NOTE / NOTE

Is nursing a kid detrimental to nonimmunological compatibility to contact-transmitted foreign bodies in female Iberian ibex (*Capra pyrenaica*)?

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Abstract: Reproductive costs may increase the susceptibility of breeding females to parasites. Compatibility may be modulated by immunity and nonimmunological factors. However, experimental tests attempting to unravel the role of nonimmunological compatibility to parasites are scarce. We experimentally infected breeding and nonbreeding females with pseudoectoparasites (PEPs) to analyse how nursing a kid affects neatness in the Iberian ibex (*Capra pyrenaica* Schinz, 1838). Our results revealed that nursing a kid does not seem detrimental to neatness in female Iberian ibex in terms of nonimmunological compatibility to contact-transmitted foreign bodies. Consequently, it seems that increased susceptibility of breeding females to contact-transmitted parasites may be mainly mediated by increased exposure or increased immunological compatibility to parasites.

Key words: Capra pyrenaica, Iberian ibex, contact-transmitted parasitism, cost of reproduction, host compatibility, kid nursing, ungulates.

Résumé : Les coûts de reproduction peuvent accroître la susceptibilité des femelles reproductrices envers des parasites. La compatibilité envers les parasites peut être modulée par le système immunitaire et des facteurs non-immunologiques. Cependant, rares sont les expériences tentant de révéler le rôle des facteurs non-immunologiques de compatibilité avec les parasites. Nous avons expérimentalement infecté avec de pseudoecotoparasites (PEPs) des femelles de bouquetin ibérique (*Capra pyrenaica*) ayant un cabris ou pas, pour analyser les effets potentiels de la reproduction sur la compatibilité nonimmunologique à des corps étrangers transmis par contact. Nos résultats suggèrent que les femelles suitées ne seraient pas plus compatibles avec les PEPs que les femelles n'ayant pas de cabri. La plus grande susceptibilité aux parasites des femellesreproductives pourrait donc plutôt dépendre d'une exposition accrue aux parasites ou d'une plus grande compatibilité immunologique avec ces derniers.

Mots-clés : Capra pyrenaica, bouquetin ibérique, parasites transmis par contact, coût de reproduction, compatibilité de l'hôte, allaitement de cabris, ongulés.

Introduction

Reproductive effort and parental care can have a cost in terms of lifetime fitness (Gross 2005), which is often mediated by increased susceptibility, sensu lato, to parasites (through exposure and (or) compatibility) (Christe et al. 2000; Combes 2001; Pelletier et al. 2005; Cripps et al. 2011).

Host compatibility to parasites refers to the probability that the parasite and potential host live together durably after the encounter or, in other words, the predisposition of hosts as suitable environments for potential parasites (Combes 2001). This compatibility is determined by the capacity of potential hosts to provide the necessary resources for the parasite (spatial resources, metabolic resources, etc.) and by the capacity of the potential host to negatively affect or destroy the parasite (via immune-defense systems or other mechanisms) (Combes 2001). Host compatibility to parasites may be modulated by factors such as anatomical characteristics, be-

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havior, and immunity (Hart 1990; Murray 1990; Hart 1994; Sarasa et al. 2009, 2010, 2011*a*). Behavior such as grooming or rubbing of body parts against solid structures can effectively remove foreign bodies from the host body surface, although the effectiveness of such behaviors is modulated by the accessibility to different host body parts and by the characteristics of the host's coat (Hart 1990; Murray 1990; Hart 1994). Midges can crawl through the hair coat of cattle, but maybe not through the dense fleece of sheep, which tend to be bitten around the head or feet (Muller and Murray 1977). Positive correlations were reported between infestation of the tick *Boophilus microplus* (Canestrini, 1888), hair length, and coat thickness in cows (Veríssimo et al. 2002). Even the variability in the seasonal loss of winter hair in the host has substantial effects on the microhabitat conditions of the body surface of the host and on its compatibility to ectoparasites. For instance, the louse *Hoplopleura acanthopus* (Burmeister, 1839) was only found on the fore-part of the body of the common vole (*Microtus arvalis* (Pallas, 1778)) in autumn but was distributed over the whole body when the louse was abundant in early spring; it is possible that lice are lost with the pelage when the winter coat is shed (Vysotskaya 1950; Murray 1990). Shearing and solar radiation affect populations of the sheep-biting louse (*Damalinia ovis* (Schrank, 1781)) in the fleece of sheep (Murray 1968). The premature loss of winter hair might be linked to antiparasitic strategies (Mooring and Samuel 1999). The shedding of the coat may be delayed when animals are in poor condition (Yeates 1955) and this delay may favor the development of lice (Murray 1957). The efficiency of antiparasitic behavior varies seasonally and, combined with molting and the resultant microclimatic changes in the pelage, plays an important role in modulating host compatibility to ectoparasites (Murray 1990). In terms of host compatibility to parasites, estimates of the relative importance of nonimmunological factors—that is, the synergy between behavioral and anatomical characteristics—independently of the effects of immunity are few (Mougeot et al. 2005; Sarasa et al. 2009, 2011*a*). This synergy between the host's anatomical characteristics and the behavioral factors favoring the cleaning of the host's body surface (Murray 1990) determines the neatness of the host, which is defined as the state of being free from foreign bodies and particles such as parasites in an absolute or relative sense (Sarasa et al. 2011*a*).

In mammals, reproductive costs have been mostly recorded in terms of activity budget and of energetic balance (Mysterud et al. 2004; Rughetti and Festa-Bianchet 2011), but the costs in terms of parasitism are only partly understood.

Male mammals have been the object of numerous studies on the costs of reproduction (Mysterud et al. 2004) that have highlighted the fact that sexual displays and the mating period are associated with altered homeostasis (Barboza et al. 2004) and with more favorable conditions for parasites (Pelletier et al. 2005). Nevertheless, nonimmunological compatibility to contact-transmitted foreign bodies is not necessarily at its greatest level during the rutting season (Sarasa et al. 2011*a*). Female mammals also make a costly investment during gestation and lactation (Clutton-Brock et al. 1989). This reproductive effort has been reported to be associated with modifications in maternal behavior (Grignolio et al. 2007; Murray et al. 2009), lower resistance to parasites (Festa-Bianchet 1989; Christe et al. 2000), and greater parasite loads in breeding females than in nonbreeding females (at least in bats and ungulates) (Rubenstein and Hohmann 1989; Okello-Onen et al. 1999; Pearce and O'Shea 2007; Zhang et al. 2010; Sundari et al. 2012). However, to our knowledge, the relative importance of nonimmunological factors in the compatibility of female hosts to parasites is an issue that is still poorly understood.

The aim of the present study was to test experimentally how nursing a kid affects nonimmunological compatibility to contact-transmitted foreign bodies in female Iberian ibex (*Capra pyrenaica* Schinz, 1838) (Sarasa et al. 2012). Contact-transmitted parasitism (e.g., sarcoptic mange caused by the itch mite, *Sarcoptes scabiei* De Geer, 1778) is a major determining factor in the ecology, population dynamics, and management practices of the Iberian ibex (Pérez et al. 2011; Sarasa et al. 2010, 2011*a*, 2011*b*). Recent studies on this biological model have revealed that behavioral and immunological factors probably intervene in parasitic infestations and their importance will depend on season, sex, age, and previous exposure, although these factors will not necessarily act in concert (Sarasa et al. 2010, 2011*a*). Antiparasitic behavior alone (e.g., grooming), was unable to explain the interindividual differences in host neatness and in nonimmunological compatibility to foreign bodies (Sarasa et al. 2011*a*), a finding that should urge biologists to reappraise the study approaches of the interindividual heterogeneity in compatibility to ectoparasites.

In male ungulates, reproductive investment has been reported to be negatively associated with investment in cleaning behavior and with susceptibility to parasites (Mooring and Hart 1995; Mooring et al. 1996, 2006). Reproductive investment in females could be linked to similar trade-offs given that in ungulates lactating females partly compensate for the costs of lactation through behavioral trade-offs to meet their daily energetic requirements (Hamel and Côté 2008). In nursing females, a lactation-related increase in prolactin occurs, which might induce reduced grooming rates, allowing greater vigilance over potential predators (Hart and Pryor 2004). Nursing is accompanied by deep physiological changes and hormonal levels modulate differences in hair characteristics between different parts of the body and between different females (Riggott and Wyatt 1983; Poindron et al. 1988; Sağsöz et al. 2004; Craven et al. 2006). Thus, increased nonimmunological compatibility to parasites —mediated by behavior and pelage characteristics—could occur in lactating females compared with non-nursing females. If nursing favors nonimmunological compatibility to contact-transmitted parasites, we would expect foreign bodies to have a longer lifespan on nursing females than on non-nursing females.

Materials and methods

The experiment was performed from August 2007 to March 2008 in a large enclosure (35 ha) containing a stock reservoir population of 87 Iberian ibex in Espacio Natural de Sierra Nevada (ENSN; 37°9′N, 3°31′E), Granada, southern Spain. The studied ibex were marked as kids with numbered ear tags and range freely within this enclosure. These ibex had previously developed tolerance to the observer (Sarasa et

Table 1. Model selection for the effects of nursing a kid on the half-lifespan of pseudoectoparasites (PEPs) on female Iberian ibex (*Capra pyrenaica*) from a stock reservoir population in Sierra Nevada, Spain, from 2007 to 2008.

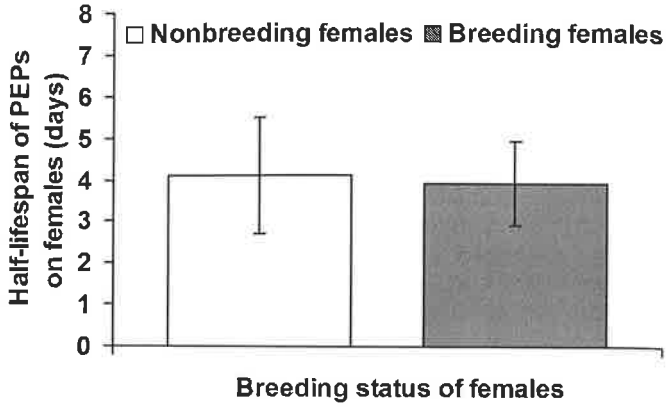
Model	K	AIC_c	ΔAIC_c	W_i	Deviance explained
P + A	3	91.45	0.00	0.79	0.78
P + A + N	4	94.38	2.94	0.18	0.78
P + A + N + A × N	5	97.76	6.32	0.03	0.79

Note: Sample size equals 20. Model variables are as follows: P, period of replication of the experiment; A, age of the female; N, breeding status. K is the number of estimated parameters. AIC_c is Akaike's information criterion corrected for small sample size; lower values indicate a superior model fit to observed data. ΔAIC_c is the difference in AIC_c values between the model and the most parsimonious model; the larger ΔAIC_c is, the less plausible it is that the fitted model is the best model given the data set. W_i is the Akaike weight of the model. (Burnham and Anderson 2002; Wood 2006).

al. 2009, 2011*a*). The natural food supply in the enclosure was complemented on a daily basis with additional forage provided in seven different mangers and in the surrounding areas to prevent the monopolization of feeding sites and food by dominant individuals (Appleby 1980).

To avoid interobserver variability, all the fieldwork was carried out by the first author. The experiment was based on a infection protocol using pseudoectoparasites (PEPs) whose characteristics have been previously described (Sarasa et al. 2009). PEPs consist of waxed wooden triangular markers that mimic innocuously several "mechanical" features of ectoparasites in host species (Sarasa et al. 2009). The hypoallergenic wax allows PEPs to became attached to the surface of the animal's coat without irritating the skin. Whatever the preestablished parasitic community of the host, real contact-transmitted parasites attempting to colonize a new host have to overcome the microhabitat conditions of the host body surface prior to successfully establishing themselves. Likewise, PEPs operate under the effects of the mechanical conditions of the microhabitats of the host's body surface, which are modulated by coat characteristics and affected by behavior such as grooming and rubbing (Sarasa et al. 2009, 2011*a*). Consequently, PEPs enable the importance of the nonimmunological features that influence the compatibility between hosts and contact-transmitted parasites to be investigated while, at the same time, "controlling" for parasite biology. We characterized the outcome of the confrontations between host and PEPs as an indicator of host compatibility and neatness, defined as the state of being free from foreign bodies and particles—for example, parasites—in an absolute or relative sense (Sarasa et al. 2011*a*). Food was used to attract all the ibex into a small bottlenecked space that is habitually used for managing animals in the large enclosure. In the selection of the infected ibex, we ensured that both nursing and non-nursing females were represented. The infections of the females was not performed until kids were 4 months old to avoid weakening the mother–kid linkage (Livezey 1990). When handled, animals were blindfolded, physically restrained, and infected with PEPs over their whole skin surface according to a standardized protocol:

Fig. 1. Effect of nursing a kid on the half-lifespan of pseudoectoparasites (PEPs) on female Iberian ibex (*Capra pyrenaica*) from a stock reservoir population in Sierra Nevada, Spain, from 2007 to 2008. Bars represent the mean half-lifespan of the PEPs on females and their related standard errors. Nonbreeding females: $n = 9$; breeding females: $n = 11$.



each ibex host had a specific PEP color code and were "infected" by 44 PEPs distributed homogeneously over the whole skin surface. Animals were then released into the large enclosure (day 0 postinfection, D0ppi). The number of PEPs on each individual was monitored daily for 3 weeks using 10 × 40 Bushnell binoculars and a Canon EOS 400D camera with a 70–300 mm lens. Although PEPs can be contact-transmitted between individuals, in this study we only recorded the loss of PEPs from each ibex relative to D0ppi because PEP transmission networks are beyond the scope of this study.

Our experimental procedure had been previously used to analyze interseasonal variability in host neatness as part of an experiment in which different females were infected in five replication periods (from September to March) (Sarasa et al. 2011*a*). To obtain comparable groups, 20 females within the range of the observed reproductive age (3–8 years) were included in this analysis (11 nursing and 9 non-nursing females; Supplementary Table S1[1]). We analyzed the effect of nursing a kid on the half-lifespan of the PEPs on females (the number of days after infection when only 22 or fewer PEPs were still on the host) to focus the study on interindividual variability in neatness, rather than on the progressive loss of PEPs over time (Sarasa et al. 2009). Antiparasitic behavior was not considered in this analysis because, as we have shown previously, this type of behavior is unable to explain accurately compatibility to contact-transmitted foreign bodies (Sarasa et al. 2011*a*). The season and the age of the females modulated the loss of PEPs (Sarasa et al. 2011*a*) and so we compared the model including only these two factors with (*i*) the model including also the "nursing" factor and (*ii*) the model including the interaction between "age" and "nursing" factors. Thus, we were able to test the potential effect of the nursing status while controlling for the effects of age and season on neatness.

We used general additive models (GAM) (Wood 2006) that describe the shape of the relationship between the re-

[1]Supplementary Table S1 are available with the article through the journal Web site (http://nrcresearchpress.com/doi/suppl/10.1139/z2012-095).

sponse variable and the explanatory variable even when nonlinear associations are expected (such as between season and neatness). We performed a model selection based on Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). This procedure identified the most parsimonious model, which is characterized by the lowest AIC_c value (Burnham and Anderson 2002). The relative importance (RI) of the examined variables derived from the multimodel inference were commented upon (Burnham and Anderson 2002). All analyses were performed using the R version 2.12.1 statistical packages (R Development Core Team 2010).

Results

Results show that the half-lifespans of the PEPs did not differ between nursing and non-nursing females (Table 1, Fig. 1). The model selection revealed that the model including only period and age of females was the best of the tested models. Relatively, the variables of greatest importance were period and age, thereby revealing the impact that these two factors have on variability in PEP lifespan ($RI_{period} = 1$; $RI_{age} = 1$). The "nursing" factor and the interaction between "age" and "nursing" only had a low relative importance ($RI_{nursing} = 0.21$; $RI_{age \times nursing} = 0.03$) and were excluded from the best model explaining the observed pattern for the data at hand. The models including the "nursing" factor and the interaction between "age" and "nursing" had an Akaike difference of greater than two units (respectively, 2.94 and 6.32), which shows that such models add little support for our data set. The explained deviance of the fitted models showed that the season and the age of females explained most of the observed variability in the length of the half-lifespan of the PEPs on females (more than 78%; Table 1).

Discussion

During our study period, nursing a kid did not seem to be detrimental to neatness in female Iberian ibex. Our experiment refines the understanding of potential parasitic costs of breeding in females (Rubenstein and Hohmann 1989; Okello-Onen et al. 1999; Pearce and O'Shea 2007; Zhang et al. 2010; Sundari et al. 2012) because the reproductive effort of nursing was not found to result in increased compatibility to pseudoectoparasites in female Iberian ibex. Females maintained the stability of their nonimmunological barriers that modulate compatibility to contact-transmitted foreign bodies, even during lactation. Consequently, the potential increased susceptibility of breeding females to contact-transmitted parasites would seem to be unconnected to their nonimmunological compatibility to ectoparasite colonization. Nonimmunological factors affecting compatibility to ectoparasites can potentially affect both the colonization—the moment the parasite arrives on the animal's coat—and the establishment or development of the parasite, which is the period the parasite is living durably in or under the coat. Nevertheless, future studies could develop this distinction further to fully assess the potential effects of reproduction on parasites that are already established successfully on females, particularly in different seasons from those of our study period. Our study suggests indirectly that the potential increased susceptibility in breeding females to contact-transmitted parasites may be mediated by greater exposure or greater immunological compatibility to parasites. Correlative and experimental studies have revealed for many mammalian species that a relaxation of immune defenses to parasites occurs in breeding females (Christe et al. 2000; Houdijk 2008; Jones et al. 2011). Thus, future studies should analyze potential immunological differences in terms of nursing status in female Iberian ibex. It is also well known that breeding female ungulates exhibit differential use of space compared with nonbreeding females. In deer, parturition often occurs in specific sites such as marshes and meadows (Ciuti et al. 2006) and in mountain ungulates on rocky slopes (Grignolio et al. 2007), a differential use of space that is usually interpreted as an antipredator strategy (Grignolio et al. 2007). Thus, a further challenge will be to analyze whether such a differential use of space could induce differential exposure to contact-transmitted parasites as, for example, occurs in kangaroos with trophically transmitted parasites, where the energetic demands of reproduction increase exposure in breeding females to faecal-contaminated areas and to infection by gastrointestinal parasites (Cripps et al. 2011).

Our experiment suggests that nursing female Iberian ibex do not show reduced neatness. Consequently, the increased susceptibility of breeding females to contact-transmitted parasites may be mediated, above all, by the increased exposure or increased immunological compatibility to parasites.

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