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Associations in male plumage ornamentation and reproductive parameters in the Icelandic Black-tailed Godwit *Limosa limosa islandica*

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Colourful breeding plumage ornamentation is widespread among birds. Males are often more ornamented than females, and such sexual dimorphism may have arisen through sexual selection, driven by female choice and male-male competition. However, in the nominate subspecies of the sexually dimorphic Black-tailed Godwit *Limosa l. limosa*, paler males are mated with females that invest more into reproduction, and it was suggested that a reduction of male–male competition for high quality nesting sites was one reason for this. Paler males breed in higher densities, which facilitate better group anti-predator defence and thus can increase the reproductive value of a clutch. If male–male competition for nesting sites drives sexual selection of plumage ornamentation in godwits, we expect plumage ornamentation to be positively correlated with female reproductive investment in populations experiencing strong male–male competition. We test this in the Icelandic subspecies *L. l. islandica*, where a population increase has led to enhanced competition for nesting sites among males. We test whether more ornamentation in Icelandic males is related to reproductive parameters. We assessed coloration in males on the basis of photos taken of birds captured on the nest in 1993 and videos of birds at their nests in 2008. We found no relationship between male breeding plumage ornamentation and timing of egg-laying. However, more ornamented males were mated with females that laid larger eggs in both years, opposite to the pattern found in the nominate species. This suggests that male plumage ornamentation may indeed be a sexually selected signal in godwits, and that intraspecific competition may be important.

INTRODUCTION

Many bird species show conspicuous plumage ornamentation and sexual plumage dimorphism (Hill & McGraw 2006). Theory of sexual selection predicts that sexual dimorphism can be due to males either signalling their ability to compete for mates and territories to other males (male–male, or intrasexual competition) or their reproductive fitness prospects to prospective mates (female choice, or intersexual competition) (Andersson 1994). To be reliable, such signals should be costly (Pomiankowski 1988, Zahavi 1975). Indeed, more exaggerated, colourful and conspicuous plumage ornamentation in males is often positively correlated with male condition, male–male competitive abilities, female choice and reproductive investment, reproductive success and male viability (for reviews see Andersson 1994, Hill 2002, Hill & McGraw 2006).

In migratory birds, early arriving males are expected to be better able to secure territories of high quality (Kokko 1999). Early arrival on the breeding grounds in godwits and other long-distance migrants is often correlated to an earlier onset of breeding, and in turn to a higher reproductive output (Bêty *et al.* 2003, Drent *et al.* 2003, Gunnarsson 2005a, 2006a, but

see Schroeder *et al.* 2010a). To arrive early, birds must be able to migrate faster or leave the staging grounds earlier (Drent *et al.* 2003). Such migratory quality of male birds can be signalled by plumage ornamentation (Piersma & Jukema 1993, Piersma *et al.* 2001, but see Drent *et al.* 2003).

Both the European mainland subspecies *Limosa limosa limosa*, and the Icelandic subspecies of the Black-tailed Godwit *L. l. islandica* are sexually dimorphic for breeding plumage and size – males are the more colourful and smaller sex (Table 1, Groen & Yurlov 1999, Gunnarsson *et al.* 2006b, Schroeder *et al.* 2008). The Icelandic subspecies winters in Western Europe and breeds almost exclusively in Iceland (Gill *et al.* 2007). Godwits of both subspecies secure their future nesting site soon after arrival on the breeding grounds, and both sexes stay there for the whole pre-breeding period (Van den Brink *et al.* 2008). Males display to females and compete with other males by aerial and ground displays and fights (Cramp & Simmons 1983), which are assumed to be more effective when males are more ornamented (Jönsson & Alerstam 1990).

Surprisingly Black-tailed Godwit males of the nominate race, in the Netherlands with a less colourful plumage were mated with females that laid larger eggs (Schroeder *et al.*

2009). This is likely to be the reason why sexual plumage dimorphism is currently less pronounced than it was 150 years ago, and why males nowadays look more like females (Schroeder *et al.* 2009). Paler male godwits being preferred by females has been attributed to large-scale land-use changes on the breeding grounds in the Netherlands, where a large part of the *limosa* population breeds. The higher food availability in nitrogen-enriched agricultural grasslands (Beintema *et al.* 1995) likely led to a decrease in male–male competition for nesting sites, which might have led to a relaxation of selection pressures. The proposed mechanism is via breeding density: paler males may be able to breed in higher densities (if food is plentiful), which facilitate better and more successful anti-predator behaviour (Schroeder 2010). Hence females paired with paler males invest more in their clutch, because it has a lower chance of being depredated than nests of females paired with more colourful males. As a consequence, plumage ornamentation of males may have become less important in the *limosa* subspecies, benefiting males who did not invest in a costly, colourful breeding plumage (Schroeder *et al.* 2009).

Contrastingly, Icelandic godwits started using a higher percentage of low quality habitats both on the breeding and wintering grounds during their remarkable population increase over the past century (Gunnarsson *et al.* 2005a, 2005b). *Islandica* males that arrive earliest on Iceland after spring migration secure territories in high quality breeding habitat and subsequently benefit from high reproductive success (Gunnarsson *et al.* 2005a, b). During the population increase, and likely due to a lack of more high quality habitat, Icelandic godwits also started to populate less suitable habitat for breeding, and the population became partitioned by habitat quality (Gunnarsson *et al.* 2005b). Thus apparently high-quality habitat is not available in sufficient quantities for all Icelandic godwits. Hence one can conclude that male–male competition for nesting sites should be relatively strong in Icelandic godwits, at least on high quality breeding grounds. And if male plumage ornamentation plays a role in intrasexual competition in the Icelandic subspecies, too, we expect that in *islandica* godwits, male ornamentation should be positively related to correlates of reproductive success. In this study, we examined the correlations between sexually dimorphic breeding plumage traits of male Icelandic Black-tailed Godwit and egg volume and timing of breeding.

MATERIAL AND METHODS

Fieldwork

We gathered data on breeding Icelandic godwits in high quality breeding grounds during two field trips to Iceland in 1993

and 2008. In 1993, GJG and NMG collected data on 34 godwit nests on lowland grassland areas in northern and southern Iceland (see also Gerritsen & Groen 1995). That year, 20 nests were located on the derelict airfield at Kaldaðarnes (63°55'N, 21°10'W), between the towns of Selfoss and Eyrarbakki), where Black-tailed Godwits bred at a high density. This area and the surrounding estuarial grasslands are among the oldest traditionally-used nesting sites of the Icelandic Black-tailed Godwit (T.G. Gunnarsson pers. comm.). In the Skogar reserve in N Iceland (65°45'N, 20°26'W), 14 additional nests were found. This area is a silted, fertile floodplain, and habitat quality is high. In total, that year 15 male and 22 female Icelandic godwits were caught on their nest with claptraps. Photographs of the back and front with one wing stretched out were taken of each bird caught. At three nests both the male and the female were caught. On all 34 nests, egg-length and egg-width were measured to the nearest mm and incubation status was determined by measuring the angle of a floating egg in water following Van Paassen *et al.* (1984).

In 2008, JS, MR, VvdB and JvG collected data on 17 Icelandic godwit nests during the breeding season in the area of the derelict air field of Kaldaðarnes (see above). Eggs were treated similarly as in 1993, but adult birds were not caught. Instead, we obtained videos of the adults using small, battery-powered digital camcorders that were placed in close proximity (1.5 m) to the nest. These camcorders (Technaxx C-2000 and Technaxx C-8000) recorded the nest site and birds returning to their nests for 45–125 minutes. On these videos, plumage could easily be scored (for a detailed description of this method see Van den Brink *et al.* 2008). We continued to place camcorders until we had video footage of both parents; on average each nest was videotaped four times. This method allowed us to obtain video footage on both males and females at 14 nests.

Plumage assessment

Experienced observers (JS and JvG) scored three features of the plumage that have been shown to be sexually dimorphic in Black-tailed Godwits and could reliably be scored on both, photos and videos (Schroeder *et al.* 2008): (1) orange intensity, the intensity of orange colour on the breast and neck on a scale of 1 (no orange) to 5 (dark reddish plumage); (2) back-score, the proportion of pigmented breeding feathers on the back and wings of the bird in relation to the total amount of feathers on a scale of 1 (no breeding feathers) to 5 (all back and wings covered in breeding feathers); and (3) breeding feathers, the absolute number of breeding feathers on the back of the bird was counted (for more detailed description and justification, see Schroeder *et al.* 2008). Photos

Table 1. Differences between Icelandic Black-tailed Godwits and the nominate species.

Trait	*islandica*	*limosa*
Degree of plumage dimorphism	More pronounced[1,2]	Less pronounced[3]
Degree of size dimorphism	More pronounced[1,2]	Less pronounced[3]
Direction of population trend	Increasing[1]	Decreasing[1]
Breeding habitat	Lowland marshes, dwarf-birch bogs, with small numbers in extensively managed agricultural grassland[1]	Intensively managed agricultural grassland, small numbers in extensively managed agricultural grassland[1]
Expected strength of competition for high quality nesting sites	High	Low
Correlation between breeding plumage and egg volume	Positive[4]	Negative[5]

References: [1] Gill *et al.* 2007, [2] Gunnarsson *et al.* 2006b, [3] Schroeder *et al.* 2008, [4] this study, [5] Schroeder *et al.* 2009.

and videotapes were scored (by JvG and JS) without previous knowledge of the reproductive parameters. Within and between observer-repeatability was high ($R > 0.9 \pm 0.1$ *SE*, for all variables, repeatability was calculated following Lessells & Boag 1987). In our individually colour ringed population of breeding Black-tailed Godwits in the Netherlands, we have found that within individual godwits, data scored from different source media (video and photographs) are highly repeatable. We could, comparing molecular sex assignment (Schroeder *et al.* 2010b) and plumage scores of colour ringed individuals compared with birds on videos confirm relatively reliable visual sex assignment based on morphology (unpubl. data JS, Gunnarsson *et al.* 2006b, Schroeder *et al.* 2008, 2009, 2010b). Thus, although a more quantitative method of plumage scoring might seem preferable, our method, especially the videos, allows increasing sample size without catching and disturbing breeding birds. Further, spectrophotometer measurements are not suitable for strongly heterogenic plumage coloration that contains small elements of different colour in most traits, and are therefore not suitable for godwits (see Schroeder *et al.* 2008).

Data preparation and statistical methods

Egg volume was calculated by the formula length*width^2*0.52 (Romanoff & Romanoff 1949). Egg volume is more variable than clutch size, because godwits nearly always lay a clutch of 4 eggs (Beintema *et al.* 1995). In this study, >90% of all nests contained four eggs when we visited those that had only recently been started, and it can be assumed that smaller clutches occur mainly through partial predation. Larger *limosa* godwit eggs hatch heavier chicks and chicks in a better condition have a higher chance of survival (Schekkerman *et al.* 2009, Schroeder 2010). We had no data on individual fledging success, which cannot be reliably determined without the use of colour marks or radio transmitters on chicks and adults (Roodbergen & Klok 2008, Schekkerman *et al.* 2008, 2009). Therefore, for our purposes, we use average egg-volume per nest as a correlate of reproductive success. Laying-date was estimated by subtracting the laying (5 days) and incubation period (23 days) from the predicted hatching date (Beintema *et al.* 1995). Egg-volume can be related to date and we tested for the relationship between laying-date and egg-volume with a linear model where we modelled year and location as fixed effects on the intercept.

We calculated z-scores of all plumage scores per year to correct for the two different methods by subtracting the annual average from an individual raw score (Quinn & Keough 2002). Due to strong multicollinearity, we collapsed all plumage traits in a principal component analysis. The first principal component explained 82% of the variation in plumage scores (eigenvalue = 2.45), and all scores load positively on this component (loadings: orange: 0.81, back-score: 0.95, breeding feathers: 0.95). Birds that score high on this first principal component (PC1) have a brighter orange plumage and their backs are covered to a larger extent and number in ornamented feathers. We use this PC1 as an indication of plumage ornamentation in Black-tailed Godwits. We assessed normality of PC1 scores visually (Gelman & Hill 2006). Females on video tapes had a crafty way of sneaking back underneath the grass canopy to sit on their nest which resulted in poor footage of their plumage and missing values for some of the plumage scores. Therefore, apart from the analysis of assortative mating, our study focuses on the males that are expected to be the gender under strongest sexual selection and thus of most interest.

We tested for assortative mating on raw plumage traits between females and males incubating the same nest with Spearman's rank correlation test, and on PC1 with Pearson correlation (both two-tailed). We were interested in the relationship between male plumage ornamentation, timing of breeding and egg-volume. Since the relationship between reproductive success and plumage may depend on local conditions, like nest density or strength of male–male competition, we employed linear mixed models, where location (breeding area in north or south Iceland) was modelled as random effects on the intercept, year as a fixed effect, and PC1 as a covariate, and the interaction between the latter two. The random terms were never significant, but we added them to the most parsimonious model to correct for any potential bias. Different plumage characteristics can signal different information (Doucet & Montgomerie 2003). We therefore also used univariate analyses to describe the relationship between male plumage, laying-date and egg-volume in detail. The plumage scores were intercorrelated, with birds that are strongly ornamented in one trait being also more colourful with respect to the other traits (Schroeder *et al.* 2008). Therefore, if one would find a significant relationship with any given plumage score, it would be highly likely that a similar relationship is also present with the other scores. We do not apply Bonferroni tests since those correct Type I errors (false positive) in multiple independent tests. In the type of data we present here, however, it is more likely to result in a significant correlation if another one is significant. To prevent this type of problem we use the first principal component in the first place and we use both univariate and multivariate analysis to supplement each other.

Statistics were calculated with R.2.7.1 statistical software for Mac OS X (R Development Core Team 2008). The lme() function with the maximum likelihood procedure (nlme package) was employed for fitting linear mixed-effects models and we selected the most parsimonious model by Akaike's information criterion (Akaike 1973, Burnham & Anderson 2002), using the maximum likelihood method (ML). We report parameter estimates ±SE for the most parsimonious model, now estimated using restricted maximum likelihood method (REML), and report the significance values of each parameter coefficient when all other parameters are present in the model (Pinheiro & Bates 2000). We set $\alpha = 0.05$. Sample sizes differ due to missing values.

RESULTS

Plumage ornamentation described by PC1 did not differ between birds from 1993 and 2008 (males: t-test: $t = -0.83$, $P = 0.41$, $n_{1993} = 13$, $n_{2008} = 8$; females: $t = 0.58$, $P = 0.57$, $n_{1993} = 18$, $n_{2008} = 10$). The plumage sex dimorphism was distinctive: males were more colourful than females with respect to PC1 (Fig. 1; females: -0.44 ± 0.20 *se*, males: 0.58 ± 0.11 *se*, $t = -4.42$, $P < 0.001$, $n = 28$ females and $n = 21$ males). Males had more orange, a larger extent of breeding plumage and more breeding feathers on their backs (Wilcoxon-test: $W_{orange} = 250$, $n_{females} = 35$, $n_{males} = 29$, $P < 0.001$; $W_{back} = 295.5$, $n_{females} = 35$, $n_{males} = 29$, $P = 0.003$; $W_{feathers} = 154.5$, $n_{females} = 28$, $n_{males} = 22$, $P = 0.004$).

Average egg volume was smaller in 2008 ($40.25 \pm 0.58 \text{cm}^3$ *se*, $n = 17$) than in 1993: ($42.07 \pm 0.51 \text{cm}^3$ *se*, $n = 33$, $t = 2.35$, $P = 0.02$). Laying-date did not differ between the two years (28 May ± 1 day *se*, $t = -0.55$, $P = 0.59$, $n = 51$). There was no change of average egg volume per nest over the course of the season (Fig. 2, average egg volume: $\beta = 0.08 \pm 0.13$ *se*, $F_{1,31} = 0.36$; $P = 0.55$).
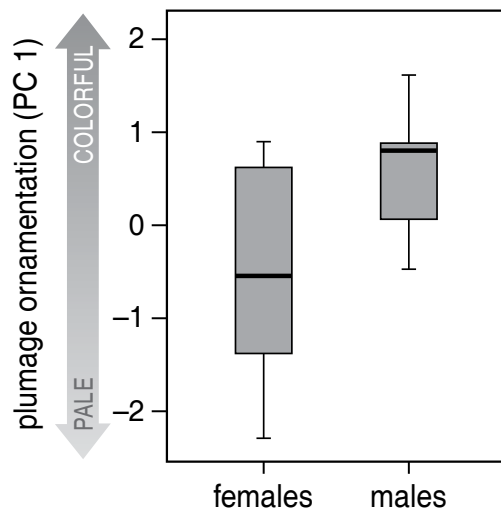
Fig. 1. Plumage ornamentation (PC 1) of male and female Icelandic Black-tailed Godwits during the breeding season. A high PC1 indicates a more ornamented breeding plumage. Whiskers depict the interquartile range of values (there where no outliers), the extent of the boxes marks the lower and upper quartile and the line inside the box gives the median value.

We found no assortative mating in relation to breeding plumage both when testing PC1 and the raw plumage scores (Table 2). However, it must be noted that in this analysis our sample size was relatively small (N = 6). Laying-date was not related to male plumage ornamentation (Fig. 3). The interaction of year and male plumage ornamentation was also not significant (model including the interaction: $\beta_{\mathrm{PC1*year}}$ = –5.45±6.94 *se, t* = –0.79; *P* = 0.44; model only including PC1 and year as main effects: β_{PC1} = 4.77±3.30 *se, t* = 1.45; *P* = 0.17; β_{year} = 0.24±0.32 *se, t* = 0.77; *P* = 0.45, *n* = 21). However, males with a more colourful plumage described by PC1 were mated with females that laid larger eggs (Fig. 3). The interaction of PC1*year was removed from the final model,

Table 2. Spearman rank correlations between breeding plumage scores of Icelandic Black-tailed Godwit males and females from the same nest. Given numbers are Spearman's rho (ρ) and one-tailed significance levels.

	ρ	*p*
Orange score (*n* = 16)	0.24	0.19
Back score (*n* = 16)	0.27	0.15
Breeding feathers (*n* = 6)	0.49	0.17
PC1 (*n* = 6)	0.30	0.28

Table 3. Spearman rank-correlations between male plumage scores (orange, back, breeding feathers) of male Icelandic Black-tailed Godwits during the breeding season and egg-volume and laying-date of the eggs they were incubating. Given numbers are Spearman's rho (ρ) and two-tailed significance levels.

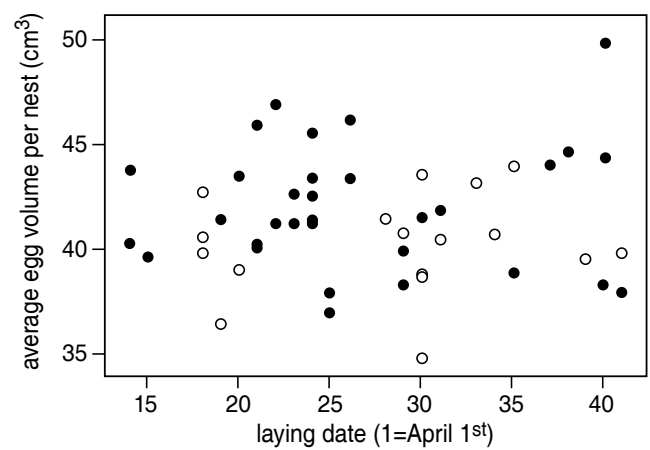|	Average egg volume		Laying date	
	ρ	*p*	ρ	*p*
Orange score (*n* = 29)	0.42	0.02	–0.10	0.61
Back score (*n* = 29)	0.31	0.11	0.18	0.33
Breeding feathers (*n* = 22)	0.38	0.08	0.15	0.50

Fig. 2. Average egg volume per Icelandic Black-tailed Godwit nests in relation to the laying date of the nest. Full circles depict nests from 1993, open circles nests from 2008.

indicating that the effect did not differ between the two years (model including the interaction: $\beta_{\mathrm{PC1*year}}$ = –2.23±2.21 *se, t-test* = –1.01; *P* = 0.33; *n* = 21). Year and the variable PC1 remained in the final model (Fig. 3, β_{PC1} = 2.45±1.12 *se, t* = 2.20, *P* = 0.04, β_{year} = –0.36±0.11 *se, t* = –3.30, *P* = 0.004, *n* = 21). Univariate correlation analyses of the raw variables supported that more colourful males were mated with females laying larger eggs. Average egg volume correlated positively with orange score while there were positive trends for the other two scores (Table 3). We found no relationship between the raw male plumage scores and laying-date (Table 3). We carried out linear regression for each dataset (1993 and 2008) separately, and the relationship between PC1 and egg-volume was marginally significant in 1993 ($F_{3,9}$= 2.40, *P* = 0.05, R^2 = 0.44, with location as a fixed factor), but not in 2008 ($F_{1,6}$= 0.57, *P* = 0.47, R^2 = 0.09, only one location).

DISCUSSION

Plumage ornamentation of male Icelandic Black-tailed Godwits was related to egg-size in 1993. The more powerful linear mixed model revealed that the pattern in 2008 could not be distinguished from that in 1993 (Fig. 3). The reason this did not show in the 2008 data in the univariate analysis may be the low sample size, or because we only used a single study area. Altogether, our study suggests that breeding plumage is a sexually selected signal in Black-tailed Godwits, and that the direction of selection may differ between the nominate and Icelandic subspecies (Schroeder *et al.* 2008, 2009).

We use egg-volume as an indicator for reproductive success because it has been shown to reflect female nutritional status at laying and female reproductive investment (Amat *et al.* 2001, Karell *et al.* 2008, Sanchez-Lafuente 2004). In godwits like in other bird species, female nutritional status is correlated to the size of the eggs laid (Schroeder *et al.* 2009). Further, egg-volume is related to chick-mass at hatching, indicating that egg-volume constrains hatchling mass, and chick body condition was related to mortality in Black-tailed Godwits (Schekkerman *et al.* 2009, Schroeder 2010). Godwit chicks are precocial and most other factors influencing the probability of fledging success are stochastic: food quality and availability, adverse weather conditions, predation and agricultural activities (Gill *et al.* 2007, Schekkerman
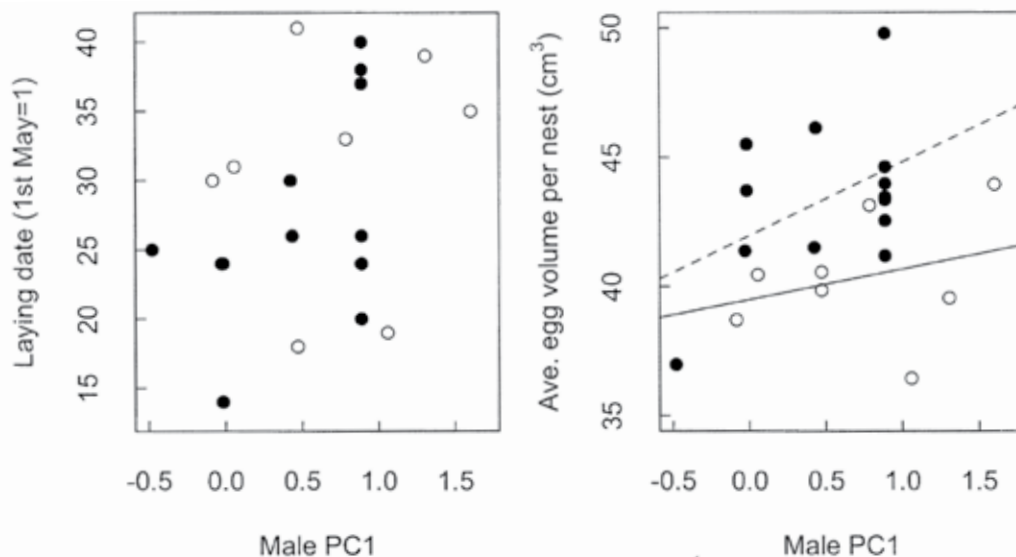
Fig. 3. Plumage ornamentation (PC1) of male Icelandic Black-tailed Godwits during the breeding season and timing of breeding and the average egg volume of the nest they were incubating. Full circles depict nests from 1993, open circles nests from 2008. Lines are linear regression lines, dashed = 1993, dotted = 2008. For statistics see text.

& Beintema 2007, Schekkerman *et al.* 2008, 2009). Thus one of the few ways a female can influence chick survival before hatching is via the amount of nutrients she allocates to her eggs. Female birds may invest more in reproduction if mated with a high quality mate (Cunningham & Russell 2000, Loyau *et al.* 2007). Thus a male godwit incubating a nest that contains relatively large eggs, in our case a more ornamented male has been able to attract a high quality female and/or a female willing to invest relatively more resources into reproduction (Fig. 3). It may also be that more ornamented males are able to secure a territory on a breeding site of high quality, which may enable females to lay larger eggs, mediated by quality or quantity of food availability. Our results support the idea that in godwits, male plumage ornamentation and female reproductive investment might directly or indirectly be linked and thus male plumage is expected to play a role in sexual selection.

Black-tailed Godwits complete moult into breeding plumage on their spring staging grounds, before arrival in Iceland. The expression of elaborated plumage ornaments must be costly if it is an honest signal of quality (Andersson 1994). If moult is costly in terms of energy or time, a more ornamented breeding plumage together with an early arrival could be an honest signal of individual quality, because such a male was able to spend time and nutrients on moult and additionally on early and/or fast migration (Drent *et al.* 2003, Kokko 1999, Piersma & Jukema 1993). Despite this, we find no relationship between timing of breeding and male plumage ornamentation (Fig. 3). Another explanation for this could be that arrival time and timing of breeding may vary between breeding areas of different quality, since those are connected with staging areas of the same quality level (Gunnarsson *et al.* 2006a), but less within (high quality) areas. In such a case, male plumage ornamentation would not be expected to vary with timing of laying within areas of equal quality. Further, if early males wait for the arrival of their females (Gunnarsson *et al.* 2006a), this would also be the case. Moreover we did not find evidence for a seasonal decline of egg-volume (Fig. 2). It may indeed be that in the high quality breeding areas studied in this paper, seasonally changing food availability

for adults is not the constraining factor when it comes to the reproductive investment decisions of females, and timing for the nutritional requirements of the precocial offspring may play a more important role (Roodbergen & Klok 2008). It is apparently important to study breeding areas of different quality, where food quality and quantity differ (Gunnarsson *et al.* 2005a).

Unlike the nominate race, where paler males are paired with females that lay larger eggs, we found that more colourful male Icelandic godwits were mated with females that laid larger eggs. In the growing Icelandic Black-tailed Godwit population, intrasexual competition is most likely higher than in the *limosa* subspecies (Gunnarsson *et al.* 2005a, b). In Iceland, it may be important to secure one of the few high quality territories for which many individuals compete, while in the Netherlands, where territory quality with respect to food for adults before egg-laying is high overall (Beintema *et al.* 1995), and reproductive success is more dependent on other variables post-hatching (Gill *et al.* 2007), this may be less important. While these conclusions are relatively speculative, it is safe to say that patterns between both subspecies are not the same, which indicates different selection pressures on male plumage traits. However, because the inverse relationship between egg-size and male plumage was found in Dutch godwits, we suggest that this pattern is most likely based on factors that differ between both subspecies and affect plumage ornamentation, with habitat differences and the population growth rate being most pronounced. Without dismissing intersexual selection, our results suggest that in Black-tailed Godwits of both subspecies, differences in intrasexual selection are most likely involved in the evolution and maintenance of sexually dimorphic plumage traits.

ACKNOWLEDGEMENTS

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