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Original Article

The condition dependence of a secondary sexual trait is stronger under high parasite infection level

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Indicator models of sexual selection predict that the expression of sexual ornaments should be condition dependent. This is only partly supported by data, as many studies do not find positive associations between ornaments and condition. The reason for this inconsistency remains poorly understood. It has been hypothesized that environmental context may explain variation in the condition dependence of sexual traits, with stronger relationships between ornaments and condition expected in harsher environments. However, field tests of this idea are scarce. We studied 9 populations of wild red grouse *Lagopus lagopus scoticus* over 11 years, and compared the relationship between ornamentation and body mass (an index of body condition) in relation to environmental variability. We used the abundance of a key parasite in this system, *Trichostrongylus tenuis*, as an index of environmental conditions. We found that both ornament expression and body mass negatively correlated with parasite infection at both population and individual levels. More interestingly, we found that the relationship between ornamentation and body mass was stronger in populations with high parasite infection levels. Our findings support the idea that the condition dependence of secondary sexual ornaments varies in relation to environmental context. In sites and years when parasites are abundant, sexual ornaments provide better signals of condition. *Key words:* genotype × environment interactions, honest signaling, indicator model, *Lagopus lagopus scoticus*, sexual selection, *Trichostrongylus tenuis*. *[Behav Ecol]*

INTRODUCTION

Indicator models of sexual selection predict that the expression of sexual ornaments should be condition dependent: The best ornaments should be displayed by individuals in prime condition, enabling potential mates or competitors to reliably assess individual condition. The reliability of this signaling is thought to be maintained by the fact that individuals in poor condition have higher relative costs of ornament expression (Zahavi 1975; Grafen 1990). Accordingly, positive relationships between ornament expression and measures of condition (understood as a pool of resources) have been widely seen in nature (Andersson 1994; Cotton et al. 2004b). However, this condition dependence of sexual ornaments may strongly change throughout an individual's lifetime or may differ between sites (e.g., Candolin 2000; Badyaev and Duckworth 2003; Cothran and Jeyasingh 2010; Dunn et al. 2010), although the reasons for such changes have been rarely analyzed and remain poorly understood.

Environmental context is considered an important factor explaining the changing condition dependence of sexual traits (Candolin 2000; Cothran and Jeyasingh 2010). The way that individuals solve the allocation trade-offs between limited resources to ornamentation versus other costly activities such as self-maintenance, is a key aspect underlying the condition dependence of sexual signals (Gustafsson et al. 1995). These trade-offs may vary between different environments (Gustafsson et al. 1995; Robinson et al. 2008; Martínez-Padilla et al. 2010). Under favorable environments, we would expect both high- and low-condition individuals to be less constrained and equally able to display larger or brighter ornaments; this could result in a decoupling of the relationship between ornament expression and condition (David et al. 2000; Cotton et al. 2004a; Fargallo et al. 2007; Cothran and Jeyasingh 2010). Therefore, the condition dependence of sexual displays may be mediated by environmental context, with stronger (i.e., steeper or tighter) ornament-condition relationships being expected under restrictive environments and weaker relationships in the most favorable environments (Candolin 2000; Fargallo et al. 2007; Vergara et al. 2012). The environmental context is a reflection of a wide range of factors, including food supply, adverse weather conditions, and indirect effects of predators, social stress, or parasites. In this paper, we explore how parasite infection levels modify the ornament-condition relationship.

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Parasites often have a central role in the resolution of life-history trade-offs in animals (reviewed by Sheldon and Verhulst 1996; Norris and Evans 2000). Parasites may decrease resources available to hosts, thus preventing investment in costly activities, such as reproduction or self-maintenance (Sheldon and Verhulst 1996; Norris and Evans 2000). There is also evidence that parasites directly affect ornament expression (Hamilton and Zuk 1982; Møller et al. 1999). Females may prefer males with the most exaggerated or brightest ornaments because these reliably indicate male qualities, such as a better immunocompetence, a reduced parasite load, or a greater ability to cope with parasites (Hamilton and Zuk 1982; Andersson 1994; Hill 2006). Parasite abundance depends on environmental factors, such as habitat characteristics, weather conditions, or host population density (Hudson et al. 2002; Altizer et al. 2006; Loiseau et al. 2010). Because of these differences in parasite abundances, the allocation trade-offs resolutions may also differ among years and populations. Under high parasite intensities, individuals should invest relatively more in parasite defense, thus decreasing the level of resources allocated to sexual ornamentation. Under such circumstances, only individuals in prime condition, better able to cope with parasites, should display more elaborate ornaments. However, when parasite abundance is low, the detrimental effects of parasites on condition may be less severe, and differences in ornament expression between high- and low-condition individuals may be relaxed. Therefore, a stronger condition dependence of sexual traits is expected under high than under low parasite intensities (Dunn et al. 2010; Edler and Friedl 2010). This prediction has been recently confirmed in a female bird (Vergara et al. 2011) but remains untested in males.

The red grouse *Lagopus lagopus scoticus* is a Tetraonid bird that displays bright red supraorbital combs, a secondary sexual trait whose size functions in inter- and intrasexual selection. Males displaying bigger combs are dominant and preferred by females (Moss et al. 1979; Redpath, Mougeot, Leckie, and Evans 2006). As predicted by the indicator models, comb size in red grouse positively correlates with several measures of condition (Mougeot et al. 2004, 2006, 2010), but there is also evidence that these relationships may be context dependent (Moss et al. 1996; Martínez-Padilla et al. 2010; Vergara et al. 2012). *Trichostrongylus tenuis* is the main parasite in this system (Hudson 1986; Redpath, Mougeot, Leckie, Elston, et al. 2006). This nematode has strong negative effects on red grouse condition indices, breeding success, survival (Delahay et al. 1995; Hudson et al. 1998; Mougeot et al. 2010), and the expression of ornaments (Mougeot, Evans, et al. 2005; Mougeot, Redpath, et al. 2005; Martínez-Padilla et al. 2007). Parasite abundance varies strongly between years and localities (Hudson 1986; Redpath, Mougeot, Leckie, Elston, et al. 2006; Watson and Moss 2008). We used this variation to study how contrasting environmental contexts affect the condition dependence of secondary sexual traits. The relationship between comb area and body mass (an index of condition, see below) in male grouse greatly varies between environmental contexts, becoming stronger under adverse conditions, particularly when the aggressiveness in the population was experimentally increased (Vergara et al. 2012). By means of testosterone implants in males, the aggressiveness in several grouse populations was experimentally modified over one and a half years (Mougeot, Evans, et al. 2005). This manipulation modified the comb area–body mass relationship, this relationship being stronger (i.e., with a steeper slope) in the areas where the aggressiveness was experimentally increased (Vergara et al. 2012). However, this experiment does not exclude a possible role for other environmental factors, such as parasites in strengthening the condition-ornament relationship. Therefore, the next logical step is to explore whether other environmental factors may alter the condition dependence of the sexual trait, and particularly, the effect of *T. tenuis* as this nematode has been considered one of the most important environmental stressors affecting this species (Watson and Moss 2008). We analyze data from 9 populations over 11 years to examine if changes in the relationship between ornament size (comb area) and condition (measured as body mass) in male red grouse are associated with *T. tenuis* abundance. We predicted lower sexual trait expression and condition, as well as stronger condition dependence of sexual traits (i.e., steeper and tighter comb area–body mass or comb-body condition index relationship; see below), in environments with higher parasite abundance.

MATERIALS AND METHODS

Between 2000 and 2011, we captured a total of 1564 male red grouse in spring and autumn in 9 populations throughout the United Kingdom (Catterick, Geltsdale, and Moorhouse in northern England; and Edinglassie, Glenn Dye, Glen Muick, Invermark, Invercauld, and Millden in Scotland, see Martinez-Padilla et al. 2011 and Supplementary data for more details). Captures were not carried out every year or season in all the study populations, but, overall, data were available for a total of 17 spring-site-years and 18 autumn-site-years, each providing different population contexts. Individuals were ringed and aged as young (<1-year old) or adult (>1-year old) from their plumage (see Cramp and Simmons 1980). We measured their comb area (maximum length × width of flattened combs, in square millimeters) as a proxy of ornament size (Mougeot et al. 2004, 2010; Martínez-Padilla et al. 2010) and their body mass (with a Pesola scale, in grams). For some males, we also measured wing length (millimeters) as an index of size and to calculate the body condition index of mass corrected for size. Body mass (corrected or not by size) in this species is strongly affected by environmental stressors such as *T. tenuis* parasites (Delahay et al. 1995; Mougeot and Redpath 2004; Mougeot et al. 2010) or aggressiveness levels in the population (Mougeot et al. 2006; Vergara et al. 2012) and positively correlates with food intake (Delahay and Moss 1996) and proxies of physiological condition (Mougeot et al. 2010) or immunocompetence (Mougeot et al. 2004). Therefore, body mass can be used as a proxy for individual condition in red grouse (Mougeot et al. 2006, 2010).

Parasite abundance

A subsample of captured individuals (including females, see Martinez-Padilla et al. 2011) per site, year, and season (mean = 39, standard deviation [SD] = 23) were kept overnight in individual boxes to collect fecal samples and released back to the wild in the early morning (Redpath, Mougeot, Leckie, Elston, et al. 2006). We used fecal egg concentration to estimate *T. tenuis* abundance (at individual level) using standard techniques (see Seivwright et al. 2004). We then calculated the geometric means of *T. tenuis* per individual in each site, season, and year as an index of infestation by parasites at population level (Redpath, Mougeot, Leckie, Elston, et al. 2006). To distinguish between *T. tenuis* abundance at individual and population levels, the average parasite abundance level in a given site-year-season is hereafter referred as to the mean parasite load at the population level.

Statistical analyses

We used general linear mixed models in SAS 9.0 Statistical Software (PROC MIXED procedure). First, we tested if ornament size and its condition dependence (i.e., the comb area–body mass

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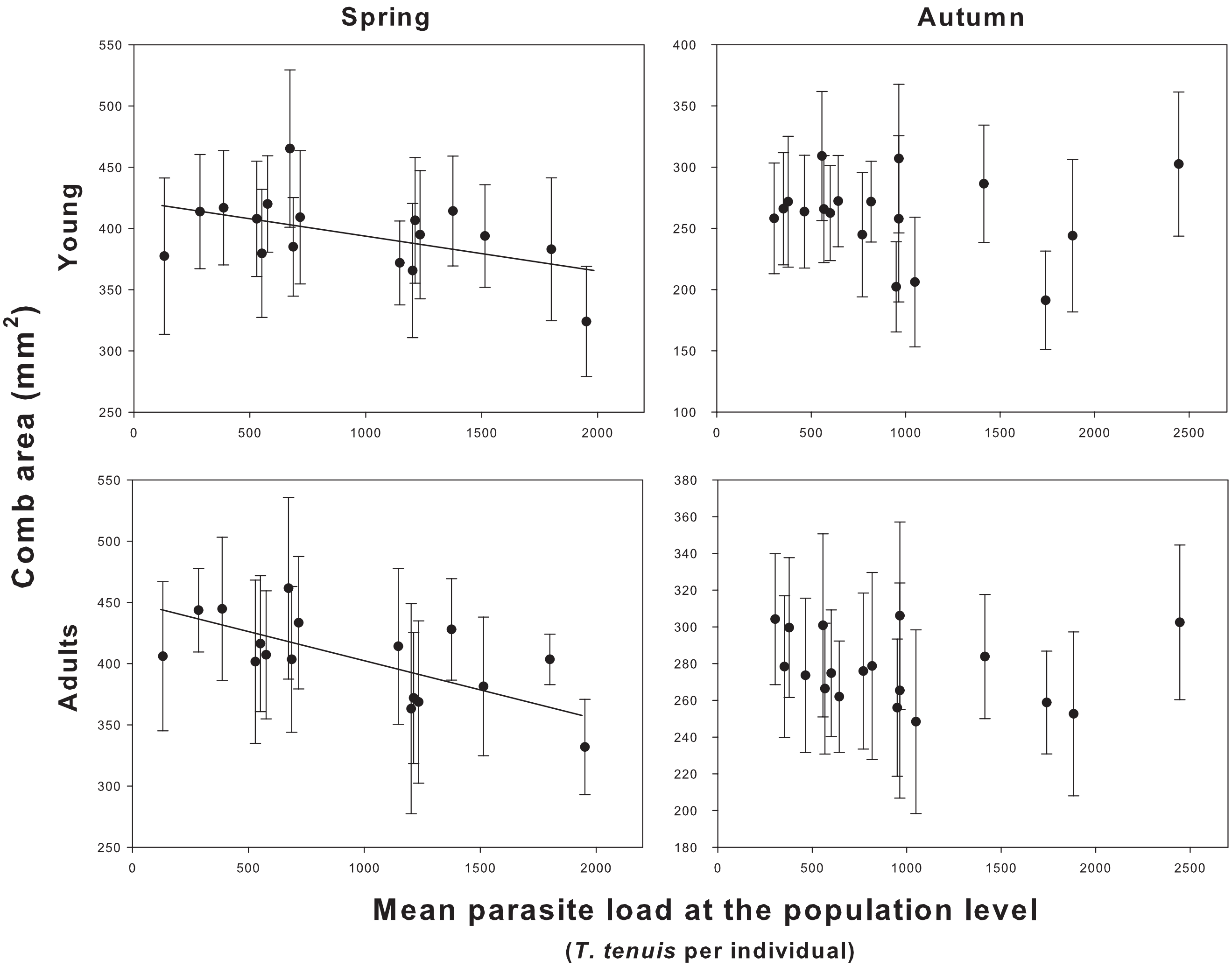

Figure 1
Mean ± SD comb area (mm^2) according to age (adults vs. young), season (spring vs. autumn), and mean parasite load at the population level. The mean parasite load at the population level is the average (geometric mean) *Trichostrongylus tenuis* abundance (worms per individual) in each population, year, and season.

relationship) varied according to the mean parasite load at the population level. To do this, comb area was the response variable, and body mass, mean parasite load at the population level, and their interaction were the explanatory terms. Second, we analyzed if body mass (response variable) varied with mean parasite load at the population level. In addition, we analyzed if the coefficients of variation ($CV = \sigma/\mu$) of comb area and individual body mass per site, year, and season were related to the mean parasite load at the population level. As this measure of parasite load was not normally distributed (Shapiro–Wilk test $P = 0.028$), we also repeated these analyses using the log-transformed mean parasite load (Shapiro–Wilk test $P = 0.63$). Finally, we also looked at the relationships between comb area, body mass, and *T. tenuis* abundances at the individual level. We also repeated all these models using a more restricted data set (with the males for which wing length was measured) and using the body condition index instead of body mass (see below). Season (spring vs. autumn) and age (young vs. adult) were included as fixed factors in all models, and the potential interactions between the studied variables were also tested and sequentially removed from models when not significant ($P = 0.05$ level). Capture date (Julian date) was also included as a covariate to correct for different sampling dates. Because we had individuals from the same site and year, we included these 2 factors as random variables in all models. Only one data point per individual was included in models, always considering the first capture of each individual. Wing length and *T. tenuis* abundance at individual level were not measured in all individuals ($n = 1268$ and $n = 763$, respectively), thus sample sizes differ between models.

RESULTS

Comb area–body mass relationship and mean parasite load at the population level

Comb area differed between age classes and seasons (both $P < 0.0001$). Adult males had larger combs than young males, and combs were bigger in spring than in autumn (Figure 1). Comb area was also negatively related to mean parasite load at the population level (Table 1), this relationship being steeper in spring than in autumn and in adults than in young (Table 1, Figure 1). Specifically, comb area was negatively related to mean parasite load at the population level in both young ($F_{1,291} = 10.71$, estimate $= -0.03$, $P = 0.001$; Figure 1) and adults ($F_{1,248} = 19.11$, estimate $= -0.03$, $P < 0.001$; Figure 1) in spring but not in autumn (young $F_{1,530} = 0.76$,

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Table 1

Effect of the mean parasite load at the population level on the relationship between comb area and body mass

Dependent variable: comb area

Explanatory	Rejected	df	*F*	*P*	Estimate ± SE
Body mass (BM)		1,1532	13.76	**<0.001**	0.068 ± 0.065
Parasite load at the population level (PPL)		1,1532	10.69	**0.001**	−0.10 ± 0.04
Age (A)		1,1532	0.00	0.967	−138.58 ± 49.39
Season (S)		1,1532	40.58	**<0.001**	170.66 ± 66.85
BM × PPL		1,1532	8.96	**0.002**	0.0001 ± 0.00005
BM × A		1,1532	0.08	0.781	0.16 ± 0.06
BM × S		1,1532	3.24	0.071	0.29 ± 0.08
PPL × A		1,1532	4.94	**0.026**	0.011 ± 0.005
PPL × S		1,1532	79.05	**<0.001**	−0.07 ± 0.008
A × S		1,1532	10.40	**0.001**	273.69 ± 84.87
BM × A × S		1,1532	10.30	**0.001**	−0.37 ± 0.11
Day of capture		1,1532	95.68	**<0.001**	1.02 ± 0.10
	BM × PPL × S	1,1531	3.15	0.075	−0.0001 ± 0.0001
	PPL × A × S	1,1530	0.23	0.629	−0.005 ± 0.010
	BM × PPL × A	1,1529	0.18	0.668	0.00004 ± 0.0001
	BM × PPL × A × S	1,1528	0.01	0.916	−0.00002 ± 0.0002

Results of the general linear mixed models analyzing the comb area–body mass relationship under different mean parasite load at the population level (average *Trichostrongylus tenuis* abundance in each population, year, and season). The model also included age (young vs. adults), season (spring vs. autumn), and associated interactions as fixed effects and included year and site as random factors. Estimates in interactions with age classes and season factors correspond to young and spring levels, respectively. df, degrees of freedom. Significant *P*-values area given in bold.

$P = 0.76$; adults $F_{1,429} = 0.01$, $P = 0.90$). In addition, comb area was positively correlated with body mass at the individual level, and this relationship was dependent on the mean parasite load at the population level (Table 1; significant comb area × mean parasite load at the population level interaction, Figure 2). As predicted, the strength of the comb area–body mass relationship varied with mean parasite load at the population level, the relationship being steeper and tighter when parasites were more abundant at the population level (Figure 2). This relationship did not differ between seasons or age classes (Table 1). Results remained similar when using the log-transformed mean parasite load at the population level instead of the untransformed variable (see Supplementary data). When using the body condition index (mass corrected for size, i.e., residuals of the body mass–wing length relationship) instead of body mass, the results were also unchanged: The relationship between comb area and body condition index was dependent on the mean parasite load at population level (body condition index × mean parasite load at the population level $F_{1,1240} = 9.31$, $P = 0.002$, slope ± standard error [SE], 0.0002 ± 0.00007, $n = 1268$). Finally, the relationship between comb area and body mass differed between seasons and age classes (i.e., body mass × age × season, see Table 1). This relationship was steeper in young (estimate ± SE, 0.38 ± 0.04) than in adults (estimate ± SE, 0.18 ± 0.04) in autumn (body mass × age $F_{1,974} = 6.02$, $P = 0.014$). In spring, the relationship between comb area body mass was similar between age classes (body mass × age $F_{1,553} = 2.94$, $P = 0.087$).

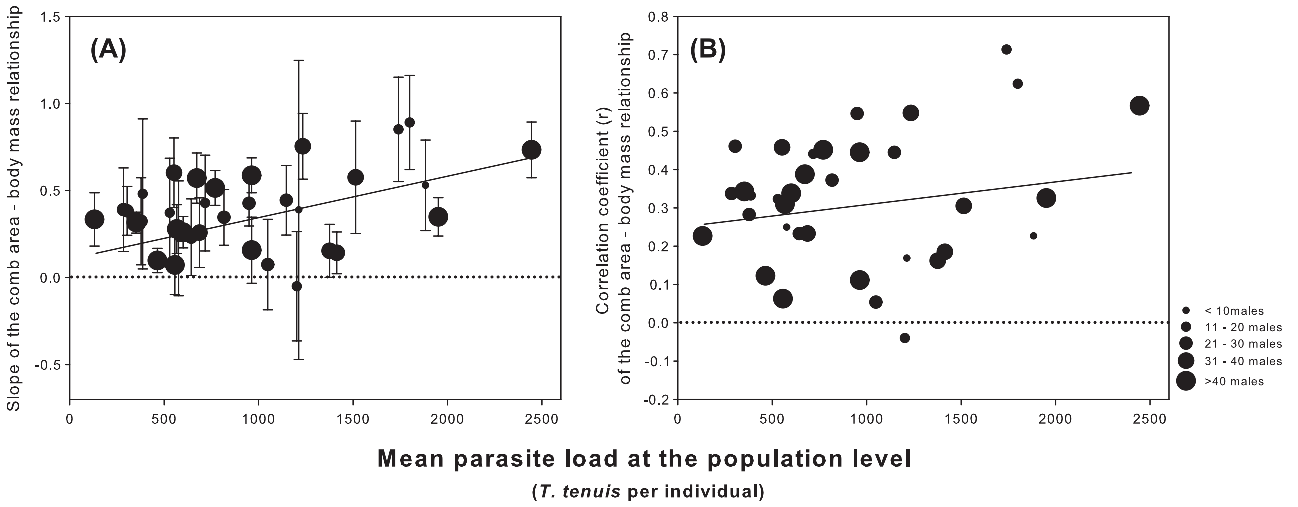

Figure 2

Variation in the condition dependence of comb area according to mean parasite load at the population level. *y* axis: (A) slopes (±SE) and (B) correlation coefficient of the comb area (mm^2)–body mass (g) relationship. *x* axis: average (geometric mean) *Trichostrongylus tenuis* abundance (worms per individual) in each population, year, and season. Different symbols represent different sample sizes in each population, year, and season.

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Table 2
Effect of the mean parasite load at the population level on male body mass

Dependent variable: body mass

Explanatory	Rejected	df	*F*	*P*	Estimate ± SE
Parasite load at the population level (PPL)		1,1539	6.70	**0.009**	−0.020 ± 0.005
Age (A)		1,1539	154.30	**<0.001**	−35.73 ± 2.83
Season (S)		1,1539	2.94	0.086	−20.23 ± 8.24
PPL × S		1,1539	8.12	**0.004**	0.018 ± 0.006
A × S		1,1539	7.79	**0.005**	13.04 ± 4.67
	Day of capture	1,1538	2.52	0.112	0.145 ± 0.09
	PPL × A	1,1537	2.19	0.139	0.006 ± 0.004
	PPL × A × S	1,1536	0.56	0.455	−0.006 ± 0.008

Results of the general linear mixed models analyzing the body mass—mean parasite load at the population level (average *Trichostrongylus tenuis* abundance per individual in each population, year, and season) relationship. The model also included age (young vs. adults), season (spring vs. autumn), and associated interactions as fixed effects and included year and site as random factors. Estimates in interactions with age classes and season factors correspond to young and spring levels, respectively. df, degrees of freedom. Significant *P*-values area given in bold.

To avoid potential problems associated with colinearity between studied variables, we also tested whether the comb area–body mass relationship varied with mean parasite load at the population level using centered body mass (individual body mass minus the average body mass of each site and year) instead of raw body mass. Centered body mass was not related to mean parasite load at the population level ($F_{1,1539} = 0.78$, $P = 0.37$), but the interaction between centered body mass and mean parasite load at the population level explaining variation in comb area remained significant ($F_{1,1532} = 7.59$, $P = 0.006$). To check that there was no bias because of the differences in the scaling of each variable, which may also make the relationship between comb area and body mass nonlinear (e.g., plateauing effect on comb area as body mass increases), we repeated the analysis using the square root transformed comb area and the cube root transformed body mass (see Vergara et al. 2011, 2012). Using the transformed values in our model did not change the relationship between mean parasite load at the population level and the comb area–body mass relationship (transformed body mass × mean parasite load at the population level $F_{1,1532} = 11.22$, $P = 0.0008$, slope ± SE, 0.001 ± 0.0003). The CV of comb area per site, year, and season was not correlated with mean parasite load at the population level ($F_{1,13} = 1.06$, $P = 0.322$), irrespective of season (nonsignificant mean parasite load at the population level × season interaction $F_{1,11} = 0.32$, $P = 0.580$).

Body mass and mean parasite load at the population level

Body mass differed between age classes, with adults being heavier than young birds, especially in autumn (Table 2; mean ± SD, adults spring = 743 ± 44, $n = 264$; adults autumn = 753 ± 49, $n = 446$; young spring = 723 ± 43, $n = 307$; young autumn = 716 ± 45, $n = 547$). In addition, body mass was negatively correlated with mean parasite load at the population level (Table 2, Figure 3), although through their interaction with season

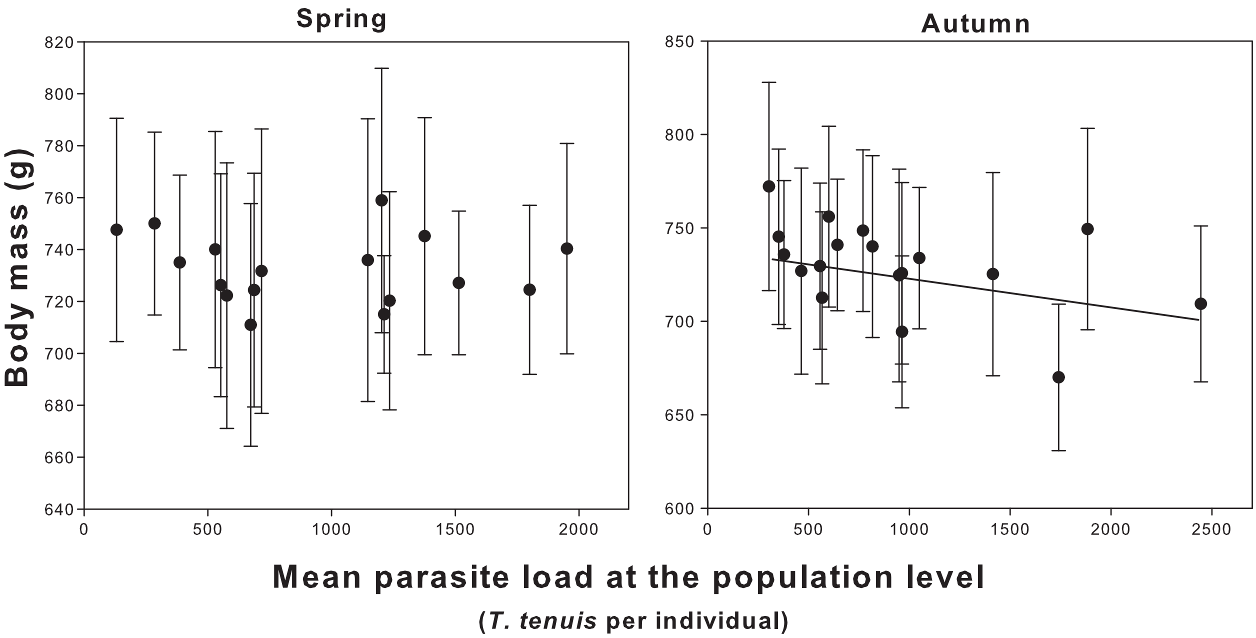

Figure 3
Mean ± SD body mass (g) according to season and mean parasite load at the population level (average *Trichostrongylus tenuis* abundance per individual in each population, year, and season).

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Table 3

Relationships between comb area (a) and body mass (b) and parasite abundance at the individual level

Variables Dependent	Explanatory	Rejected	df	F	P	Estimate ± SE
(a) Comb area	*Trichostrongylus tenuis*		1,739	5.78	**0.016**	−0.004 ± 0.001
	Age (A)		1,739	19.90	**<0.001**	−18.04 ± 4.04
	Season (S)		1,739	73.19	**<0.001**	284.37 ± 33.23
	Day of capture		1,739	24.78	**<0.001**	0.85 ± 0.17
		T. tenuis × S	1,738	3.16	0.075	−0.007 ± 0.004
		T. tenuis × A	1,737	3.69	0.055	0.007 ± 0.003
		A × S	1,736	0.06	0.806	2.08 ± 8.50
		T. tenuis × A × S	1,735	0.62	0.431	0.006 ± 0.008
(b) Body mass	*T. tenuis*		1,736	0.72	0.397	–0.001 ± 0.001
	Age (A)		1,736	38.28	**<0.001**	−28.88 ± 5.29
	Season (S)		1,736	1.79	0.180	−6.31 ± 9.49
	T. tenuis × A		1,736	2.01	0.156	−0.005 ± 0.003
	T. tenuis × S		1,736	1.60	0.206	−0.006 ± 0.004
	A × S		1,736	0.42	0.515	−6.79 ± 10.43
	T. tenuis × A × S		1,736	9.01	**0.002**	0.022 ± 0.007
		Day of capture	1,735	0.68	0.409	–0.12 ± 0.15

Results of the general linear mixed models testing for associations between comb area and body mass with *T. tenuis* abundance at individual level. The models also included age (young vs. adults), season (spring vs. autumn), and associated interactions as fixed effects and included year and site as random factors. Estimates in interactions with age classes and season factors correspond to young and spring levels, respectively. df, degrees of freedom. Significant P-values area given in bold.

(Table 2), being this relationship negative and significant in autumn ($F_{1,975}$ = 8.52, estimate = −0.01, P = 0.003; Figure 3) but not significant in spring ($F_{1,554}$ = 0.09, estimate = 0.001, P = 0.758; Figure 3). These relationships between body mass and mean parasite load at the population level were independent of age classes (Table 2). Results did not change when using the log-transformed mean parasite load at the population level instead the untransformed variable (see Supplementary data). When analyzing the body condition index instead of body mass (i.e., including wing length as a covariate in the model), the mean parasite load at the population level × season interaction remained significant ($F_{1,1242}$ = 8.65, P = 0.003, n = 1268). The CV of body mass per site, year, and season was not correlated with mean parasite load at the population level ($F_{1,13}$ = 1.08, P = 0.317), irrespective of season (parasite population mean × season $F_{1,11}$ = 2.26, P = 0.161).

Relationships between comb area, body mass, and parasite abundance at individual level

Comb area was negatively correlated with *T. tenuis* abundance at the individual level (Table 3, Figure 4). This relationship was similar between age classes and seasons, although the *T. tenuis* × age interaction and the *T. tenuis* × age × season interaction were close to significance (Table 3). Specifically, comb area was negatively correlated with *T. tenuis* at individual levels in both spring ($F_{1,92}$ = 3.97, estimate = −0.01, P = 0.049; Figure 5) and autumn in adults ($F_{1,245}$ = 5.54, estimate = −0.004, P = 0.019; Figure 5) but not in young males (spring, $F_{1,106}$ = 0.00, P = 0.977; autumn, $F_{1,260}$ = 0.54, P = 0.464). Body mass was also negatively correlated with parasite abundance at the individual level, as seen by the significant interaction with age and season (Table 3, Figure 5). In adult males, the relationship between body mass and *T. tenuis* abundance differed between seasons, although not significantly so (*T. tenuis* × season, $F_{1,344}$ = 2.59, P = 0.108), being significant and negative in spring ($F_{1,92}$ = 6.22, P = 0.014, estimate = −0.009; Figure 5) but not significant in autumn ($F_{1,246}$ = 0.16, P = 0.68; Figure 5). In young males, body mass also correlated with *T. tenuis* abundance depending on season (*T. tenuis* × season interaction, $F_{1,373}$ = 11.86, P < 0.001; Figure 5). There was a negative relationship between body mass and *T. tenuis* abundance in autumn ($F_{1,261}$ = 8.11, P = 0.004, estimate = −0.01; Figure 5) but not in spring ($F_{1,107}$ = 2.29, P = 0.133; Figure 5). When analyzing the body condition index instead of body mass (i.e., including wing length as a covariate in the model), the *T. tenuis* at individual level × age × season interaction remained significant ($F_{1,700}$ = 9.94, P = 0.001, n = 728).

DISCUSSION

The finding that male sexual ornament expression is not always positively related to condition has puzzled evolutionary ecologists and challenged the basis of some sexual selection models (Cornwallis and Uller 2009). Our results suggest that the environmental context, in terms of mean parasite abundance, would explain variation in the condition dependence of a sexual ornament under natural conditions. Our correlative data support the prediction that the abundance of parasites modifies the relationship between sexual ornament expression and condition. We showed that the relationship between comb area and body mass was stronger in grouse populations with high infection levels of their main parasite, *T. tenuis.* To the best of our knowledge, this study is the first empirical evidence that suggests that parasite infection is associated with changes in the condition dependence of a male sexual trait and fully agrees with our recent finding in female grouse (Vergara et al. 2011). Further experimental tests are now needed to corroborate the present findings.

We found that sexual trait expression, comb area, and body mass, which we used as an index of condition, positively correlated, as predicted by indicators models of sexual selection. This relationship was consistent during autumn, when intrasexual competition for territory acquisition is most intense, and spring, when territory defense, mating, and breeding occur (Hudson 1986). As predicted, the strength of the relationship became steeper and tighter as our index of environmental conditions (population parasite infection) worsened. The observed changes in the comb area–body mass relationship were consistent with increased costs for condition-dependent sexual displays in restrictive environments, which enhanced the relative differences between high- and low-condition individuals as environmental conditions worsen (Cotton et al. 2004a; Cothran and Jeyasingh 2010). A lower

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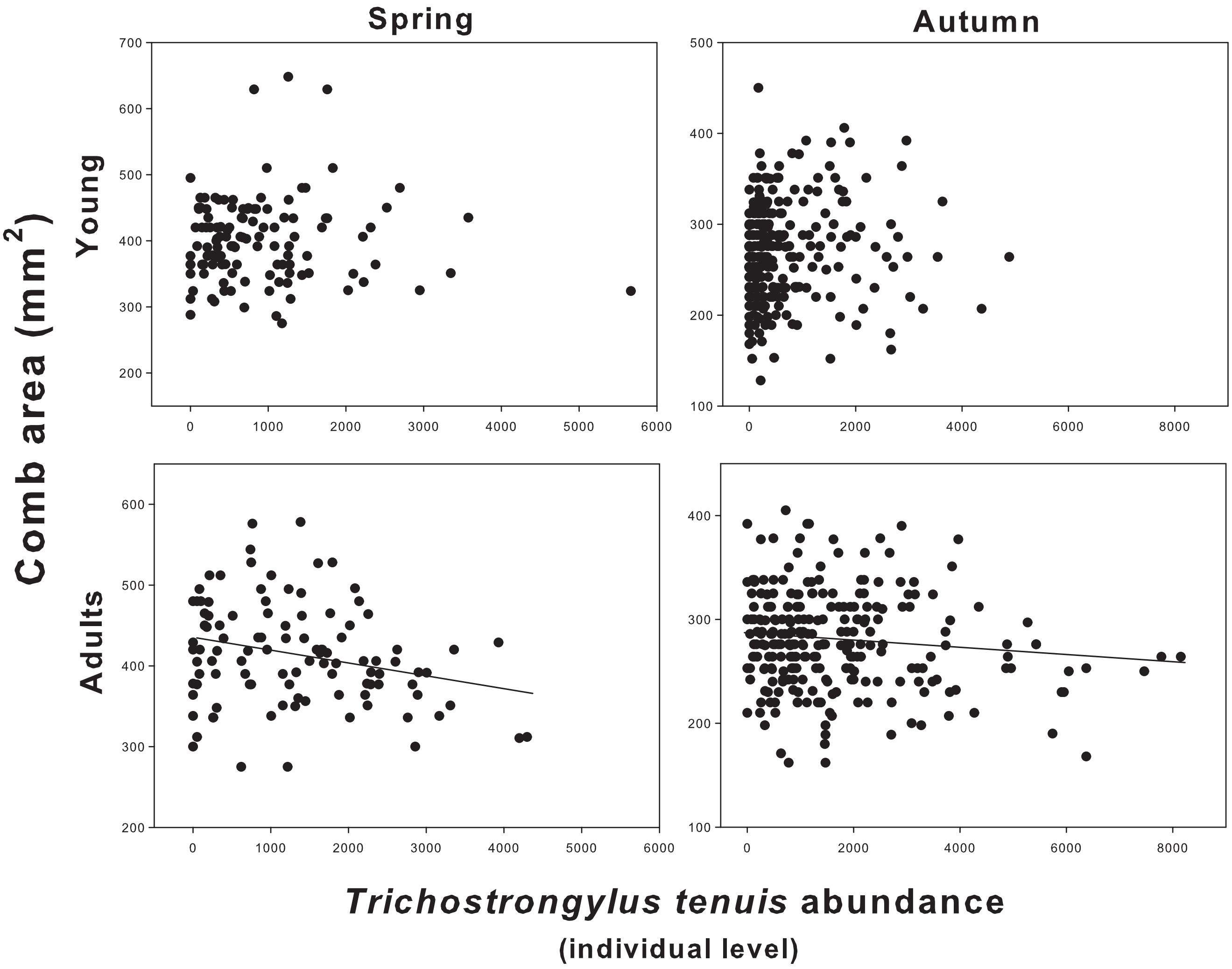

Figure 4
Relationships between comb area (mm^2) and *Trichostrongylus tenuis* abundance (worms per host) at the individual level and according to age (adults vs. young) and season (spring vs. autumn).

parasite infection was not associated with greater variance in comb area or body mass, indicating that the improved positive relationship was simply not due to a greater variance in such traits. However, there are alternative explanations for a changing comb area–body mass relationship between environments (Vergara et al. 2012). One would be that individuals may adjust their investment in sexual traits according to their survival probabilities. Under severe environments, individuals with low probabilities of survival may invest more in sexual traits, whereas individuals with more chances of surviving may save resources for more favorable conditions, with higher potential reproductive outcome (see Cornwallis and Uller 2009 and references therein). Another potential explanation for the changing comb area–body mass relationship is the genotype environment interaction hypothesis (Ingleby et al. 2010). Previous studies on birds have shown that the covariation between genetically determined ornamental coloration and body mass depends on the environmental conditions (Piault et al. 2009; Roulin 2009), suggesting that different genotypes may regulate body mass in different ways (Piault et al. 2009; Roulin 2009). Finally, if viability selection associated with investment in sexual ornaments varies among environments, different relationships between sexual traits and condition can be found across time and space (Robinson et al. 2008). Further studies will help to clarify the potential role of mechanisms other than the phenotypic plasticity one discussed above in explaining the variation in the comb area–body mass relationship found here.

Our results have further implications for our understandings of sexual selection processes. If a sexual trait (here comb size) is a better predictor of condition when parasites are more abundant, signal reliability might also be dependent on parasite abundance within a population. In consequence, changing relationships between ornament expression and the potential direct and indirect benefits for females associated with mate appraisal and choice based on ornament expression may thus emerge under environmental heterogeneity (Greenfield and Rodriguez 2004; Ingleby et al. 2010; Tolle and Wagner 2011). Our results can therefore help understanding changing female mate preferences for male ornaments under contrasted environments (Narraway et al. 2010).

Negative effect of parasites on sexual ornamentation and body mass

Males have to trade-off resource allocation between ornament expression and other costly activities, such as antiparasite defenses (Sheldon and Verhulst 1996). There is strong

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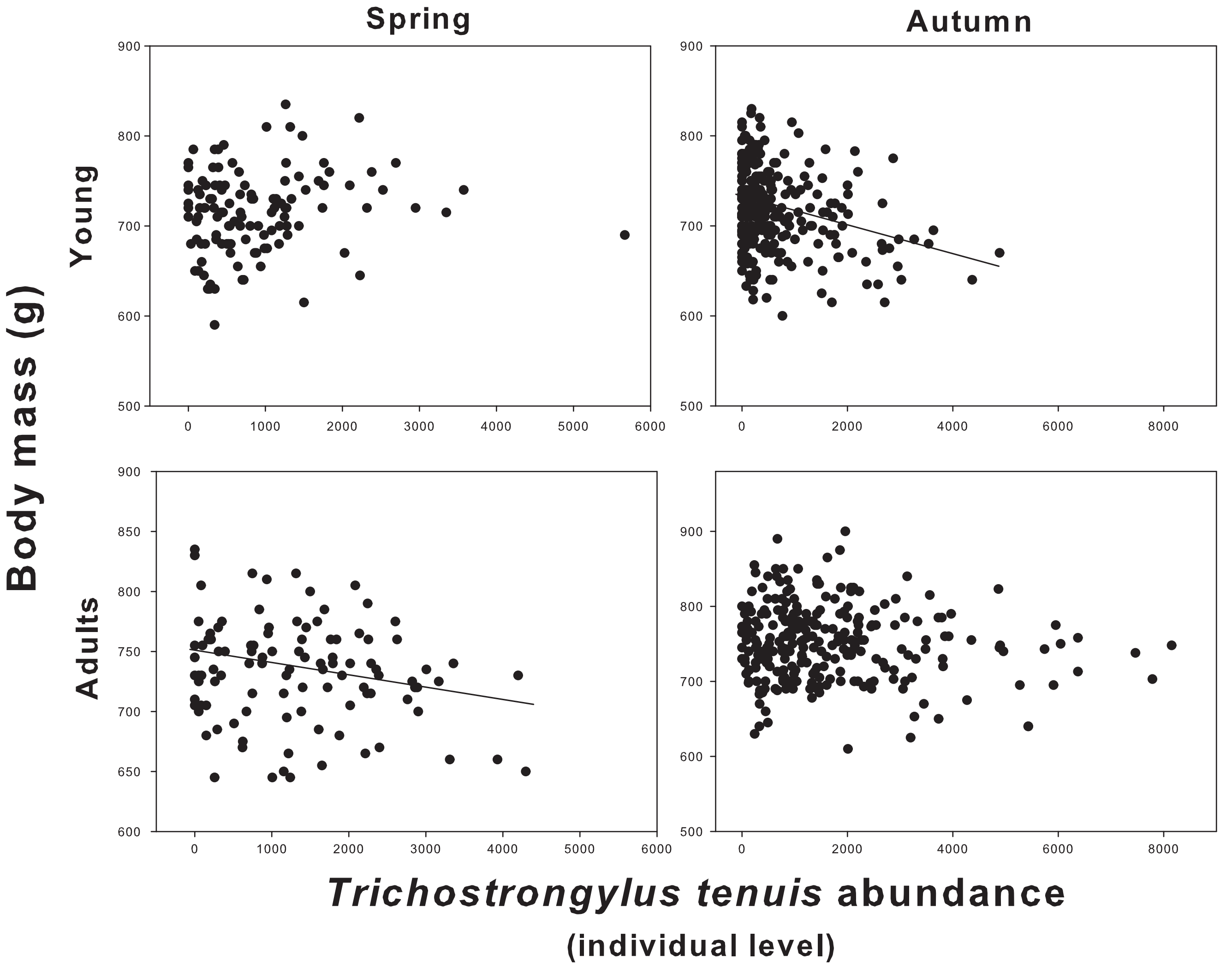

Figure 5
Relationships between body mass (g) and *Trichostrongylus tenuis* abundance (worms per host) at the individual level and according to age (adults vs. young) and season (spring vs. autumn).

evidence for increased investment in these defenses to be associated with substantially reduced sexual ornamentation (Hill 2006). In agreement, we found that the size of male red grouse combs was negatively correlated with infection levels by *T. tenuis*, at both the individual and population level. Our correlative results fully agree with the previously described negative effect of *T. tenuis* parasites on comb expression (Martínez-Padilla et al. 2010; Mougeot, Evans, et al. 2005; Mougeot, Redpath, et al. 2005; Mougeot et al. 2010). Similarly, we showed that body mass was negatively correlated with the average infection level by *T. tenuis* within the population and with parasite infestation at individual level. This result agrees with previous evidences showing that *T. tenuis* abundance negatively affected red grouse proxies of condition, including body mass, as well as breeding success and, to a lesser extent, survival (Hudson et al. 1998; Redpath, Mougeot, Leckie, and Evans 2006). We also found that the relationship between *T. tenuis* abundance and ornament size and body mass was age and season dependent. Young individuals are overall much less parasitized than adults (Hudson 1986; Mougeot, Evans, et al. 2005; Mougeot, Redpath, et al. 2005). Because of these age differences, the negative effect of *T. tenuis* on grouse should be more evident in adults than in young (Mougeot, Evans, et al. 2005), and our findings fully agree with the suggestion that *T. tenuis* parasites have stronger negative consequences on adult than young males. In spring, comb area at both population and individual level was negatively related to *T. tenuis* abundance, but these relationships were less evident in autumn. This seasonal effect could be explained by different resource allocation priorities in spring versus autumn. In autumn males may allocate more resources toward antiparasite defenses, whereas in spring males may be investing more resources toward reproduction (e.g., for displaying bigger ornaments or for display behaviors aimed at attracting mates) and be more sensitive to parasites at that time (Mougeot et al. 2006).

In conclusion, our study supports the idea that the condition dependence of secondary sexual ornaments varies across heterogeneous environments and more specifically across populations with contrasted parasite abundances. In sites and years when parasites are more abundant, the expression of sexual ornaments better indicates an individual's condition.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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