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

Introduction


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; Markussen 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; basophils 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 (Markussen 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; Markussen 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 (Markussen 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 (Markussen 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 Gruvågeidnu 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 Markussen 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