



Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*

Lucy D. Patterson¹, Albrecht I. Schulte-Hostedde*

Department of Biology, Laurentian University, Sudbury, ON, Canada

ARTICLE INFO

Article history:

Received 17 September 2010
Initial acceptance 4 November 2010
Final acceptance 10 February 2011
Available online 26 March 2011
MS. number: A10-00620R

Keywords:

behaviour
boldness
parasite load
personality
reproductive success
scramble competition
Tamias striatus
temperament

An individual's fitness is estimated by its lifetime reproductive success. In the polygynandrous sciurid mating system, male reproductive success is determined by an individual's success in locating and defending receptive females. Personality traits are differences in behavioural reactions that are heritable, consistent across contexts and over time, and may have important fitness consequences. Little research has been conducted on the effect of personality on success in the competition for mates. We examined the relationship between behavioural traits, parasite load and male reproductive success (the number of offspring sired in one year) in the eastern chipmunk. We expected that behavioural traits would affect male reproductive success either directly, through their effect on success in locating and/or defending females, or indirectly, through their effect on parasite load. We measured trappability, activity level/exploratory behaviour, struggle rate and ecto- and endoparasite load. Eighty-two chipmunks (29 adult males, 24 adult females, 29 juveniles) were genotyped to determine paternity. Assuming that trappability is an indicator of boldness, we found that bolder males had more offspring when controlling for endoparasite load. Moreover, bolder males had a higher endoparasite load, caused either by depleted energy reserves or the immunosuppressive effects of testosterone. We conclude that boldness affects reproductive success both directly and indirectly (via parasite load) in male chipmunks; however, there appears to be a trade-off between the positive direct effect and the negative indirect effect on reproductive success.

© 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

An individual's fitness is estimated by the number of offspring it produces over its lifetime (lifetime reproductive success; Neff & Pitcher 2005). An understanding of the patterns and causes of variation in reproductive success is critical to life history and mating system theory (Ribble 1992). In mammals, variation in male reproductive success can be pronounced (Le Boeuf 1974; Clutton-Brock et al. 1982) and has traditionally been attributed to traits that enable males to defend sexually receptive females from rivals (Clutton-Brock et al. 1979; Clutton-Brock 1988; Andersson 1994). In scramble competition, however, male reproductive success is correlated with traits that enable males to efficiently locate receptive females (Schwagmeyer & Woontner 1986; Schwagmeyer & Parker 1987; Schwagmeyer 1995; Schwagmeyer et al. 1998; Spritzer et al. 2005a, b; Lane et al. 2009).

Rodents are a group of mammals that frequently engage in scramble competition for mates (Waterman 2007; Lane et al. 2009).

Sciurids are a good example because, in many species, females are territorial, breed asynchronously within a local population, and are thus uneconomical to defend (Ims 1988; Murphy 1998; Waterman 2007). The sciurid mating system is best described as polygynandry (Dobson et al. 2010) because both sexes copulate with multiple partners. The two forms of precopulatory male–male competition in this mating system are competitive searching and the establishment of dominance hierarchies (Waterman 2007). In many species, male sciurids search for females and participate in mating chases, in which dominant males tends to have greater mating success (reviewed in Koprowski 1998). However, the relationship between dominance and reproductive success in this type of mating system is unclear (Dewsbury 1982) because the ability to find females may be more important than overt conflict in competitive searching. In thirteen-lined ground squirrels, for example, males that obtained an above-average number of copulations searched twice the surface area as other males (Schwagmeyer 1994).

Success in locating and acquiring mates may be influenced by personality traits. Personality and temperament have been used to describe the 'phenomenon that individual behavioural differences are consistent over time and/or across situations' (Réale et al. 2007,

* Correspondence: A. I. Schulte-Hostedde, Department of Biology, Laurentian University, 935 Ramsey Lake Road, Sudbury, ON P3E 2C6, Canada.

E-mail address: aschulte@laurentian.ca (A. I. Schulte-Hostedde).

¹ L. Patterson is now at the St Lawrence Islands National Park, 2 County Road 5, RR3, Mallorytown, ON K0E1R0, Canada.

page 294). Personality theory implies that, although behaviour may change with age or environmental conditions, differences between individuals are maintained (Réale et al. 2007). These behavioural differences, or personality traits, tend to be heritable, consistent over a broad range of contexts (feeding, mating, antipredatory behaviour, parental care, dispersal, etc.) and stable over long periods of life (Budaev 1997; Lowe & Bradshaw 2001; Gosling 2001; Dall et al. 2004; Sih et al. 2004a). Personality traits should be distinguished from idiosyncrasies (behavioural attributes distinctive to a particular individual: Réale et al. 2007), motivational states (Koolhaas et al. 1999) and ability levels (Winter & Barenbaum 1999).

There is growing evidence that personality traits have fitness consequences in wild populations (reviewed in: Dingemanse & Réale 2005; Réale et al. 2007; Smith & Blumstein 2008). They affect the age of primiparity, fledgling/weaning success, survival, reproductive success and offspring growth rate in bighorn sheep, *Ovis canadensis* (Réale et al. 2000, 2009; Réale & Festa-Bianchet 2003), great tits, *Parus major* (Dingemanse et al. 2004), red squirrels, *Tamiasciurus hudsonicus* (Boon et al. 2007), western bluebirds, *Sialia mexicana* (Duckworth 2006), and rhesus macaques, *Macaca mulatta* (Westergaard et al. 2003). Personality may also affect searching ability (Lane et al. 2009) and dominance (Wilson et al. 1994; Dingemanse & de Goede 2004), which influence success in locating and competing for mates. Females may also select mates based on personality traits (Godin & Dugatkin 1996; Forstmeier et al. 2004; van Oers et al. 2008).

Eastern chipmunks are small, monomorphic, solitary mammals that engage in a mating chase (Yahner 1978) similar to many sciurids (Koprowski 1998). During the breeding season, males significantly increase their home range and devote a substantial amount of time to locating females (Yahner 1978). On a female's day of peak oestrus, males that have congregated on her territory compete for access to her, and several may obtain copulations (Yahner 1978; Koprowski 1998). Successful copulations typically occur when a male isolates the female from competitors, either by fighting off opponents or by being the first to locate her after she has evaded the pursuing males (Elliott 1978; Yahner 1978). Scramble competition plays a significant role in this mating system because males compete to locate partners, both prior to and during the mating chase.

The main objective of this study was to determine how trappability, exploratory behaviour, activity level and struggle rate affect the annual reproductive success of male chipmunks. These behaviours have been found to vary consistently among individuals and have been described as personality traits (Réale et al. 2000; Boon et al. 2007; Martin & Réale 2008). We also tested the repeatability and the correlation among these behavioural traits to assess the extent to which they could be regarded as personality traits in this study, as defined by Réale et al. (2007).

Our first expectation was that reproductive success would increase with trappability, struggle rate, exploratory behaviour and activity level, because these behaviours should favour success in the mating chase. To be successful in the mating chase, males must locate a female in oestrus, compete aggressively with rival males, locate the female once she has evaded the chase, and/or entice her to copulate (Elliott 1978; Yahner 1978). Trappability may be used as an index of boldness because it reflects individual differences in willingness to accept the risk involved in taking the bait (Réale et al. 2000). Bolder individuals disperse further (Armitage & van Vuren 2003), are competitively superior (Ward et al. 2004; Sundström et al. 2004) and preferred by females (Godin & Dugatkin 1996). The amount that an individual struggles during handling quantifies its reaction to humans (e.g. Boivin et al. 1992; Réale et al. 2000; Martin & Réale 2008), and has been included in the shy–bold

spectrum (Réale et al. 2007). Exploratory behaviour has also been associated with dispersal (Dingemanse et al. 2003). Males that are bolder and have higher levels of activity and exploratory behaviour should have an advantage in finding receptive females prior to and during the mating chase, competing with rival males, and/or being attractive. Thus, males with these traits should have higher reproductive success.

Alternatively, trappability, struggle rate, exploratory behaviour and activity level could decrease reproductive success through their effect on parasite load. We expected individuals with higher trappability, struggle rate and levels of activity and exploratory behaviour to have increased exposure to parasites because they disperse further (Armitage & van Vuren 2003; Dingemanse et al. 2003). Activity level has been related to parasite acquisition risk in various species (Poulin et al. 1991; van der Veen 2003; James et al. 2008; Boyer et al. 2010). Parasites can decrease the energy available to the host for reproduction either directly, by using up resources, or indirectly, by changing the behaviour and food intake of the host (Milinski 1990), increasing immune activity (Lochmiller & Deerenberg 2000; Khokhlova et al. 2002; Martin et al. 2003), or increasing metabolic rate (Khokhlova et al. 2002). In addition, parasitism diminishes an individual's attractiveness to potential mates (Zuk et al. 1990). Highly parasitized males should therefore have fewer offspring. If parasite load increases with struggling rate, trappability, activity level and exploratory behaviour, we expected reproductive success to decrease with these traits as a result. Few studies have attempted to determine the effect of personality on reproductive success in wild populations (but see Réale et al. 2000, 2009; Dingemanse et al. 2003; Boon et al. 2007), or determined whether personality traits are subject to sexual selection (Schuett et al. 2010).

METHODS

Field Procedures

Study area

We monitored an eastern chipmunk population on a 5.04 ha grid situated in an area of hardwood forest in Algonquin Park, Ontario, Canada (45°30'N, 78°40'W) from April to September 2008. The grid comprised 14 lines, each counting 16 traps at 15 m intervals. Trapping occurred four times weekly using Longworth live traps (Rogers Manufacturing, West Kelowna, BC, Canada) baited with a mixture of oats and water-soaked sunflower seeds. Alternate lines were set at dawn and checked approximately 3 h later.

Handling

Captured chipmunks were transferred to a cloth bag, marked with two metal eartags (model 1005-1, National Band and Tag, Newport, KY, U.S.A.), aged (adult or juvenile), sexed, scored for reproductive condition (oestrus, lactating, scrotal, or nonreproductive), weighed and measured. New individuals were classified as juveniles if they were nonreproductive and weighed less than 80 g. A sliver of tissue from the periphery of a pinna was clipped with scissors stored at –20 °C until genetic analysis. Females were classified as being in oestrus by a swollen vagina, and as lactating if their mammary glands were visibly enlarged (Smith & Smith 1975). Males were categorized as 'scrotal' if they had enlarged testes and a black scrotum (Schulte-Hostedde et al. 2002). We used dial callipers (Series 505, Mitutoyo, Toronto, ON) to measure the skull width (zygomatic width; ± 0.1 mm).

Parasites

Chipmunks may be infected with various parasites such as ticks, fleas, mites, bot flies and intestinal cestode and nematode parasites

(Snyder 1982). To assess ectoparasite load, we combed males for fleas and mites. One combing consisted of 10 strokes from the tail to the base of the stripes at the posterior of the body, and five strokes on each hindleg. Fleas and mites were stored in 70% ethanol. Chipmunks were ideally sampled three times over the summer (mean \pm SD = 2.54 \pm 1.56). To assess intestinal parasite load, faecal samples were collected throughout the season, either from the open field arena (see below), or during handling, and stored in 70% ethanol.

Behavioural traits

Adult males were scored in two behavioural tests: a handling bag test and an open field test. The handling bag test measures struggle rate (Martin & Réale 2008). Handling bag tests were conducted outdoors at each capture, once the individual was released from the trap into the handling bag and identified as male. This was done to minimize the amount of handling prior to the handling bag test. The handling bag was suspended at arm's length for 1 min. The number of seconds that the chipmunk spent moving during that minute was determined with a stopwatch. The open field test (Martin & Réale 2008) measures the behavioural reaction of each individual to a novel environment. The open field test was conducted outdoors, in an opaque plastic arena (76 \times 42 cm at the bottom and 90 \times 53 cm at the top; height = 42 cm) with a clear, acrylic lid and 10 equally spaced holes (5 cm diameter) carved into the bottom. A grid of squares (10 \times 10 cm) was taped to the underside of the Plexiglas floor (Semenova et al. 2001). Open field tests were conducted after handling bag tests and prior to all other routine measurements. Once the chipmunk entered the arena, its behaviour was recorded for 5 min with a digital camcorder (Panasonic PV-GS60P, Mississauga, ON) placed on a tripod directly adjacent to the arena and angled such that the arena filled the field of view. Natural daylight was used as lighting, and the tests were conducted in the shade to reduce glare. The arena and lid were cleaned with dilute acetic acid (5–10%) between trials. We aimed to test each male in three open field trials to ensure the repeatability of the measurements, although this was not possible for individuals that were caught fewer than three times over the field season.

Radiotelemetry

The location of lactating females' burrows was determined to increase the probability of catching their offspring and correctly assigning the maternity of juveniles. All lactating females caught on the grid were radiocollared with a BD-2C transmitter (Holohil Systems Ltd, Carp, ON) and tracked after dusk two to three times during the breeding season. Additional traps were then placed around each located burrow that females used.

Ethical note

All experimental procedures were in accordance with guidelines from the Canadian Council on Animal Care and were approved by the Animal Care Committee at Laurentian University (AUP 2008-01-04). Eighty-two chipmunks (29 adult males, 24 adult females, 29 juveniles) were used in this study. Chipmunks may have experienced distress in the traps or during handling, tissue sampling, radiocollaring or behaviour trials. To minimize stress in the traps, we provided the animals with oats, water-soaked sunflower seeds and bedding, and we checked all traps within 5 h of setting them. Animals were monitored during handling and behavioural trials for signs of extreme stress (hyperventilation, prolonged and intense struggling, or a foot caught in the handling bag) and released immediately if any occurred. To minimize stress, open field tests were never conducted on the same day as tagging and tissue sampling. We did not take the same precaution with handling bag tests because they required less manipulation and were assumed to

be less stressful. All tagging and tissue-sampling tools were cleaned with rubbing alcohol between chipmunks. Any bleeding resulting from tissue sampling was blotted with styptic powder (Bamboo, North Hills, CA, U.S.A.). Chipmunks were released immediately after handling. Radiocollars weighed 1.57 g and were attached with collar wire and plastic tubing. This represented a mean of 1.7% (range 1.6–1.9%) of the weight of the chipmunks collared and did not impede locomotion. We removed all radiocollars at the end of the breeding season.

Laboratory Procedures

Behavioural traits

Videos from the open field tests were analysed using ActivCapt 1.0, a program written by Lowell Patterson (Solutions 4U Corp., Ottawa, ON) that aids the user in tallying the number of seconds that an individual spends engaged in focal behaviours during a video trial. We measured the proportion of time that each chipmunk spent engaged in each of the following behaviours: grooming, rearing, climbing, head-dipping, in locomotion and motionless (Martin & Réale 2008). We also counted the number of times the chipmunk dipped its head into a hole and the number of times it crossed a square (Semenova et al. 2001).

Parasites

The fleas and mites in each sample were counted. Using a dissecting microscope (Olympus SZ61) equipped with a camera (Sony XC-ST50) and Image Pro Express 5.1 software (Media Cybernetics, Silver Spring, MD, U.S.A.), we calculated the body length (μ m) of each parasite from the mean of three measurements of the distance from the clypeal tubercle to the last abdominal segment (fleas), or the distance from the tip of the chelicera to the posterior end of the ventrian shield (mites). Fleas and mites were identified to species by H. Proctor (University of Alberta, Edmonton, Canada). Faecal samples were used to estimate intestinal parasite load. We determined the number of eggs per gram of faeces (EPG) by egg floatation on a grid-etched slide using a modified McMaster technique (Rossanigo & Gruner 1991).

Genotyping

Nine microsatellite loci (Table 1) were amplified for use in paternity analysis and to assess the heterozygosity of males. DNA was extracted from tissue samples using a standard QIAGEN DNeasy extraction tissue kit (Qiagen Inc., Mississauga, ON). PCR amplification was performed in a gradient thermocycler (Eppendorf Mastercycler). For the 'Chip' primers (Peters et al. 2007), amplification was performed in 12.5 μ l volumes containing 5 ng of

Table 1

Characterization of the microsatellite loci used to genotype a population of eastern chipmunks, *Tamias striatus*, in Algonquin Provincial Park, Ontario

Locus	<i>n</i>	NA	Size (bp)	<i>H</i> _O	<i>H</i> _E	Fis	HWE
EACH-04	81	10	251–273	0.64	0.68	0.05	0.20
EACH-05	81	7	99–119	0.77	0.72	–0.06	0.24
EACH-06	80	6	161–185	0.53	0.47	–0.10	0.80
EACH-09	82	10	163–191	0.68	0.70	0.02	0.70
EACH-11	81	8	282–300	0.72	0.76	0.05	0.08
Chip14	70	15	239–303	0.83	0.86	0.03	0.10
Chip24	81	12	100–148	0.79	0.91	0.13	0.04
Chip36	81	10	91–131	0.77	0.84	0.09	0.64
Chip203	81	14	322–383	0.86	0.88	0.02	0.15

Number of chipmunks genotyped (*n*), number of alleles (NA), allele size range, observed (*H*_O) and expected (*H*_E) heterozygosities, and Hardy–Weinberg equilibrium *P* values (HWE) are given for each locus. *n*, NA, allele size, *H*_O and *H*_E were calculated in Cervus; Fis and HWE were calculated from Genepop. 'EACH' and 'Chip' loci were obtained from Anderson et al. (2007) and Peters et al. (2007), respectively.

template DNA, 0.15 mM of dNTPs (BioShop, Burlington, ON), 0.5 U of Taq (Qiagen), 0.4 μ M of each primer (IDT), 1 \times reaction buffer (Qiagen), 0.025 μ g/ μ l of BSA (Bioshop) and 2 mM of MgCl₂ (Qiagen). Amplification conditions were as follows: 5 min at 94 °C, followed by 21 cycles at 96 °C for 20 s, highest annealing temperature (58 °C for Chips 14 and 201; 59 °C for Chips 36; 63 °C for Chip 203; 64 °C for Chip 24; decreased by 0.5 °C per cycle) for 20 s, then at 72 °C for 30 s, followed by 15 cycles at 96 °C for 20 s, lowest annealing temperature (10 °C below the highest annealing temperature) for 20 s, and at 72 °C for 30 s. The PCR ended with a 10 min extension at 72 °C. For the 'EACH' primers (Anderson et al. 2007), amplification was performed in 10 μ l volumes, using 5 ng of template DNA, 0.2 mM of dNTPs (Bioshop), 0.2 μ M of each primer (IDT), 0.5 U of Taq (Qiagen), 1 \times reaction buffer (Qiagen), and 2 mM of MgCl₂ (Qiagen). The amplification conditions were as follows: 94 °C for 2 min; 94 °C for 30 s, annealing temperature (58 °C for EACH-06; 60 °C for EACH-11; 62 °C for EACH-05; 64.5 °C for EACH-09; 65 °C for EACH-04) for 30 s, and 72 °C for 30 s for 35 cycles; 72 °C for 10 min and a final extension at 60 °C for 45 min.

PCR products were sent to the Mobix lab at McMaster University (Hamilton, ON) for genotyping. The profiling results were analysed with Peak Scanner Software v.1.0 (Applied Biosystems, Inc., Streetsville, ON, Canada). We also determined that the loci followed the Hardy–Weinberg equilibrium (Genepop 4.0; Raymond & Rousset 1995; Rousset 2008), and we checked for the presence of null alleles or scoring errors (Microchecker v.2.2.3; van Oosterhout et al. 2004) and linkage between loci (Fstat v.2.9; Goudet 1995).

Paternity assignment

Paternity was assigned using a likelihood-based approach with Cervus 3.0 (Kalinowski et al. 2007). None of the loci were linked. Locus Chip 24 was not in Hardy–Weinberg equilibrium due to an excess of homozygotes. However, it was retained in the paternity analysis because it was scored reliably, and Cervus 3.0 is tolerant to null alleles and genotyping errors that could have caused this locus not to be in Hardy–Weinberg equilibrium. We used the 'Parent Pair (Sexes Known)' option for both the simulation and parentage analysis. This option was used because (1) including the population's possible maternal genotypes increases the accuracy of paternal assignments and (2) the identities of both parents were unknown. The simulations were run for 10 000 cycles, and the parameters were the following: the average number of candidate mothers (22) and fathers (28), the proportion of candidate mothers (0.95) and fathers (0.85) sampled, the proportion of loci typed (0.982), the estimated proportion of loci mistyped (0.01), the minimum number of typed loci for an individual to be considered (4), and the method of confidence calculation (delta). The relaxed confidence level was set to 80% and the strict confidence level was set to 95%. Maternity assignments were confirmed by radiotelemetry and capture data whenever possible.

Statistical Analyses

Statistical analyses were performed in SPSS 15.0 (SPSS, Chicago, IL, U.S.A.), Genstat 12.0 (Payne et al. 2009) and R 2.10.0 (R Development Core Team 2009).

Behavioural variables

As not all behavioural tests were performed on all individuals, there was some variation in sample size among the tests. An index of trappability was formed from the residuals of the regression between the number of captures and the minimum number of trapping days that the individual was known to be on the grid (date of last capture – first capture + 1). Trappability can be used as an index of boldness because it reflects individual differences in

willingness to accept the risk involved in taking the bait (Réale et al. 2000). An activity/exploration index was extracted from the behaviours measured in the open field test via a principal component analysis (PCA; Martin & Réale 2008). The efficiency of the PCA analysis is improved by multivariate normality (Quinn & Keough 2002). To improve univariate and thus multivariate normality, we applied a log transformation ($\log(x+1)$) to the number of crosses and head-dips and to the percentage of time spent grooming, climbing, rearing and head-dipping, and we applied a square-root transformation to the percentage of time spent in locomotion. Only the first component was retained as the activity/exploration index to be used in subsequent analyses, because (1) the second component was not a good indicator of activity and exploration (see Results, Table 2) and (2) the other components were rejected following the Kaiser–Guttman rule (Kaiser & Norman 1991).

To obtain a single value for activity/exploration, we first conducted a linear mixed model with the first principal component (Z1) as the dependent variable, Julian date and trial order as fixed effects and chipmunk identity as a random effect. The interaction was subsequently removed from the model because of non-significance. From this model, it was determined that trial order had a significant effect on Z1 (see Results). Since some individuals had only two trials, using the mean of all three trials could produce inconsistencies. For this reason, only the first two trials were averaged to obtain a single value of activity/exploration per individual.

A mixed model was also run to determine which factors influenced handling bag trials. The mixed model included struggle rate as a dependent variable, chipmunk identity as the random effect and weather, reproductive condition, observer and trial order as fixed effects. To avoid overparameterization, no interactions were included in this model. Struggle rate was significantly affected by the observer (see Results). An ANOVA with a Tukey's test was then run to determine which observer(s) were significantly different. One observer was significantly different from the other two. All values recorded by this outlying observer were removed from the data set. The struggle rate score was obtained by taking the mean of all trials remaining in the data set for each individual. The behaviour scores for trappability, struggle rate and activity/exploration were used as independent variables in subsequent analyses.

To determine the extent to which the measured behaviours are personality traits, we determined the repeatability of each trait, and determined the correlation among variables. We measured repeatability because the repeatability of a trait sets an upper limit to its heritability (Boake 1989). The repeatability of struggle rate and activity/exploration was determined by calculating the intra-individual correlation coefficient (ICC; Lessells & Boag 1987; Hruschka et al. 2005) via a generalized linear mixed model. Repeatability could not be assessed for trappability in this way because we only obtained a single measurement per individual. However, if behaviour is consistent over time, then behavioural scores for the second half of the summer should correlate with scores from the first half. Thus, we divided the trapping season in half and calculated trappability scores for early and late summer following methods outlined above. We then ran a linear regression with the scores for early summer as the independent variable and those for late summer as the dependent variable. Females and juveniles were included in the calculations to determine the repeatability of trappability to increase the sample size.

We also ran pairwise Pearson's correlations between variables. Since a large proportion of the literature defines personality as a suite of correlated behaviours (e.g. Costa & McCrae 1992; Koolhaas et al. 1999; Sih et al. 2004a, b), a correlation among

traits would lend support to the hypothesis that these are personality traits.

Finally, to determine whether trappability scores could be an index of dominance rather than personality, we tested whether age and size affected trappability. Age and body size significantly correlate with dominance in many species of tree squirrels (reviewed in [Koprowski 1998](#)) and other mammals (e.g. [Clutton-Brock 1988](#); [Le Boeuf & Reiter 1988](#)). If trappability represents dominance, then it should correlate with age and body size. No correlation is expected if trappability represents boldness, however, because personality traits are relatively stable throughout an individual's life ([Boissy 1995](#); [Koolhaas et al. 1999](#); [Bouchard & Loehlin 2001](#)). To determine the effect of body size and age on trappability of males, we ran a linear model with skull width and age class (juvenile or adult) as independent variables and the trappability score as the dependent variable. The interaction term was removed because it was not significant ($t_{1,35} = -0.22$, $P = 0.83$).

Parasite variables

Both ectoparasite load and intestinal ('endo-') parasite load were quantified. Three ectoparasite variables were considered: abundance, total length of ectoparasites (as an index of parasite biomass) and species richness. Ectoparasite abundance was defined as the total number of fleas and mites obtained from each individual sampled ([Rózsa et al. 2000](#)), whereas species richness was calculated as the number of flea and mite species and the total length of ectoparasites was calculated as the sum of the lengths of all fleas and mites. These three measurements contribute to parasite load because larger and more numerous parasites consume more resources, whereas maintaining several means of immune defence against different parasite species is more costly for the host ([Taylor et al. 1998](#); [Jokela et al. 2000](#)). To control for sampling effort, we ran a linear regression on the ($\log + 1$) of each ectoparasite variable and the number of combings. The ectoparasite variables were logged because the relationships were exponential. The residuals from each regression were used as indices of ectoparasite abundance, species richness and length. Because all three indices were strongly correlated, we ran a PCA to obtain a single value as an index of ectoparasite load. The first component from the PCA was the only component retained as per the Kaiser–Guttman rule ([Kaiser & Norman 1991](#)). Endoparasite load was quantified as the mean number of eggs per gram of faeces (EPG) and log-transformed to improve normality.

Parasite load sometimes varies on a temporal basis (e.g. [Gorrell & Schulte-Hostedde 2008](#); [Filipiak et al. 2009](#)), which might cause inconsistencies between individuals first caught and sampled at different periods of the summer. To ensure that parasite load was consistent over the summer, we grouped the data into three time periods: early summer (May/June), mid-summer (July) and late summer (August/September). We calculated the mean EPG and ectoparasite load per individual per time period. We performed a linear mixed model with time period as the fixed effect, chipmunk identity as the random effect and mean EPG as the dependent variable. EPG was log-transformed to improve normality of the residuals.

Direct reproductive success

The direct effect of personality on reproductive success (RS) was assessed by running a backward stepwise regression with the personality variables (trappability, struggle rate, activity/exploration) as independent variables and number of offspring (NO) as the dependent variable. The stepwise regression was based on a generalized linear model (GLM) with a Poisson distribution and a log link function. The final model (trappability) was then run as

a GLM (Poisson distribution, log link function). The model was overdispersed ($\chi^2_{24} = 40.37$, $P = 0.02$). This was corrected by using a quasi-Poisson distribution, thereby preventing the statistical test from being overly liberal ([Burnham & Anderson 2002](#)).

Reproductive success via parasite load

To determine whether parasite load affected reproductive success, we ran a GLM (Poisson distribution, log link function) with EPG and ectoparasite load as independent variables and the NO as the dependent variable. We then determined how personality affected the EPG, the only significant term in the previous model. We ran a backward stepwise regression (GLM, normal distribution, identity link function) of personality traits (trappability, activity/exploration, struggle rate) on EPG, followed by a GLM of the final model obtained. This backward stepwise regression had the same parameters as the regression of personality variables on the NO. Finally, we ran a GLM (Poisson distribution, log-link function) of the most significant terms of the final parasite model and final personality model on the NO. The purpose of this analysis was to determine the joint effect of personality and parasite load on reproductive success.

Males captured primarily on the periphery of the grid may have been caught less often, resulting in lower trappability scores, and/or may have mated with unsampled females, thereby biasing our estimate of reproductive success. To determine whether our measures of trappability and reproductive success were biased, we designated males as being 'interior' or 'peripheral', and conducted two tests. The first test consisted of an ANOVA with trappability as the dependent variable and the interior/peripheral designation as the independent variable. The second test consisted of a GLM (Poisson distribution, log link function) with the number of offspring as the dependent variable and the interior/peripheral designation and number of times caught as the independent variables. The interaction term was removed because it did not contribute to the model (deviance = -0.24 , $P = 0.71$).

RESULTS

Behavioural Variables

The linear regression used to obtain the trappability index ($R^2 = 0.74$, $F_{1,28} = 78.39$, $P < 0.001$) was both significant. In terms of the activity/exploratory behaviour index, the first component (eigenvalue 4.71; Z1 in [Table 2](#)) from the PCA on the variables from the open field trials explained 58.9% of the variance and were strongly positively correlated ($R^2 > 0.6$) with all variables except for grooming and motionless. The second component (eigenvalue 1.32, explaining 16.5% of the variance) correlated strongly only with the

Table 2

Component loadings from the principal component analysis for the open field test data conducted on 24 male eastern chipmunks, *Tamias striatus*, in Algonquin Park, Ontario

Variable	Component	
	Z1	Z2
Grooming	0.356	0.806
Climbing	0.669	-0.407
Head dips	0.635	-0.478
Rearing	0.698	0.279
Crosses	0.929	-0.002
Head dipping	0.829	-0.329
Locomotion	0.890	0.279
Motionless	-0.950	-0.127

Only the first principal component (Z1) was retained because the second component (Z2) only poorly correlated with behaviours reflecting activity and exploration.

loadings for grooming (Table 2). The activity/exploration scores for each trial were significantly influenced by trial order (LMM: $F_{1,41} = 9.60$, $P = 0.004$) but not date ($F_{1,41} = 0.13$, $P = 0.72$). Conversely, only observer significantly affected struggle rate of each trial (LMM: observer: $F_{2,2867} = 14.74$, $P < 0.0001$; trial order: $F_{1,287} = 1.57$, $P = 0.21$; weather: $F_{2,287} = 0.81$, $P = 0.45$; date: $F_{1,287} = 0.03$, $P = 0.86$). The lack of effect of trial order implies that there was no habituation. Struggle rate scores of observer 2 were significantly different from those of observer 1 (Tukey's HSD test: difference score = -11.8 , $P < 0.001$) and observer 3 (difference score = -8.05 , $P < 0.001$), but the scores of observers 1 and 3 did not differ significantly (difference score = -3.76 , $P = 0.35$).

None of the behavioural traits were correlated (Pearson correlation: trappability and activity/exploration: $r_{19} = 0.10$, $P = 0.65$), (trappability and struggle rate: $r_{19} = 0.22$, $P = 0.30$, struggle rate and activity/exploration: $r_{19} = -0.35$, $P = 0.11$). The Z score for activity/exploration ($df = 24$, $\tau^2 = 0.48$, $\sigma^2 = 0.51$, $ICC = 0.52$) and the struggle rate ($df = 26$, $\tau^2 = 79.50$, $\sigma^2 = 202.44$, $ICC = 0.28$) were moderately repeatable. The trappability scores from early summer reliably predicted those in late summer ($R^2 = 0.43$, $F_{1,25} = 18.84$, $P < 0.001$), suggesting that trappability is highly repeatable. Skull width ($t_{1,36} = 0.58$, $P = 0.56$) and age class ($t_{1,36} = 0.40$, $P = 0.69$) did not significantly affect trappability.

The overall model testing the effect of skull width and age class on the trappability of males was not significant ($R^2 = 0.01$, $F_{2,36} = 0.17$, $P = 0.84$), and neither were the independent variables (skull width: $t_{1,36} = 0.58$, $P = 0.56$; age: $t_{1,36} = 0.40$, $P = 0.69$).

Parasite Load

The linear regressions used to create all three ectoparasite variables were significant (abundance: $R^2 = 0.57$, $F_{1,22} = 29.42$, $P < 0.001$; length: $R^2 = 0.54$, $F_{1,22} = 25.69$, $P < 0.001$; species richness: $R^2 = 0.51$, $F_{1,22} = 22.92$, $P < 0.001$). All three indices were strongly correlated ($R^2 = 0.73$ – 0.85 , $P < 0.001$). The first component from the PCA (eigenvalue = 2.80) used to create a single ectoparasite index explained 93% of the variance. Ectoparasite abundance (0.58), length (0.59) and number of species (0.57) were all positively correlated with this component ($N = 23$). The ectoparasite load index and EPG were not correlated (linear regression: $R^2 = 0.001$, $t_{1,16} = 0.16$, $P = 0.87$). Finally, time period did not affect ectoparasite load (LMM: $F_{2,2} = 0.993$, $P = 0.50$) or EPG (LMM: $F_{2,9} = 1.74$, $P = 0.23$), indicating that the sampling method was repeatable.

Reproductive Success

Eighty-two chipmunks (29 adult males, 24 adult females, 29 juveniles) were genotyped. Twenty offspring were assigned a mother at the 95% confidence level. For paternal assignments, 18 of 29 offspring were assigned a father at the 80% confidence level for either the pair (father–offspring) or the trio (mother–father–offspring) delta score. Of the 18 offspring assigned a father at the 80% confidence interval, 13 were also assigned a father at the 95% confidence level.

The values for all individual terms in the four models tested (A–D) are given in Table 3. The backward stepwise regression of personality traits on the number of offspring yielded trappability as the only term in the final model. Once the overdispersion ($\chi^2_{24} = 40.29$, $P = 0.04$) of the model was corrected, the trappability model was not significant (GLM: $F_{1,25} = 2.02$, $P = 0.17$; Model A). Number of offspring decreased with EPG (GLM: $\chi^2_{2,17} = 4.22$, $P = 0.02$; Model B). When trappability and EPG were included together in a GLM, the full model ($\chi^2_2 = 11.71$, $P = 0.003$) and each of the terms were significant (Model C). Behavioural traits

Table 3

Sample size (N), estimate, standard error (SE), t value or Wald's statistic (χ^2) and P value for each independent variable in the linear and generalized linear models that were run to explore the relationship between behavioural traits, parasite load and reproductive success in a population of male eastern chipmunks, *Tamias striatus*, in Algonquin Park, Ontario

	N	Estimate	t or Wald's (χ^2) [*]	P
Model A (offspring)				
Trappability	26	0.05	1.92	0.18
Model B (offspring)				
Ectoparasite index	20	0.24	1.27	0.20
EPG	20	-1.35	-2.74	0.006
Model C (offspring)				
Trappability	21	0.07	5.54	0.019
EPG	21	-1.44	9.86	0.002
Model D (EPG)				
Activity/exploration	16	-0.05	-0.50	0.62
Trappability	16	0.03	2.98	0.009*
Struggle rate	16	-0.02	-1.84	0.09

Dependent variables are in brackets: number of offspring and eggs per gram of faeces (EPG).

* The t value is given for multiple regressions; the Wald's statistic is given for Poisson regressions (see text). Significant values are shown in bold.

significantly affected EPG ($R^2 = 0.40$, $F_{3,16} = 3.46$, $P = 0.04$). EPG increased with both trappability and struggle rate (Model D), although the effect of struggle rate only approached statistical significance.

In the tests of edge effects, peripheral males had lower trappability scores, but the difference only approached statistical significance (ANOVA: $F_{1,24} = 3.88$, $P = 0.06$). The number of offspring sired, however, did not depend on the raw number of times a male was caught (GLM: $t_{1,23} = 0.79$, $P = 0.44$) or on his designation as 'peripheral' or 'interior' (GLM: $t_{1,23} = 1.69$, $P = 0.10$).

DISCUSSION

In our first analysis, we found no effect of behavioural traits on the number of offspring sired by male eastern chipmunks. However, more trappable males had higher intestinal parasite loads. Moreover, reproductive success increased with trappability, although this relationship only became evident when controlling for endoparasite load.

The most likely explanation for the patterns observed is that trappability is an indicator of boldness. Shyness and boldness refer to the willingness of an individual to take risks, with bolder individuals taking more risks (Wilson et al. 1994). Bolder males are assumed to be more likely to risk entering an enclosed space to acquire food. Trappability may also reflect activity level and exploratory behaviour (Boon et al. 2008; Boyer et al. 2010), although we found no correlation between trappability and activity/exploratory behaviour in the open field test. One possibility that we cannot address is that heavily parasitized male chipmunks have higher trappability because of reduced energy resources (Moore & Wilson 2002). Parasites induce changes in host behaviour (Klein 2003; Thomas et al. 2005), and higher energy requirements may drive parasitized individuals to take advantage of 'riskier' food sources. Boyer et al. (2010), however, found no causal influence of tick load on Siberian chipmunk activity/exploration or trappability.

Two factors are typically assessed to qualify behavioural traits as personality: repeatability and correlations among traits (e.g. Dingemans et al. 2002; Boon et al. 2007; Martin & Réale 2008). Repeatability sets an upper limit to heritability (Boake 1989), which is necessary for natural selection. Docility and activity/exploration were moderately repeatable in our study and have previously been found to be repeatable in eastern chipmunks (Martin & Réale

2008). Furthermore, trappability in early summer strongly predicted trappability in late summer. Trappability, struggle rate and activity/exploration in open field tests, however, were not correlated. While this lack of correlation weakens the case for presence of personality in eastern chipmunks, it cannot be entirely discounted, because a lack of correlation does not necessarily imply a lack of personality traits (Réale et al. 2007). Different traits may be controlled by different hormones or genes (Koolhaas et al. 1999; Ketterson & Nolan 1999). Our result that males on the periphery of the grid had lower trappability scores suggests that factors other than personality (e.g. wandering off the study area) may have influenced trappability. Nevertheless, trappability has been used as a measure of boldness (Réale et al. 2000) and activity/exploration (Boon et al. 2008; Boyer et al. 2010) in other species.

Bold male chipmunks may be dominant, travel further from their burrows and/or be more attractive to females. Bolder individuals are more aggressive than (Huntingford 1976; Riechert & Hedrick 1993) and competitively superior to (Ward et al. 2004; Sundström et al. 2004) their shyer conspecifics. Dominance may enhance reproductive success via increased success in direct male–male competition (Andersson 1994). In many sciurids, dominant males monopolize females and obtain the most copulations during mating chases (reviewed in: Koprowski 1998; Waterman 2007). High levels of testosterone, which are associated with dominance (Pelletier et al. 2003; Sands & Creel 2004), concurrently suppress the immune system (Folstad & Karter 1992), thereby leading to an increase in parasites and pathogens (Moore & Wilson 2002; Mougeot et al. 2006). If highly trappable chipmunks are more dominant, this may explain the apparent increase in intestinal parasites in these individuals. Males with high levels of testosterone may be bolder and more dominant, and thus have higher reproductive success through higher success in direct male–male competition, but they may also suffer higher parasite loads. However, dominance is unlikely to be a strong predictor of reproductive success in chipmunks. Yahner (1978) found that, if there were seven or more males in a mating bout, dominant male eastern chipmunks were so busy chasing away rivals that they never copulated. Since mating chases in eastern chipmunks are commonly composed of 8–12 males (Elliott 1978), dominance may in fact hamper reproductive success. Furthermore, we found no effect of size or age class on trappability. Because dominance generally correlates with age and body size in sciurids (reviewed in Koprowski 1998), larger and older male chipmunks should be more trappable if boldness correlates with dominance. The lack of effect implies that boldness is unrelated to dominance in chipmunks, which is consistent with findings from other species (Beauchamp 2000; Réale et al. 2000). In mountain chickadees, *Poecile gambeli*, conversely, dominance is negatively correlated with exploration (Fox et al. 2009).

Bolder male chipmunks may also travel further from their burrows. Exploratory, bold and/or aggressive individuals use larger home ranges (Boon et al. 2008) and disperse further from their natal area (Fraser et al. 2001; Dingemanse et al. 2003; Duckworth & Badyaev 2007). During the breeding season, male chipmunks devote most of their time to locating the home ranges of females and the female within that home range (Yahner 1978). A larger home range increases the encounter rate with potential mates (Fisher & Lara 1999; Spritzer et al. 2005a, b), which is why male home ranges increase drastically during the breeding season in sciurids (Farentinos 1979; Edelman & Koprowski 2006; Lane et al. 2009) and in other species with scramble competition (Ruby 1978; Morreale et al. 1984; Gibbons et al. 1990; Schwarzenberger & Klingel 1995; Say & Pontier 2004). Boldness would thus be advantageous during the competition to find females. The increase in endoparasite load found in bold chipmunks may be the result of

energy trade-offs that lead to a weakened immune system (Sheldon & Verhulst 1996; Pelletier et al. 2005). Males that have invested heavily in searching and competing for females have reduced energy reserves (Millesi et al. 1998; Lane et al. 2010), and thus may trade off energy for the immune system for other life history functions. This has been used as a general argument in mammals (Moore & Wilson 2002) and may be at work here in chipmunks.

Lastly, boldness may be attractive to female chipmunks, as found in guppies (Godin & Dugatkin 1996). Boldness may indicate overall male quality in guppies because bolder fish are better informed about potential predators (Dugatkin & Godin 1992), more likely to survive encounters with predators (Godin & Davis 1995) and have a higher feeding rate (Wilson et al. 1993; Godin & Crossman 1994). Thus, boldness could serve as an indicator of desirable 'good genes' (Welch et al. 1998). However, if bold males have a high endoparasite load, they would be less attractive to females (Zuk et al. 1990) that can detect infections via odour cues (Kavaliers & Colwell 1995; Penn & Potts 1998; Zala et al. 2004).

There appears to be an effect of boldness on male reproductive success that is mediated by endoparasite load. Adopting a broader perspective to understand the relative role of behaviour and parasites on reproductive success is now required for both males and females. Subsequent studies can examine this issue by experimentally manipulating parasite load and energy reserves by parasite removal and food supplementation. This would test the hypothesis that bolder males are energetically stressed during the mating season, leading to a depressed immune system and a higher parasite load. Similar patterns may be occurring in females during the most costly reproductive period, lactation (Millar 1987). Moreover, direct behavioural observations during mating chases would clarify the links between the behaviours measured in this study and success in the mating chase. Finally, long-term studies that examine the effects of behaviour and parasites on lifetime reproductive success will better characterize the fitness benefits of contrasting behavioural and life history strategies (Wolf et al. 2007; Biro & Stamps 2008).

Acknowledgments

This work was supported by the Natural Sciences and Engineering Research Council of Canada, the Canadian Foundation for Innovation and Ontario Ministry of Research and Innovation, and Laurentian University.

References

- Anderson, S. J., Fike, J. A., Dharmarajan, G. & Rhodes, O. E. 2007. Characterization of 12 polymorphic microsatellite loci for eastern chipmunks (*Tamias striatus*). *Molecular Ecology Notes*, **7**, 513–515.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Armitage, K. B. & van Vuren, D. H. 2003. Individual differences and reproductive success in yellow-bellied marmots. *Ethology, Ecology and Evolution*, **15**, 207–233.
- Beauchamp, G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, **137**, 301–314.
- Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361–368.
- Boake, C. R. 1989. Repeatability: its role in evolutionary studies of mating behaviour. *Evolutionary Ecology*, **3**, 173–182.
- Boivin, X., Le Neindre, P., Chupin, J. M., Garel, J. P. & Trillat, G. 1992. Influence of breed and early management on ease of handling and open-field behaviour of cattle. *Applied Animal Behaviour Science*, **32**, 313–323.
- Boissy, A. 1995. Fear and fearfulness in animals. *Quarterly Review of Biology*, **70**, 165–191.
- Boon, A. K., Réale, D. & Boutin, S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, **10**, 1094–1104.

- Boon, A. K., Réale, D. & Boutin, S. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels (*Tamiasciurus hudsonicus*). *Oikos*, **117**, 1321–1328.
- Bouchard, T. J. & Loehlin, J. C. 2001. Genes, evolution, and personality. *Behavioural Genetics*, **31**, 243–274.
- Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J.-L. 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology*, **79**, 538–547.
- Budaev, S. V. 1997. "Personality" in the guppy (*Poecilia reticulata*): a correlational study of exploratory behaviour and social tendency. *Journal of Comparative Psychology*, **111**, 399–411.
- Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*. 2nd edn. New York: Springer-Verlag.
- Clutton-Brock, T. H. 1988. Reproductive success. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 472–485. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour*, **27**, 211–225.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Costa, P. T. & McCrae, R. R. 1992. Four ways five factors are basic. *Personality and Individual Differences*, **13**, 653–665.
- Dall, S. R., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.
- Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Quarterly Review of Biology*, **57**, 135–159.
- Dingemans, N. J. & de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, **15**, 1023–1030.
- Dingemans, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1165–1190.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–938.
- Dingemans, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B*, **270**, 741–747.
- Dingemans, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B*, **271**, 847–852.
- Dobson, F. S., Way, B. M. & Baudoin, C. 2010. Spatial dynamics and the evolution of social monogamy in mammals. *Behavioral Ecology*, **21**, 747–752.
- Duckworth, R. A. 2006. Behavioural correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, **17**, 1011–1019.
- Duckworth, R. A. & Badyaev, A. V. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 15017–15022.
- Dugatkin, L. A. & Godin, J.-G. 1992. Prey approaching predators: a cost–benefit perspective. *Annales Zoologici Fennici*, **29**, 233–252.
- Edelman, A. J. & Koprowski, J. L. 2006. Seasonal changes in home ranges of Abert's squirrels: impact of mating season. *Canadian Journal of Zoology*, **84**, 404–411.
- Elliott, L. 1978. Social behaviour and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions to Zoology*, **265**, 1–107.
- Farentinos, R. C. 1979. Seasonal changes in home range size of tassel-eared squirrels *Sciurus aberti*. *Southwestern Naturalist*, **24**, 49–62.
- Filipiak, L., Mathieu, F. & Moreau, J. 2009. Caution on the assessment of intestinal parasitic load in studying parasite-mediated sexual selection: the case of blackbirds coccidiosis. *International Journal of Parasitology*, **39**, 741–746.
- Fisher, D. O. & Lara, M. C. 1999. Effects of body size and home range on access to mates and paternity in male bridled naitail wallabies. *Animal Behaviour*, **58**, 121–130.
- Folstad, I. & Karter, A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, **139**, 603–622.
- Forstmeier, W., Coltman, D. W. & Birkhead, T. R. 2004. Maternal effects influence the sexual behaviour of sons and daughters in the zebra finch. *Evolution*, **58**, 121–130.
- Fox, R. A., Ladage, L. D., Roth, T. C. & Pravosudov, V. V. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, **77**, 1441–1448.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. & Skalski, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist*, **158**, 124–125.
- Gibbons, J. W., Greene, J. L. & Congdon, J. 1990. Temporal and spatial movement patterns of sliders and other turtles. In: *Life History and Ecology of the Slider Turtle* (Ed. by J. W. Gibbons), pp. 201–215. Washington, D.C.: Smithsonian Institution Press.
- Godin, J.-G. J. & Crossman, S. L. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. *Behavioral Ecology and Sociobiology*, **34**, 359–366.
- Godin, J.-G. J. & Davis, S. A. 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society B*, **259**, 193–200.
- Godin, J.-G. J. & Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, U.S.A.*, **93**, 10262–10267.
- Gorrell, J. & Schulte-Hostedde, A. I. 2008. Patterns of parasitism and body size in red squirrels (*Tamiasciurus hudsonicus*). *Canadian Journal of Zoology*, **86**, 99–107.
- Gosling, S. D. 2001. From mice to men: what can I learn about personality from animal research? *Psychology Bulletin*, **127**, 45–86.
- Goudet, J. 1995. FSTAT (vers. 1.2): a computer program to calculate *F*-statistics. *Journal of Heredity*, **86**, 485–486.
- Hruschka, D. J., Kohrt, B. A. & Worthman, C. M. 2005. Estimating between- and within-individual variation in cortisol levels using multilevel models. *Psychoneuroendocrinology*, **30**, 698–714.
- Huntingford, F. A. 1976. The relationship between antipredator behaviour and aggression among conspecifics in the three-spined stickleback. *Animal Behaviour*, **24**, 245–260.
- Ims, R. A. 1988. Spatial clumping of sexually receptive females induces space sharing among male voles. *Nature*, **335**, 541–543.
- James, C. T., Noyes, K. J., Stumbo, A. D., Wisenden, B. D. & Goater, C. P. 2008. Cost of exposure to trematode cercariae and learned recognition and avoidance of parasitism risk by fathead minnows *Pimephales promelas*. *Journal of Fish Biology*, **73**, 2238–2248.
- Jokela, J., Schmid-Hempel, P. & Rigby, M. C. 2000. Dr. Pangloss restrained by the Red Queen: steps towards a unified defence theory. *Oikos*, **89**, 267–274.
- Kaiser, H. F. & Norman, W. T. 1991. Coefficients alpha for components. *Psychological Reports*, **69**, 111–114.
- Kalinowski, S. T., Taper, M. L. & Marshall, T. C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.
- Kavaliers, M. & Colwell, D. D. 1995. Discrimination by female mice between the odours of parasitized and non-parasitized males. *Proceedings of the Royal Society B*, **261**, 31–35.
- Ketterson, E. D. & Nolan, V. 1999. Adaptation, exaptation, and constraint: a hormonal perspective. *American Naturalist, Supplement*, **154**, S4–S25.
- Khokhlova, I. S., Krasnov, B. R., Kam, M. & Degen, A. A. 2002. Energy cost of ectoparasitism: the flea *Xenopsylla ramesis* on the desert gerbil *Gerbillus dasyurus*. *Journal of Zoology*, **258**, 349–354.
- Klein, S. L. 2003. Parasite manipulation of the proximate mechanisms that mediate social behaviour in vertebrates. *Physiology and Behaviour*, **79**, 441–449.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van DerVegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blockhuis, H. J. 1999. Coping style in animals: current status in behaviour and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.
- Koprowski, J. L. 1998. Conflict between the sexes: a review of social and mating systems of the tree squirrels. In: *Ecology and Evolutionary Biology of the Tree Squirrels* (Ed. by M. Steele, J. Merritt & D. Zygers), pp. 33–41. Martinsville, Virginia: Virginia Museum of Natural History.
- Lane, J., Boutin, S., Gunn, M. & Coltman, D. 2009. Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology*, **78**, 296–304.
- Lane, J. E., Boutin, S., Speakman, J. R. & Humphries, M. M. 2010. Energetic costs of male reproduction in a scramble competition mating system. *Journal of Animal Ecology*, **79**, 27–34.
- Le Boeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. *American Zoologist*, **14**, 163–176.
- Le Boeuf, B. J. & Reiter, J. 1988. Lifetime reproductive success in northern elephant seals. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 344–362. Chicago: University of Chicago Press.
- Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Lochmiller, R. L. & Deerenberg, C. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*, **88**, 87–98.
- Lowe, S. E. & Bradshaw, J. W. S. 2001. Ontogeny of individuality in the domestic cat in the home environment. *Animal Behaviour*, **61**, 231–237.
- Martin, J. G. & Réale, D. 2008. Temperament, risk assessment, and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, **75**, 309–318.
- Martin, L. B., Scheuerlein, A. & Wikelski, M. 2003. Immune activity elevates energy expenditure of house sparrows: a link between direct and indirect costs? *Proceedings of the Royal Society B*, **270**, 153–158.
- Millinski, M. 1990. Parasites and host decision-making. In: *Parasitism and Host Behaviour* (Ed. by C. J. Barnard & J. M. Behnke), pp. 95–116. London: Taylor & Francis.
- Millar, J. S. 1987. Energy reserves in breeding small rodents. *Symposia of the Zoological Society of London*, **57**, 231–240.
- Millesi, E., Huber, S., Dittami, J., Hoffman, I. & Daan, S. 1998. Parameters of mating effort and success in male European ground squirrels, *Spermophilus citellus*. *Ethology*, **104**, 298–313.
- Moore, S. L. & Wilson, K. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. *Science*, **297**, 2015–2018.
- Morreale, S. J., Gibbons, W. & Congdon, J. D. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). *Canadian Journal of Zoology*, **62**, 1038–1042.
- Mougeot, F., Redpath, S. M. & Pieltney, S. B. 2006. Elevated testosterone increases parasite intensity in male red grouse. *Behavioral Ecology*, **17**, 117–125.
- Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution*, **52**, 8–18.

- Neff, B. D. & Pitcher, T. E. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology*, **14**, 19–38.
- van Oers, K., Drent, P. J., Dingemans, N. J. & Kempenaers, B. 2008. Personality is associated with extrapair paternity in great tits, *Parus major*. *Animal Behaviour*, **76**, 555–563.
- van Oosterhout, C., Hutchinson, W. F., Wills, D. P. & Shipley, P. 2004. Microchecker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535–538.
- Payne, R. W., Murray, D. A., Harding, S. A., Baird, D. B. & Soutar, D. M. 2009. *GenStat for Windows. Introduction*. 12th edn. Hemel Hempstead: VSN International. <http://www.vsn.co.uk/resources/documentation/genstat-guide-introduction/>.
- Pelletier, F., Bauman, J. & Festa-Bianchet, M. 2003. Fecal testosterone in bighorn sheep (*Ovis canadensis*): behavioural and endocrine correlates. *Canadian Journal of Zoology*, **81**, 1678–1684.
- Pelletier, F., Page, K. A., Ostiguy, T. & Festa-Bianchet, M. 2005. Fecal counts of lungworm larvae and reproductive effort in bighorn sheep, *Ovis canadensis*. *Oikos*, **110**, 473–480.
- Penn, D. & Potts, W. K. 1998. Chemical signals and parasite-mediated sexual selection. *Trends in Ecology & Evolution*, **13**, 391–396.
- Peters, M. B., Glenn, J. L., Svete, P., Hagen, C., Tsyusko, O. V., Decoursey, P., Lieutenant-Gosselin, M., Garant, D. & Glenn, T. C. 2007. Development and characterization of microsatellite loci in the eastern chipmunk (*Tamias striatus*). *Molecular Ecology Notes*, **7**, 877–879.
- Poulin, R., Rau, M. E. & Curtis, M. A. 1991. Infection of brook trout fry, *Salvelinus fontinalis*, by ectoparasitic copepods: the role of host behaviour and initial parasite load. *Animal Behaviour*, **41**, 467–476.
- Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- R Development Core Team 2009. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Raymond, M. & Rousset, F. 1995. GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.
- Réale, D. & Festa-Bianchet, M. 2003. Predator-induced selection on temperament in bighorn ewes. *Animal Behaviour*, **65**, 463–470.
- Réale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J. & Festa-Bianchet, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, **22**, 1599–1607.
- Ribble, D. O. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *Journal of Animal Ecology*, **6**, 457–468.
- Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-related behavioural traits in the spider, *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour*, **46**, 669–675.
- Rossanigo, C. E. & Gruner, L. 1991. Accuracy of two methods for counting eggs of sheep nematode parasites. *Veterinary Parasitology*, **39**, 115–121.
- Rousset, F. 2008. Genepop'007: a complete re-implementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources*, **8**, 103–106.
- Rózsa, L., Reiczgel, J. & Majoros, G. 2000. Quantifying parasites in samples of hosts. *Journal of Parasitology*, **86**, 228–232.
- Ruby, D. E. 1978. Seasonal changes in the territorial behaviour of the iguanid lizard *Sceloporus jarrovi*. *Copeia*, **3**, 430–438.
- Sands, J. & Creel, S. 2004. Social dominance, aggression and faecal glucocorticoids levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour*, **76**, 387–396.
- Say, L. & Pontier, D. 2004. Spacing pattern in a social group of stray cats: effects on male reproductive success. *Animal Behaviour*, **68**, 175–180.
- Schuett, W., Tregenza, T. & Dall, S. R. X. 2010. Sexual selection and animal personality. *Biological Reviews*, **85**, 217–246.
- Schulte-Hostedde, A. I., Millar, J. S. & Gibbs, H. L. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution*, **56**, 2519–2529.
- Schwagmeyer, P. L. 1994. Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology*, **98**, 265–276.
- Schwagmeyer, P. L. 1995. Searching today for tomorrow's mates. *Animal Behaviour*, **50**, 759–767.
- Schwagmeyer, P. L. & Parker, G. A. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour*, **35**, 1015–1025.
- Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioral Ecology and Sociobiology*, **19**, 359–364.
- Schwagmeyer, P. L., Parker, G. A. & Mock, D. W. 1998. Information asymmetries among males: implications for fertilization success in the thirteen-lined ground squirrel. *Proceedings of the Royal Society B*, **265**, 1861–1865.
- Schwarzenberger, T. & Klingel, H. 1995. Range utilisation and activity of radio-collared yellow-necked mice *Apodemus flavicollis* Melchior, 1834. *Zeitschrift für Säugetierkunde*, **60**, 20–32.
- Semenova, T. P., Anoshkina, I. A., Khomut, B. M. & Kolaeva, S. G. 2001. Seasonal peculiarities of behaviour of ground squirrel *Citellus undulatus* in holeboard and open field tests. *Behavioural Processes*, **56**, 195–200.
- Sheldon, B. & Verhulst, S. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, **11**, 317–321.
- Sih, A., Bell, A. M. & Johnson, J. 2004a. Behavioural syndromes: an evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Sih, A., Bell, A. M., Johnson, J., Chadwick, J. & Ziemba, R. E. 2004b. Behavioural syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277.
- Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.
- Smith, D. A. & Smith, L. C. 1975. Oestrus, copulation, and related aspects of reproduction in female eastern chipmunks, *Tamias striatus* (Rodentia: Sciuridae). *Canadian Journal of Zoology*, **53**, 756–767.
- Snyder, D. P. 1982. *Tamias striatus*. *Mammalian Species*, **168**, 1–8.
- Spritzer, M. D., Solomon, N. G. & Meikle, D. B. 2005a. Influence of scramble competition for mates upon the spatial ability of male meadow voles. *Animal Behaviour*, **69**, 375–386.
- Spritzer, M. D., Meikle, D. B. & Solomon, N. G. 2005b. Female choice based on male spatial ability and aggressiveness among meadow voles. *Animal Behaviour*, **69**, 1121–1130.
- Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I. & Jarvi, T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, **15**, 192–198.
- Taylor, L. H., Mackinnon, M. J. & Read, A. F. 1998. Virulence of mixed-clone and single-clone infections of the rodent malaria *Plasmodium chabaudi*. *Evolution*, **52**, 583–591.
- Thomas, F., Adamo, S. & Moore, J. 2005. Parasitic manipulation: where are we and where should we go? *Behavioural Processes*, **68**, 185–199.
- van der Veen, I. T. 2003. Is body size or activity of copepods related to ingestion of parasite larvae? *Parasitology*, **126**, 173–178.
- Ward, A. J., Thomas, P., Hart, P. J. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology Sociobiology*, **55**, 561–568.
- Waterman, J. 2007. Male mating strategies in rodents. In: *Rodent Societies: an Ecological and Evolutionary Perspectives* (Ed. by J. O. Wolff & P. W. Sherman), pp. 27–41. Chicago: University of Chicago Press.
- Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, **280**, 1928–1930.
- Westergaard, G. C., Cleveland, A., Trenkle, M. K., Lussier, I. D. & Higley, J. D. 2003. CSF 5-HIAA concentration as an early screening tool for predicting significant life history outcomes in female specific-pathogen-free (SPF) rhesus macaques (*Macaca mulatta*) maintained in captive breeding groups. *Journal of Medical Primatology*, **32**, 95–104.
- Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993. Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442–446.
- Winter, D. G. & Barenbaum, N. B. 1999. History of modern personality theory and research. In: *Handbook of Personality: Theory and Research* (Ed. by L. A. Pervin & O. P. John), pp. 3–27. 2nd edn. New York: Guilford Press.
- Wolf, M., Sander van Doorn, G., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–585.
- Yahner, R. 1978. The adaptive nature of the social system and behaviour in the eastern chipmunk, *Tamias striatus*. *Behavioral Ecology and Sociobiology*, **3**, 397–427.
- Zala, S. M., Potts, W. K. & Penn, D. J. 2004. Scent-marking displays provide honest signals of health and infection. *Behavioral Ecology*, **15**, 338–344.
- Zuk, M., Thornhill, R., Ligon, J. D. & Johnson, K. 1990. Parasites and mate choice in red jungle fowl. *American Zoologist*, **30**, 235–244.