Acta Oecologica 53 (2013) 38–48

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer

Gema Escribano-Avila [a,*], Nathalie Pettorelli [b], Emilio Virgós [a], Carlos Lara-Romero [a], Jorge Lozano [a], Isabel Barja [c], Felipe S. Cuadra [d], Marisa Puerta [d]

[a] Departamento de Biología y Geología, Universidad Rey Juan Carlos, Departamental I. C/Tulipán s/n, E-28933 Móstoles, Madrid, Spain
[b] Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK
[c] Unidad de Zoología, Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, C/Darwin 2, 28049 Madrid, Spain
[d] Departamento de Fisiología Animal, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, C/Jose Antonio Navais, 12, Ciud ad Universitaria, 28040 Madrid, Spain

ARTICLE INFO

Article history:
Received 19 July 2013
Accepted 14 August 2013
Available online

Keywords:
Stress
Non-invasive
Habitat quality
Immune function trade-off
Environmental change

ABSTRACT

According to the Cort-Fitness Hypothesis, higher stress levels (glucocorticoids) in vertebrates are correlated to lower fitness. However, recent studies have failed to validate this hypothesis. A proposed wider framework suggests that reproduction can be perceived as an overload adds up to other environmental challenges that individuals must adjust to. In this case, elevated glucocorticoids could help individuals to allocate resources to reproduction without comprising other functions, leading to the expectation of a positive cort-fitness relationship. This has been proposed as the Cort-Adaptation Hypothesis. Stress levels result from a complex interaction between the environment and the neuroendocrine system of animals. Accounting for physiological functions involved in how animals cope with their environment would help to clarify the relationship between glucocorticoids and animal performance. We used roe deer (*Capreolus capreolus*) inhabiting diverse habitats in the Iberian Peninsula to: i) test the Cort-Fitness and Cort-Adaptation hypotheses by indexing fitness using a comprehensive physiological approach which takes into account fundamental physiological functions and their trade-offs; and ii) evaluate the link between primary productivity and individuals' condition in a seasonal environment. We evaluated spatial and temporal variation in stress levels, reproductive hormone levels, nutritional status and immune function from fecal samples collected in 2010. Lower stress levels were related to better condition in non-reproductive seasons but not to higher primary productivity. In contrast, stress levels were always positively related to reproductive condition, which was better in most productive habitats. Summer and winter were the less productive seasons and the more challenging for the species in the habitat gradient studied. In winter, reproductive condition traded off against immune function being biased toward immune function in less productive habitats. In summer reduced primary productivity limited roe deer nutritional and immunological condition but not reproductive condition. Overall our results match both the Cort-Fitness and Cort-Adaptation Hypotheses.

1. Introduction

Biodiversity loss is presently occurring at a faster rate than throughout the entire history of the planet (Millenium Ecosystem Assessment, 2005) due to an increase in anthropogenic threats such as habitat loss, degradation and fragmentation, over-exploitation, pollution and climate change (Parmesan and Yohe, 2003; Vitousek, 1994). Understanding and predicting how these threats affect biodiversity and ecosystem functioning is a major focus of the scientific community (Loreau et al., 2001). However, if conservation and management efforts are to be successful, not only do we need to understand how species presence and distribution are impacted by global environmental change (Araujo and Rahbek, 2006), but we also need to identify the mechanisms which allow organisms to cope with their changing environments (Romero and Wikelski, 2001; Wingfield, 2008).

Most studies that examine how animal populations manage their variable environments have focused on the stress levels of populations to changing conditions. These studies are generally

* Corresponding author. Tel.: +34 914888288; fax: +34 91 664 7490.
E-mail addresses: gema.escribano@urjc.es, gema.escribano.avila@gmail.com (G. Escribano-Avila).

1146-609X/$ – see front matter © 2013 Elsevier Masson SAS. All rights reserved.
http://dx.doi.org/10.1016/j.actao.2013.08.003

based on indexing stress levels using glucocorticoids (GC) or their metabolites in urine or faeces (GCm) as a quality indicator of condition (Boonstra, 2004; Busch et al., 2011; Creel et al., 2002; Gobush et al., 2008; Lanctot et al., 2003; Romero and Wikelski, 2001) since stress response is the link between an individual's perception of the environment and physiology (McEwen and Wingfield, 2003). When an animal perceives a stressor (e.g. predator, competitor), its nervous system sends a signal to the endocrine system triggering an increase in GC secretion in the blood, which allows the animal to allocate energy to respond to the stressor. However, when a stressful stimulus is present for a long period of time, high GC concentrations remain in the blood, which can have detrimental effects on certain systems, such as the immune and reproductive systems (Romero, 2004). Hence, individuals with high GC or GCm levels are expected to be in poor condition and have low relative fitness (Husak and Moore, 2008; Wingfield and Sapolsky, 2003). This hypothesis is generally referred to as the Cort-Fitness Hypothesis (Bonier et al., 2009).

In recent years, empirical evidence has cast doubts on the credibility of this hypothesis. For instance, Taillon and Côté (2008) failed to find a correlation between higher GC or GCm levels and fitness or condition in white-tailed deer (*Odocoileus virginianus*). A recent study on the relationship between GC or GCm and fitness found an array of positive, negative and non-significant results (Bonier et al., 2009). This lack of consistency could be due to the involvement of GC in several complex functions such as temperature maintenance, immunity, social interactions and reproduction (Mormede et al., 2007; Sapolsky et al., 2000). Bonier et al. (2009) have proposed a wider approach when interpreting the Cort-Fitness Hypothesis which includes reproduction as pivotal function in which GC play an important role. Reproduction is one of the most demanding processes of animal life-history (Williams, 1966), and during this period elevated GC could help to allocate the necessary resources for animals to successfully overcome reproduction without compromising other functions such as immunity or temperature maintenance (e.g. by mobilizing reserves tissues to make them available). This hypothesis is referred to as the Cort-Adaptation hypothesis (Bonier et al., 2009) according to which a positive relationship between fitness and GC could be expected during the reproductive period. Thus, the interpretation of GC levels might require complementary information on the state of reproduction and other relevant physiological functions such as immunity and nutritional conditions (Romero, 2004). In this sense, some authors have highlighted the importance of considering the trade-offs between stress response and fitness correlates of condition to accurately interpret GC or GCm results for conservation issues (Busch and Hayward, 2009; Hayward et al., 2011).

In the last few decades, roe deer have been expanding their range to the central Iberian Peninsula, forcing the species to cope with a gradient in habitat suitability from the preferred humid broadleaved forest to xeric agricultural environments with severe summer droughts (Acevedo et al., 2005; Tellería and Virgós, 1997; Virgós and Tellería, 1998). This natural expansion provides an excellent opportunity to study the physiological changes that allow animals to survive in such a wide habitat gradient. In this paper we assess roe deer (*Capreolus capreolus*) sensitivity to different habitat conditions using a holistic physiological approach. We used several indicators of fundamental physiological functions such as stress levels (indexed by fecal GCm), reproductive condition (fecal metabolites of progesterone, estradiol and testosterone), nutritional status (fecal nitrogen) and immune function (fecal IgA) to perform an empirical test of the cort-adaptation and cort-fitness hypotheses for the reproductive cycle of the species and determine the potential use of these physiological variables as indicators of habitat quality perceived by roe deer. We expected the measured physiological indicators to relate differently at the individual-level depending on the reproductive moment. During the rut season (summer), we expected to find a positive relationship between reproductive hormones (for both sexes), GCm and the measured indicators of immune function and nutritional condition, verifying the Cort-Adaptation hypothesis. Winter and spring are the periods of pregnancy and parturition/lactation, respectively, in which the reproductive hormones progesterone (P_4) and estradiol (E_2) play a major role in placenta maintenance and milk gland development (Ryg, 1986). In these periods, we expected to find a positive relationship between P_4, E_2, GCm, nutritional and immune condition indicators. During the non-reproductive season (autumn), we expected to find a negative correlation between GCm and condition-related variables (immune function and nutrition) and non-significant relationship with reproductive hormones, verifying the Cort-Fitness hypothesis.

If our expectations in relation to the Cort-Fitness and Cort-Adaptation hypotheses were validated at the individual level, we would expect the magnitude of the variables to be controlled by primary productivity at the population-level. For instance, on the reproductive seasons if the Cort-adaptation hypothesis better fits the obtained data, we would expect the levels of reproductive hormones, GCm and condition related variables to be higher in more productive habitats (Bonier et al., 2009,Pettorelli et al., 2005, 2006).

2. Material and methods

2.1. Study area

The study area occupies around 2000 km^2 in the Sierra de Guadarrama and Sierra de Altomira in central Spain (Fig. 1). We studied an environmental gradient from 800 to 1700 m. Average annual precipitation and temperature ranges are 527–974.5 mm and 7.75–13 °C, respectively (http://opengis.uab.es/wms/iberia/) (Table S1). The vegetation above 1200 m is composed of alpine grasslands, natural pinewoods and plantations of Scots pines (*Pinus sylvestris*). Between 1000 and 1200 m, the landscape is dominated by mosaics of humid pastures and broadleaved vegetation, mainly Pyrenean oak (*Quercus pyrenaica*). Below 1000 m, the most abundant formations are mosaics of pasture sclerophyllous vegetation where holm oak (*Quercus ilex*) is the predominant species. The lower parts of the mountains are occupied by extensive crops of wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*), where holm forests have a patchy distribution (Tellería and Virgós, 1997). According to environmental characteristics (precipitation, temperature and vegetation type), we identified five dominant habitats (Pine, Oak, Holm, Xeric and Crops). Three to four populations were studied in each habitat (Table S1). A roe deer population was defined as an individual or group of individuals partly inhabiting a 50 ha home range centered on the sampling location (Guillet et al., 1996). To maximize the number of individuals sampled, we established three to four 50 ha plots per habitat type separated by at least 2 km (Fig. 1). Based on local densities (FIDA, 2008), we estimated that there was an average of eight roe deer in each of the study plots in the Pine, Oak, Holm and Crops habitats (range 4–12) and four in each plot of the Xeric habitat (range 3–9). More details are facilitated on the Section 2.3. In each plot we performed two linear transects of 400 m to characterize non-forest habitat composition (Table S2).

2.2. Primary productivity

Primary productivity for each habitat was assessed using the Normalized Vegetation Difference index (NDVI), which has been