

# Pseudoectoparasites: a new tool for exploring the relationship between host behaviour and ectoparasites

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Host encounter and host compatibility are the main hypotheses proposed to explain uneven patterns of parasitism (Combes 2001; Guégan et al. 2005). These hypotheses suggest, respectively, intrinsic differences in exposure to infestations because of, for example, behaviour or ecology and uneven responses or 'tolerance' to parasites as a result of, for example, behaviour or immunology.

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Uneven parasitism has often been related to immunology (Zuk 1996; Zuk & McKean 1996). Nevertheless, the causal effect of host behaviour variability on the biased distribution of pathogens is a subject of increasing interest (Altizer et al. 2003). As the first line of defence against parasitic assaults (Hart 1994), behaviour is strongly relevant in understanding parasitism (see Barnard & Behnke 1990). Most studies emphasize the impact of pathogens on host behaviour or antiparasitic features (Dobson 1988; Barber et al. 2000; Moore 2002; Thomas et al. 2005). Studies on host behaviour as a determining factor in parasitism often report relationships between the timing of infestations and the seasonality of behaviour (Tinsley 1990). Nevertheless, 'permissive' exposure and behavioural inequalities at the between-individual scale still remain poorly studied dimensions of this question (Bundy & Blumenthal 1990).

Studies on the link between host behaviour and parasitism use either direct or indirect methods. The direct approach involves, when possible, the use of antiparasitic treatment (Fox & Hudson 2001; Ferrari et al. 2003); otherwise real infestations are commonly

used (Berriatua et al. 1999; Skerratt 2003; Chronert et al. 2007), but

these have ethical problems and sanitary risks. Although the direct approach is generally considered to be more informative, it does not allow investigators to focus on behaviour as the determining factor independently of the host immune system. Indirect approaches, which partly resolve such problems, may involve several methods. Although costly and difficult, a first alternative is the use of direct behavioural observation, which still plays a key role in current knowledge of the subject (e.g. Mooring et al. 2006). Nevertheless, this method is often limited to observable individuals over a set period of time and thus is potentially exposed to a number of confounding factors. A second option is biotelemetry, which provides new tools that partly solve the limitations on fieldwork (e.g. Ji et al. 2005; Schaubert et al. 2007) and reduce costs (despite still being very expensive; see Cooke et al. 2004; Ropert-Coudert & Wilson 2005). However, neither direct observation nor biotelemetry provides direct knowledge of the relationship between host behaviour and pathogen transmission, and both often need to be used in parallel with epidemiological data to encompass assumptions on the relationship between, for example, interindividual distance and the probability of infestation. Finally, fluorescent pigments and biomarkers are another interesting approach to the exploration of social or trophic interactions, especially in small species (Dickman 1988; Fisher 1999; Knowlton & Olmstead 2001; Papillon et al. 2002). Nevertheless, the use of this type of marker in the analysis of behaviour in relation to ectoparasitism in medium-sized and large hosts is difficult to put into practice. Thus, a new tool with the advantages of current approaches and without their drawbacks may improve current perspectives and substantially enrich our knowledge of how host behaviour influences ectoparasitism in these host species.

We investigated the potential of a new type of marker in the study of host behavioural traits that are relevant to parasitism. First, we designed 'pseudoectoparasites' (PEPs) that fitted our research goals and conformed to ethical specifications. Second, we tested the stability of PEP characteristics over time and during different seasons. Given that PEPs are prone to desiccation, just as the survival of free-living stages of parasite species is determined by the climate (Arlan et al. 1989; Tembely 1998; O'Connor et al. 2006), we would expect a decrease in the infectivity of PEPs over time (prediction 1) and differences in the infectivity of PEPs between seasons (prediction 2). Third, in a medium-sized ungulate we tested the infectivity of such PEPs under a low invasive protocol (infestation of feeding points with PEPs) and then monitored the short-term dynamics in PEPs on hosts as an indicator of infective persistence. Given that differential exposure may explain uneven parasitism (Bundy & Blumenthal 1990; Lajeunesse et al. 2004) and as access to food, especially all at feeding points, is often linked to dominance (Appleby 1980; Jullien et al. 1988; Jørgensen et al. 2007), we would expect a greater prevalence of PEPs in males than in females (prediction 3) and in adults than in juveniles (prediction 4), as well as a greater prevalence of PEPs with increased body weight (prediction 5). Given that ungulate body weight usually differs according to sex and increases with age, especially as a result of growth (Granados et al. 2001; Lesage et al. 2001), we assessed the relative effects of all factors by taking into account the effects of sex and age on body weight. Ungulates perform antiparasitic and maintenance behaviours (Murray 1990) and so after pseudoinfestation we would expect infested animals to lose their PEPs with time (prediction 6). Finally, according to the 'body size principle' that has emerged from the programmed grooming model (Hart et al. 1992), smaller animals should lose their PEPs more quickly than larger ones and so we would expect a faster return to an 'uninfested status' in females than in males (prediction 7) and a faster return in juveniles than in adults (prediction 8).

## METHODS

### Pseudoectoparasites

The markers had to fit our protocols, be easy to monitor and nonaggressive to hosts, and had to mimic the more 'mechanical' features of ectoparasites (e.g. adherence and infectivity), regardless of the host immune system. In this study we used triangular markers made of wood, all of the same green colour (Fig. 1). Given the methodological purpose of this test, we made the markers customizable. For example, the PEPs can be used with a single colour (as in our test) or with a number of colours (Fig. 1) depending on experimental requirements. The different shape of each end of a triangular PEP increases the number of two-colour combinations compared to a rectangular form (four versus three possibilities; Fig. 1). In designing the markers we took into consideration potential adaptations in further experiments, for example on the dispersion of PEPs from several pseudoparasitic sources infested with individualized coloured PEPs. Although we monitored the markers from short distances (often below 20 m) in the current experiment, they were visible for up to 80 m in favourable conditions (we used a Swarovski spotting telescope 20–60x). However, their visibility might depend on the type of host and the environment and their design may need to be changed for other experiments. To attach the PEPs to the host, we used a commercial and hypoallergenic wax (Trimona Handball Wax; Johann Tripmacker, Braunschweig, Germany). PEPs became attached to the surface of the coat and had little contact with the skin. The wax (which is hypoallergenic and approved for human use) was only in contact temporarily with the coat and no effect on the skin was observed. After the PEPs dropped off, the little remaining wax also disappeared rapidly when the hosts scratched themselves against trees.

### Experimental Study Site

The tests were performed on a stock reservoir of Iberian ibex, *Capra pyrenaica*, in Dilar, Espacio Natural de Sierra Nevada

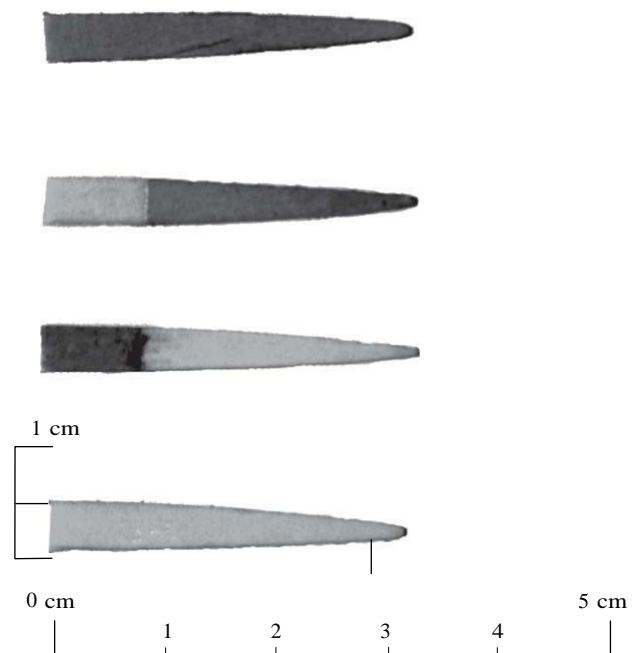


Figure 1. Pseudoectoparasites.

(ENSN; 37° 9' N, 3° 31' E) Granada, southern Spain. This enclosure protects 66 individually marked ibexes (41% males and 59% females), ranging freely over 35 ha, whose normal feeding is complemented daily by additional forage placed in mangers.

### Stability of PEP Characteristics

The average life span of the free-living stages of ectoparasites such as sarcoptic mange, *Sarcoptes scabiei*, is less than 7 days in laboratory conditions resembling those in which natural infestations take place (Arlian et al. 1989; Pérez et al. 1997). Since we used PEPs to explore how the host's behaviour affects infestations by contact-transmitted parasites such as *Sarcoptes*, we tested the stability of PEP characteristics over a week. We placed 80 PEPs on metallic supports exposed to the weather. To monitor the desiccation rate of waxed PEPs, we tested the adherence of a different set of 10 PEPs each day (from day 0 to day 7) by calculating as an indicator of adherence the number of strokes with a soft brush needed to remove each PEP from the metallic supports. To test the stability of the PEP desiccation rate between seasons, we repeated this protocol in five periods that are potentially of interest for further work on the timing of ectoparasitic infestations (1: August–September 2007; 2: October–November 2007; 3: November–December 2007; 4: January–February 2008; 5: March 2008).

### Test Procedure

To avoid interobserver variability, M.S. carried out the entire field procedure. During March 2007 he verified that all ibexes used the feeding mangers and tolerance to the observer was developed over 2 weeks. Next, and to test the ability of PEPs to infest medium-sized hosts under a low invasive protocol, 150 PEPs were placed on the edges of the seven mangers of the enclosure just prior to daily feeding. Animals were monitored at 5, 30 and 72 h after the pseudoinfestation of the mangers to estimate the short-term dynamics of PEPs on ibexes (infective ability and persistence).

The total prevalence of PEPs in the experimental group ( $p_{\text{group}}$ ) was estimated by the percentage of observed ibexes with PEPs. Prevalence by sex or age was estimated by considering separately males and females ( $p_{\text{males}}$  and  $p_{\text{females}}$ ), and juveniles and adults ( $p_{\text{juveniles}}$  and  $p_{\text{adults}}$ ). We considered females up to 2 years old and males up to 4 years old to be juveniles and all the remaining animals to be adult as per their allometric growth and ossification rate (Granados et al. 2001; Serrano et al. 2006).

### Statistical Analysis

All analyses were performed using the R 2.6.2 statistical package (R Development Core Team 2008).

### Stability of PEP characteristics

We used generalized linear models (GLMs) to test the effects of time (number of days since the placing of the PEPs) and season

(1–5) on the indicator of adherence (dependent variable). We used an information-theoretical approach (see Whittingham et al. 2006) based on Akaike's information criterion (AIC, Burnham & Anderson 2002) and chose the most parsimonious model (lowest AIC, which points out the model that provides an accurate approximation to the structural information in the data at hand, see Burnham & Anderson 2002) out of the possible subsets, ranging from the null model (intercept only) to a model with explanatory variables and two-order interactions. Models with Akaike differences of less than two units and the relative importance of examined variables were studied (RI, which quantifies the evidence for the importance of each variable in the set of models, see Burnham & Anderson 2002), especially if the Akaike weight ( $W_i$ ) of the best models was moderate or low (Anderson et al. 2000, 2001).

### Pseudoinfestation and short-term dynamics of PEPs

To test the inequalities of exposure to infestation (host encounter hypothesis) at 5 h after infestation of the mangers, we used GLMs. We tested the effects of ibex sex, age and body weight on the individual pseudoparasitic status (infested or not by PEPs, dependent variable). To take into account the effects of sex and age on body weight we used in the analysis the residuals of body weight on age in the logistic model estimated separately for males and females (sex–age-specific body weight). We again used an information-theoretical approach (see above), but we based model selection on Akaike's information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002).

Finally, to test the determining factors of the short-term dynamics of PEPs on their hosts (infective persistence, longitudinal data), we analysed the loss of PEPs in animals that were PEP-infested 5 h after infestation of mangers (host compatibility hypothesis) using mixed-model analyses as recommended by Paterson & Lello (2003). We tested the effects of time after infestation and of the sex and age of ibexes (independent variables) on individual pseudoparasitic status (PEP-infested or not, dependent variable). We again used an information-theoretical approach based on Akaike's information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002), as described above.

## RESULTS

### Stability of PEP Characteristics

The characteristics of PEPs changed with time, but did not differ between seasons. The analyses of the stability of PEP adherence showed that, independently of season, the time from the infestation was the most important parameter ( $W_i$  ¼ 0.79, RI ¼ 1) to explain the observed variability of adherence (Table 1).

### Pseudoinfestation of Ibexes by PEP

Although no attraction or repulsion behaviour was observed, numerous ibexes were infested by PEPs at 5 h after infestation of

Table 1  
Model selection in the analysis of pseudoectoparasite characteristics

Model	N	K	AIC	DAIC	L (gi/x)	$W_i$	Relative importance
Time	400	3	–607.12	0.00	1.00	0.79	Time: 1.00
Time þ season	400	7	–603.21	3.91	0.14	0.11	Season: 0.21
Time þ season þ time × season	400	11	–603.07	4.05	0.13	0.10	
Null model	400	2	–241.65	365.47	0.00	0.00	
Season	400	6	–235.45	371.67	0.00	0.00	

K ¼ number of estimated parameters; AIC ¼ Akaike's information criterion; DAIC ¼ difference in AIC between the model and the most parsimonious model; L(gi/x) ¼ Probability of the model being the Kullback–Leibler best model given the data set;  $W_i$  ¼ Akaike weight of the model, see Burnham & Anderson (2002).

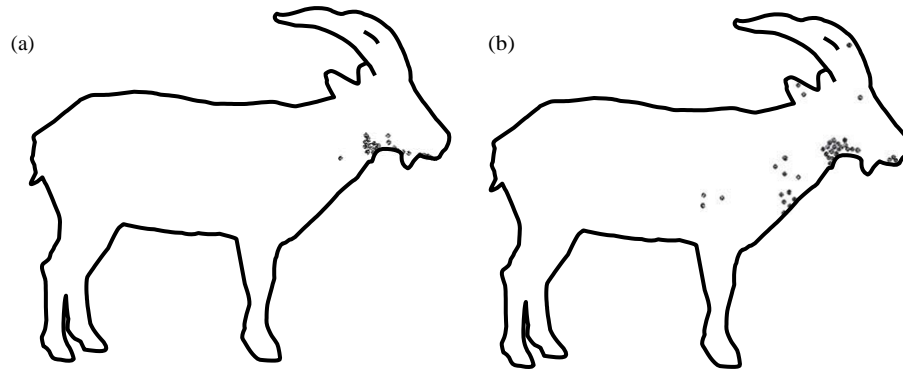


Figure 2. Localization of pseudoectoparasites on their hosts (a) at 5 h and (b) pooled results at 72 h after infestation of mangers.

mangers (Fig. 2). Prevalence of PEPs was high ( $p_{\text{total}} \approx 47.4\%$ ) and influenced mainly by the sex and age of animals. In general, males ( $p_{\text{males}} \approx 64.7\%$ ;  $p_{\text{females}} \approx 33.3\%$ ) and juvenile individuals ( $p_{\text{juveniles}} \approx 59.0\%$ ;  $p_{\text{adults}} \approx 31.2\%$ ) were the most infested (Fig. 3). According to the observed prevalences, the model that included the effect of age was the best ( $W_i \approx 0.23$ ), suggesting that the age of the animals is the main factor explaining the distribution of PEPs among the hosts. Three additional models had substantial support (sex  $\beta$  age, sex, sex  $\beta$  age  $\beta$  sex  $\times$  age models; Table 2), highlighting the sex-dependent slope of the relationship between age and probability of infestation (Fig. 3). Among the set of candidate models, the RI of age was the highest, followed by sex and sex-age-specific body weight, supporting the hypothesis that the age of hosts is the main determinant of the observed PEP prevalences (Table 2).

#### Dynamics of PEPs on their Hosts

The life span of PEPs on hosts was limited and differences were found according to age, but not to sex. For the data on the development of infestation, the model that included time  $\beta$  age was the best ( $W_i \approx 0.38$ ), followed by the model that included time ( $W_i \approx 0.30$ ), indicating a faster progressive loss of PEPs in adults than in juveniles (Fig. 4). Among the explanatory variables, time had the highest RI, and then age and sex (Table 3).

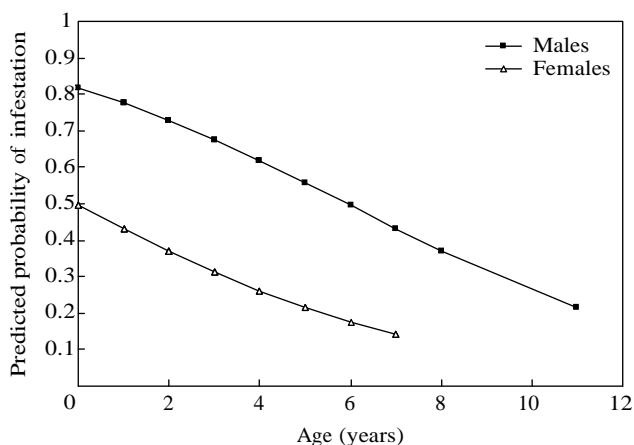


Figure 3. Predicted probability of infestation by pseudoectoparasites in terms of the sex and age of hosts at 5 h after infestation of mangers.

#### DISCUSSION

In this study we tested a new tool for exploring the role of host behaviour in ectoparasite transmission. Our results showed that PEPs could be a promising alternative since they can be used in contrasting seasons and they have features in common with ectoparasites as discussed below.

#### Characteristics of PEPs

The adherence of PEPs changed over time (as per our prediction 1), but did not differ between seasons (which contrasts with our prediction 2) probably because of the stability of the commercial wax we used, which is made for use in all seasons. Our results thus suggest that the infective ability of PEPs decreases over time; similarly, free-living stages of ectoparasites have limited life spans, and PEPs could be useful for exploring interseasonal variation in host behavioural traits.

#### Pseudoinfestation

The high prevalence observed 5 h after infestation of mangers underlines the fact that fixed feeding points represent a serious pathogenic risk to individuals. Although supplementary feeding is a widespread management tool, it should be used with care in wildlife population maintenance to avoid counterproductive pathogenic infection (see Gortázar et al. 2007). Our results also suggest that there is an uneven risk of infestation between individual subclasses, which supports the host encounter hypothesis. Males and juveniles were the most infected individuals, findings

Table 2  
Model selection in the analysis of pseudoectoparasitic infestation

Model	N	K	AICc	DAICc	L(gi/x)	$W_i$	Relative importance
Age	37	2	50.97	0.00	1.00	0.23	Age: 0.72
Sex $\beta$ age	37	3	51.66	0.69	0.71	0.16	Sex: 0.56
Sex	37	2	52.26	1.29	0.53	0.12	BW: 0.32
Sex $\beta$ age $\beta$ sex $\times$ age	37	4	52.92	1.95	0.38	0.09	
Age $\beta$ BW	37	3	53.12	2.15	0.34	0.08	
Null model	37	1	53.16	2.19	0.33	0.08	
Sex $\beta$ age $\beta$ BW	37	4	53.97	3.00	0.22	0.05	
Sex $\beta$ BW	37	3	54.54	3.57	0.17	0.04	
Age $\beta$ BW $\beta$ age $\times$ BW	37	4	55.28	4.31	0.12	0.03	
BW	37	2	55.33	4.36	0.11	0.03	

BW  $\approx$  sex-age-specific body weight; K  $\approx$  number of estimated parameters; AICc  $\approx$  Akaike's information criterion corrected for small sample sizes; DAICc  $\approx$  difference in AICc between the model and the most parsimonious model; L(gi/x)  $\approx$  probability of the model being the Kullback-Leibler best model given the data set;  $W_i$   $\approx$  Akaike weight of the model; see Burnham & Anderson (2002).

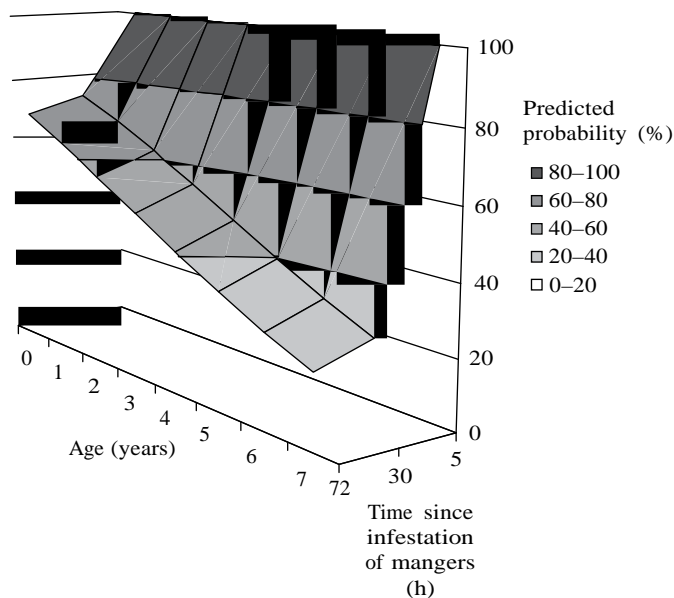


Figure 4. Predicted probability of remaining infested by pseudoectoparasites in terms of the time elapsed since infestation of manger and host age.

that agree with our prediction 3 but contradict our prediction 4. In addition, no effect of the sex–age-specific body weight was detected (contrary to our prediction 5). The observed sex-biased infestation seems to support the role of preferential access to feeding points and dominance in the observed pattern. However, the age bias and the apparent lack of a role for sex–age-specific body weight also suggest that the subject is of greater complexity. Taking into account the height of infested mangers and the smaller size of juveniles, there may be greater contact at feeding between the manger and the body of animals in juveniles than in adults. Nevertheless, the Iberian ibex is a sexually dimorphic ungulate and the observed sex inequalities do not seem to support this hypothesis. The observed age bias could also be caused by a greater tolerance shown by the highest-ranked ibex to the lowest-ranked animals than to intermediated-ranked ones, as reported by Bonanni et al. (2007) in cats, *Felis silvestris catus*, and possibly also backed up by kinship discrimination (Ceacero et al. 2007). Such patterns could lead to uneven diets such as those reported by Dennehy (2001).

Furthermore, PEPs seemed to have a limited life span on hosts, as stated in our prediction 6. Thus, PEPs could be an interesting tool for use in the study of both short-term processes of host surface cleaning and of the start of infestations, as illustrated by the similarity between the observed distribution of PEPs on hosts (Fig. 2) and the initial stage of mange infestation described in the Iberian ibex (León-Vizcaíno et al. 1999). No effect of sex was detected on the loss of PEPs by hosts, which disagrees with our prediction 7. The life span of PEPs on adult hosts did, however, seem to be shorter than on juvenile individuals, contrary to our prediction 8. This paradoxical age inequality in the loss of PEPs underlines the need to investigate further the factors determining surface cleaning by taking into account frequency and also the efficiency of related behaviours. However, the small sample size of infested hosts, the small number of PEPs on each host and the short period during which PEP loss was monitored (among other potentially confounding factors) could have biased our results on PEP loss according to sex and age. Thus, further work should specifically focus on such inequalities to verify these detected trends.

Table 3  
Model selection in the analysis of loss of pseudoectoparasites by their host

Model	N	K	AICc	DAICc	L(gi/x)	W <sub>i</sub>	Relative importance
Time $\beta$ age	18	3	63.16	0.00	1.00	0.38	Time: 0.98
Time	18	2	63.67	0.51	0.78	0.30	Age: 0.60
Time $\beta$ age $\beta$ sex	18	4	66.18	3.01	0.22	0.08	Sex: 0.21
Time $\beta$ age $\beta$ time $\times$ age	18	4	66.20	3.03	0.22	0.08	
Time $\beta$ sex	18	3	66.54	3.38	0.18	0.07	
Time $\beta$ sex $\beta$ time $\times$ sex	18	4	69.68	6.51	0.04	0.01	
Time $\beta$ age $\beta$ sex $\beta$ time $\times$ age	18	5	69.76	6.60	0.04	0.01	
Time $\beta$ age $\beta$ sex $\beta$ sex $\times$ age	18	5	69.84	6.68	0.04	0.01	
Time $\beta$ age $\beta$ sex $\beta$ time $\times$ sex	18	5	69.87	6.71	0.03	0.01	
Age	18	2	70.85	7.69	0.02	0.01	

K % number of estimated parameters; AICc % Akaike's information criterion corrected for small sample sizes; DAICc % difference in AICc between the model and the most parsimonious model; L(gi/x) % probability of the model being the Kullback–Leibler best model given the data set; W<sub>i</sub> % Akaike weight of the model; see Burnham & Anderson (2002).

## Conclusions

Despite being a simple tool tested under a low invasive protocol, the use of PEPs seems to be able to mimic parasitic infestation in a medium-sized host species. Our test also underlined the role of sex and age in determining behavioural factors of infestations, as suggested by other authors (Bundy & Blumenthal 1990; Lajeunesse et al. 2004). Further studies using PEPs with more targeted protocols may enrich our knowledge of factors such as surface cleaning efficiency, interindividual infestation of contact-transmitted diseases, scratching site selection and the interindividual heterogeneity of behaviour. Although the aim of using PEPs is not to substitute for existing methods for studying the relationship between parasitism and host behaviour, this new method is nevertheless a promising and complementary approach that may further our understanding of previously poorly studied dimensions of the interactions between host behaviour and parasitism.

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