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Personality predicts ectoparasite abundance in an asocial sciurid

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Abstract

Parasitism is a consequence of complex interactions between host, parasite, and their shared environment, and host behavior can influence parasite risk. Animal personality (i.e., consistent behavioral differences that are repeatable across time and context) can influence parasitism with more explorative individuals typically hosting greater parasite loads. Host "sociality" is known to impact parasite risk with more social individuals typically at higher risk of acquiring or transmitting parasites, but other behaviors could also be important. We quantified personality in least chipmunks (*Tamias minimus*), including repeatability of behavioral traits, and determined whether these personality traits affected ectoparasite prevalence and abundance. We measured personality using standardized hole-board tests and quantified ectoparasitism of 39 least chipmunks over 2 years at a site in southeastern Manitoba, Canada. We found that activity and exploration were repeatable within the context of the hole-board test for least chipmunks, which suggests that these traits reflect personality. More exploratory individuals hosted a greater abundance of ectoparasites compared to less exploratory individuals. Our results are consistent with past studies implicating personality as a factor in host–parasite dynamics and suggest that exploration may be an important behavioral correlate of parasite acquisition.

KEYWORDS
behavior, consistent individual differences, host–parasite dynamics, least chipmunk, repeatability

1 | INTRODUCTION

Parasites are ubiquitous and can influence host population dynamics (Hudson, Dobson, & Lafferty, 2006; Tompkins, Dunn, Smith, & Telfer, 2011), regulate ecological processes (e.g., predator–prey dynamics, Hudson, Dobson, & Newborn, 1992), influence agricultural operations (e.g., crop pest *Meligethes viridescens*, Mason et al., 2003), and act as vectors for human disease (e.g., Malaria, Greenwood & Mutabingwa,

2002). Both microparasites (i.e., microbes with rapid reproduction within a host) and macroparasites (i.e., multicellular species with low reproductive output) can therefore impact ecological and agricultural systems, and public health. Understanding the intersecting properties of hosts, parasites, and their shared environment is critical for predicting potential outcomes at the population level (Scholtof, 2006).

Host species characteristics such as population density (Ebert, 1995), demography (Le Cœur et al., 2015; Webber, Czenze, & Willis, 2015b; Webber, McGuire, Smith, & Willis, 2015a), and behavior (Moore, 2002; VanderWaal & Ezenwa, 2016) are important

determinants of parasitism. For gregarious host species, risk of parasitism typically increases as a function of host contact rate and subsequent social interactions (Alexander, 1974; Altizer et al., 2003). For instance, in the social gidgee skink (*Egernia stokesii*), greater social connectivity increased risk of infection with blood parasites and ticks (Godfrey, Bull, James, & Murray, 2009). Similarly, social allogrooming in meerkats (*Suricata suricatta*) increased the likelihood of acquiring *Myobacterium bovis*, the causative agent of tuberculosis (Drewe, 2010). For species that do not maintain stable social groups, transmission dynamics are mediated by other factors such as allometry (Han, Park, Jolles, & Altizer, 2015), space use (Han et al., 2015), and reproductive energetics (Patterson, Neuhaus, Kutz, & Ruckstuhl, 2015). For example, in red squirrels (*Tamiasciurus hudsonicus*), males tend to host more fleas than females during the mating season and females host more fleas during lactation, presumably because squirrels cannot allocate energy to grooming or immune function during these energetically costly times of year (Patterson et al., 2015). The reproductive season represents a period when males occupy larger home ranges as they search for potential mates. Han et al. (2015) predicted that this kind of behavioral shift could increase risk of macroparasite infestation for a range of smaller-bodied carnivores and primates.

Animal personality, or consistent individual differences in behavior, could also influence risk of parasitism. Personality can influence space use (Boyer, Réale, Marmet, Pisanu, & Chapius, 2010) and dispersal (Harrison et al., 2014), which could affect risk of parasitism (Barber & Dingemanse, 2010) and potentially influence the dynamics of parasite transmission and acquisition among hosts. Variation in activity levels or exploratory tendencies among individuals could be particularly important for ectoparasite infection because many ectoparasites are free-living and have environmental reservoirs. Free-living ectoparasites are habitat-dependent (Hudson et al., 1992) so hosts that are more active or explore their environments more thoroughly may face greater infestation than less active or explorative individuals (Barber & Dingemanse, 2010; but see Bordes, Morand, Kelt, & Van Vuren, 2009 and Lindenfors et al., 2007). For example, Boyer et al. (2010) found that the activity–exploration axis of personality and space use predicted tick load for Siberian chipmunks (*Tamias sibiricus*). Thus, individual personality traits, which may be linked to dispersal or home range size (e.g., Boyer et al., 2010; Harrison et al., 2014), could influence risk of acquiring ectoparasites.

Personality variation has been extensively studied in free-ranging rodents (e.g., Boon, Réale, & Boutin, 2007; Le Cœur et al., 2015; Montiglio, Garant, Thomas, & Réale, 2010; Timonin et al., 2011). Chipmunks are among the most diverse mammalian genera in North America (23 species, Sullivan et al., 2014) and ectoparasite communities of chipmunks are well documented (e.g., Jameson, 1999; Timm, 1975). Personality variation has also been studied in two common species (e.g., *Tamias striatus* in North America, Martin & Réale, 2008; *T. sibiricus* in Europe, Le Cœur et al., 2015) but least chipmunks (*T. minimus*), which are among the most common and wide-spread chipmunks (Verts & Carraway, 2001), have not been studied in this context. Additional data from this and other species would be useful to facilitate future comparative analyses. Like other chipmunks, *T. minimus* is

typically asocial and is also subordinate to *T. striatus*, a sympatric species (Carey, 1978).

We studied least chipmunks to test two hypotheses. First, we tested whether putative personality traits measured in a standard hole-board test were repeatable within individuals over time. Second, we tested the hypothesis that personality influences ectoparasite prevalence and abundance in least chipmunks. We predicted that more active and exploratory individuals would host higher intensities of ectoparasites because these individuals would be most likely to encounter infested conspecifics or environmental reservoirs of ectoparasites.

2 | METHODS

2.1 | Study site and subjects

All procedures were approved by The University of Winnipeg Animal Care Committee and conducted under a Manitoba Conservation Wildlife Scientific Permit (WB0612). We trapped least chipmunks in Sandilands Provincial Forest, Manitoba (49°22′37″N, 96°6′31″W) between June 1 and August 1, 2013, and July 27 and August 1, 2014. Sandilands Provincial Forest is located in transitional lowland boreal forest dominated locally by jack pine (*Pinus banksiana*) and red pine (*P. resinosa*) (Scott, 1996). Our trapping grid consisted of eight rows, each with 10 Sherman live traps placed at 10 m intervals with four smaller trapping grids (four rows, each with five traps) in adjacent areas. Trapping occurred at least four times a week and we baited traps with a mixture of peanut butter, rolled oats, and apple slices. Traps were set at, or shortly after, dawn and subsequently checked every 2 hr.

2.2 | Capture

Chipmunks were transferred from traps into cloth bags prior to behavioral testing and ectoparasite sampling (Patterson & Schulte-Hostedde, 2011). Individuals were tagged using uniquely numbered ear tags (National Band and Tag Company, Newport, Kentucky) or with a passive integrated transponder (PIT tag; Trovan Ltd. ID 100-01, Douglas, UK) injected subcutaneously in the interscapular region. Chipmunks were considered juvenile if they were <35 g at first capture and were not visibly reproductive. Juvenile least chipmunks begin to disperse from natal burrows in mid-July (Sheppard, 1969), which was consistent with the distribution of captured chipmunks we identified as juvenile based on mass and reproductive status. Adult males were identified as "scrotal" if they had enlarged testes and a dark scrotum (Schulte-Hostedde, Millar, & Gibbs, 2002), and females were identified as pregnant or lactating based on gentle palpation of the abdomen and enlarged mammary glands (Smith & Smith, 1975). All captured females were either lactating or post-lactating, and we did not capture any juvenile females, so we considered all females reproductive. We weighed each chipmunk with an electronic balance (±0.1 g; Model HH 320, Ohaus, Parsippany, NJ, USA), and measured body length (±0.1 mm; without tail) using digital calipers (Canadian Tire, Toronto, ON, Canada). We calculated a body condition index

(BCI) by dividing mass by body length and used this metric for subsequent analyses.

2.3 | Quantifying personality

We quantified personality using a hole-board test (File & Wardill, 1975; Martin & Réale, 2008). The test consisted of a rectangular arena (58 cm long × 42 cm wide × 26 cm deep) made from an opaque plastic storage container with a transparent Plexiglas cover. The test consisted of four blind holes (2 cm diameter × 5 cm deep) drilled into the floor of the test. Two outer holes were positioned further from the entrance, 5 cm away from the back and side wall of the test. Inner holes were positioned closer to the entrance, 10 cm from the front wall, and 15 cm away from the side wall. These holes are thought to differentiate between exploration and general activity because the animal is stationary while it investigates the hole (File & Wardill, 1975; Martin & Réale, 2008). A start chamber (16 cm long × 8 cm wide) was fastened to the front of the test with a small sliding door separating the start chamber from the test chamber.

Trials were 10 min long and were recorded using a digital video camera (Panasonic HX-DC2, Dual Camera) mounted on a tripod adjacent to the test. Trials were conducted outdoors with natural lighting between 800 and 1,600 under a tent with mesh screen sides to decrease glare. After each trial, the test and start chambers were cleaned thoroughly using a mixture of soap and water to remove residual scent, which could affect behavior of chipmunks in subsequent trials. Hole-board tests were repeated for individuals as they were recaptured to quantify repeatability of behavioral traits identified as important components of personality in other chipmunk species (Boyer et al., 2010; Martin & Réale, 2008).

Videos were scored for a range of behaviors assessed in previous studies of rodents (e.g., Boon et al., 2007; Martin & Réale, 2008; Patterson & Schulte-Hostedde, 2011). The length of time an individual spent in the entrance chamber before entering the test chamber was recorded as latency to enter, with a maximum possible latency of 60 s (Martin & Réale, 2008). Ten-minute behavioral trials began once the animal entered the hole-board test, after latency to enter was recorded. We scored locomotion (time spent moving forward), rearing (number of times an individual raised its front limbs off the floor), number of escape attempts (jumping toward the roof of the enclosure), duration of grooming, time spent motionless, frequency of head dips (number of times an individual explored holes on the floor), and the number of fecal pellets produced during the trial. We also superimposed one vertical and one horizontal line over the video, intersecting at the centre of the hole-board test, to quantify locomotion as the number of times an individual crossed each line (i.e., line crossing). We counted all instances when at least half of the test individual's body crossed over a line as a single line cross.

2.4 | Ectoparasites

We assessed ectoparasitism using two metrics: (i) Prevalence was quantified as the presence or absence of ectoparasite infestation and (ii) abundance was quantified as the number of ectoparasites on each chipmunk, including zeroes (i.e., individuals that did not have any ectoparasites). Ectoparasite prevalence and abundance were determined immediately after behavioral trials by combing the fur on the dorsal surface of the head, back, and flanks, a procedure that disturbed any ectoparasites in the fur. We then re-examined each individual by gently blowing on the ventral and dorsal surfaces of the torso, which disturbed any ectoparasites that may have been missed by the comb. We collected ectoparasites found on chipmunks in the field by removing them with tweezers and storing them in ethanol for subsequent identification.

Chipmunks were parasitized with fleas, mites, and lice. We identified five species of fleas: *Eumolpianus eumolpi eumolpi* (commonly parasitizes least chipmunks, Verts & Carraway, 2001), *Ceratophyllus vison* (generally parasitizes tree squirrels, Galloway & Christie, 1990; Patrick & Wilson, 1995), *Ctenophthalmus pseudagyrtes pseudagyrtes* and *Megabothris quirini* (both commonly parasitize mice, voles, and shrews, Baker, 1904, Buckner, 1964; Holland, 1985; Waterman, Macklin, & Enright, 2013), and *Hystrichopsylla dippiei dippiei* (a generalist flea that parasitizes a range of rodent species, Buckner, 1964; Hastriter & Haas, 2005; Timm, 1975). Although some of the flea species we identified more commonly parasitize other rodents (e.g., squirrels, mice, or voles), all five species have previously been observed parasitizing *T. minimus* (Buckner, 1964; Hastriter & Haas, 2005; Timm, 1975). Adult fleas jump onto the host to feed and can easily move from one host to another (Lindsay & Galloway, 1997). We pooled fleas from all species together for subsequent statistical analysis given relatively small sample sizes for each individual species. We identified one nymph of a sucking louse (*Hoplopleura arboricola*), a species that has previously been observed parasitizing least chipmunks (Timm, 1975). All mites were likely members of the genus, *Androlaelaps*, although we did not identify mites to species. Mite and louse eggs hatch and develop directly on the host, where they subsequently feed during their nymphal and adult stages (Radovsky, 1994), and cannot survive off the host for extended periods of time. We detected only one chipmunk with one louse so we were unable to conduct statistical analyses for this group.

2.5 | Statistical analysis

All analyses were conducted using R (version 3.1.1 GUI 1.65, R Development Core Team 2014). Principal component analysis (PCA) was used to reduce behavioral variables measured in the hole-board test into a smaller number of principal component (PC) scores (Martin & Réale, 2008). Prior to conducting PCA, we scaled and centered raw data by subtracting variable mean values from each individual value and dividing by the variable standard deviation, which ensures that the first component describes the most variance. The number of principal components retained was based on the Kaiser–Guttman criterion (eigenvalues >1, Kaiser, 1991). PC scores were used as representative values for given personality traits in subsequent analysis (see Section 3).

We did not recapture any chipmunks between years, so our repeatability (*r*) analysis reflected within-year repeatability of personality

TABLE 1 Summary of results for principal component analysis of behavioral responses of least chipmunks in a hole-board test (N = 69). See Section 2.3 in methods for details

Behavioral variable	PC1 (Activity)	PC2 (Exploration)	PC3 (Vigilance)
Line crossing	0.41*	−0.22	0.19
Locomotion	0.52*	−0.06	0.01
Freezing	−0.51*	0.08	0.21
Latency to enter	0.09	0.62*	−0.13
Number of head dips	−0.24	−0.51*	0.13
Fecal pellets	−0.16	−0.44*	−0.32
Escape attempts	0.35	−0.04	0.49*
Grooming	0.09	0.09	−0.62*
Rear attempts	0.26	−0.29	−0.39*
Standard deviation	1.83	1.27	1.15
% Total variation	37.50	18.00	14.60

*Variables that loaded strongly (PC score >0.4) on a given principal component axis.

traits. We repeated the hole-board test at least twice for 23 individuals, where the second trial occurred, on average, 8 days after the initial trial (range: 2–25 days). We obtained only one measurement for 16 individuals. Following Martin, Nussey, Wilson, and Réale (2011), we included individuals with one measurement in our repeatability analysis to increase power. To calculate repeatability, we used the rptR package in R (Stoffel, Nakagawa, & Schielzeth, 2017). We fit models with Gaussian error structure and included test number (1, 2, or 3) and numbers of days between personality trials as fixed effects and individual identity as a random effect (Nakagawa & Schielzeth, 2010). Repeatability was therefore quantified by calculating the proportion of variation between groups (V_{ind}) attributable to the residual variance among groups (V_{res}) for each personality trait (Dingemanse & Dochtermann, 2013):

$$r = \frac{V_{ind}}{(V_{ind} + V_{res})} \qquad (1)$$

Based on the distribution of repeatability values synthesized by Bell, Hankison, and Laskowski (2009), we defined repeatability values of <0.2 as weak, values ≥0.2, but ≤0.40 as moderate, and values >0.4 as strong.

We also calculated r for ectoparasite abundance and prevalence using the rptR package (Stoffel et al., 2017). For ectoparasite abundance, we fit our repeatability models with a Poisson distribution and logit link, while for ectoparasite prevalence we fit our repeatability models with a binomial distribution and square-root link (Nakagawa & Schielzeth, 2010). For both sets of models, we included year and number of days between captures as fixed effects and individual identity as a random effect. There were many uninfested chipmunks (see Section 3), so we also calculated the proportion of chipmunks that changed from uninfested to infested from their initial capture to second capture.

We assessed normality for all variables. Ectoparasite distribution was overdispersed and thus did not meet the criteria for Gaussian or Poisson distributions (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Therefore, we used generalized linear mixed models (GLMMs) with a negative binomial distribution to assess effects of

predictor variables on ectoparasite abundance, and GLMMs with a binomial distribution to assess effects of predictor variables on ectoparasite prevalence. For our models of ectoparasite abundance and prevalence, we included PC1 (activity), PC2 (exploration), mean-centered and scaled BCI (i.e., body mass divided by body length), demographic (i.e., adult male, adult female, or juvenile male), and interactions between demographic and each of PC1, PC2, and BCI, as fixed effects. We also included individual identity and year (2013 or 2014) as random effects. We did not include PC3 (vigilance) in our models because it was not repeatable (see below) and thus did not meet the definition of personality. None of the interactions we included in our global models were significant, so we removed them from subsequent models and present results for models without interactions. We ran a single model to test for effects of our covariates on each of ectoparasite abundance and prevalence. We assessed significance at α = 0.05 and all values are mean ± SD unless otherwise noted.

3 | RESULTS

We conducted 69 hole-board tests and quantified ectoparasite abundance for 39 individual chipmunks 1.5 ± 0.67 times each (range: 1–3 tests per individual) in 2013 (n = 20) and 2014 (n = 19). We retained the first three PC scores, which combined to explain 70% of the total variance in the data (Table 1). The first component (PC1) was comprised of behaviors such as locomotion and line crossing so we interpreted PC1 as an index of activity. The second component (PC2) was comprised of behaviors such as the total number of head dips and the latency to enter the hole-board test so we interpreted PC2 as an index of exploration. The third component (PC3) was comprised of behaviors such as grooming, number of escape attempts, and rearing, behaviors which have previously been interpreted as anxiety or vigilance. We therefore interpreted PC3 as an index of vigilance. Activity and exploration were strongly repeatable (r = .49 ± .14 [SE] and r = .54 ± .13, respectively), while vigilance (r = 0 ± .10) was not repeatable (Table 2).

Including multiple captures of the 39 individuals, ectoparasite prevalence (i.e., presence of at least one ectoparasite) was 57.9% (40/69), while overall ectoparasite abundance was 2.25 ± 4.70 (range: 0–30; Table 3). Mite prevalence was 17% (12/69), while abundance of mites was 1.2 ± 4.4 (range: 0–30; Table 3). Flea prevalence was 53% (37/69), while abundance of fleas was 0.97 ± 1.4 (range: 0–8; Table 3). In 2013, we recaptured chipmunks, on average, 2.5 ± 1.6 times (range 0–7 recaptures), while in 2014, we recaptured chipmunks, on average, 1.6 ± 1.1 times (range 0–4 recaptures). On average, recapture latency, that is, days between recaptures, was 4.8 ± 6.4 days (range 1–31 days).

Overall ectoparasite prevalence (r = .20 ± .11 [SE]) and abundance (r = .33 ± .16) were moderately repeatable (Table 4). Flea prevalence (r = .06 ± .06) and abundance (r = .05 ± .08) were not repeatable between captures, while mite prevalence (r = .76 ± .29) and abundance (r = .47 ± .15) were strongly repeatable between captures (Table 4). Of chipmunks that we initially captured with at least one ectoparasite, 44% (10/23) of these changed infection status on subsequent

captures. For fleas alone, nearly half of chipmunks that hosted at least one flea at first capture (47%, 11/23) hosted no fleas at second capture; however, only 17% (4/23) of individuals switched from hosting mites to not hosting mites between captures.

Consistent with our hypothesis, exploration in the hole-board test was positively related to ectoparasite abundance (Table 5; Figure 1), although there was no relationship between exploration and prevalence (Table 5). Our model predicted an increase of 1.46 ectoparasites per unit increase in individual exploration behavior. For perspective, this corresponds with an approximate abundance of 0 parasites for the least explorative individual we assessed and approximately 7.5 ectoparasites for the most explorative individual (Figure 2; Table 5). There was no relationship between activity and ectoparasite abundance or ectoparasite prevalence (Table 5). We found a significant effect of BCI on ectoparasite abundance, with chipmunks in better body condition hosting higher ectoparasite abundance than individuals in worse condition (Table 5; Figure 2). We found no differences in ectoparasite abundance, and a moderate difference in ectoparasite prevalence

TABLE 2 Summary of generalized linear mixed-effects models estimating repeatability for activity, exploration, and vigilance in least chipmunks (*Tamias minimus*). All models included assay (1, 2, or 3) and days between trials as fixed effects and included individual identity as a random effect. "Ind Var" refers to among-individual variation, while "Resid Var" refers to residual variation (i.e., unexplained within-individual variation)

Behavioral repeatability	Estimate ± *SE*	*t*-value	Ind Var	Resid Var	Repeatability
Activity (PC1)			1.627	1.659	0.49
Intercept	0.84 ± 0.48	1.7			
Assay	−0.52 ± 0.30	−1.7			
Days between trials	0.02 ± 0.01	0.4			
Exploration (PC2)			0.939	0.795	0.54
Intercept	−0.28 ± 0.34	−0.8			
Assay	0.32 ± 0.21	1.5			
Days between trials	−0.03 ± 0.03	−1.0			
Anxiety (PC3)			0	1.244	0
Intercept	0.56 ± 0.36	1.6			
Assay	−0.48 ± 0.24	−2.0			
Days between trials	0.07 ± 0.03	2.2			

TABLE 3 Summary of flea, mite, and louse prevalence, abundance, and intensity for 39 individual least chipmunks (*n* = 39 individuals, *N* = 69 captures). Ectoparasite abundance (i.e., ectoparasites per chipmunk, regardless of infection status) and ectoparasite intensity (i.e., number of ectoparasites per parasitized chipmunks) for all chipmunks displayed as mean ± *SD* (range) for both first capture and all captures of all individuals combined

Ectoparasite group	Number parasitized	Number unparasitized	Overall abundance	Overall intensity
First capture only				
Fleas	20	19	0.97 ± 1.6 (0–8)	2.0 ± 1.9 (1–8)
Mites	7	32	1.5 ± 5.4 (0–30)	13.8 ± 11.1 (1–30)
Lice	1	38	0.02 ± 0.2 (0–1)	1.0 (1–1)
Overall	23	16	2.54 ± 5.6 (0–30)	4.47 ± 6.9 (1–30)
All captures combined				
Fleas	37	32	0.97 ± 1.4 (0–8)	1.9 ± 1.5 (1–8)
Mites	12	57	1.2 ± 4.4 (0–30)	11.2 ± 11.1 (1–30)
Lice	1	68	0.01 ± 0.1(0–1)	1.0 (1–1)
Overall	40	29	2.25 ± 4.7 (0–30)	4.02 ± 5.8 (1–30)

among demographics with males hosting higher prevalence than females (Table 5).

4 | DISCUSSION

We identified behavioral traits in one context (i.e., the hole-board test) that were repeatable across time in least chipmunks. Although the strict definition of personality refers to traits that are repeatable across both time and context, we still use the term personality because our repeatability values were so high and the traits we quantified are virtually identical to those observed in other closely related species (e.g., Boyer et al., 2010; Martin & Réale, 2008). We found a positive relationship between one of these traits (i.e., exploration) and ectoparasite abundance. Our results suggest that more exploratory individuals face greater risk of acquiring ectoparasites than less exploratory individuals and add to a growing literature suggesting that personality traits can influence risk of acquiring and transmitting parasites and pathogens (for review, see Barber & Dingemanse, 2010; Kortet, Hedrick, & Vainikka, 2010).

Activity and exploration, but not vigilance, were repeatable in our study, consistent with the occurrence of personality in this species. These values of repeatability were higher than median values quantified in a meta-analysis by Bell et al. (2009). Although the time between our experimental trials (1–25 days) was relatively low, animals were consistently active or explorative across

TABLE 4 Summary of generalized linear mixed models (fit with a binomial distribution) estimating repeatability for overall ectoparasite, flea, and mite prevalence and abundance. All models included year (2013 or 2014) and days between captures as fixed effects and included individual identity as a random effect

	Repeatability of prevalence estimates			Repeatability of abundance estimates		
	Estimate ± *SE*	*z*-value	*r*	Estimate ± *SE*	*z*-value	*r*
Overall ectoparasitism			.20			.33
Intercept	−0.95 ± 0.48	−2.0		−0.49 ± 0.36	−1.4	
Year (2014)	1.66 ± 0.13	2.4		0.62 ± 0.47	1.3	
Days since capture	0.12 ± 0.06	1.9		0.02 ± 0.02	1.2	
Flea parasitism			.06			.05
Intercept	−1.08 ± 0.39	−2.7		−0.55 ± 0.27	−2.1	
Year (2014)	1.44 ± 0.53	2.7		0.27 ± 0.34	0.8	
Days since capture	0.11 ± 0.05	1.9		0.03 ± 0.01	1.9	
Mite parasitism			.76			.47
Intercept	−4.24 ± 2.52	−1.6		−6.1 ± 1.89	−3.2	
Year (2014)	1.95 ± 1.48	1.3		2.32 ± 1.61	1.4	
Days since capture	−0.001 ± 0.11	−0.01		−0.15 ± 0.07	−2.3	

TABLE 5 Summary of generalized linear mixed models (GLMMs) assessing the effect of candidate variables on total ectoparasite abundance and prevalence for 39 least chipmunks. Families were set to negative binomial distributions for ectoparasite abundance models, and binomial distributions for ectoparasite prevalence models. Fixed effects included demographic, mean-centered, and scaled body condition index (BCI), as well as PC1 (activity) and PC2 (exploration). An asterisk represents significance (α = 0.05). Note: Repeatability estimates were calculated using separate models generated via the "rpt" function (see Section 2) because residual variances for GLMMs with non-Gaussian distributions are fixed

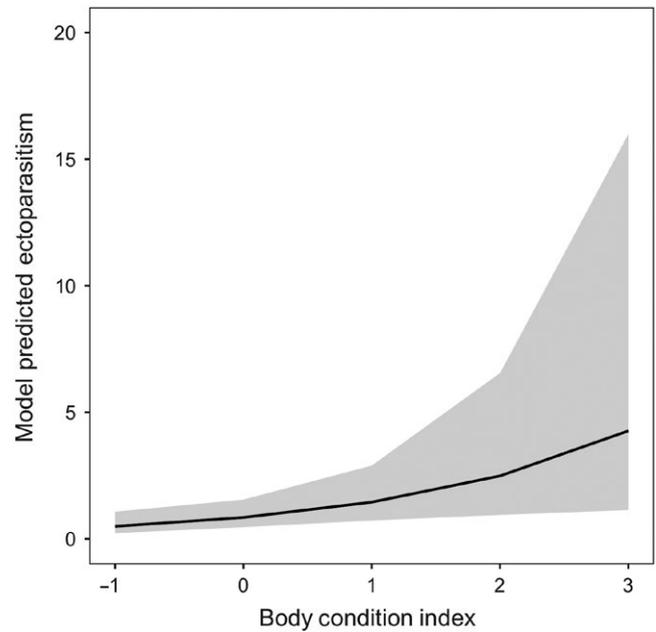|	Ectoparasite abundance			Ectoparasite prevalence		
Fixed effects	Estimate ± *SE*	*z*-value	*p*-value	Estimate ± *SE*	*z*-value	*p*-value
Intercept	−0.85 ± 0.58	−1.4	.14	−0.65 ± 1.0	−0.6	.52
Demographic						
Adult male[a]	0.84 ± 0.70	1.2	.22	1.34 ± 0.75	1.9	.06
Juvenile male[a]	1.21 ± 0.79	1.5	.12	1.89 ± 0.94	2.0	.04*
BCI	0.54 ± 0.21	2.6	.009*	0.12 ± 0.34	−0.4	.70
PC1 (Activity)	0.08 ± 0.08	1.0	.29	−0.20 ± 0.10	−1.0	.34
PC2 (Exploration)	0.38 ± 0.15	2.5	.01*	−0.26 ± 0.26	−1.0	.32
Variance components	Variance ± *SD*			Variance ± *SD*		
Individual	2.08 ± 1.44			0		
Year	0			1.42 ± 1.93		

[a]Relative to adult females.
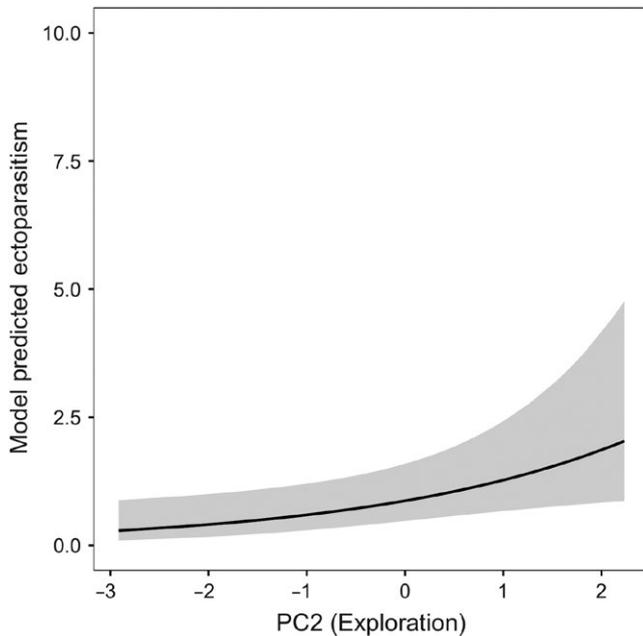
FIGURE 1 Relationship between ectoparasite abundance and exploration (PC2) measured in a hole-board test for 39 individual least chipmunks. The trend line was generated using generalized linear mixed models fit with negative binomial distribution and accounts for the effects of individual identity and year as random effects in the model (see Section 2 for details)

FIGURE 2 Relationship between ectoparasite abundance and mean-centered and scaled body condition index (BCI). The trend line was generated using generalized linear mixed models fit with negative binomial distribution and accounts for the effects of individual identity and year as random effects in the model (see Section 2 for details)

trials, even over days or weeks. Our results represent a possible first step to understanding the ecological consequences and evolutionary trajectory of behavioral phenotypes in least chipmunks (Dochtermann, Schwab, & Sih, 2015). Although repeatability of a given trait does not confirm heritability, it suggests the possibility that the trait is heritable and represents the upper bound of heritability (Dochtermann et al., 2015). Thus, our results leave open the possibility that activity and exploration could be subject to evolutionary change in this species.

We found some support for our hypothesis that personality influences ectoparasite infestation in least chipmunks. As we expected, more exploratory individuals had higher ectoparasite abundance, which is consistent with research showing that activity also affected ectoparasite abundance in Siberian chipmunks (Boyer et al., 2010). We did not find evidence to support our hypothesis that more active chipmunks would host greater ectoparasite abundance than less active individuals, and activity did not predict the presence or absence of ectoparasites. One explanation for the differences we observed between ectoparasite abundance and prevalence could be that prevalence is a coarse, categorical measure of ectoparasitism. Abundance ranged widely from 1 to 30 ectoparasites per chipmunk and, therefore, provides a more precise index than presence/absence. Thus, behavioral variation may be more likely to predict this continuous index of ectoparasitism (Barber & Dingemanse, 2010).

Our results suggest that more exploratory individuals are more likely to encounter and acquire ectoparasites. Typically, ectoparasites are transmitted via direct host–host contact, or alternatively, from an environmental reservoir such as a nest, den, or roost of a

potential host. For instance, in tree swallows (*Tachycineta bicolor*), fleas lay eggs in nests of parasitized hosts (Harriman, Dawson, Clark, Fairhurst, & Bortolotti, 2013) so nests represent an environmental reservoir. Least chipmunks are presumably asocial outside the breeding season, so more exploratory least chipmunks likely have greater exposure to ectoparasites via contact with environmental reservoirs such as nests or burrows of conspecifics or heterospecifics, as opposed to physical contact with conspecifics. Specifically, activity and exploration may be linked to dispersal tendencies (e.g., Canestrelli, Bisconti, & Carere, 2016; Harrison et al., 2014) or home range size (e.g., Boyer et al., 2010), which in turn could facilitate contact with parasites in the environment. While it is possible that we captured dispersing chipmunks in our study, juvenile dispersal in chipmunks typically occurs in spring and is also male-biased (e.g., Messier, Garant, Bergeron, & Réale, 2012). Moreover, nearly all juvenile males were recaptured at least once (20/21: 96%), suggesting that dispersal had already occurred and that individuals in our study were residents. We suggest that future studies attempt to quantify the rate at which asocial species, like chipmunks, contact environmental reservoirs of ectoparasites, which could be measured using individuals fitted with PIT tags and readers randomly distributed to represent localized ectoparasites (Harper & Batzli, 1996). It would also be useful to quantify the social tendencies of chipmunks to determine the proportion of ectoparasites acquired from conspecifics vs. the environment.

With the addition of our study, there are now three species of chipmunk (i.e., *T. striatus*, *T. sibiricus*, and *T. minimus*) for which personality has been quantified (Boyer et al., 2010; Martin & Réale, 2008). Among

sympatric chipmunks, anecdotal evidence suggests that *T. minimus* can be displaced from preferred habitat in the presence of the much larger *T. striatus* (Verts & Carraway, 2001). We encourage researchers to quantify personality for additional chipmunk species and to study potential interspecific variation in personality, or behavioral tendencies, among sympatric species. It could be useful to consider species-specific behavioral tendencies within a niche-partitioning framework and determine how individual personality traits vary within and among species and niches (Bolnick et al., 2003). For sympatric species that likely share many of the same general ecological characteristics, such as least and eastern chipmunks, inter- and intraspecific niche partitioning may be particularly important for individuals to reduce competition. Similarly, in an eco-energetic context, Careau, Bininda-Emonds, Thomas, Realé, and Humphries (2009) found an interaction between exploration and basal metabolic rate across muroid species, suggesting a possible coevolutionary relationship between energetics and personality (Careau et al., 2009; see also Wolf, Van Doorn, Leimar, & Weissing, 2007).

Although we cannot confirm cause–effect relationships in our study, we hypothesize that personality traits in our study animal are more likely to influence ectoparasite intensity and not the other way round. Some parasites can manipulate host behavior to facilitate transmission (e.g., *Toxoplasma gondii*, da Silva & Langoni, 2009), but these parasites are typically endoparasites with intermediate and definitive hosts (e.g., acanthocephalans, Moore, 1984). It seems unlikely that ectoparasites we observed (i.e., fleas and mites) manipulate host behavior to influence transmission dynamics (Poulin, 2000; Poulin & Maure, 2015; but see Kavaliers, Colwell, & Choleris, 1999). We did not experimentally manipulate parasite intensity; however, we did remove ectoparasites from individuals after behavioral trials and before releasing them (see Section 2). If ectoparasite abundance were a driving force of exploration in chipmunks, we would expect low repeatability values for exploration, as individual behavior should have changed after we reduced parasite loads. Instead, we observed levels of repeatability that were high relative to past studies (Bell et al., 2009). There was also no difference in behavior of Siberian chipmunks in previous studies after experimental addition or removal of *Ixodes* ticks (Boyer et al., 2010). Our results on repeatability of parasite prevalence, at least for mites, lend some support to this hypothesis. Mites are relatively immobile and appear unlikely to leave their hosts. Individuals that had high mite intensities on their first capture tended to re-acquire similar levels of mites between captures days or weeks apart, suggesting that their exploration leads to this repeated infestation. Fleas on the other hand are mobile ectoparasites and the majority of the flea community lives in the nest as opposed to on a host. Thus, the lack of repeatability for flea infestation could reflect occasional occurrences when fleas remain on the host when they leave the nest. Adult fish lice (*Argulus coregoni*) parasitizing rainbow trout (*Oncorhynchus mykiss*) switched hosts more frequently as a function of mate searching (Bandilla, Hakalahti-Sirén, & Valtonen, 2008), which could also explain some inconsistencies in repeatability scores for ectoparasite abundance and intensity that we observed.

We cannot rule out the possibility that the pattern we observed reflects an indirect link between chipmunk personality and ectoparasite abundance affected by some factor we were not able to measure. For example, more explorative individuals may prefer certain types of habitat that tend to harbor more parasites than other habitat types, which could have led to the pattern we observed. For instance, parasitoids of *Melanagromyza aeneoventr* were more abundant on thistles in fields that were left fallow (i.e., not seeded that year) than thistles in fields with actively growing crops (Kruess, 2003), presumably leading to differences in environmental presence of parasitoids based on habitat type. If variation in use of different habitat types is influenced by individual personality, chipmunks could potentially encounter parasites at different rates because of their habitat preferences rather than as a direct consequence of their personality traits. However, this seems unlikely for our data because, as noted above, the reservoir from which chipmunks likely acquire most of their ectoparasites is the burrow (i.e., the same habitat type for all individuals). In our view, a more likely explanation for our results is that the most explorative chipmunks investigate additional burrows on the landscape and acquire more parasites as a result.

We also observed a positive effect of body condition (Figure 2) on ectoparasite abundance as well as differences in ectoparasitism between age and sex classes. The relationship between body condition and ectoparasitism is equivocal for mammals, with some studies identifying negative relationships (Neuhaus, 2003; Zahn & Rupp, 2004) and others observing positive relationships (Gorrell & Schulte-Hostedde, 2008; Webber et al., 2015b). Our results suggest that ectoparasites of least chipmunks tend to infest larger hosts, possibly to take advantage of greater resources available and/or reduced competition among parasites on a larger host (Møller, 2000). Moreover, we observed moderate differences in ectoparasite prevalence between age and sex classes. Juvenile and adult males hosted higher ectoparasite prevalence than females, which is well established in rodents (e.g., Hillegasse, Waterman, & Roth, 2008; Perez-Orella & Schulte-Hostedde, 2005). While the effect of age and/or sex on ectoparasitism may be seasonal (Patterson et al., 2015), males presumably host higher prevalence than females due to sex-specific variation in natural history, with male-biased dispersal and/or larger home ranges in males.

Personality also plays a larger role in both animal and human immunology. Individuals with shy personality traits may experience increased responsiveness of the hypothalamic–pituitary–adrenal (HPA) axis, which can eventually decrease overall health (see Cavigelli, 2005). While stress may increase an individual's susceptibility to disease, it is still unclear how it might impact host–parasite dynamics. In many small mammals, stress and anxiety can be indicated by increased grooming (Katz & Roth, 1979; Menzies, Timonin, McGuire, & Willis, 2013), which can be costly if other important behaviors (such as foraging or mating) are neglected, but may be effective for removing ectoparasites. While we did not directly measure HPA function in least chipmunks, our results suggest that vigilance-related behaviors (perhaps increasingly present in more anxious individuals) are not the main drivers of ectoparasitism in this species.

Our results suggest that personality influences parasitism in least chipmunks. Despite the possibility that active or exploratory individuals have greater access to resources and mates (Biro & Stamps,

2008), increased parasite risk introduces a possible trade-off for least chipmunks with exploratory personalities. It is possible that distinct personalities are maintained within populations because of balancing selection (Penke, Denissen, & Miller, 2007) and trade-offs like parasite risk may play a role in that process. The influence of personality on parasite infection risk that we observed may be especially important on the broader scale of transmission dynamics. Generally, a small number of individuals are responsible for transmitting most infections (Lloyd-Smith, Schreiber, Kopp, & Getz, 2005), although the driving factors of this process remain unclear. For least chipmunks, personality appears to influence transmission dynamics, and this link should be investigated within the broader context of space use (Canestrelli et al., 2016) and interspecific interactions to better understand the implications for individual fitness and population dynamics.

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