ORIGINAL ARTICLE

Kristin Lagesen · Ivar Folstad

Antler asymmetry and immunity in reindeer

Abstract Fluctuating asymmetry (FA) measures an individual's ability to undergo identical development in bilaterally symmetrical characters and may indicate sensitivity to environmental stress. FA in ornamental characters is often positively related to parasite intensities, which are important environmental stressors. Parasites affect and are affected by several parts of the immune system, and the ability to resist parasites may be signalled via FA in ornaments. In this study we examined reindeer antlers, which show FA, demonstrated to be caused by parasite infections. We measured antler FA, immune parameters (i.e. densities of different classes of leukocytes, IgG levels and abomasal lymph node numbers) and intensity of abomasal nematodes in free-ranging 1.5-year-old male reindeer slaughtered in the early part of their rutting period. We found a relationship between parasite intensity and immune parameters suggesting that our measures of immune activity reflect density of current parasite infections. More important, these immune parameters were associated with FA in both the main beam length and numbers of antler tines. The immune parameters were, however, only weakly correlated to antler size. This indicates that FA, but not size, of antlers grown during exposure to a multitude of environmental stressors may reveal information about individual immunity that can be important for host-parasite interactions. Antler FA may therefore communicate an individual's quality during the rut in reindeer.

Key words Antler · Fluctuating asymmetry · Immunity · Parasites · Reindeer

K. Lagesen · I. Folstad (✉)
Department of Ecology, Institute of Biology,
University of Tromsø, N-9037 Tromsø, Norway
e-mail: ivarf@ibg.uit.no,
Tel.: +47-77-644384, Fax: +47-77-64560

Introduction

Models of sexual selection suggest that the phenotypic expression of ornamental characters may depend on the quality of the carrier (Zahavi 1975, 1977; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Folstad and Karter 1992; Folstad and Skarstein 1997). By choosing mates on the basis of ornamental characters, selectors may acquire mates in good physical condition capable of providing high-quality parental care (Hoelzer 1989; Hill 1991) or, given heritable qualities, mates that can sire young of high genetic quality (Hillgarth 1990; Norris 1993; Petrie 1994; von Schantz et al. 1994; Møller 1996b).

If both mate preference for large ornaments and ornament size are heritable, mate preference may cause directional selection on ornament size and lead to genetic fixation of the trait (Lande 1981; Kirkpatrick 1982). However, if ornaments are to reliably reflect heritable qualities, additive genetic variance must be maintained. Infectious organisms (i.e. parasites) may be of particular importance for maintaining this genetic variance as they, in theory, can create genetic co-evolutionary cycles of changing host resistance and parasite virulence (Hamilton and Zuk 1982; Eshel and Hamilton 1984; Hamilton et al. 1990). Consequently, parasites may affect the ability of individuals to develop ornamental characters.

Bilaterally symmetrical ornaments are expected to be perfect symmetrical because the same genome encodes development of the character on both sides. These characters, however, often exhibit fluctuating asymmetry (FA), which is defined as small random deviations from perfect bilateral symmetry where the signed size differences between the two sides of a character are normally distributed with a mean value of zero (Van Valen 1962; Palmer and Strobeck 1986; Leary and Allendorf 1989; Parsons 1990, Møller and Swaddle 1997). The degree of FA is often higher in ornamental than in non-ornamental traits, because directional selection for

large ornament size may decrease developmental stability in ornamental as compared to non-ornamental traits. Consequently, ornamental FA may be a particularly good indicator of an individual's ability to cope with genetic or environmental stress (Møller and Swaddle 1997).

Parasites may be one important environmental stressor (Livshits and Kobyliansky 1991; Møller 1996a), and both observational and experimental studies have repeatedly shown that parasite intensities are positively related to the degree of ornamental FA (Møller 1992, 1996b; Folstad et al. 1996; Markusson and Folstad 1997; Møller and Swaddle 1997). Parasitic infections may thus lead to increased FA, which can have important implications for mate choice as symmetrical individuals are often preferred over asymmetrical ones (Møller and Pomiankowski 1993a; Møller 1996b).

The environment created by the host's immune system influences parasitic organisms. Leukocytes, lymphoid organs and immunoglobulins are important components of this environment. There are five major classes of leukocytes, which all have different main functions: neutrophils carry out phagocytosis; basinophils release histamines; eosinophils destroy parasitic worms; monocytes execute phagocytosis in the circulatory system, and lymphocytes (B-cells and T-cells) can kill pathogens and are involved in antibody-mediated responses with immunoglobulins (Vander et al. 1994). Lymphocytes arise, multiply and are stored in peripheral lymphoid organs such as lymph nodes. Immunoglobulins are proteins that function as B-cell receptors and antibodies, and mammals have five major classes: IgA, IgD, IgE, IgG and IgM, with IgG the most abundant. The ability to generate an immune response to parasitic infections may be influenced by host genetics (Gasbarre et al. 1993; Sorci et al. 1997) and there is now considerable support for heritable parasite resistance in vertebrates (Wakelin 1978, 1985; Wakelin and Blackwell 1988; Wakelin and Apanius 1997). Thus, as parasites negatively affect ornamental symmetry, symmetry may reflect heritable parasite resistance and individuals selecting mates with symmetrical ornaments may consequently produce more parasite-resistant offspring than randomly mating individuals.

Reindeer (*Rangifer tarandus tarandus*) are hosts of several species of parasites and have antlers showing FA (Markusson and Folstad 1997). Under *ad libitum* feeding conditions, reindeer treated against parasites develop less FA in antlers than untreated individuals (Folstad et al. 1996). Additionally, both free-ranging and *ad-libitum*-fed reindeer show a positive correlation between parasite intensities and antler FA (Folstad et al. 1996; Markusson and Folstad 1997). Antler size, on the other hand, is unrelated to parasite intensities both under *ad libitum* feeding regimes (Folstad et al. 1996) and among free-ranging animals (Markusson and Folstad 1997). Moreover, parasite removal does not influence the size of antlers among reindeer under *ad libitum* feeding conditions (Folstad et al. 1996). Thus, parasites seem to affect symmetry in antlers, even when they are grown under exposure to a multitude of environmental stressors, but do not, on the other hand, influence antler size.

In our present study we have, therefore, mainly focused on the individual qualities reflected in antler FA, rather than those reflected by antler size. More precisely, in an attempt to better understand the relationship between antler FA and immunity, we conducted a cross-sectional, observational study on immunological parameters (e.g. density of lymphocytes in blood samples) and antler FA in free-ranging male reindeer during the early part of the rutting period. Since there is a relationship between parasite intensities and antler FA among males in this period (Markusson and Folstad 1997), we also expected immunological parameters to be related to antler FA. However, as the present knowledge about what characterises an individual with a high-quality immune system (in terms of, for example, density of lymphocytes) seems scanty, we had no a priori predictions about the directions of these relationships. That is, we did not know whether symmetrical males should be expected to have high or low lymphocyte densities. Therefore, to facilitate the interpretation of our immunological variables, we also included a parasitological examination of the animals. This examination enabled us to make a rough evaluation of the importance of our immunological variables and, additionally, helped us understand what, for example, high lymphocyte densities would mean in terms of parasite intensities. The parasitological examination was restricted to counting the abomasal nematodes, which are prevalent parasites that may be of particular importance for free-ranging reindeer hosts (Halvorsen 1986; Bye 1987; Arneberg et al. 1996).

Methods

The animals

We examined 35 1.5-year-old semi-domestic reindeer stags from a herd in the district Orda in the West-Finnmark reindeer management area, northern Norway. Stags were randomly selected from the herd and as approximately 90% of the 1.5-year-old males were slaughtered in this district in 1995, the sampled individuals were considered representative of their cohort. The animals were slaughtered within a period of 3 h on 15 September 1995 at Guovdageaidnu slaughterhouse. The animals had not been treated with antihelmintics.

Morphometric data

Dressed body weight was measured to the nearest 0.1 kg. After removing meat and fat from the jaws by boiling, the length of the right and left side of the lower jaw was measured according to von den Driesch (1976). Measurements were made with a slide caliper to the nearest 0.1 mm. Jaw length was used to calculate non-ornamental FA. We measured total antler length according to Markusson and Folstad (1997), which includes the length of all parts of the antler. The main beam was measured on the inside from the burr to the outer tip. Tines were measured from the split-off from the main beam to the tip (Fig. 1). All measurements were made with a tape measure to the nearest 0.1 cm. The methods used for
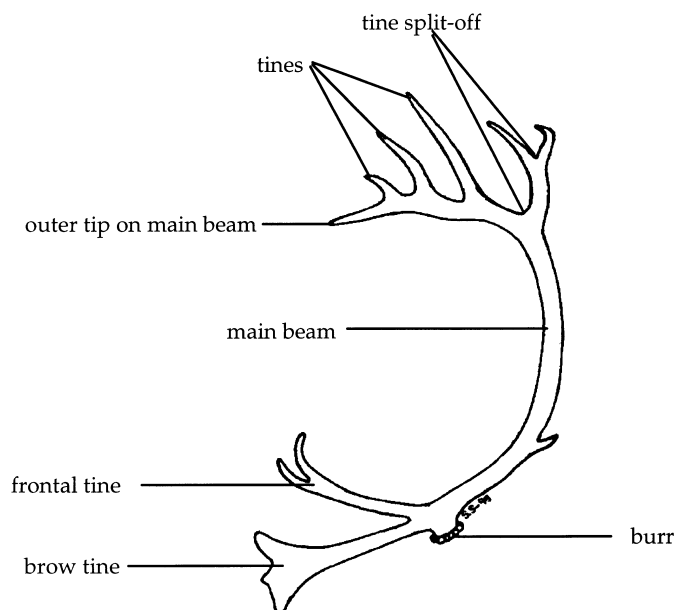
Fig. 1 Antler nomenclature. All parts of the antlers were measured when measuring total antler length (i.e. length of the *main beam* from the outer tip to the *burr*, length of all *tines* from their *split-off* from the main beam, length of *frontal tine* and length of *brow tine* including tines on frontal and brow tine)

measuring antler and jaw size ensure high repeatability (see Markusson and Folstad 1997). The number of tines was counted as all tines branching off from the main beam, except the outer tip on the main beam. We investigated FA in the sample by calculating both relative and absolute asymmetry (Palmer 1994) for the bilateral traits: total antler length, main beam length, number of tines and jaw length. Absolute asymmetry is the absolute value of the difference between the right and the left side of a trait in an individual. Relative asymmetry is absolute asymmetry divided by the mean trait size.

Blood sampling

Blood was collected in containers, both with and without EDTA as anticoagulant, from the common carotid arteries of each reindeer within 1 min of slaughter and immediately after the throat was cut.

Haematocrit measures

Blood from containers without EDTA was used to fill three heparinized capillary tubes of 200 µl from each individual. The tubes were centrifuged at 1200 rpm for 4 min, and the total length of liquid in each tube and the length of the erythrocyte layer were measured with a digital slide caliper. These data were used to determine the haematocrit value. The mean haematocrit value from the three tubes was used in later analyses. This method ensures high repeatability (Saino et al. 1995).

Immunological data

Leukocyte counts

Blood from containers without EDTA was used to make blood smears. These were fixed in 70% ethanol and stained by the May-Grunwald-Giemsa staining method. After staining they were scanned at × 100 magnification and erythrocytes and leukocytes, classified according to Hawkey and Dennett (1989) as lymphocytes,

monocytes, eosinophils, neutrophils and basinophils, were counted. In each smear 100–102 leukocytes were counted, depending on the number of leukocytes present in the last microscopic field containing leukocytes. The corresponding number of erythrocytes in the same fields were also counted. From this we calculated the relative frequency of leukocytes of each class with respect to the total population of leukocytes and the number of leukocytes per 10,000 erythrocytes. These counts made it possible to estimate the number of leukocytes from each class and this number was multiplied by the haematocrit values, following Skarstein and Folstad (1996), to obtain an estimate of the density of circulating leukocytes of each class in each reindeer.

Gamma-globulin assay

Blood in a container with EDTA was centrifuged at 5000 rpm for 15 min within 2 h of sampling. Plasma was removed and transferred to a 1.8-ml tube and immediately frozen. This plasma was later used to estimate the total amount of IgG for each individual. Gamma-globulin was assayed by densitometry after electrophoretic separation of plasma proteins on agarose gels (Saino and Møller 1996).

Lymph nodes

Lymph nodes were dissected from the abomasal mesenteries of the part lying in the fat between the abomasum and omasum and counted. These lymph nodes may be of particular importance for the immunological environment of abomasal nematodes.

Parasitological data

Parasitological data were obtained by estimating intensities of adult abomasal nematodes. Adult female and male nematodes were subsampled according to Bye (1987). The parasitological term "intensity" is defined as the number of abomasal nematodes in each infected host.

Statistical analyses

Statistical analyses were done using Statsoft Statistica for Windows 5.0B. Distributions of all data, except intensities of abomasal nematodes, met the assumption of normality (Kolmogorov-Smirnov one-sample tests); nematode intensities were log-transformed to meet the assumption of normality. Pearson product-moment correlation was used when testing bivariate relationships. We adjusted for multiple comparisons according to Rice (1989), and report the effect of these adjustments. In accordance with Kleinbaum et al. (1988), we used multiple stepwise regression analysis, backward elimination procedure, when testing multivariate relationships, where F to remove was set to 6.09 and F to enter to 7.0 in order to keep only the independent variables with significant partial correlation coefficients in the model. When using multivariate analysis, we first checked for colinearity between the independent variables to see if it was necessary to conduct ridge regression to remove the effect of colinearity. The largest correlation coefficient between independent variables was 0.86, and we consequently did not conduct ridge regression. The significance level chosen was 5%.

Results

Descriptive statistics

Descriptive statistics of morphometric, immunological and parasitological data are given in Table 1. None of

Table 1 Descriptive statistics of morphometric, immunological and parasitological data from 1.5-year-old male reindeer, with information on sample size (*n*), arithmetic mean (*Mean*), standard deviation (*SD*), minimum (*Min.*) and maximum values (*Max.*). Data were sampled from all animals, but sample size varies as a consequence of damage to some of the traits during slaughtering (e.g. jaws were fractured) or examination (e.g. blood smears were too thick to identify the different classes of leukocytes). Antler and jaw lengths are given as mean lengths and fluctuating asymmetry (*FA*) as absolute asymmetry

Parameter	*n*	Mean	SD	Min.	Max.
Dressed body weight (kg)	35	23.30	3.29	18.60	34.80
Jaw length (cm)	31	21.53	0.68	20.21	23.30
Main beam length (cm)	35	37.60	5.11	26.00	48.00
Total antler length (cm)	35	67.05	14.08	35.85	97.30
Number of tines	35	3.23	1.13	1	6
FA in jaw length	31	0.08	0.05	0.00	0.21
FA in main beam	35	1.88	1.44	0.00	4.80
FA in total antler length	35	6.66	4.60	1.30	18.20
FA in number of tines	35	1.03	0.99	0	4
Number of lymph nodes	27	8.78	2.99	4	15
Basinophils	18	0.001	0.001	0.000	0.005
Eosinophils	18	0.001	0.001	0.000	0.004
Neutrophils	18	0.017	0.012	0.0028	0.051
Lymphocytes	18	0.009	0.006	0.0019	0.028
Monocytes	18	0.001	0.001	0.0000	0.003
IgG	30	0.230	0.088	0.00007	0.383
Nematode intensities	27	2825.11	1793.7	930	10,600

the right-minus-left values for antlers and jaws, except number of tines and absolute asymmetry in total antler length, differed significantly from a normal frequency distribution with a mean of zero (Kolmogorov-Smirnov one-sample test). Additionally, none of the signed-value distributions departed from normality for skewness or kurtosis, except for number of tines which had a significantly different kurtosis ($t = 2.3$, $df = 34$, $P = 0.01$, Student *t*-test) and showed a leptokurtic frequency distribution (Table 2).

FA in antlers and jaws

As there was no significant relationship between length and absolute FA of any of the morphological characters examined (*r*-values range from −0.12 to 0.23 with *P* always > 0.18), there was no need to remove the effect of length on asymmetry estimates (Møller 1990; Palmer 1994) and absolute FA was consequently used instead of relative FA. Moreover, the variance in relative FA of total antler length was significantly larger than variance in relative FA of jaw length ($F_{2,30} = 1293.2$, $P < 0.001$,

F-max test, Sokal and Rohlf 1981) and mean relative FA in total antler length was also significantly larger than mean relative FA in jaw length ($t = -9.39$, $df = 30$, $P < 0.001$, Student's *t*-test). FA in jaw length was only significantly correlated with FA in number of tines, but this association, which is negative (Table 3), is no longer significant after correcting for multiple comparisons.

Confounders

None of the measurements of FA was significantly related to body mass (*r*-values range from −0.24 to 0.13 with *P* always > 0.17) or the log-transformed abomasal nematode intensities (*r*-values range from −0.11 to 0.28 with *P* always > 0.16). Body mass was, on the other hand, correlated with both the log-transformed intensities of abomasal nematodes ($r = 0.42$, $P = 0.02$, $n = 27$) and the concentration of IgG ($r = -0.38$, $P = 0.04$, $n = 30$). These associations are however not significant after sequential Bonferroni adjustment (Rice 1989) and body mass was consequently not controlled for in later analyses.

Table 2 Descriptive data on FA in antlers and jaws in 1.5-year-old male reindeer, with information on sample size (*n*), and *mean*, *skewness* and *kurtosis* of the left-minus-right (*R–L*) character value

Character	*n*	R–L		
		Mean ± SE	Skewness ± SE	Kurtosis ± SE
Total antler length (cm)	35	−0.14 ± 1.38	0.14 ± 0.40	−0.30 ± 0.78
Main beam length (cm)	35	0.44 ± 0.40	−0.10 ± 0.40	−0.34 ± 0.78
Number of tines	35	−0.12 ± 0.24	−0.02 ± 0.40	1.79 ± 0.78
Jaw length (mm)	31	0.25 ± 0.17	0.12 ± 0.42	−1.04 ± 0.82

Table 3 Pearson product-moment correlations between antler FA and jaw FA of 1.5-year-old male reindeer, with correlation coefficients (r) and significance level (P). Sample size is 31 for all tests. None of the P-values are significant after controlling for multiple comparisons

Character	Jaw FA	
	r	P
FA in number of tines	−0.42	0.02
FA in antler length	0.14	0.46
FA in the main beam	0.26	0.15

Parasites and immune parameters

A stepwise regression model, with a backward elimination procedure, with log-transformed intensities of the abomasal nematodes as the dependent variable and the estimated level of immune parameters as independent variables, significantly explained most of the variation in parasite intensities among animals. The estimated levels of neutrophils, monocytes, lymph node number and IgG were significantly correlated with nematode intensities, while the estimated level of lymphocytes, eosinophils and basinophils were not significantly related to nematode intensities (Table 4).

Antlers and immune parameters

The examined immune parameters could not significantly explain the variation in main beam length and number of tines ($F_{1,10} = 0.6$, $P = 0.45$, and $F_{1,10} = 2.5$, $P = 0.14$, respectively). Total antler length, on the other hand, showed a negative association with monocytes in the stepwise regression model with immune parameters as independent variables ($F_{1,10} = 17.7$, $R^2 = 0.64$, $P = 0.002$).

The regression model showed that the estimated levels of immune parameters were not related to FA in total antler length or FA in jaw length (all F-values for independent variables < 6.09). However, the immune parameters explained a significant amount of both the variation in FA in number of tines and in FA of the main beam. The estimated levels of basinophils and

Table 4 Stepwise regression analysis, with a backward elimination procedure, of abomasal nematode intensities and levels of immunological parameters in 1.5-year-old male reindeer. Dependent variable: log-transformed abomasal nematode intensities. Regression model: $F_{4,7} = 15.23$, $r = 0.95$, $R^2 = 0.90$, $P = 0.0015$, $n = 12$

Independent variable	Partial correlation coefficient	R^2	P
Neutrophils	0.94	0.75	0.00015
Monocytes	−0.93	0.69	0.00030
Lymph node number	−0.88	0.34	0.00196
IgG	0.71	0.02	0.03107

Table 5 Stepwise regression analysis, with a backward elimination procedure, of FA in number of tines in the antlers and level of immunological parameters in 1.5-year-old male reindeer. Dependent variable: FA in number of tines in the antlers. Regression model: $F_{2,9} = 6.80$, $r = 0.78$, $R^2 = 0.60$, $P = 0.016$, $n = 12$

Independent variable	Partial correlation coefficient	R^2	P
Basinophils	−0.78	0.48	0.005
Eosinophils	0.65	0.48	0.029

Table 6 Stepwise regression analysis, with a backward elimination procedure, of FA in main beam of antlers and levels of immunological parameters in 1.5-year-old male reindeer. Dependent variable: FA in antler main beam. Regression model: $F_{5,6} = 49.49$, $r = 0.99$, $R^2 = 0.98$, $P = 0.000085$, $n = 12$

Independent variable	Partial correlation coefficient	R^2	P
IgG	−0.97	0.01	0.00005
Basinophils	−0.96	0.74	0.00015
Lymph node number	−0.96	0.44	0.00016
Lymphocytes	0.86	0.77	0.00667
Neutrophils	0.79	0.90	0.01886

eosinophils were significantly related to FA in number of tines (Table 5) whereas the estimated levels of IgG, basinophils, lymph node number, lymphocytes and neutrophils were significantly related to FA in the main beam (Table 6). Conducting these analyses with relative instead of absolute FA in antlers produces very similar results to those presented here.

Discussion

The immune parameters examined in 1.5-year-old male reindeer were significantly related to abomasal nematode intensities and to the FA of antlers, but not to antler size. This suggests that immune responses to parasites may be signalled through antler FA rather than by antler size.

In general, individuals with large ornaments seem to experience less developmental instability than individuals that develop small ornaments, despite the additional cost of developing large ornaments (Smith et al. 1982; Møller 1990; Manning and Chamberlain 1993). This suggests that individuals with large ornaments are better able to cope with genetic and environmental stress than individuals with small ornaments. The ability to develop large and symmetrical ornaments may thus reflect individual qualities (Møller 1990, 1996b; Møller and Pomiankowski 1993b). This study did not, however, find the expected negative relationship between antler length and FA in antler length, which has previously been documented among 1.5-year-old male reindeer (Markusson and Folstad 1997). This questions the generality of the association between size and asymmetry of antlers in

reindeer, but the lack of association could also be caused by the relative low range of character values within the examined cohort of animals (Palmer 1994).

Ornamental traits usually show a higher degree of FA than non-ornamental traits (Møller and Pomiankowski 1993a) and, in accordance with previous studies, we found a significantly larger variance in relative FA in total antler length than in relative FA in jaw length. Moreover, mean relative FA was also larger in total antler length than in jaw length. The higher level of FA in ornamental compared to non-ornamental characters suggests that antlers may be more sensitive to developmental stress than jaws. This is in accordance with the assumption that directional selection for ornament size may lead to a high degree of FA in these traits (Møller 1990, 1994). Moreover, antler FA was not positively related to FA in jaws. Therefore, FA in ornamental characters does not seem to reflect overall body FA, and this is in agreement with previous studies both on male reindeer (Markusson and Folstad 1997) and barn swallows (Møller 1990, 1994). Jaw asymmetry in the examined animals developed over a period of 1.5 years, while the asymmetry of antlers may reflect developmental instability over a growth period of 3–4 months. This suggests that antlers and jaws, which reflect developmental instability over different time spans, may be influenced by different environmental stressors in the highly seasonal subarctic habitat of reindeer.

Reindeer parasites are seasonal stressors (Halvorsen 1986) that influence development of symmetry in antlers (Folstad et al. 1996). At the time of the rut, 1.5-year-old males show a positive relationship between FA in antlers and the intensity of parasitism, estimated from densities of abomasal nematodes and parasitic propagules in faeces (Markusson and Folstad 1997). The present study was not designed to examine the relationship between the parasitic infrapopulations (i.e. the parasite community of one host) and antler morphology, and abomasal nematode counts were the only parasite counts included. The lack of association between this particular group of parasites and antler FA documented in this study is also common to the previous studies (Folstad et al. 1996; E. Markusson, personal communication). These former studies document, however, that there is an association between FA in antlers and parasite intensities when a more conclusive evaluation of the parasite infrapopulations of reindeer is undertaken (Folstad et al. 1996; Markusson and Folstad 1997).

The importance of parasite counts in the present study is related to the evaluation of the examined immune parameters. The estimated levels of IgG, neutrophils and monocytes, and number of lymph nodes in the abomasal mesentery, were all significantly related to the variation in abomasal nematode intensity. This could have been anticipated. Neutrophils and monocytes are both involved in immune responses to nematodes (Venturiello et al. 1993) where they carry out phagocytosis (Vander et al. 1994), and, in lymph nodes, B-lymphocytes produce IgG after antigen presentation

(Vander et al. 1994). We cannot, of course, determine cause and effect, but a tentative explanation for the directions of the observed relationships is that low numbers of monocytes and lymph nodes results in increased parasite intensities whereas increased parasite intensity results in higher neutrophil and IgG levels. We note that IgG levels have been reported to respond to increased infections of gastrointestinal nematodes, including *Ostertagia* spp. (Gasbarre et al. 1993; Hilderson et al. 1993), which are the most common species of abomasal nematodes in reindeer (Bye 1987). Even if our estimates of both individual immunocompetence and parasite intensities are far from conclusive, the associations documented in this study clearly suggest that our immune measurements may be of importance for the host-parasite interactions.

Ornaments have been suggested to have evolved as signals of immune system function (Folstad and Karter 1992; Folstad and Skarstein 1997) and the immune parameters examined are significantly related to antler FA. They are, however, not good predictors of antler size. This is as expected because parasite intensities and antler size have been shown to be unrelated in both experimental and observational studies on reindeer (Folstad et al. 1996; Markusson and Folstad 1997). The association between ornamental FA and immune parameters in reindeer is not in accordance with that reported from house sparrows (*Passer domesticus*) where FA in the size of the badge, a trait subjected to a directional mate preference, was unrelated to the size of the bursa of Fabricius (Møller et al. 1996). The lack of a relationship between the size of an immunologic organ and ornamental FA in house sparrows could have several explanations. For example, the measured immune feature may not reflect the quality of relevant individual immune function in house sparrows. A similar critique may also apply to this study, but among the seven parameters investigated, the estimated levels of IgG, basinophils, neutrophils, lymphocytes and lymph node number significantly explained 98% of the variation in FA in the antler main beam. Additionally, basinophil and eosinophil levels significantly explained 60% of the variation in FA in number of tines. The directions of the specific relationships between immune parameters and measurements of antler FA are difficult to understand, and an individual with a high level of IgG will, for example, be characterised by a high intensity of abomasal nematodes and a low FA in antler main beam. An individual with a high number of abomasal lymph nodes, on the other hand, will have few abomasal nematodes and low FA in antler main beam. These relationships would have been more easily understood if physiological trade-offs had been expected between immunological activity and the degree of ornamental FA. However, as signals of developmental stability may have evolved as amplifiers rather than as handicaps (Hasson 1990, 1997), antler FA may be reliable because of design and not because of costly trade-offs between ornamental development and immune activity. Consequently there need not be dif-

ferent physiological costs for immune activity on symmetrical versus asymmetrical males, only different benefits from a given immune activity. The explanations for the directions of the relationships between the examined immune parameters and antler FA must consequently await further studies, but in sum they do suggest that the variation in FA, but not size, of full-grown antlers may be explained by immune system functions that could be important for host-parasite interactions.

The adaptive significance of antlers as weapons is obvious, but they may also operate as ornamental signals of individual quality (Clutton-Brock 1982). Antler size and complexity are correlated with fighting success and dominance (Topinski 1974; Bartos et al. 1988), and FA in palm length of antlers is a good predictor of dominance in male fallow deer (*Dama dama*, Maylon and Healy 1994). In reindeer, FA in total antler length reveals information about parasite burden (Markusson and Folstad 1997), while FA in main beam of antlers and FA in number of antler tines may signal information about individual immune functions important for host-parasite interactions. Thus, antler morphology may be a complex signal that reveals detailed information about differences in individual quality that may be of importance in both inter- and intrasexual communication during rut.

References

Arneberg P, Folstad I, Karter AJ (1996) Gastrointestinal nematodes depress food intake in naturally infected reindeer. Parasitology 112:213–219

Bartos L, PernerV, Losos S (1988) Red deer stags rank position, body weight and antler growth. Acta Theriol 33:209–217

Bye K (1987) Abomasal nematodes from three Norwegian wild reindeer populations. Can J Zool 65:677–680

Clutton-Brock TH (1982) The function of antlers. Behavior 79:109–125

Driesch A von den (1976) A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin 1. Peabody Museum of Archaeology and Ethnology, Harvard University Press, Cambridge, Mass

Eshel I, Hamilton WD (1984) Parent-offspring correlation in fitness under fluctuating selection. Proc R Soc Lond B 222:1–14

Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. Am Nat 139:603–622

Folstad I, Skarstein F (1997) Is male germ line control creating avenues for female choice? Behav Ecol 8:109–112

Folstad I, Arneberg P, Karter AJ (1996) Antlers and parasites. Oecologia 105:556–558

Gasbarre LC, Leighton EA, Davies CJ (1993) Influence of host genetics upon antibody-responses against gastrointestinal nematode infections in cattle. Vet Parasitol 46:81–91

Halvorsen O (1986) Epidemiology of reindeer parasites. Parasitol Today 2:334–339

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218:384–386

Hamilton WD, Axelrod R, Tanese R (1990) Sexual reproduction as an adaption to resist parasites (a review). Proc Natl Acad Sci USA 87:3566–3573

Hasson O (1990) The role of amplifiers in sexual selection: an integration of the amplifying and the Fisherian mechanisms. Evol Ecol 4:277–289

Hasson O (1997) Towards a general theory of biological signaling. J Theor Biol 185:139–156

Hawkey CM, Dennett TB (1989) A color atlas of comparative veterinary haematology. Wolfe, London

Hilderson H, Vercruysse J, Degraaf DC, Bastiaensen P, Fransen J, Berghen P (1993) The presence of an early L(4) larvae population in relation to the immune response of calves against *Ostertatia ostertagi*. Vet Parasitol 47:255–266

Hill FE (1991) Plumage color is a sexual selected indicator of male quality. Nature 350:337–338

Hillgarth N (1990) Parasites and female choice in the ring necked pheasant. Am Zool 30:227–233

Hoelzer GA (1989) The good parent process of sexual selection. Anim Behav 38:1067–1078

Kirkpatrick M (1982) Sexual selection and the evolution of female choice. Evolution 36:1–12

Kleinbaum DG, Kupper LL, Muller KE (1988) Applied regression analysis and other multivariable methods. Duxbury, Pacific Grove, Calif

Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favoured by sexual selection. Am Nat 124:309–323

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proc Natl Acad Sci USA 78:3721–3723

Leary RF, Allendorf FW (1989) Fluctuating asymmetry as an indicator of stress: implications for conservation biology. Trends Ecol Evol 4:214–217

Livshits G, Kobyliansky E (1991) Fluctuating asymmetry as a possible measure of developmental homeostasis in humans: a review. Hum Biol 63:441–466

Manning JT, Chamberlain AT (1993) Fluctuating asymmetry, sexual selection and canine teeth in primates. Proc R Soc Lond B 251:83–87

Markusson E, Folstad I (1997). Reindeer antlers: visual indicators of individual quality? Oecologia 110:501–507

Maylon C, Healy S (1994) Fluctuating asymmetry in antlers of fallow deer, *Dama dama*, indicates dominance. Anim Behav 48:248–250

Møller AP (1990) Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Anim Behav 40:1185–1187

Møller AP (1992) Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characters. J Evol Biol 5:691–699

Møller AP (1994) Sexual selection in the barn swallow (*Hirundo rustica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. Evolution 48:658–670

Møller AP (1996a) Parasitism and developmental instability of hosts: a review. Oikos 77:189–196

Møller AP (1996b) Sexual selection, viability selection, and developmental stability in the domestic fly *Musca domestica*. Evolution 50:746–752

Møller AP, Pomiankowski A (1993a) Fluctuating asymmetry and sexual selection. Genetica 89:267–279

Møller AP, Pomiankowski A (1993b) Why have birds got multiple sexual ornaments? Behav Ecol Sociobiol 32:167–176

Møller AP, Swaddle JP (1997) Asymmetry, developmental stability, and evolution. Oxford University Press, Oxford

Møller AP, Kimball RT, Erritzøe J (1996) Sexual ornamentation, condition, and immune defence in the house sparrow *Passer domesticus*. Behav Ecol Sociobiol 39:317–322

Norris K (1993) Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362:537–539

Palmer AR (1994) Fluctuating asymmetry analyses: a primer. In: Markow TA (ed) Developmental instability: its origins and evolutionary implications. Kluwer, Dordrecht, pp 335–364

Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, patterns. Annu Rev Ecol Syst 17:391–421

Parsons PA (1990) Fluctuating asymmetry: an epigenetic measure of stress. Biol Rev Camb Phil Soc 65:131–145

Petrie M (1994) Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 371:598–599

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Saino N, Møller AP (1996) Sexual ornamentation and immunocompetence in the barn swallow. Behav Ecol 7:227–232

Saino N, Møller AP, Bolzern AM (1995). Testosterone effects on the immune system and parasite infestations in the barn swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. Behav Ecol 64:397–404

Schantz T von, Grahn M, Gøransson G (1994) Intersexual selection and reproductive success in the pheasant *Phasianus colchicus*. Am Nat 144:510–527

Skarstein F, Folstad I (1996) Sexual dichromatism and the immunocompetence handicap: an observational approach using arctic charr. Oikos 76:59–367

Smith MH, Chesser RK, Cothran EG, Johns PE (1982) Genetic variability and antler growth in a natural population of white-tailed deer. In: Brown RD (ed) Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, pp 365–368

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

Sorci G, Møller AP, Boulinier T (1997) Genetics of host-parasite interactions. Trends Ecol Evol 12:196–200

Topinski P (1974) The role of antlers in establishment of the red deer herd hierarchy. Acta Theriol 19:509–514

Van Valen L (1962) A study of fluctuating asymmetry. Evolution 16:125–142

Vander AJ, Sherman JH, Luciano DS (1994) Human physiology: the mechanisms of body function. McGraw-Hill, New York

Venturiello SM, Giambartolomei GH, Costantino SN (1993) Immune killing of newborn *Trichinella* larvae by human leucocytes. Parasite Immunol 15:559–564

Wakelin D (1978) Genetic control of susceptibility and resistance to parasitic infections. Adv Parasitol 16:219–308

Wakelin D (1985) Genetic control of immunity to helmintic infections. Parasitol Today 1:17–23

Wakelin D, Apanius V (1997) Immune defence genetic control. In: Clayton DH, Moore J (eds) Host-parasite evolution: general principles and avian models. Oxford University Press, Oxford, pp 30–58

Wakelin D, Blackwell JM (1988) Genetics of resistance to bacterial and parasitic infection. Taylor and Francis, London

Zahavi A (1975) Mate selection – a selection for a handicap. J Theor Biol 53:205–214

Zahavi A (1977) The cost of honesty. J Theor Biol 67:603–605

Communicated by S. Creel