as after arrival on the still snow-covered tundra, might thus incur the highest relative cost of hosting cestodes and acanthocephalans. If this reasoning is correct, males should try hard to select ‘clean’ females. To explain why females do not usually get as rufous as the males, we may bear in mind that growing feathers as well as developing eggs require specific rare nutrients that need storing in advance (e.g. Selman and Houston, 1996). Thus, there may be a fecundity cost of the plumage ornament which limits the expression in females (Fitzpatrick et al., 1995).

Wedekind (1992, 1997) pointed out that different secondary sexual traits could well indicate resistance to different classes of parasites and pathogens. Given the different demands on males and females, there may be sex-related differences in the predictive value of a particular ornament. Studies of indicator mechanisms in
sexual selection routinely depict females as the choosy sex and males as the sex that has to advertise specific qualities (e.g. Møller et al., 1999). Yet, the advantage of having a high-quality mate applies to both sexes, especially in monogamous birds with biparental care such as bar-tailed godwits (Fitzpatrick, 1994; Fitzpatrick et al., 1995). By choosing a male with a high-quality ornament, a female bar-tailed godwit, rather than to select for parasite resistance, may choose a partner that has proven to be capable of combining and completing the acts of flight, fuel storage and moult (Piersma and Jukema, 1993; Piersma et al., 1996). This ability may have a genetic basis, and it may not. In any case, we predict that as a result of mutual sexual selection, bar-tailed godwits will mate assortatively with respect to plumage scores. Such ‘mutual’ sexual selection has been demonstrated in a monogamous alcid in which both sexes carry a crest, the crested auklet Aethia cristatella (Jones and Hunter, 1993).

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List of References


