Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*

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Summary

1. Although behaviours can contribute to the heterogeneity in parasite load among hosts, links between consistent individual differences in behaviour and parasitic infection have received little attention. We investigated the role of host activity and exploration on hard tick infestations of marked individuals in a population of Siberian chipmunks *Tamias sibiricus* introduced in a suburban French forest over 3 years.

2. Individual activity-exploration profiles were assessed from 106 hole-board tests on 73 individuals, and chipmunks' trappability and trap diversity were used respectively as indices of their activity-exploration and space use on a sub-sample of 60 individuals. At each capture, we counted the total number of ticks per head of chipmunk.

3. We found significant and consistent individual differences in activity-exploration, trappability, trap diversity and tick load, and could estimate individual indices for these four variables, corrected for confounding effects of year, season, body mass and sex.

4. Using a path analysis, we found an indirect effect of activity-exploration on tick load: tick load increased with space use, which in turn was positively affected by trappability in the field. Trappability was itself positively related to activity-exploration in the hole board. Habitat type affected tick load, independently of behavioural traits. A second path model revealed a lack of either direct or indirect influence of tick loads on chipmunks' personality and trappability.

5. Our results show that host personality-related patterns in space use can lead to a non-random parasite distribution among hosts.

Key-words: activity-exploration, ixodid infestation, parasite, path analysis, personality

Introduction

Throughout the last decade, evolutionary biologists have developed a growing interest in inter-individual variations in behaviour often referred to as personality (Wilson *et al.* 1994; Sih *et al.* 2004; Réale *et al.* 2007). In an ecological context, personality refers to consistent behavioural differences between individuals over time and/or across situations (Sih *et al.* 2004; Réale *et al.* 2007). Importantly, these individual differences persist after controlling for the effects of factors such as of sex, age or reproductive state (Réale *et al.* 2007).

The evolutionary reasons for the maintenance of consistent differences in personality traits have recently received an increased attention from behavioural ecologists (Sih *et al.* 2004; Dingemanse & Réale 2005; Réale *et al.* 2007). In particular, fluctuating selection related to environmental heteroge-

neity in space and time may maintain variance in behaviour traits in a wild population (Sih *et al.* 2004; Dingemanse & Réale 2005; Boon, Réale & Boutin 2007; Réale *et al.* 2007). Consistent individual differences in activity, exploration, boldness or aggressiveness have been shown to have consequences for dispersal (Fraser *et al.* 2001; Dingemanse *et al.* 2003; Duckworth & Badyaev 2007) or space use (Boon, Réale & Boutin 2008). In a heterogeneous environment, high activity or through exploration may thus be advantageous if it increases the chance of discovering important resources (Wolf *et al.* 2007). This advantage may, however, be counterbalanced by potential fitness costs associated with increased chance of encountering predators (Jonsson, Koskela & Mappes 2000; Biro *et al.* 2004; Brodin & Johansson 2004a, b; Sih *et al.* 2004; Boon *et al.* 2008). In the same way, difference in activity may also affect the probability of meeting with parasite infective stages (Wilson *et al.* 1993). Furthermore, the role of host behaviour has sometimes been cited as a potential

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explanation of the heterogeneity in macroparasite distribution among hosts (Poulin, Rau & Curtis 1991; Brown *et al.* 1994; Ostfeld, Miller & Hazler 1996; Brunner & Ostfeld 2008). Host behaviour can increase the risk of being infected by parasites and diseases (Poulin *et al.* 1991; Brown *et al.* 1994; Krasnov *et al.* 2005; Natoli *et al.* 2005; Easterbrook *et al.* 2007). Genetics and social interactions have also been involved in explaining heterogeneities in parasitic infections (Easterbrook *et al.* 2007). However, few studies have focused on the possible influence of individual personality on infection by parasites (Wilson *et al.* 1993; Natoli *et al.* 2005; Easterbrook *et al.* 2007).

In this study, we studied the link between consistent individual differences in activity and exploration, space use and hard tick loads in a population of Siberian chipmunk *Tamias sibiricus* (Laxmann, 1769), introduced into a suburban forest near Paris, France (Chapuis 2005). We measured activity-exploration of individual chipmunks by looking at their response to a novel environment test, using the so-called hole-board test (Martin & Réale 2008a, b). In this population chipmunks feed mainly larvae and nymph of *Ixodes ricinus* (Linnaeus, 1758) (Vourc'h *et al.* 2007). Using a confirmatory path analysis (Shipley 2004; Thomas *et al.* 2007; Favre, Martin & Festa-Bianchet 2008) we investigated the causal effects of consistent differences in activity-exploration between chipmunks and habitat on measures of individual activity in a familiar environment, space use and tick load indices. Activity in a familiar environment and space use were assessed by trappability and trap diversity respectively (Boon *et al.* 2008). Prior to this analysis, we controlled for environmental factors and host characteristics known to have a potential influence on these variables.

Previous works have shown that personality (i.e. boldness and exploration) could affect the tendency of an individual to enter a trap (see review in Biro & Dingemanse 2009). We thus predicted that more active and exploratory chipmunks in the hole board should be trapped more often and should visit a larger variety of traps compared with less active and exploratory animals. We also expected that chipmunks with a larger home range have more chance of encountering ticks than chipmunks with small home ranges, and therefore have higher tick loads than the latter ones. We also tested the direct link between chipmunks' personality and tick load, and investigated the inter-relationships between chipmunks personality, habitat characteristics, space use and tick load. Parasites are known to manipulate their host behaviour (Klein 2003; Thomas, Adamo & Moore 2005), thus a second path model was executed with the same variables but in which we tested if Tick Load Index had a direct causal effect on chipmunk activity-exploration in the hole-board, trappability and trap diversity indices.

Materials and methods

ANIMALS AND STUDY AREA

Field work was conducted in the temperate forest of Sénart, 22 km south-east of Paris, France (48°39′N–2°29′E; 3200 ha).

The study site (Parc de la Faisanderie) was a 14-ha area surrounded by a fence. Two main kinds of habitat are found within the site: a semi-open oak grove (6·0 ha) and a closed oak-hornbeam grove (6·5 ha). Grassland and buildings represented 1·5 ha of the study area (Marmet, Pisanu & Chapuis 2009). The Siberian chipmunk, a solitary, sedentary and central place foraging Sciurid rodent, is native to Asia and was introduced as pets in Europe in the 1960s. The first individuals were observed in Sénart in the early 1970s (Chapuis 2005).

The chipmunk population was monitored using the capture–mark–recapture method with 104 baited live-traps covering the study site. Fifty-two traps were placed in the closed habitat and another 52 in the semi-open habitat and near buildings. Throughout 2005, 2006 and 2007, during the entire chipmunk active period (i.e. from February/March to November/December), two capture sessions were carried out each month, one every 2 weeks, for three and for five consecutive days alternately. Traps were checked four times a day, twice in the morning and twice in the afternoon, at 2 h of intervals. Individuals were ear-tagged and implanted with a transponder chip. With each trapping event, the date, hour and trap location were recorded, as well as chipmunk identity, age (adult or juvenile), sex and body mass. After being handled and examined chipmunks were released at their point of capture.

HOST AND PARASITE

In Sénart, the Siberian chipmunk feed four tick species, of which *Ixodes ricinus* represents 90% of the larvae and 99% of the nymphs (Vourc'h *et al.* 2007). At the first capture of a chipmunk within a capture session, we counted exhaustively tick larvae, nymphs and adults by direct observation of the head of the host (Craine, Randolph & Nuttall 1995; Schmidt, Ostfeld & Schauber 1999). Two consecutive tick counts during two consecutive capture sessions were therefore separated by at least 15 days and were considered independent of each other as complete turn-over of immature stages of feeding *Ixodes* spp. on a rodent host is known to be less than a week (Pérez-Eid 2007). Adult ticks were rarely found on chipmunks (i.e. 41 adults on 2413 examinations and 84 636 counted ticks over the 3 years). We thus only considered the number of larvae and nymphs for further analyses.

BEHAVIOURAL TEST

We used a hole-board test (File & Wardill 1975) already employed on other Sciurids (Boon *et al.* 2007; Martin & Réale 2008b). Tests were performed in the field, directly after the capture of chipmunks. The testing arena was 70 × 35 × 32 cm white box, with a transparent Plexiglas lid and with four holes (diameter = 4·0 cm; depth = 4·5 cm) on the floor (for more information see Martin & Réale 2008b). After its capture, the chipmunk was isolated during 5 min in the entrance lock of the arena. Then we opened the hole-board door to let it enter into the arena. Chipmunks that did not enter after 5 min were gently pushed inside and were recorded with a latency to enter of 5 min. Chipmunk behaviours were then recorded for 5 min in the hole board with a camcorder and then released at their point of capture. The arena was cleaned after each test with a cloth and alcohol diluted in water. Videos were analysed with The Observer Video-Pro 5.0 software (Noldus, Wageningen, The Netherlands), which allowed us to measure the time and frequency of each behaviour variable following the ethogram proposed by Martin & Réale (2008b; see Table 1).

Table 1. Principal component analysis loadings for each behaviour observed during hole-board tests on Siberian chipmunk in Sénart forest

Behavioural variables	Component 1	Component 2	Component 3
Immobility	**−0·44**	< 0·01	−0·05
Locomotion	**0·37**	−0·20	−0·02
Head-dip	**0·32**	−0·27	−0·21
Locomotion-scan	**0·31**	**0·43**	0·04
Jump	**0·32**	**0·41**	< −0·01
Sniff	**0·35**	**−0·37**	−0·05
Climb	0·26	**0·44**	−0·04
Groom	0·07	−0·22	**0·49**
Excrements	0·12	−0·13	**0·70**
Entrance latency	−0·10	0·17	**0·42**
Scan	0·25	0·13	0·12
Rear	0·27	−0·28	−0·13
Standard deviation	2·11	1·40	1·10
Total variance (%)	37·1	16·3	10·1

Bold type indicates behaviours that had a major contribution to a component. For more details on behavioural variables see Materials and methods.

STATISTICAL ANALYSES

Principal component analysis

We ran 106 hole-board tests on 73 individuals, including 31 individuals with two or three tests. These replicated measures allowed for the estimation of the repeatability of the behavioural response to the hole board over time (Réale *et al.* 2000). For the same individual, two consecutive tests were separated by 10 days minimum (mean = 23 - days, range = 10–70).

In 2005, one juvenile and four adult females, and two juvenile and two adult males were tested. In 2006, 15 juvenile and 24 adult females, and 18 juvenile and seven adult males were tested. A principal component analysis (PCA) was executed on hole-board data to reduce the number of behavioural variables (Boon *et al.* 2007; Martin & Réale 2008b). Prior to PCA, the variables locomotion, locomotion-scan, rear, climb, sniff, head-dip, groom, excrements and immobility were normalized using a square-root transformation and the variable jump with a logarithm transformation. Only the principal components explaining the greater part of the total variance were retained with the Kaiser-Guttman criterion (Martin & Réale 2008b).

Individual behavioural profiles

For these analyses we used the data from the 106 tests run on 73 individuals. For each component we first ran a linear-mixed model (LMM; Pinheiro & Bates 2000; Crawley 2007) with chipmunk identity (id thereafter) as a random effect and year of test, day, hour, sex, age, test order for the same individual (i.e. first, second or third test) and if it was the first chipmunk capture in its life or not as fixed effects. We then selected fixed effects using a stepwise backward procedure based on t tests (using α = 5% as the level to reject a fixed effect). To test for the significance of the random effect we compared the fit of the LMM with a linear model (LM) excluding chipmunk id. A likelihood ratio test (LRT) was carried out between the two selected models (Pinheiro & Bates 2000; Martin & Réale 2008b). The use of LMM allowed us to control for pseudoreplication of the data

that occurs with repeated measures on the same individual, and to estimate the variance because of individuals and the repeatability of behaviours (Crawley 2007). Finally, a best linear unbiased predictor (BLUP) for random effect was used to estimate individual behavioural profiles (Pinheiro & Bates 2000; Martin & Réale 2008b). Behavioural profiles were used as indices of personality of each chipmunk.

Trappability and trap diversity indices

Live-trapping data are commonly used to estimate animal movements and space use (Jonsson *et al.* 2000). Thirteen individuals used to test for individual behavioural profiles in 2006 were captured in a part of the forest where the chipmunk population was not monitored on a regular basis, and were thus excluded from subsequent analyses because of biased estimates in number of different traps used. Henceforth, we used for further analyses a sample of 60 chipmunks with a complete trap history: 12 juveniles and 23 adult females, and 18 juveniles and seven adults males.

Using data within the same year in which the individual was tested with the hole board (i.e. 2005 or 2006 depending on the chipmunk), we calculated an individual trappability and trap diversity indices. These two indices were estimated from the residuals of the LM of number of captures or number of different traps as a function of the length of capture period (i.e. the number of capture days executed between the first animal capture and the last one in a year), periphery variable (i.e. the proportion of chipmunk captures in traps at the periphery of the capture network), chipmunk sex, age and second order interactions.

To analyse the link between individual personality and trapping characteristics we needed to verify that trapping characteristics were consistent across years for the same individual (i.e. trapping characteristics as an expression of personality). Using a restricted sample of 34 individuals that were caught in at least two successive years between 2005 and 2007 (*n* = 78 tests), we used a LMM procedure to estimate individual consistency across years in the number of captures and the number of different traps. Number of captures was log transformed, and number of different traps was square root transformed prior to analyses. We included the length of the capture period, year, chipmunk sex, age and periphery variable as fixed effects, and id as a random effect.

Individual Tick Load Index

To analyse the link between the different behaviours and tick load we needed to restrict our tick data set to the year a chipmunk was tested in the hole board (i.e. hole-board year: 2005 or 2006, depending on the chipmunk). During that hole-board year, we determined an individual Tick Load Index using a similar LMM procedure as above on the number of ticks counted in each capture session (range from 0 to 381 ticks for one count). This analysis allowed us to estimate repeatability of tick load within the hole-board year. Tick number was log transformed prior to the analyses. Chipmunk id was used as a random effect, and fixed effects considered were the day when ticks were counted, day^2, year, host sex, age, body mass and their two way interactions (*n* = 294 instances for 60 individuals). We integrated day^2 within the models as we noticed a quadratic relationship between tick abundance and day in the course of the trap season. We also added a temporal autocorrelation between day and tick load, in the same LMM as we supposed that two measures of tick number were more correlated when they were closer in time. Not controlling for autocorrelation can lead to bias the estimation of fixed effects in the model (Pinheiro & Bates 2000). We tested the importance of this autocorre-

lation by executing a LRT between the two LMM, with and without this autocorrelation (Pinheiro & Bates 2000). A BLUP was used on the best LMM to obtain an individual Tick Load Index. We finally estimated the repeatability of tick infestation across years for individuals who were trapped at least two successive years using the same fixed effects (n = 479 observations for 34 individuals; in this analysis year was redundant to chipmunk age and could not be included in the model, and autocorrelation was not tested).

Path analyses

A path model is organized in function of an *a priori* logically, biologically or experimentally based arrangement that allows testing for direct or indirect relationships in the cause-effect linkages between several variables (Scheiner, Mitchell & Callahan 2000; Shipley 2004). Parasite aggregation among hosts is often explained as the result of both host characteristics and environmental factors (Brunner & Ostfeld 2008). We hypothesized that tick load could have been directly or indirectly linked back to chipmunk personality and habitat characteristics through patterns of active-exploratory and spacing behaviours (Fig. 1a).

First, host behaviours may play a central role in increased encounter rates of parasites (Poulin 1996). Individual differences of personality should thus contribute to the heterogeneity of parasite burden in a host population. Intrinsically more active and exploratory chipmunks should be trapped more often (individual Trappability Index) and in more different traps (individual Trap Diversity Index) than lowly active-exploratory individuals (Fig. 1a). Male rodents, which cover longer distances and occupy larger home ranges than females were also more infested (Randolph 1975; Ostfeld *et al.* 1996; Krasnov *et al.* 2005). As more mobile chipmunks have a greater probability of encountering questing ticks, and the same for those using a bigger space, trappability and trap diversity indices were presumed to influence tick load (Fig. 1a). Second, we hypothesized that habitat shelter different densities of ticks (Fig. 1a), because environmental conditions, such as vegetation structure, soil composition and moisture, determine ticks activity and abundance at a small spatial scale (Mejlon 2000; Randolph *et al.* 2000). We thus tested the causal effect of personality on habitat selection and tick load (Fig. 1a). Third,

habitat characteristics could affect both trappability and trap diversity indices and in turn tick load (Fig. 1a). Habitat features such as the quantity, quality and diversity of available resources, soil conditions for burrows, or vegetation structure are known to change rodents' locomotion, activity, exploration and home range (Mahan & Yahner 1999; Vásquez, Ebensperger & Bozinovic 2002). In our analysis, the individual habitat index was estimated as the proportion of traps a chipmunk was taken in the closed oak-hornbeam grove (range 0–100%). Finally, we consider the possibility that personality differences could affect tick load through differences in immunity (Koolhaas 2008), although we did not have enough information to predict the sign of the relationship (Fig. 1a). As parasites can influence behaviours of their hosts (Thomas *et al.* 2005), we propose an alternative hypothesis to link tick load and chipmunk behaviour (Fig. 1b). In this model, ticks are assumed to both increase chipmunks' activity and exploration in the hole-board, and their trappability and trap diversity in the field. In this second model, all the other relationships between habitat, tick load and behaviour are identical to model 1.

The previous models used in this paper allowed us to obtain single characteristic measures per individual per variable integrated in the path analysis. In this way, we took into consideration factors that could influence the studied variables, but which were not included into our path analyse to simplify it and as some of these factors were categorical (Petraitis, Dunham & Niewiarowski 1996). Path coefficients of our causal scheme were calculated with LM and correspond to the standardized partial regression coefficients. All variables were rank encoded for path analyses, and we then used the d-sep test to evaluate if one of these two alternative chains of causality could be rejected (Shipley 2004). We executed basis sets and analysed independence (or partial independence) of all possible pairs of variables of a path model, except significant ones (Shipley 2004). For this, pairs of variables were tested one by one with LM by integrating only causal parents of the pair tested. Finally, the agreement between the empirical data and the predicted pathways was evaluated calculating the Fisher's C statistic, $C = -2 \Sigma \ln(p_i)$, where (p_i) are the new probabilities of pairs of variables tested for independence (Shipley 2004; Thomas *et al.* 2007). C follows a chi-square distribution with $2k$ degrees of freedom, where k is the total
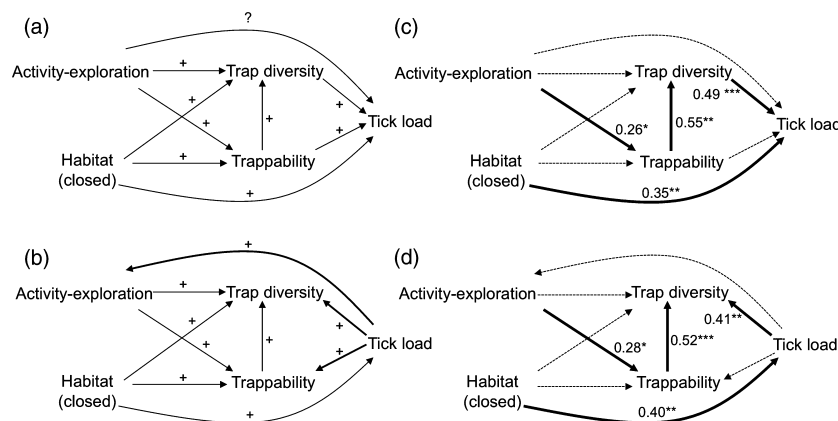

Fig. 1. Path analysis diagrams linking the active-explorative personality of Siberian chipmunks in Sénart forest (obtained with a hole-board test), their habitat, activity (Trappability Index) and space use (Trap Diversity Index) with their tick load: (a) the *a priori* hypothesized causal path model and (b) an alternative structure of causal relationships ('+' or '?' represent the predicted links between two variables, and thick lines in (b) represent relationships, which differ from model (a) and (b) respectively), and (c) and (d) are their corresponding significant pathways and associated standardized path coefficients. Arrows indicate the direction of causality assumed in models. All variables were encoded in ranks *P < 0·05, **P < 0·01, ***P < 0·001. See the text for the justification of path models and variable descriptions.

number of pairs tested for independence in a path model. A probability below the significance level of 0·05 leads to the rejection of the causal model (Shipley 2004; Thomas *et al.* 2007).

Statistical analyses were executed with ʀ software (R Development Core Team 2006) and residual distributions of each model were verified using scatter and quantile–quantile plots.

Results

INDIVIDUAL BEHAVIOURAL PROFILES

The first three components of the PCA were retained and explained 63% of the total variance (Table 1). The first one (PC1) associated the following behaviours: locomotion, head-dip, locomotion-scan, jump and sniff, with immobility opposed at this behavioural unity (Table 1). The second one (PC2) opposed locomotion-scan, jump and climb with sniff (Table 1). Entrance latency, groom and excrements were associated on the third axis (PC3; Table 1).

Chipmunk id explained a significant proportion of the variance of PC1 and behaviours of this axis were repeatable for the same individual (repeatability = 55%, LRT = 9·16, d.f. = 1, P = 0·002). However, the id effect did not significantly improve models on the two other components retained (PC2: LRT = 1·21, d.f. = 1, P = 0·271 and PC3: LRT = 2·31, d.f. = 1, P = 0·128 respectively). Consequently, we chose to treat only PC1 in our study as it was the only one showing significant behavioural differences between individuals. Thus individual behavioural profiles of 'activity-exploration' were calculated from this component. Chipmunks' exploration and activity decreased with the increase in the number of tests per individual (second test: t_{31} = −7·40, P < 0·001; third test: t_{31} = −3·95, P < 0·001). No significant effects of the year, day, hour, sex, age and first capture were found (results not shown here).

TRAPPABILITY AND TRAP DIVERSITY INDICES

Length of capture period was positively related to number of captures, and to trap diversity within the same year in which the individual was tested with the hole board (Table 2). Chipmunks inhabiting areas close to the periphery of our capture network were trapped less (Table 2). Year, sex, age and second order interactions were not significant (Table 2; all P > 0·05; Fig. 2a). There was a significant interaction between sex and age on the number of different traps used by an individual, adult males using significantly more traps than other categories (Table 2; Fig. 2b).

Using the restricted sample of individuals that were caught in at least two successive years between 2005 and 2007 (see Materials and methods), we observed significant and consistent individual differences across years in the capture number (repeatability = 36%, LRT = 4·64, d.f. = 1, P = 0·031), and a strong tendency for the diversity of visited traps (repeatability = 34%, LRT = 3·81, d.f. = 1, P = 0·051). Results for fixed effects in these two models were similar to the models in Table 2, and are therefore not shown here.

Table 2. Mixed model on (a) number of traps (log transformed) and (b) number of different traps (square root transformed) in which chipmunks were caught within the same year of which they were tested with the hole board

	Coefficient ± SE	d.f.	*t*-Value	*P*-value
(a) No. traps Variable[a]				
Length of capture period	0·066 ± 0·003	1,57	17·41	< 0·001
Periphery[b]	−0·004 ± 0·002	1,57	−2·09	0·041
(b) No. different traps Variable[c]				
Length of capture period	0·046 ± 0·004	1,55	12·59	< 0·001
Sex (female)[d]	0·562 ± 0·179	1,55	3·14	0·003
Age (adult)	0·450 ± 0·167	1,55	2·69	0·009
Sex (female) × age (adult)	−0·547 ± 0·237	1,55	−2·31	0·025

Chipmunk id was included in the model as a random effect (see text for more information). Results from this analysis were used in the path analysis.
[a]Year, sex, age and second order interactions were not significant and were excluded from the model.
[b]Proportion of chipmunk captures in traps at the periphery of the capture network.
[c]Year and periphery were not significant and were excluded from the model.
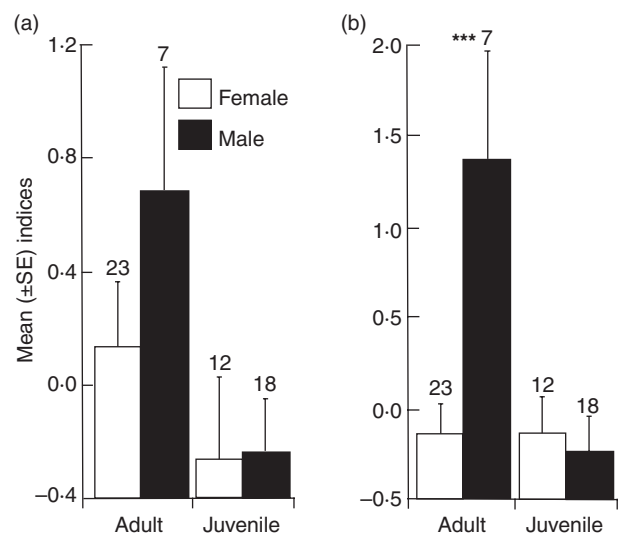[d]Category of reference are presented in parentheses.

Fig. 2. Variation in mean (a) trappability (log transformed) and (b) trap diversity (square root transformed) according to age and sex in Siberian chipmunk at Sénart in 2006. Data were corrected for length of capture period. Sample size is indicated above SE bars apply to all graphs (***P < 0·001).

TICK LOAD INDEX

Overall number of tick nymphs varied between 0 and 55 (mean ± SE = 18·00 ± 0·45), and number of larvae between 0 and 350 per individual (mean ± SE =
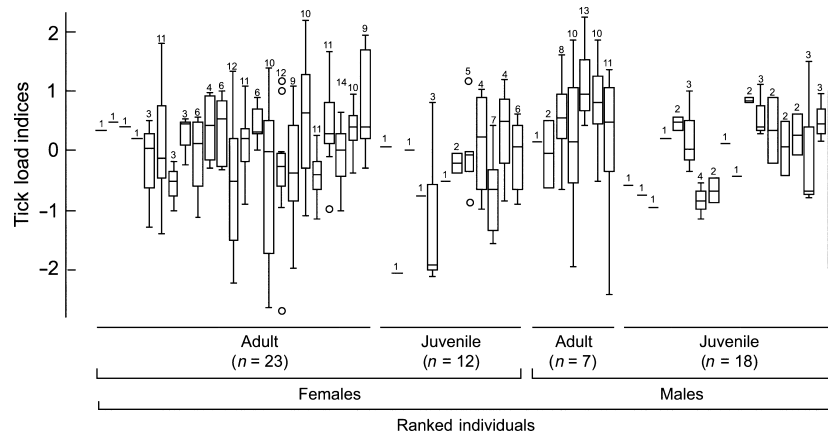
Fig. 3. Boxplot representation of individual variation in tick load in adult and juvenile, females and males Siberian chipmunks analysed at Sénart between 2005 and 2007 Tick load was log transformed and corrected for days, days², year and host body mass. Individual within an age-sex class were ranked according to trap diversity. Number of measures per individual is specified under the 5% percentile (if not specified $n = 1$).

32·76 ± 2·62) respectively. Number of nymphs was strongly correlated with number of larvae per chipmunk ($r = 0.73$, $t = 18.14$, d.f. = 292, $P < 0.001$). There were significant individual differences in tick load harboured by chipmunks (LRT = 42·55, d.f. = 1, $P < 0.001$; Fig. 3) and an integrated temporal autocorrelation improved the LMM (LRT = 53·56, d.f. = 1, $P < 0.001$). Consequently, we predicted the BLUP based on the LMM with the autocorrelation. Tick load was weakly but significantly repeatable within the hole-board year (repeatability = 10%). Tick load showed a quadratic relationship with day of capture with a peak in June (Table 3). Chipmunks had significantly more ticks in 2006 compared with 2005 (Table 3). Males had more ticks than females in 2005 but not in 2006 (year × sex interaction), and juveniles had fewer ticks than adults. Heavier juveniles had more ticks (body mass × age) and juveniles harboured more ticks with advancing days (age × day interaction; Table 3). We found significant consistent individual differences in tick loads across successive years (repeatability = 39%, LRT = 140·89, d.f. = 1, $P < 0.001$). Fixed effect results

for this across-year model were similar to those for the within hole-board year model and are not shown here.

CONFIRMATORY PATH ANALYSES

The structural equations, with the path coefficients (±SE), derived from our first causal path model (Fig. 1a) were:

$$\text{Trappability} = 23 \cdot 25(4 \cdot 47) \\ + 0 \cdot 24(0 \cdot 13)\text{Activity - exploration}$$

$$\text{Trap diversity} = 13 \cdot 76(3 \cdot 85) + 0 \cdot 55(0 \cdot 11)\text{Trappability}$$

$$\text{Tick load} = 8 \cdot 21(5 \cdot 09) + 0 \cdot 35(0 \cdot 12)\text{Habitat} \\ + 0 \cdot 38(0 \cdot 11)\text{Trap diversity}$$

The more chipmunks were active-exploratory the more they were trapped, but they did not go in a higher variety of traps (Fig. 1c). Chipmunk activity-exploration did not affect

Table 3. Mixed model on tick load (number of ticks counted on an individual; log transformed) in the same year of which the chipmunk was tested with the hole board

Variable[a]	Coefficient ± SE	d.f.	*t*-Value	*P*-value
Day	0·003 ± 0·002	1,229	1·63	0·105
Day²	−0·0002 ± 0·00002	1,229	−7·13	<0·001
Year (2005)[b]	0·957 ± 0·287	1,55	3·33	0·001
Sex (female)	1·468 ± 0·445	1,55	3·30	0·002
Age (adult)	−3·817 ± 0·944	1,55	−4·04	<0·001
Body mass	0·003 ± 0·007	1,229	0·36	0·719
Day × age (adult)	0·016 ± 0·005	1,229	3·14	0·002
Year (2005) × sex (female)	−1·165 ± 0·492	1,55	−2·37	0·021
Age (adult) × body mass	0·025 ± 0·010	1,229	2·37	0·019

Chipmunk id was included in the model as a random effect (see text for more information). Results from this analysis were used in the path analysis.
[a]Two-way interactions that were not significant were excluded from the model.
[b]In the parentheses denotes the category of reference.

Table 4. Basis sets, tests of conditional independence and the Fisher's C statistic associated with a priori path model (a) and an alternative one (b) presented in Fig. 1

Model (a)				Model (b)			
Basis set	t-Value	Partial r	P	Basis set	t-Value	Partial r	P
3_‖_2 ‖{1}	1·733	0·232	0·088	1_‖_5 ‖{2}	−1·200	−0·168	0·235
4_‖_1 ‖{3}	−0·303	−0·034	0·763	3_‖_2 ‖{1}	1·733	0·232	0·088
4_‖_2 ‖{3}	0·168	0·020	0·867	3_‖_5 ‖{1, 2}	0·786	0·108	0·435
5_‖_1 ‖{2, 4}	−1·714	−0·191	0·092	4_‖_1 ‖{3, 5}	0·461	0·049	0·646
5_‖_3 ‖{1, 2, 4}	−1·228	−0·168	0·225	4_‖_2 ‖{3, 5}	−1·181	−0·137	0·243
10 d.f., C = 13·44, P > 0·20				10 d.f., C = 13·12, P > 0·20			

'X_‖_Y |{Z_i, Z_j, …}' means that X and Y are hypothesized to be independent conditional of the combined set of {Z_i, Z_j, … } and 'Ø' represents an empty set. The model is rejected if the C probability is < 0·05. Basis set numbers refer to: 1 (active-explorative temperament profile), 2 (habitat), 3 (Trappability Index), 4 (Trap Diversity Index), 5 (Tick Load Index). All the variables were encoded in ranks.

habitat use (Fig. 1c). Trappability positively affected trap diversity, which in turn was positively related to tick load. Habitat type was directly linked to tick load, as chipmunks inhabiting the closed habitat were more infested than those inhabiting the semi-closed habitat. Considering the basis set, this path model was not rejected ($P > 0·20$; Table 4).

The structural equations derived from the second path model (Fig. 1b) were:

$$\text{Tick load} = 18 \cdot 26(4 \cdot 46) + 0 \cdot 40(0 \cdot 13)\text{Habitat}$$

$$\text{Trappability} = 23 \cdot 25(4 \cdot 47) \\ + 0 \cdot 24(0 \cdot 13)\text{Activity - exploration}$$

$$\text{Trap diversity} = 4 \cdot 25(4 \cdot 44) + 0 \cdot 50(0 \cdot 10)\text{Trappability} \\ + 0 \cdot 36(0 \cdot 10)\text{Tick load}$$

In this alternative diagram habitat had only an impact on tick load, with chipmunks inhabiting the closed habitat being more infested than chipmunks inhabiting the semi-closed one (Fig. 1d). As in the first model, we observed the pathway linking activity-exploration to trappability, and in turn trappability to trap diversity (Fig. 1d). Tick load did not influence either activity-exploration or trappability, directly or indirectly. Tick load was positively related to trap diversity. With a $P > 0·10$, this model could not be rejected (Table 4), despite the fact that it did not fit the data as well as the first hypothesis.

Discussion

Understanding the processes associated with the heterogeneity in parasite distribution on their hosts is fundamental to ecological and epidemiological research. It is generally admitted that parasites could induce changes in their host behaviour (Klein 2003; Thomas et al. 2005). There is also evidence for the effect of host behaviour on its rate of encounter with a parasite (Brink et al. 1967; Randolph 1975; Poulin et al.

1991). However, the consequences of personality differences on host susceptibility of infestation by a parasite have rarely been investigated yet (Wilson et al. 1993; Natoli et al. 2005; Easterbrook et al. 2007). Our results show that consistent individual differences in activity-exploration measured in the hole board influenced indirectly tick load in chipmunks, through activity (i.e. trappability) and space use (i.e. trap diversity), suggesting that according to its personality a host can run different risks of encountering parasites in their home range. The results of our alternative path analysis model and the fact that individual chipmunks did not change their behavioural reactions to the hole board as a result of an increase in tick load (N. Boyer, unpublished data) suggest that tick load did not modify chipmunks' activity-exploration in the hole board. Variation in activity patterns has been proposed to explain differences in parasite load among age-sex categories in a population or among species (e.g. Mohr 1961; Randolph 1975; Nilsson & Lundqvist 1978; Poulin 1996). Our results show that the same process can lead to heterogeneity in parasite load among individuals that differ consistently in their activity and exploration. These results also have important implications for the evolution of host–parasite interactions; selection on heritable variation in activity-exploration could lead to potential evolutionary changes in space use and activity behaviour in a host population as a result of parasite infestation. Being highly active and exploratory can be advantageous in feeding or mating contexts, but can also be costly because it increases the chance of encountering a predator (Jonsson et al. 2000; Biro et al. 2004; Brodin & Johansson 2004; Sih, Kats & Maurer 2003; Boon et al. 2008), or parasites (this study). Parasites may thus also play an important role in the maintenance of personality variation.

We found consistent differences in activity-exploration between individuals in the hole board ($r = 0·55$), indicating that these behavioural differences could not be explained by environmental conditions prior to or during the hole-board test alone (for other estimates on Sciurids see: Boon et al. 2007; Martin & Réale 2008b). Exploration and activity could not be separated and decreased with the number of hole-board tests passed, and activity-exploration in the hole board did not vary specifically according to sex or age classes.

Furthermore, individual personality differences were also expressed as individual consistency across years in trappability ($r = 0.36$) and the diversity of traps visited ($r = 0.34$), and individual differences in trappability were related to differences in activity-exploration in the hole board (as in red squirrels; Boon *et al.* 2008).

The existence of a pattern linking personality differences with space use in animals seems increasingly supported, with exploratory, bold or aggressive individuals using larger home ranges (Boon *et al.* 2008), or dispersing farther from their natal area (Fraser *et al.* 2001; Dingemanse *et al.* 2003; Duckworth & Badyaev 2007). In chipmunks adult males had larger home ranges than females (Marmet *et al.* 2009), and juvenile males disperse farther than females (Loew 1999; Marmet *et al.* 2009). However, contrary to our expectations, habitat type did not affect chipmunks' trappability and trap diversity. Trap diversity used as an index of space use could be biased if more exploratory individuals entered the first trap they met more readily than less exploratory individuals. This bias, however, will only underestimate the relationships found between personality, space use and tick load observed in this study.

One of our goals was to control for potential factors affecting tick load prior to test for individual differences in tick load within a year or across years. Ticks appeared on Siberian chipmunks from the end of March to November with a higher abundance in June. This pattern has been often reported for ticks, with abundances varying throughout the course of a year depending on climatic conditions (Mejlon 2000; Randolph *et al.* 2000), and is in accordance with estimates of Ixodid abundance in the vegetation and stages feeding on chipmunks over the study period (Pisanu *et al.*, unpublished data). Tick loads were higher in male chipmunks than in females. Such male bias has been often observed in host–parasite systems (Randolph 1975; Poulin 1996; Moore & Wilson 2002). Differences in immune system and in level of steroid hormones could explain such sexual differences (Hughes & Randolph 2001). Higher risk of infestation in males compared with females has also been explained by sexual differences in spacing behaviour (Ostfeld *et al.* 1996; Poulin 1996; Krasnov *et al.* 2005). In the absence of information on both testosterone and resistance differences between the sexes, we cannot reject these hypotheses. However, our results suggest that higher tick load in males is caused in part by larger home range sizes and higher activity in males than in females (this study and Marmet *et al.* 2009; Pisanu *et al.*, unpublished data). Chipmunk adults were more infested than juveniles, which could be as a result of an increase, with age, in the body surface available for ticks. Moreover, changes in infection predisposition and/or in exposition probably happen with age. After having considered variation in tick load caused by season, sex or age, we found that some chipmunks consistently harboured more ticks than others. Individual consistency differences in tick load were detectable across years ($r = 0.39$) and to a lower extent within the same year ($r = 0.10$). Hosts seemed therefore unequal with respect to parasite infections. Although immune system efficiency could explain chipmunk id effect on their parasite burden, our results indicate that differences in tick load among individuals can hardly be explained by personality-related characteristics other than activity-exploration behaviour. For example, although habitat type affected tick load, personality did not seem to affect habitat choice in this chipmunk population. In the same way, personality did not show any direct link with tick load. Therefore, the only path through which personality can be linked to tick load is through differences in trappability, which in turn affects positively trap diversity. The alternative model could not support the hypothesis that ticks were responsible for individual behavioural differences in the hole board. In this model, tick load was only related to trap diversity, but did not show any direct link with trappability and activity-exploration measured in the hole board. Furthermore, adult of Ixodid ticks stay on their host for a maximal period up to 8 days, even less for younger stages (Pérez-Eid 2007), while we analysed consistent individual differences in behaviour over several months. This long-term study allowed us to estimate behavioural profiles for periods that were much longer than the feeding period by a tick on a host. These results suggest that the model assuming that personality affects space use and tick load might be more probable than the one assuming that tick load was responsible for the link between behaviour in the hole-board, trappability and trap diversity.

We found higher tick loads for chipmunks inhabiting the closed habitat, where free-living stages of *I. ricinus* survive better because of the relative humidity of the forest undergrowth (Mejlon 2000; Randolph *et al.* 2000). The closed forest is also the main roe deer (*Capreolus capreolus* Linnaeus 1758) resting area, whereas deer use the open habitat less often and essentially for foraging (Pisanu & Chapuis, unpublished data). Habitat use by the deer may thus affect the density of ticks and therefore tick loads on chipmunks.

Conclusion

Using chipmunks and ticks as a model, we show that animals' activity and exploration can also be costly by increasing exposure to questing parasites. As questing tick larvae are highly clumped in space (Ostfeld *et al.* 1996; Mejlon 2000), possessing a larger home range increases the probability of encountering these larval tick concentrations and a greater number of other stages. Models have been created to study the effects of host population density and composition on the parasite and pathogens' persistence (Rosà *et al.* 2006). Our study confirms the necessity for integrating individual host characteristics in these models (Brunner & Ostfeld 2008). As individual personality seems to influence the host–parasite interactions, it could be taken into account in control programs of parasites and infectious diseases. Studies have already shown that focused control efforts on individuals having a central place in disease transmission would decrease infection risks by 80% and thus be more efficient than a random elimination (Woolhouse *et al.* 1997; Perkins *et al.* 2003). Individuals whose personality promotes a high

parasite infestation could be responsible for the greater part of parasite transmission in a population and thus play a primordial role in parasite and disease persistence (Woolhouse *et al.* 1997; Natoli *et al.* 2005; Perkins *et al.* 2003).

Acknowledgements

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