

Original Article

Neatness depends on season, age, and sex in Iberian ibex *Capra pyrenaica*

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Heterogeneity in host compatibility is one of the main hypotheses proposed to explain uneven resistance to parasites and uneven parasite load between hosts. It suggests that differences between hosts modulate their predispositions as suitable environments for their potential parasites. Interesting studies of antiparasitic behavior have reported the existence of behavioral traits that are capable of removing foreign particles and of reducing the success of parasitic infections. These traits favor host neatness, although little is known about the heterogeneity of neatness. We used a standardized pseudo-infection with pseudo-ectoparasites (PEPs) to test the effects of sex, age, and season on the loss of PEPs by hosts as a means of exploring the factors determining neatness in the Iberian ibex *Capra pyrenaica*. Behavioral observations were also performed to analyze investment in antiparasitic behavior in terms of sex, age, and season. The life span of PEPs peaked in the period December–January, decreased with host age, and was longer in females than in males. Investment in antiparasitic behavior is also associated with both sex and age and season but in a different pattern with interactions between such factors. Our results disagree with the hypothesis that small-bodied animals should be less compatible to carry contact-transmitted particles, such as ectoparasites, in comparison with larger animals. This preexisting hypothesis is thus an inadequate way of predicting host neatness. Consequently, our experiment underlines the importance that nonimmunological traits play in determining heterogeneity in host compatibility to contact-transmitted foreign bodies and helps improve understanding of neatness and of host–parasite systems. *Key words*: antiparasitic behavior, body size principle, *Capra pyrenaica*, ectoparasites, grooming, host compatibility, neatness, ungulates. [*Behav Ecol* 22:1070–1078 (2011)]

INTRODUCTION

Heterogeneity in host compatibility, which suggests that differences between hosts modulate their predisposition as suitable environments for potential parasites, is one of the main hypotheses posited to explain uneven resistance and uneven parasite load between hosts (Combes 2001). Numerous studies to date have focused on physiological traits and, above all, on immunity (Zuk 1996; Norris and Evans 2000; Martin et al. 2006), but an increasing body of evidence suggests that behavior also plays a key role (Altizer et al. 2003; Perkins et al. 2008, 2009; Gear et al. 2009). In recent decades, interesting studies of antiparasitic behavior have reported numerous behavioral traits that affect the success of parasites in colonizing, establishing, and proliferating on hosts (Mooring et al. 1996a, 1996b). These traits enhance in a global sense the neatness of the host, defined as the state of being free from foreign bodies and particles—for

example, parasites—in an absolute or relative sense. Grooming, which can be broadly defined as consisting of all forms of body surface care (Mooring et al. 2004), is a costly process (Giorgi et al. 2001) that supposes trade-offs with other activities (Giorgi et al. 2001; Hawlena, Bashary, et al. 2007). Individuals engage in this type of behavior to differing degrees (Mooring and Hart 1997). Nonimmunological defenses are under-considered in studies focused on invertebrates (Parker et al. 2011), and in vertebrates, grooming each other (“allogrooming”) can have several social functions beyond hygiene (Fruteau et al. 2009; Kutsukake and Clutton-Brock 2010; Tiddi et al. 2011). As a result, the hygienic function of antiparasitic behaviors was particularly highlighted in vertebrate species that mostly perform self-grooming (Cotgreave and Clayton 1994; Murray 1990), and interindividual differences were more deeply analyzed in ungulates (Mooring and Hart 1995; Mooring et al. 2004). On the basis of behavioral observations, 2 opposing models addressing the parasite-control of function of grooming were proposed. Animals may groom in response to stimulation, for example, from parasites bites (“stimuli-driven” grooming), or animals may groom prophylactically as a result of a central mechanism (“programmed-driven” grooming) (Hart et al. 1992). Based on behavioral observations, the “body-size principle” was presented as a possible reflection of increased vulnerability

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to ectoparasites through a greater body surface to mass ratio (Hart et al. 1992). The body-size principle, resulting from the “programmed grooming model,” suggests that small-bodied animals should groom at a higher rate and consequently have fewer ectoparasites in a comparison with larger animals (Hart et al. 1992). Thus, according to this principle, juveniles would groom more than adults (Mooring and Hart 1997; Mooring, Hart, et al. 2006) and, in dimorphic species, females would groom more than males (Mooring et al. 2002). To date, this principle has been mainly tested in ungulates (Mooring et al. 2000, 2002, 2004; Mooring, Hart, et al. 2006; Mooring, Patton, et al. 2006). In terms of non-immunological defenses against parasites and based on this prevailing body-size principle, adult males are often assumed to be more prone than other host classes to colonization by contact-transmitted foreign entities (such as ectoparasites). Thus, adult males may have higher densities of ectoparasites than females and juvenile (Schalk and Forbes 1997; Moore and Wilson 2002), in part due to their supposed lower investment in antiparasitic behavior (Hart et al. 1992). This expected nonimmunological predisposition to parasite colonization and the “immunocompetence handicap” hypothesis (Folstad and Karter 1992) might even act additively to produce uneven distribution of parasites. Testosterone stimulates the development of characteristics used in sexual selection and at the same time reduces immunocompetence (Folstad and Karter 1992). Androgens would mediate the suppression of antiparasitic behavior as well (Mooring et al. 1998; Mooring, Patton, et al. 2006).

However, recent studies have highlighted the fact that the body-size principle might not be as generalized and preponderant as expected and place doubt on the ability of the body-size principle to predict host neatness. Grooming, for example, has been observed to take place less often in juveniles than in adults in the desert rodent *Meriones crassus* (Hawlena, Bashary, et al. 2007; Hawlena et al. 2008), Cape ground squirrels *Xerus inauris* showed no sex differences in terms of autogrooming (Hillegass et al. 2008), and the preliminary results of a test procedure using pseudoectoparasites (PEPs) did not match predictions based on the body-size principle (Sarasa et al. 2009). Thus, these studies indicate that there is a need to study variability in neatness further and to analyze its consistency with predictions derived from the body-size principle.

In this study, we used PEPs (Sarasa et al. 2009) to test experimentally the role of key factors of individual heterogeneity in patterns of uneven neatness in a sexually dimorphic ungulate, the Iberian ibex *Capra pyrenaica* (Pérez et al. 2002). Observations of behavior were also performed to analyze investment in antiparasitic behavior. According to the body-size principle, we expected to find greater investment in antiparasitic behavior in small ibexes than in large ones (Mooring and Hart 1997; Mooring et al. 2002; Mooring, Hart, et al. 2006). Thus, we expected neatness (expressed as the investment in antiparasitic behavior and the ability to remove PEPs) to decrease with age (prediction 1) and males to be less neat than females (prediction 2).

In addition, host–pathogen interactions are usually highly status dependent. More specifically, the mating season might signal a period of change in the levels of physiological modulators of grooming behavior (Mooring, Patton, et al. 2006) and in investment in antiparasitic behavior (Mooring et al. 1996a). These changes relate to the link between host behavior and opportunism in parasite life cycles (Tinsley 1990), and in the case of the ecology of the Iberian ibex, autumn rutting is generally considered to be the starting point and hence one of the main determining factors of the seasonal outbreaks of sarcoptic mange caused by the

contact-transmitted mite *Sarcoptes scabiei* (Pérez et al. 1997; León-Vizcaíno et al. 1999). This burrowing mite consumes living cells and tissue fluid from the skin of its host (Pence and Ueckermann 2002). Sarcoptic mange is a major determining factor of Iberian ibex ecology, population dynamics, and management practices (Pérez et al. 2002, 2011; Sarasa et al. 2010, 2011). Thus, during the mating season, we expected to find a season-dependent reduction in antiparasitic behavior coinciding with a peak in the life span of colonizing ectoparasites and of PEPs, as well as greater neatness during the rest of the year (prediction 3).

MATERIALS AND METHODS

Study site

The experiment was performed in a large enclosure (35 ha) containing a stock reservoir population of Iberian ibex (Espacio Natural de Sierra Nevada [ENSN], lat 37°9' N long 3°31' E, Granada, southern Spain). This enclosure was built in the 1990s to protect a pool of ibexes trapped in the surrounding Sierra Nevada Natural Space from mange. The enclosure that contains the stock reservoir population only prevents exposure of the mange-free ibexes inside to potentially many ibexes on the outside. As a result, the stock reservoir population is free of mange but not free of other parasites. During the study period, 41 males and 46 females that had been marked as kids with numbered ear tags, ranged freely within this enclosure. Ibexes had previously developed tolerance to the observer (Sarasa et al. 2009) to avoid the behavioral alterations associated with the presence of a human observer (Crofoot et al. 2010). The natural food supply available in the enclosure was complemented on a daily basis with additional forage provided in several mangers and their surrounding areas to prevent the monopolization of feeding sites and food by dominant individuals (Appleby 1980).

Experimental procedure

To avoid interobserver variability, all the fieldwork was carried out by the first author. The experiment was based on a pseudo-infection protocol using PEPs whose characteristics have been previously described (Sarasa et al. 2009). PEPs are waxed wooden triangular markers that mimic innocuously contact-transmitted parasitic infections in host species (Sarasa et al. 2009). PEPs mimic several mechanical features of ectoparasites and can be transmitted by contact to hosts. PEPs are under the effects of the microhabitat conditions of the body surface of their host, just as real contact-transmitted parasites do (Sarasa et al. 2009). Nevertheless, the host–PEP interaction is only an imitation of real host–parasite interactions because PEPs are unaffected by host immunity, are innocuous to the host, and do not exhibit microhabitat preferences (e.g., parasite mobility and preferences [Murray 1990; Crompton 1997; Christe et al. 2007; Khokhlova et al. 2011]) (Sarasa et al. 2009). Consequently, PEPs enable the importance of the nonimmunological features that influence the compatibility between hosts and contact-transmitted parasites to be investigated, while controlling for parasite biology. Whatever the preestablished parasitic community of the host, real contact-transmitted parasites attempting to colonize a new host have to overcome to the microhabitat conditions of the host body surface prior to successfully establishing themselves. Likewise, PEPs are under the effects of the microhabitat conditions of the host body surface that lead to PEPs loose (Sarasa et al. 2009), and we characterized the outcome of such confrontations as an indicator of host compatibility and neatness. PEPs were

prepared just prior to animal manipulation (before dawn) to minimize handling time and to optimize the features of the PEPs during pseudoinfection. Food was used to attract all the ibexes into a small bottlenecked space that is habitually used for managing animals in the large enclosure. In the selection of the pseudoinfected ibexes, we ensured that all sex- and age-classes were represented (Supplementary Table S1). When handled, animals were blindfolded, physically restrained, and each pseudoinfected with 44 PEPs distributed over the whole skin surface of the host according to a standardized protocol (each host had different color PEPs). Animals were then released into the large enclosure (Day 0 post-pseudoinfection = D0ppi). The dynamics of the PEPs on each individual were monitored daily for 3 weeks using 10 × 40 Bushnell binoculars and a Canon EOS 400D camera with a 70–300 mm lens. The short-range observation distance and extensive photographic data were key factors in the fine monitoring of the dynamics of the PEPs.

Rutting in the Iberian ibex occurs in autumn between mid-November and mid-December (Fandos 1991). Contact-transmitted parasites are supposed to take advantage of the mating season to propagate within populations and the peak in occurrence of major parasites such as *S. scabiei* takes place between January and March (Pérez et al. 1997; León-Vizcaíno et al. 1999; Granados et al. 2007). To examine inter-seasonal variability of host neatness before, during, and after these key periods in the ecology of the Iberian ibex, the whole experimental procedure was repeated 5 times (I: end of August–early September 2007; II: mid October–early November 2007; III: end of November–mid December 2007; IV: mid-January–early February 2008, and V: March 2008). PEPs were found to be a suitable tool for this purpose because their characteristics (in particular their adherence) were stable between the considered periods (Sarasa et al. 2009). During the experiment, we also recorded the peak of the rutting season, that is, the period in which tending and courting behavior in males is especially intense and frequent and in which females do not systematically avoid and are more receptive to courting males. Different individual hosts were considered for each season to avoid inter-seasonal autocorrelation. A total of 57 individuals were pseudoinfected and monitored throughout the experiment (Supplementary Table S1).

Observational study

To examine investment in antiparasitic behavior related to age, sex, and season, we also scan-sampled behavior

(Altmann 1974) in the year after the pseudoinfections using the same calendar of 5 sampling periods. This protocol was based on the relative phenological stability of the biology of the Iberian ibex, well illustrated by the fact that the peak in rutting occurred as normal in mid-November during the years of pseudoinfection and behavioral observations, as described by previous studies of the life cycle of the species (Fandos 1991). For each period, 9–13 samplings were performed (70% in morning and 30% in afternoon), during which the behavior of all the observed animals (individually marked with ear tags) was scan sampled to estimate the relative importance (RI) of antiparasitic behavior in their activity budgets and its seasonality. We distinguished “intra-specific cleaning behavior” (ISCB) from “exo-scratching behavior (ESB).” ISCB is the maintenance of the coat using teeth, horns, or any other part of the body and includes self-grooming, allogrooming, and hindleg scratching described in other studies (Mooring et al. 2002, 2004; Mooring, Patton, et al. 2006). ESB is the voluntary rubbing of parts of the body on environmental components such as trees, fences, or rocks. Note that ESB is not normally considered in major studies of antiparasitic behavior (Mooring et al. 2000, 2002, 2004), maybe due to the difficulties in sampling such behavior in free-ranging individuals and in deficient environments such as zoological parks. Nevertheless, alternative strategies to ISCB such as ESB (including wallowing) or cleaning symbiosis could be consistently associated with parasite life cycles (McMillan et al. 2000) and might even be highly effective in removing parasites (Bezuidenhout and Stutterheim 1980). During our observations, we also recorded rutting behavior (tending and courting behavior in males). Samplings were performed at least 6 h apart and almost always 24 h apart in order to reduce/avoid temporal autocorrelation.

Analysis

In our behavioral data set, we analyzed the factors associated with the mean investment in antiparasitic behavior per individual in order to focus the study on the importance of explanatory variables rather than on the rarity of occurrence of antiparasitic behavior. Thus, the mean investment in total and in categories of antiparasitic behavior was estimated for each individual in each replication period. As suggested by Verbeke and Molenberghs (2000), we performed an exploratory data analysis of our behavioral data set. We tested for temporal autocorrelation (a relationship

Table 1
Model selection for effects of sex, age, and season on the half-life span of PEPs on their hosts

Model	Sample size	<i>K</i>	AICc	ΔAICc	<i>L</i> (gi/ <i>x</i>)	<i>w</i> _{<i>i</i>}	Dev-Expl	RI
P + A + S	57	5	234.29	0.00	1.00	0.39	0.71	P: 1.00
P + A + S + A × S	57	6	236.52	2.23	0.33	0.13	0.71	A: 1.00
P + A + S + P × A	57	11	236.58	2.29	0.32	0.12	0.79	S: 0.84
P + A + S + S × P	57	6	236.81	2.52	0.28	0.11	0.71	P × A: 0.23
P + A	57	4	236.92	2.64	0.27	0.10	0.69	A × S: 0.20
P + A + P × A	57	11	238.31	4.02	0.13	0.05	0.78	P × S: 0.17
P + A + S + S × P + A × S	57	7	239.13	4.85	0.09	0.03	0.71	
P + A + S + P × A + A × S	57	13	239.57	5.28	0.07	0.03	0.81	
P + A + S + P × A + S × P	57	12	239.84	5.55	0.06	0.02	0.80	
P + A + S + P × A + S × P + A × S	57	14	242.99	8.70	0.01	0.01	0.81	

Only the 10 best models are reported. P, period of replication of the experiment; A, age of the host; S, sex of the host; ×, interaction; *K*, number of estimated parameters; AICc, Akaike Information Criterion corrected for small sample size; lower values indicate a superior model fit to observed data. ΔAICc, difference of AICc between the model and the most parsimonious model; the larger the ΔAICc, the less plausible it is that the fitted model is the best model given the data set. *L*(gi/*x*), probability of the model being the best model given the data set. *w*_{*i*}, Akaike weight of the model. Dev-Expl, Deviance explained by the fitted model. RI, RI of factors (Burnham and Anderson 2002; Wood 2006).

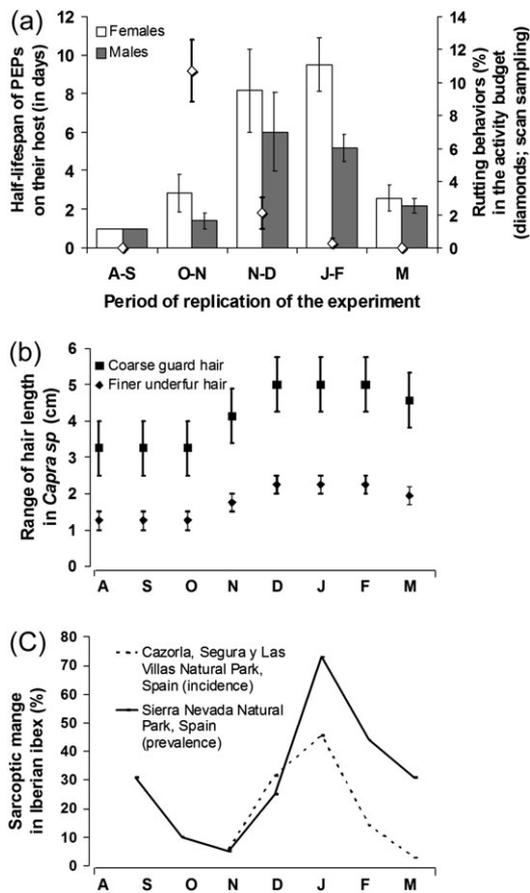


Figure 1

Comparison of (a) seasonality in the life span of PEPs on their hosts, (b) hair-coat length in *Capra sp.*, and (c) sarcoptic mange *Sarcoptes scabiei* in 2 populations of Iberian ibex *Capra pyrenaica*. The x axis represents months of the year: A = August, S = September, O = October, N = November, D = December, J = January, F = February, M = March. (a) Bars represent the mean half-life span of PEPs on their hosts and their related standard errors according to host sex and the replication period of the experiment; diamonds represent the phenology of investment in rutting behavior (mean values and their related standard errors); (b) lines represent the ranges of hair length for coarse guard hair (squares) and for finer underfur hair (diamonds) according to season in *Capra sp.*, redrawn from Couturier (1962); (c) black line: prevalence of sarcoptic mange in samples (% of samples with mange) during an outbreak in the Sierra Nevada Natural Park in Spain, redrawn from Pérez et al. (1997); dashed line: incidence (% of new cases) of sarcoptic mange infections within a group during an outbreak in the Cazorla, Segura y Las Villas Natural Park in Spain, redrawn from León-Vizcaíno et al. (1999).

between values separated from each other by a given time lag) using the Durbin–Watson (DW) test. In our data set, temporal autocorrelation was not significantly different to zero (total antiparasitic behavior (TAPB): DW = 1.8313; P value = 0.4053). Thus, we analyzed our behavioral data as independent variables.

In our experimental data set, we analyzed the factors that determined the half-life span of the PEPs on their hosts (the number of days after pseudoinfection when only 22 or fewer PEPs were still on the host) in order to focus the study on interindividual variability in neatness rather than on the progressive loss of PEPs over time (Sarasa et al. 2009).

For both the behavioral and the experimental data sets, the effects of the period (detailed above) and of the sex and age of

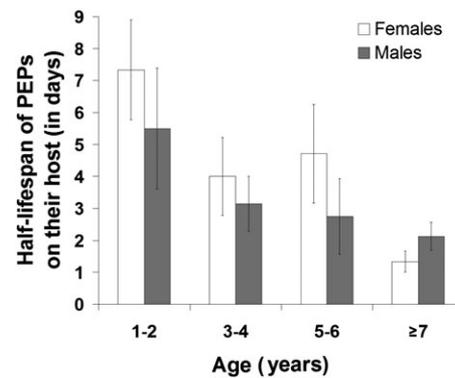


Figure 2

Effect of host age on the half-life span of the PEPs on hosts. Bars represent the mean half-life span of the PEPs on their hosts and their related standard errors.

animals were examined. For the behavioral data set, we first analyzed the total investment in antiparasitic behavior and, subsequently, analyzed separately ISCB and ESB. We used an information-theoretic approach with generalized additive models (GAMs) based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002; Wood 2006). The model selection in our analyses identified the most parsimonious model with the lowest AICc (Burnham and Anderson 2002) from the possible subsets, which ranged from the null model (MO, intercept only) to a model with all explanatory variables and their 2-order interactions. Models with Akaike differences of fewer than 2 units and the RI of the examined variables derived from the multimodel inference were commented upon (Burnham and Anderson 2002). The RI of predictor variables was measured by the sum of the Akaike weights of all the models in which the variable in question appears (minimum RI = 0 and maximum RI = 1; Burnham and Anderson 2002). All analyses were performed using the R 2.12.1 statistical packages (R Development Core Team 2010).

RESULTS

Half-life span of PEPs on their hosts

Period, ibex age, and sex affected the half-life span of PEPs on their hosts; interactions between factors had unsubstantial effects for the data at hand (Table 1). The model including these 3 main factors appeared as the best in the model selection (Table 1). The RI of period and age were the highest, indicating their impact on the variability in the life span of PEPs (RI = 1, Table 1). The half-life span of PEPs peaked in the period December–January, approximately a month and a half after the observed high point of the rutting season (Figure 1a) and after the observed low point of investment in TAPB, as per following chapter. In addition, the half-life span of the PEPs decreased gradually with the age of the host (Figure 2). The sex of the host was also an important factor in determining the half-life span of PEPs, although its RI was slightly lower than those of period and age (Table 1). The half-life span of the PEPs was longer in females than in males (Figure 1a). Interactions between explanatory variables were excluded from the best model in explaining the observed pattern for the data at hand (Table 1). The explained deviance of the fitted models suggests that the considered factors explain most of the observed variability in the length of the half-life span of the PEPs on their hosts (Table 1).

Table 2
Model selections for the effects of sex, age, and season on antiparasitic behavior in Iberian ibex

Model	Sample size	<i>K</i>	AICc	Δ AICc	$L(gi/x)$	w_i	Dev-Expl	RI
a) Model selection for effects of sex, age, and season on TAPB in Iberian ibex								
P + A + S + P × A	115	17	988.22	0.00	1.00	0.44	0.44	P: 1.00
P + A + P × A	115	16	989.20	0.99	0.61	0.27	0.42	A: 1.00
P + A + S + P × A + A × S	115	18	990.92	2.71	0.26	0.11	0.44	S: 0.72
P + A + S + P × A + S × P	115	18	990.99	2.77	0.25	0.11	0.44	P × A: 0.95
P + A + S + P × A + S × P + A × S	115	19	993.73	5.52	0.06	0.03	0.44	A × S: 0.15
P + A + S	115	9	994.49	6.27	0.04	0.02	0.30	P × S: 0.15
b) Model selection for effects of sex, age, and season on ISCB in Iberian ibex								
P + A + S + P × A	115	27	734.24	0.00	1.00	0.50	0.57	P: 1.00
P + A + S + P × A + A × S	115	28	735.97	1.74	0.42	0.21	0.58	A: 1.00
P + A + S + P × A + S × P	115	28	736.02	1.78	0.41	0.21	0.58	S: 0.98
P + A + S + P × A + S × P + A × S	115	29	738.30	4.06	0.13	0.07	0.58	P × A: 1.00
P + A + P × A	115	25	741.25	7.02	0.03	0.02	0.52	A × S: 0.28
P + A + S	115	7	749.69	15.45	0.00	0.00	0.24	P × S: 0.27
c) Model selection for effects of sex, age, and season on ESB in Iberian ibex								
P + A + P × A	115	15	834.86	0.00	1.00	0.62	0.41	P: 1.00
P + A + S + P × A	115	16	836.90	2.04	0.36	0.22	0.41	A: 1.00
P + A + S + P × A + S × P	115	17	839.22	4.36	0.11	0.07	0.41	S: 0.38
P + A + S + P × A + A × S	115	17	839.40	4.54	0.10	0.06	0.41	P × A: 0.99
P + A + S + P × A + S × P + A × S	115	18	841.87	7.01	0.03	0.02	0.41	A × S: 0.08
P + A	115	9	844.95	10.09	0.01	0.00	0.28	P × S: 0.09

Only the 6 best models are reported. P, period of replication of the experiment; A, age of the host; S, sex of the host; ×, interaction; *K*, number of estimated parameters; AICc, Akaike Information Criterion corrected for small sample size; Δ AICc, difference of AICc between the model and the most parsimonious model; $L(gi/x)$, probability of the model being the best model given the data set; w_i , Akaike weight of the model. DevExpl, Deviance explained by the fitted model. RI, RI of factors (Burnham and Anderson 2002; Wood 2006).

Investment in antiparasitic behavior

Period, age, and sex, sometimes in interaction, affect investment in antiparasitic behavior (Table 2). In the analyses of TAPB (Table 2a), the best model highlighted the fact that the 3 main factors and the interaction between age and period of the year had substantial effects on the observed variability of TAPB. Investment in TAPB showed nonlinear variations over seasons ($RI_{\text{Period}} = 1$), with a fall from the end of summer to November and a rise from November to March (Figure 3a). This relationship with season interacted with the effect of age ($RI_{\text{Age}} = 1$; $RI_{\text{Period} \times \text{Age}} = 0.95$). Despite the fact that young ibexes invested more in TAPB than adults at the end of summer, the trend was inverted in January–February. In the remaining seasons, the effect of age was less clear (autumn) or nonlinear (March) (Figure 4a). The sex of ibexes had an additive effect because males invested more in TAPB than females (Figure 3a), although the RI of sex was lower than those of age and season ($RI_{\text{Sex}} = 0.72$). In our analyses of TAPB, this lower importance of sex in comparison with age and period was also highlighted by the second model with substantial support (Δ AICc < 2), which just included period, age, and their interaction. In autumn, males were not observed to invest in antiparasitic behavior and investment of females was low, and our analyses of TAPB detected no substantial effect of the interaction between season and sex for the data at hand ($RI_{\text{Period} \times \text{Sex}} = 0.15$).

The respective analyses of ISCB and of ESB provide better understanding of the factors associated with investment in antiparasitic behavior. In the analyses of ISCB (Table 2b), the best model also highlighted the fact that the 3 main factors and the interaction between age and period played a substantial role in the observed variability. Investment in ISCB showed nonlinear variations over seasons ($RI_{\text{Period}} = 1$), a decrease from the end of summer to November and a rise from November to end of winter (Figure 3b). Nevertheless, in the model selection referring to ISCB, 2 additional models had

substantial support (Δ AICc < 2; Table 2b). These models suggest that the interactions “sex–period” and “sex–age” probably affected the observed variability in ISCB. The greater investment in ISCB by males was more pronounced at the end of summer and in March than in autumn–winter (Figure 3b; $RI_{\text{Sex}} = 0.98$, $RI_{\text{Period} \times \text{Sex}} = 0.27$, Table 2b). Furthermore, the season-dependent effect of age on ISCB passed from a mostly negative relationship at the end of summer to a bell-shaped one at the end of winter, although these relationships were more pronounced in males than in females (Figure 5; $RI_{\text{Age} \times \text{Sex}} = 0.28$, Table 2b).

In the analyses of ESB (Table 2c), the best model only included period, age, and their interaction. Investment in ESB was lower at the end of summer and autumn than in winter and early spring (Figure 3c; $RI_{\text{Period}} = 1$, Table 2c) and this effect of the season interacted with the effect of age ($RI_{\text{Period} \times \text{Age}} = 0.99$, Table 2c). The relationship between age and investment in ESB changed from mostly negative at the end of summer to mostly positive at the end of winter (Figure 4b). No substantial effect of sex was detected in ESB for the data at hand.

DISCUSSION

Our results provide clear evidence that both antiparasitic behavior and neatness with regard to PEPs vary with season, age, and sex in Iberian ibex, although these proxies of host neatness exhibit different patterns. To our knowledge—at least among vertebrates—this is the first experiment to characterize neatness inequalities independently of the host immune system and preferences of real parasites.

Neatness, seasons, and hair coat

The observed patterns corroborate the hypothesis that neatness patterns are season dependent but do not fulfill the

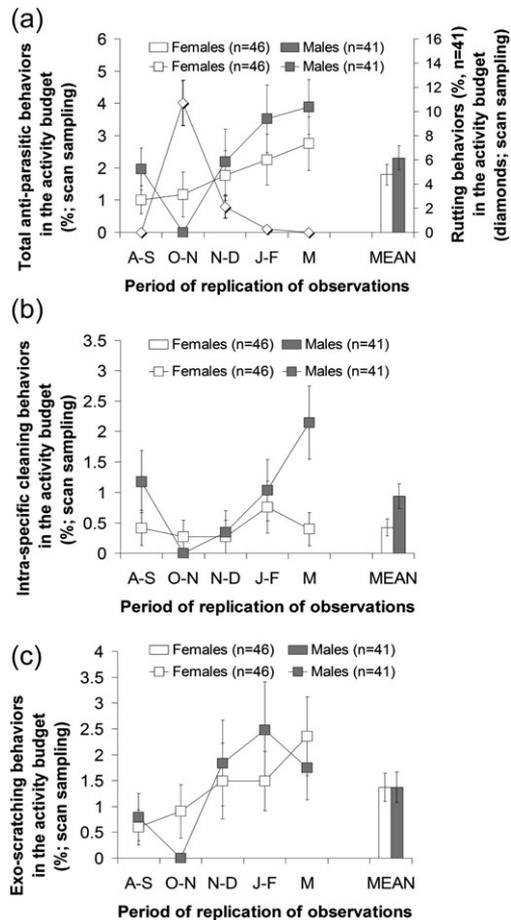


Figure 3

Investment in antiparasitic behavior in the activity budget (%) according to host sex and of the replication period of the observations. A = August, S = September, O = October, N = November, D = December, J = January, F = February, M = March. (a) Bars and squares represent the investment in TAPB and diamonds represent the phenology of investment in rutting behavior (mean values and their related standard errors for both); (b) bars and squares represent investment in ISCB including the self-grooming, allogrooming, and hindleg scratching described in other studies (mean values and their related standard errors for both); (c) bars and squares represent investment in exo-scratching cleaning behavior corresponding to rubbing of parts of the body on environmental components such as trees or rocks (mean values and their related standard errors for both).

prediction of a peak in the half-life span of the PEPs during the rutting season. Nevertheless, the expected low point of investment in TAPB during the rutting season was fulfilled. Thus, although antiparasitic behavior may remove efficiently contact-transmitted particles ranging from bacteria to macroparasites (Mooring et al. 1996b; Kohari, Sato and Nakai 2009), our results suggest that antiparasitic behavior alone may not explain the pattern of PEP life span and of neatness. Figure 1a shows that the observed peak of the half-life span of the PEPs occurs in mid-winter, approximately a month and a half after the low point in investment in TAPB that occurs during the rutting season (Figure 3a). This trend suggests that winter-linked traits, such as hair-coat characteristics, may play a greater role in surface cleaning efficiency and neatness maintenance by hosts. Other authors have related hair-coat characteristics to grooming (Mooring and Samuel 1998, 1999) and parasitism (Veríssimo et al. 2002). Mooring and Samuel (1998)

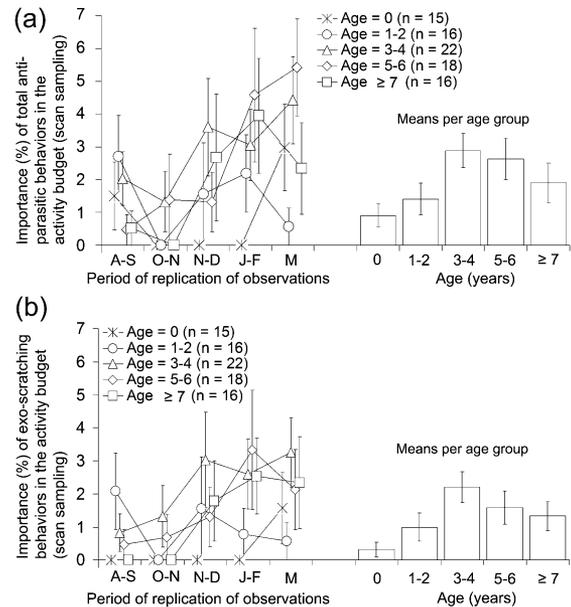


Figure 4

Investment in TAPB and in exo-scratching cleaning behavior in the activity budget (%) according to host age and the replication period of the observations. Bars represent mean values and their related standard errors. (a) TAPB. (b) Exo-scratching cleaning behavior consisting of rubbing parts of the body on environmental components such as trees or rocks. A = August, S = September, O = October, N = November, D = December, J = January, F = February, M = March.

suggested that a dense hair coat might in fact act as a physical barrier against the establishment of ectoparasites. Nevertheless, our study shows that PEPs had a longer life span in winter, the period in which ibexes had their longest hair coats (Figure 1b) (Couturier 1962). Moreover, coat thickness and hair length have been found to correlate positively with tick infection in bovinds (Veríssimo et al. 2002), whereas moose *Alces alces* infected with winter ticks *Dermacentor albipictus* showed a premature loss of winter hair (McLaughlin and Addison 1986; Mooring and Samuel 1999). Consequently, long hair coats might in fact facilitate parasite colonization and could be negatively linked to neatness. Hair-coat length might be a trait modulated by a trade-off between the advantages it gives during the rigors of winter and its parasite-related disadvantages. This hypothesis is supported by the overlapping seasonality of hair length in caprids (Couturier 1962), the life span of PEPs on Iberian ibex, and the infections of sarcoptic mange in Iberian ibex (Pérez et al. 1997; León-Vizcaino et al. 1999), all of which are illustrated in Figure 1. It also agrees with the conditional handicap theory (Pomiankowski 1987; Iwasa et al. 1991), which suggests that secondary sexual traits such as sex-specific hair coats that serve as honest signals of individual quality (Andersson 1994) are costly to produce and maintain. Relationships between mammalian hair coats and factors such as sex, age, dominance, and reproductive potential are consistent with the principle of intersexual selection based on hair-coat signaling (Hinsz, Matz and Patience 2001; Derocher et al. 2005; Loehr et al. 2008; Davis et al. 2010). In *C. pyrenaica*, sexual dimorphism in hair coat was, for the moment, just recorded in hair color (Fandos 1991), although even hair color has been related to parasitism in other ungulate species (Rødven et al. 2009). Thus, compatibility to contact-transmitted parasites might be a cost of hair-coat signaling and the links between coat characteristics and parasitism need to be studied further if

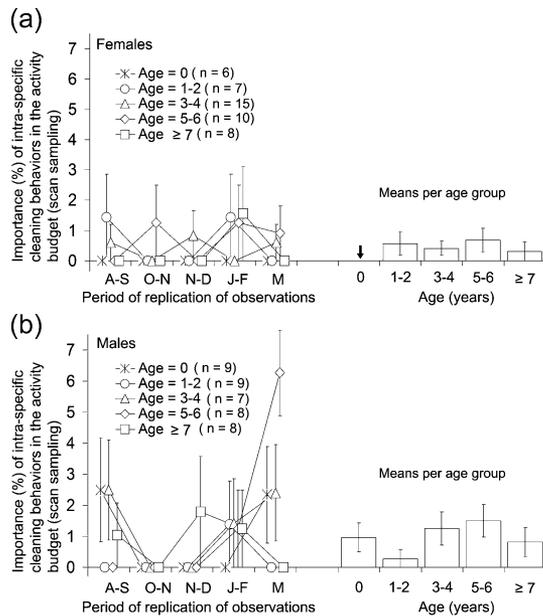


Figure 5 Investment in ISCB in the activity budget (%), including the self-grooming, allogrooming, and hindleg scratching described in other studies according to host age and sex and the replication period of the observations. Bars represent mean values and their related standard errors. (a) Females. (b) Males. A = August, S = September, O = October, N = November, D = December, J = January, F = February, M = March. Arrow indicates value equal to zero.

we are to improve our understanding of hair-coat correlates (Loehr et al. 2008) and selection (Moorcroft et al. 1996).

Neatness and the “body-size principle”

Investment in antiparasitic behavior and the half-life span of the PEPs in our Iberian ibex population was modulated by the sex and age of the hosts, but in patterns that contradict the predictions made on the basis of the body-size principle derived from the “programmed grooming model” (Hart et al. 1992). Life span of PEPs was greater on juveniles than on adults, although the relationship between age and investment in antiparasitic behavior showed a different season-dependent pattern. This mismatch also suggests that antiparasitic behavior by itself may be unable to explain the pattern of PEP life spans and of host neatness. These results agree with the age patterns observed in Iberian ibex during the preliminary bench test of the PEPs (Sarasa et al. 2009) and with the mismatch between investment in antiparasitic behavior and parasite densities observed in rodents (Hawlena, Bashary, et al. 2007; Hawlena et al. 2008). Moreover, investment in antiparasitic behavior was lower in females than in males, at least at the end of summer and in early spring via ISCB, and PEP life span was greater on females than on males throughout the experiment. These findings suggest again that antiparasitic behavior alone might be unable to explain the pattern of PEP life span and of neatness. Our results on the effect of sex also disagree with the predictions based on the body-size principle (Hart et al. 1992) but do match previous studies that found less investment in grooming in female than in male birds (Cotgreave and Clayton 1994) and better survival of parasites on female than on male bats (Christe et al. 2007). Males are often immunologically disadvantaged compared with females (Folstad and Karter 1992; Sarasa et al. 2010), although in some cases, males

may have nonimmunological advantages compared with females that lessen their compatibility to new parasite colonization. These nonimmunological advantages of males against parasites may at least partially compensate for their relative immunological defenselessness (Folstad and Karter 1992).

An interesting challenge that should be accepted by future studies is to discriminate the RI of the potential origins of uneven nonimmunological compatibility of hosts to new colonizing parasites (or to PEPs). Such potential origins include prophylaxis (e.g., programmed-driven grooming) and response to stimulation (e.g., stimuli-driven grooming) within behavioral defenses against parasites, although morphological inequalities, such as inequalities in hair coat, may be important as well. To unravel potential associations between neatness, social rank, and even fitness will also be useful for identifying selective processes at work. For the moment, the body-size principle alone, as derived from the programmed grooming model (Hart et al. 1992), still seems to be an inaccurate way of predicting investment in antiparasitic behavior, compatibility to new parasite colonization, and neatness in hosts. Nevertheless, no mechanisms should be excluded at this point. As suggested by other authors, alternative cleaning modes (e.g., ESB, exposition to solar radiation, and rainfall) and alternative antiparasitic strategies (e.g., molt phenology, cleaning symbiosis) may be better predictors of neatness than grooming frequency (Lenouvel et al. 2009) or might even act simultaneously on host neatness. Confounding factors inherent to the ecology of parasites probably blur direct correlations between grooming behavior and ectoparasite loads: parasites may actively choose their hosts (Christe et al. 2007; Hawlena et al. 2007; Khokhlova et al. 2011), intraspecific competition between parasites on hosts is also a powerful force (Hawlena, Abramsky, et al. 2007), and host-parasite immunological interactions differ between one host and another (Lloyd 1995; Wikel et al. 1996; Sarasa et al. 2010).

Neatness is a complex concept that, when related to parasites, integrates the effects of immunological and nonimmunological factors. This study challenges the idea that the body-size principle derived from the programmed grooming model (Hart et al. 1992) can accurately predict investment in antiparasitic behavior, compatibility to new parasite colonization, and host neatness. Accurate estimates of the RI of both immunological and nonimmunological factors are required if we are to obtain more complete and accurate knowledge of these questions.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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