SHORT COMMUNICATION

The ornament–condition relationship varies with parasite abundance at population level in a female bird

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Abstract Environmental heterogeneity is expected to create variation in the ornament–condition relationship. This topic has been studied in males with less attention being given to females. Here, we explore inter-population variation in the relationship between the size of a male-like trait, supra-orbital combs, and body mass in female red grouse *Lagopus lagopus scoticus*. We used the abundance of the nematode *Trichostrongylus tenuis*, a parasite with strong negative effects on this species, as a proxy of environmental conditions. We studied six populations over 5 years and showed that the comb size–body mass relationship varied with mean parasite abundance, with stronger ornament–condition relationships in populations with higher parasite infection levels. Our study supports the idea that environmental conditions, and in particular parasite infection levels, may affect the reliability of female ornaments as condition indicators.

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Introduction

Signaling theories of sexual selection predict that ornament expression honestly reflects individual quality. The reliability of this signaling is thought to be maintained because only individuals that are of high (genetic) quality or in better physiological condition can afford the cost of displaying exaggerated conspicuous traits (Zahavi 1975). Although these ideas are widely accepted, and indeed positive associations between ornaments and measures of condition or fitness have been extensively shown (Cotton et al. 2004a), why this trend is often not found remains largely unexplored (Cornwallis and Uller 2009).

One explanation for the changing ornament–condition relationship is that environmental heterogeneity creates variation in the average expression of ornament size, of condition or of both (i.e., the condition-dependence relationship; Cotton et al. 2004a, b; Cothran and Jeyasingh 2010). The latter predicts that the relative differences between low- and high-quality individuals in sexual trait expression may be constrained or enhanced because of favorable or adverse environmental conditions, respectively (Cotton et al. 2004b; Cothran and Jeyasingh 2010, but see Hoffmann and Merilä 1999). As a consequence, environmental conditions should affect the strength of the relationship between ornament expression and measures of condition (i.e., its condition dependence), these being

stronger under more restrictive environmental contexts (Candolin 2000; Fargallo et al. 2007). Changing ornament–condition relationships can also be explained by genotype × environment interactions, i.e., alternative genotypes are adapted to different environmental conditions (Ingleby et al. 2010). For instance, previous findings in birds have shown that the co-variation between genetically determined colored traits and body mass depends on environmental conditions (Roulin et al. 2008; Piault et al. 2009). This suggests that different genotypes may regulate body mass in different ways (Roulin et al. 2008; Piault et al. 2009). Moreover, if viability selection associated with investment in sexual traits varies among environments, different ornament–condition relationships can be found between years and populations (Robinson et al. 2008). To date, such studies have focused mostly on male traits, with very little attention being paid to date to female traits (but see Doutrelant et al. 2008; Roulin 2009), despite their potential for acting as reliable condition indicators (Hegyi et al. 2008; Vergara et al. 2009; Martínez-Padilla et al. 2011).

The red grouse *Lagopus lagopus scoticus* is a game species that lives in the moorlands of the UK. This species displays red supra-orbital combs during social/sexual interactions. Combs are smaller in females than on males (Mougeot et al. 2005), but their size is condition dependent and positively correlated with fitness components in both sexes (MacColl et al. 2000; Mougeot et al. 2004, 2006; Seivwright 2004; Redpath et al. 2006a; Martínez-Padilla et al. 2011). In male grouse of the genus *Lagopus*, comb size functions in both male–male competition and female choice (Moss et al. 1979; Holder and Montgomerie 1993; Bart and Earnst 1999; Redpath et al. 2006a). Males with bigger combs are dominant, more aggressive, hold larger territory, and are preferred by females as they more often pair with more than one female (see Moss et al. 1979; Redpath et al. 2006a and references there-in). Although less studied than in males, several evidences suggest a similar quality advertising function of comb size in female grouse. Females erect their combs and display them in inter-sexual displays, as well as during hostile encounters with other females when defending their territory or mate (Watson and Jenkins 1964). In addition, females with bigger combs are those that pair with more aggressive males, i.e., those holding larger territories (Redpath et al. 2006a), and there is positive assortative mating by comb size (Haines 2010).

Red grouse have great temporal and spatial variation in their level of infection by *Trichostrongylus tenuis* (Redpath et al. 2006b). This nematode has well-documented strong negative effects on the condition, ornamentation, and fitness of both male and female grouse (Delahay et al. 1995; Redpath et al. 2006b; Martínez-Padilla et al. 2010, 2011). We used the abundance of this parasite in a given site and year as a proxy of environmental context, with sites and years where parasites are more abundant being those of a priori worse environmental conditions. We analyzed six populations over 5 years, covering a wide range of environmental conditions. We explored whether the relationship between female comb size and body mass as a proxy of condition (Martínez-Padilla et al. 2011) changes associated to the average *T. tenuis* abundance in a given site and year. Previous studies have highlighted that the condition dependence of male comb size may be context dependent (Martínez-Padilla et al. 2010), with stronger ornament–condition relationships (i.e., steeper slopes) under more competitive environments (Moss et al. 1996; Vergara et al., unpublished data). Here, we focus on females and explore whether the contrasted environmental contexts, and specifically the infection levels by *T. tenuis* parasites in the population, are associated with different comb size–body mass relationships. Adverse conditions should enhance the relative differences between low- and high-quality individuals (Cotton et al. 2004b; Cothran and Jeyasingh 2010), so we predicted that the comb size–body mass relationship should vary according to mean parasite infection levels, with steeper slopes being found in those sites and years with higher parasite abundances.

Methods

General procedures

In 2001–2002 and 2009–2011, we captured and individually marked 373 female red grouse in spring from six UK populations, three in western Scotland, Edinglassie (57°12′N, 03°07′W), Glen Muick (56°56′N, 03°06′W) and Invermark (56°54′N, 02°50′W), and three sites in northern England, Catterick (54°20′N, 01°51′W), Gelstdale (54°52′N, 2°38′W), and Moorhouse (54°44′N, 02°23′W). The average distance between nearest populations was 31 km (range, 16–58 km), and the furthest apart were separated by ca. 300 km. In all sites heather, *Calluna vulgaris* is the predominant vegetation. Gelstdale and Moorhouse are managed as reserves (by RSPB and English Nature, respectively) while the rest of sites are managed for red grouse shooting (see Martínez-Padilla et al. 2011 for more details). Captures were carried out in the following years for each population: Catterick (2002, 2009–10), Edinglassie (2001), Geltsdale (2009–10), Glen Muick (2001–02), Invermark (2001, 2011), and Moorhouse (2002, 2009). Overall, data were available from 12 site-years. Each female was ringed, and we determined age (young, <1-year-old or adult, >1-year-old) from plumage characteristics, measured body mass (grams) and comb area (length × width, square millimeters) as an index of trait size (Mougeot et al. 2005; Martínez-Padilla et al. 2011).

Parasite population mean

A sample of individuals (average=40, range=17–107), including females and males, were captured for each site and year and kept overnight in boxes to collect fecal samples (Redpath et al. 2006b). We used fecal egg concentration to estimate *T. tenuis* abundance using a previously validated method (Seivwright et al. 2004) routinely used for red grouse (Redpath et al. 2006b). Parasite abundance does not differ between sexes (Mougeot et al. 2005), so we used data from both sexes to calculate "parasite population mean," i.e., average (geometric mean) *T. tenuis* abundance in each site -year.

Statistical analyses

We used General Linear Mixed Models in SAS 9.0 (PROC-MIXED procedure). We analyzed if the comb area–body mass relationship varied with parasite population mean. Comb area was the response variable with body mass, parasite population mean, and their interaction as explanatory terms. We included age (young vs. adult; combs are larger in old females; Martínez-Padilla et al. 2011), capture date of each female (1=1 January) as explanatory terms, and site and year as random variables in models.

In a separate model, we also analyzed whether the comb area–body mass varies with parasite population mean in a non-linear way by including a quadratic term (parasite population mean^2) in the model and by testing for a body mass × parasite population mean^2 interaction. Such a quadratic (plateau like) relationship could be predicted if fecundity compromises investment in ornamentation only, or more, under adverse conditions as compare with favorable environments (Morales et al. 2009). We used the Satterthwaite method to calculate degrees of freedom. In some rare cases, the same female was recaptured in different years. If so, we only used one data per female, that of the first capture, in the analyses. We repeated the models twice, first using untransformed comb size data, which were normally distributed, and second using the square root transformed comb area, and the cube root transformed body mass. The second analysis was conducted to check if there was no bias because of the different xscaling of each variable, which may also make the relationship between both variables non-linear (e.g., plateauing effect on comb area as body mass increases). In addition, to verify that unequal sample sizes between site-year were not an issue, we repeated our analysis with a subsample of eight (that is our minimum sample size) randomly selected individuals per site and year. Note that the Satterthwaite correction was not used in this case, given the balanced sample size. Lastly, to avoid potential problems associated with the collinearity of variables (body
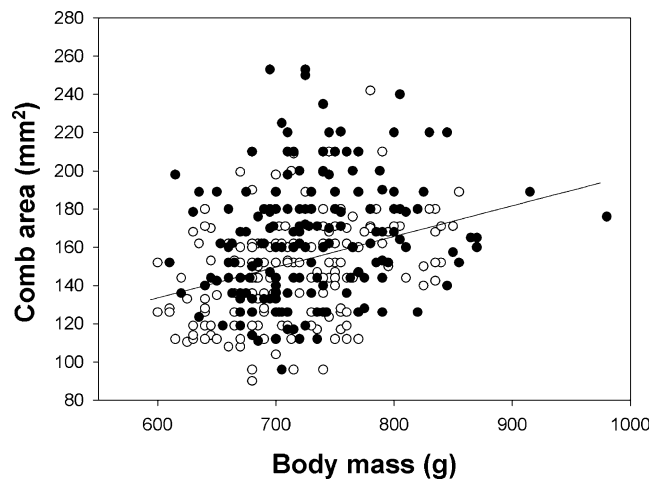

Fig. 1 Relationship between comb area (square millimeters) and body mass (grams) in female red grouse. *White and black circles* represent young and adult females, respectively

mass being negatively correlated with parasite population mean: GLMM, $F_{1,39.3}$=5.36, P=0.021, estimate=−0.01), we used centered body mass (individual body mass minus average body mass of the population) instead of body mass (centered body mass being not significantly related to parasite population mean; $F_{1,370}$=0.14, P=0.70).

Results

Comb area and body mass were overall positively correlated ($F_{1,364}$=14.27, estimate=0.11±0.03, P<0.001, Fig. 1; see also Martínez-Padilla et al. 2011). The relationship was linear (Fig. 1) and did not differ between age classes (body mass × age, $F_{1,357}$=0.21, P=0.649). However, the comb area–body mass relationship varied according to parasite population mean (Table 1). As predicted, the slope of this relationship was steeper as parasite population mean increased (Fig. 2). Neither body mass^2 nor the body mass × parasite population mean^2 interaction was significant (both P> 0.148), so we had no evidence of a quadratic relationship. Using the square root transformed comb area and cube root transformed body mass values in our model did not change the results (Table 1). Similarly, the interaction between body mass and parasite population remained significant when using a reduced but balanced dataset of only eight individuals per site and year ($F_{1,76}$=6.81, estimate=0.0002±0.00001, P=0.010). Using centered body mass (individual body mass minus average body mass of the population) instead of body mass, the interaction between centered body mass and parasite population mean explaining variation in comb area also remained significant ($F_{1,360}$=3.90, estimate=0.0001± 0.00007, P=0.049). The coefficients of variation (CV = σ/μ) for both comb area ($F_{1,6}$=4.77, estimate=0.00003±

Table 1 Effect of parasite population mean on the female comb area–body mass relationship

Response term	Explanatory term	Rejected term	df	F	P	Estimate±SE
Comb area	Parasite population mean (PPM)		1, 242	5.33	0.021	−0.077±0.033
	Body mass		1, 235	0.24	0.621	−0.03±0.07
	Age		1, 367	32.73	<0.001	−16.58±2.89
	PPM × body mass		1, 258	5.40	0.020	0.0001±0.00004
	Day of capture		1, 11.2	6.58	0.010	0.35±0.13
		PPM × age	1, 358	0.14	0.708	−0.001±0.004
		Body mass × age	1, 355	0.13	0.722	−0.01±0.05
		PPM × body mass × age	1, 356	0.97	0.326	−0.00009±0.00009
Square root comb area	Parasite population mean (PPM)		1, 315	3.89	0.049	−0.007±0.003
	Cubic root body mass		1, 314	0.08	0.781	−0.18±0.67
	Age		1, 362	28.77	<0.001	−0.59 ±0.11
	PPM × cubic root body mass		1, 320	3.99	0.046	0.0008±0.00004
	Day of capture		1, 20	7.69	0.011	0.015±0.005
		PPM × age	1, 356	0.01	0.908	−0.00002±0.0001
		Cubic root body mass × age	1, 359	0.16	0.692	−0.19±0.48
		PPM × cubic root body mass × age	1, 358	0.47	0.493	−0.0005±0.0008

Year and site were included as random factors. Parameter estimates ± SE for the model with untransformed comb area were as follows: year= 51.13±132.82, Z=0.38, P=0.350; site=53.94±88.75, Z=0.61, P=0.271. Parameter estimates ± SE for the model with root squared comb area were as follows: year=0.18±0.26, Z=0.71, P=0.239; site: 0.04±0.07, Z=0.55, P=0.290. Parameters given for "age" are those of young females. Terms were sequentially removed when not significant (P=0.05) following a backward procedure

0.00001, P=0.071) and body mass ($F_{1,4.27}$=7.01, estimate=6.13 e^{-6}±2.31e^{-6}, P=0.053) were not correlated with parasite population mean (untransformed variables and year and site included as random factors). We thus had no obvious evidence that the stronger relationships found between body mass and comb area when parasites were more abundant were due to greater variances in these parameters.

Discussion

Our study shows that the ornament–condition relationship in a female bird varies with parasite infection at population level. This is consistent with the hypothesis that the condition dependence of female sexual traits is mediated by environmental conditions. Any indicator of worsened environmental condition is likely associated with a reduced individual body condition and also possibly a reduced sexual trait expression (Cothran and Jeyasingh 2010). We used average *T. tenuis* abundance in a given site and year as an index of environmental context because of the well-known negative effects of this parasite on the condition, fitness, and ornamentation of red grouse (Delahay et al. 1995; Redpath et al. 2006b; Martínez-Padilla et al. 2010, 2011). Indeed, *T. tenuis* have been shown by experiment to reduce female red grouse body mass and comb area (Delahay and Moss 1996; Martínez-Padilla et al. 2011). Here we found that the comb area–body mass relationship greatly varied across sites and years with different parasite abundance levels, the relationship being stronger when parasites were more abundant. It has been suggested that
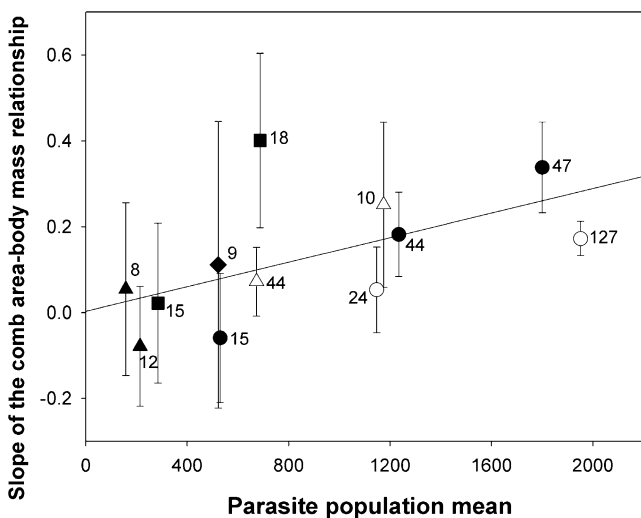

Fig. 2 Relationships between parasite population mean and the slopes (±SEM) of the comb area (square millimeters)–body mass (grams) relationship. *Different symbols* highlight different populations. *Numbers next to symbols* refer to sample sizes (number of females per site and year)

the trade-off between investment in ornamentation and other reproductive traits (e.g., egg formation) becomes more important under adverse conditions (Chenoweth et al. 2006; Morales et al. 2009). If so, we would predict a quadratic rather than a linear relationship in the strength of the ornament–condition relationship according to the environmental conditions: weak relationships under favorable conditions because most individuals may reach both increased ornament expression and body condition, stronger relationships at intermediate levels of environmental quality because the enhanced differences between low- and high-quality individuals under such conditions, and again weak ornament–condition relationships under extremely adverse conditions because fecundity compromises investment in ornamentation. Interestingly, we showed that the slope of the ornament–condition relationship decreased in the population with the highest parasite abundance (see Fig. 2). Within our data range, we had no evidence of a quadratic relationship, possibly no studied population had extremely high mean parasite abundances. Indeed, previous works on red grouse indicate that *T. tenuis* has marked negative effects above parasite intensities of ca. 3,000 worms per bird (Hudson et al. 1992). Nevertheless, our results suggest that the capacity of comb area as a predictor of body mass is influenced by the current parasite infection level in the population. To the best of our knowledge, our results constitute the first empirical evidence that the reliability of a female ornament as an indicator of condition varies with parasite abundance. In the future, this finding should be corroborated through experimental studies. As *T. tenuis* can also be affected by factors such as temperature or rainfall (Moss et al. 1993), experiments should now be conducted to demonstrate a direct role of this nematode in mediating the ornament–condition relationship.

Although far from being fully understood, changing relationships between ornament expression and costly phenotypic traits have been found in males across contrasted environments (Candolin 2000; Fargallo et al. 2007). Our results are consistent with the patterns observed in male red grouse, as previous findings showed that the slope of the comb area–body mass relationship is higher under more adverse environments in terms of aggressiveness in the population (Moss et al. 1996) and infection by *T. tenuis* (Vergara et al., unpublished data). Our results thus support the same prediction (varying relationships between costly phenotypic traits in contrasted environments) but for a female conspicuous trait. Several explanations for this stronger ornament–condition relationship under more restricted environments have been proposed. Adverse and favorable environments may increase or decrease, respectively, the relative differences between low- and high-quality individuals in sexual trait expression (Cotton et al. 2004b; Cothran and Jeyasingh 2010). If so, the ornament–condition relationship

may change between contrasted environments, with steeper relationships expected under adverse conditions (Candolin 2000; Fargallo et al. 2007; Doutrelant et al. 2008). These patterns can also be explained by allocation priorities towards ornamentation as opposed to self-maintenance needs that differ between contrasted environments (Martínez-Padilla et al. 2010) or by genotype × environment interactions, as for instance when genetically determined ornamentation co-varies with condition according to environmental conditions (Roulin et al. 2008; Piault et al. 2009). Further studies are needed to distinguish between these or other alternatives. Irrespective of the mechanism behind the observed pattern of change in the comb area–body mass relationship across environments, the importance of our results lays in that changing environmental conditions likely affect the reliability of the female conspicuous trait as a condition indicator. This idea is attracting growing interest in sexual selection studies focusing on male ornaments because the unreliability of ornaments may compromise the operation of sexual selection mechanisms (e.g., promoting wrong preferences, see Ingleby et al. 2010). Our study indicates that these concepts, initially developed for male ornaments, also apply to female conspicuous traits, which at least in some cases, may also have evolved or may be maintained via sexual selection processes. Therefore, for adequately testing the intra- or inter-sexual selection of female conspicuous traits, the environmental context should be taken into account.

In conclusion, our study stresses out that the environmental context may modify the ornament–condition relationship in females, as it does in males (Cothran and Jeyasingh 2010), a pattern that may compromise the value of female conspicuous traits as indicators of condition.

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