No island-effect on glucocorticoid levels for a rodent from a near-shore archipelago

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ABSTRACT

17   Island rodents are often larger and live at higher population densities than their mainland
18   counterparts, characteristics that have been referred to as "island syndrome". Island syndrome
19   has been well studied, but few studies have tested for island-mainland differences in stress
20   physiology. We evaluated island syndrome within the context of stress physiology of white-
21   footed mice (*Peromyscus leucopus*) captured from 11 islands and 5 mainland sites in Thousand
22   Islands National Park, Ontario, Canada. Stress physiology was evaluated by quantifying
23   corticosterone (a stress biomarker), the primary glucocorticoid in mice, from hair and its related
24   metabolites from fecal samples. White-footed mice captured in this near-shore archipelago did
25   not display characteristics of island syndrome, nor differences in levels of hair corticosterone or
26   fecal corticosterone metabolites compared with mainland mice. We suggest that island white-
27   footed mice experience similar degrees of stress in the Thousand Islands compared with the
28   mainland. Although we did not find evidence of island syndrome or differences in glucocorticoid
29   levels, we identified relationships between internal (sex, body mass) and external (season)
30   factors and our hormonal indices of stress in white-footed mice.

INTRODUCTION

33   Studying island ecosystems and species has been central to the development of ecological and
34   evolutionary theory (Foster, 1964; MacArthur & Wilson, 1967; Van Valen, 1973; Lomolino et
35   al., 2012; Warren et al., 2015). Island communities tend to have low species diversity compared
36   with mainland systems (Losos & Ricklefs, 2009), including fewer native predators (Blackburn et
37   al. 2004). In response to decreased predator pressure and interspecific competition, combined

38   with changes in food availability on islands, small mammals evolve towards gigantism upon
39   arrival to islands while larger species often display dwarfing (Lomolino et al., 2012). This
40   pattern, observed across numerous archipelagos, contributes to the evolutionary trend called the
41   "island rule" (Van Valen, 1973). Behavioural and morphological changes co-occur in small
42   mammals following island colonization, with individuals becoming less aggressive to
43   conspecifics and demonstrating less predator avoidance behaviour (Adler & Levins, 1994).
44   The combination of increased body size with changes in behaviour and demography has been
45   referred to as "island syndrome" in rodents (Adler & Levins, 1994). Although morphological and
46   behavioural traits associated with island syndrome have been relatively well-characterized, few
47   studies have focused on the effect of island life on stress physiology (but see (Clinchy et al.,
48   2004; Müller et al., 2007).
49   When an animal encounters a perceived stressor, its hypothalamic-pituitary-adrenal
50   (HPA) axis is activated, resulting in increased secretion of glucocorticoid hormones (GCs;
51   Sapolsky, Romero & Munck, 2000). Multiple environmental factors can influence GC levels,
52   including predation (Clinchy et al., 2011; Sheriff, Krebs & Boonstra, 2011), food availability
53   (Kitaysky, Wingfield & Piatt, 1999; Walker, Wingfield & Boersma, 2005) and population
54   density (Boonstra & Boag, 1992; Harper & Austad, 2004; Dettmer et al., 2014; Blondel et al.,
55   2016). Elevated GC levels are involved in preparation for future stressors by shifting resources
56   from reproduction and digestion toward replenishing energy stores used during the initial stress
57   response (Romero & Wingfield, 2016). Although short-term elevations of GCs are presumed to
58   be adaptive, chronically elevated GCs may correlate negatively with indices of wildlife health
59   (Stothart et al., 2016), condition (Injaian et al., 2019), and survival (Wilkening and Ray, 2016).
60   In wildlife studies, stress has traditionally been evaluated by quantifying circulating GC
61   levels from blood samples (Sapolsky, 1982; Wingfield, Smith & Farner, 1982). However, there
62   is increasing interest in quantifying GCs from less-invasive alternative sources, including saliva,
63   feces and hair (Sheriff et al., 2011). Importantly, comparing measures of GC levels in different
64   materials allows for stress to be evaluated over different time scales (Sheriff et al., 2011). For
65   example, wild eastern chipmunks (*Tamias striatus*) from more open environments had higher
66   fecal cortisol metabolites than those from more forested areas; however, there was no difference
67   in long term stress between the two groups based on hair cortisol (Mastromonaco et al., 2014).
68   Although concerns have been raised regarding interpretation of both fecal (Goymann, 2012) and
69   hair GCs (Sharpley, Kauter & McFarlane, 2009; Keckeis et al., 2012; Stewart et al., 2018), a
70   meta-analysis suggests they are useful metrics for quantifying an individual's response to
71   environmental stressors (Dantzer et al., 2014).
72   Hair GC levels are influenced by both internal and external factors (Romero &
73   Wingfield, 2016; Heimbürge, Kanitz & Otten, 2019). Hair GC levels vary within individuals
74   between body regions (Macbeth et al., 2010; Acker, Mastromonaco & Schulte-Hostedde, 2018)

75   and among individuals by age (Dettmer et al., 2014), body size (Waterhouse et al., 2017),
76   condition (Cattet et al., 2014), sex (Stewart et al., 2018), food availability (Cattet et al., 2014)
77   and season (Martin & Réale, 2008). Further, a study of captive rhesus macaques showed that
78   hair GC levels increased with population density (Dettmer et al., 2014). Fecal GC levels are also
79   influenced by internal and external factors in wild mammals (Hayssen, Harper & DeFina, 2002;
80   Smith et al., 2012; Mastromonaco et al., 2014).
81   Animals display a range of physiological adaptations to island life. For example,
82   immunological differences exist between bluebirds (*Sialia sialis*) from Bermuda and the
83   continental United States (Matson et al., 2014). Caviomorph rodents from small islands have
84   lower basal metabolic rates than their mainland counterparts (Arens & McNab 2001). With
85   respect to stress physiology, circulating corticosterone levels were lower in blue tits (*Parus*
86   *caeruleus*) from the island of Corsica than mainland France (Müller et al., 2007). Although
87   some data are available for changes in glucocorticoid levels in response to island life for birds,
88   demonstration of a pattern similar to the island rule or island syndrome is lacking. The ecological
89   factors shown to affect GC levels in wildlife (e.g., predation, competition, and resource
90   availability) are also thought to account for island syndrome in rodents (see Adler & Levins,
91   1994). Given that island syndrome is largely attributed to decreased predation pressure
92   experienced by island rodents (Adler & Levins, 1994), and that low predation is associated with
93   low GC levels (Clinchy et al., 2011), we predicted that populations of island rodents displaying
94   island syndrome would also have lower GC levels than their mainland relatives.
95   Although many island-mainland comparisons of behavioural and physiological
96   characteristics have been made using wildlife from isolated oceanic islands (Müller et al., 2007;
97   Novosolov, Raia & Meiri, 2013; Matson et al., 2014; Cuthbert et al., 2016), evidence of island
98   syndrome in rodents has been found in relatively near-shore archipelagos in both freshwater and
99   marine environments (Lomolino, 1984; Adler & Tamarin, 1984). The Thousand Islands are an
100 archipelago in the St. Lawrence River, whose islands are divided between Canada and the United
101 States. The Thousand Islands region has served as the site for numerous studies of island
102 biogeography in small mammals (Lomolino, 1982, 1984; Werden, 2012; Werden et al., 2014).
103 Mammalian species richness in the Thousand Islands is positively related to island area
104 (Lomolino, 1982), and the body size of meadow voles (*Microtus pennsylvanicus*) and short-
105 tailed shrews (*Blarina brevicauda*) increases with the degree of isolation from the mainland
106 (Lomolino, 1984). On the basis of these trends in species richness and morphology, we selected a
107 portion of the islands belonging to Thousand Islands National Park in Ontario, Canada as our
108 study site. As a study species, we focused on white-footed mice (*Peromyscus leucopus*) because
109 they are the most abundant small mammal in Thousand Islands National Park (Werden et al.,
110 2014), and *Peromyscus* has been the focus of many studies that provide the basis for island
111 syndrome (Adler & Levins, 1994).

112   The current study had two aims: 1. To test if white-footed mice in the Thousand Islands
113   display characteristics of island syndrome, including greater body mass and higher relative
114   abundance than their mainland counterparts, and 2. To test if there were differences in stress
115   physiology between island and mainland mice. We tested these aims under the hypothesis that
116   island syndrome includes changes in stress physiology. To test our hypothesis, we compared
117   corticosterone (the major GC in mice and rats; Keeney, Jenkins & Waterman, 1995) in hair
118   ($CORT_{hair}$), and its metabolites in feces ($CORT_{feces}$), of white-footed mice captured at multiple
119   island and mainland locations in a near-shore archipelago; from sites in Thousand Islands
120   National Park in Ontario, Canada. We predicted that if white-footed mice in the Thousand
121   Islands were more abundant and larger than mainland mice (as expected by "island syndrome"),
122   then island mice would also have lower $CORT_{hair}$ and $CORT_{feces}$ levels. Because aspects of island
123   syndrome in rodents are affected by island area and distance from the mainland (Adler & Levins,
124   1994), we also predicted that white-footed mice would have lower GC levels on the smaller and
125   more isolated islands in the archipelago. Finally, we evaluated how body mass affected CORT in
126   white-footed mice, and whether CORT varied between seasons and with population density.
127

MATERIALS & METHODS

129   The Trent University Animal Care Committee (protocol numbers 23877 and 24341) approved all
130   procedures prior to working with the animals. Trapping in the Thousand Islands National Park
131   was approved via a Parks Canada Research and Collection Permit (No. 22959).
132

Study species and location

134   The white-footed mouse is a small, nocturnal rodent that inhabits deciduous and mixed forests in
135   the eastern United States and southern edge of Canada (Werden et al., 2014). White-footed mice
136   in Ontario breed from April – August, and females have litters of approximately 5 individuals on
137   average (Millar, Wille & Iverson, 1979). Female white-footed mice in southern Ontario produce
138   1-4 litters per year (Harland, Blancher & Millar, 1979). Moulting in *Peromyscus* precedes or
139   follows energetically costly periods such as reproduction, and begins in March in white-footed
140   mice in the nearby state of New York (Pierce & Vogt, 1993). Our small mammal trapping period
141   coincided with the breeding season, when most individuals would be displaying their summer
142   pelage.
143   All trapping locations were located in Thousand Islands National Park in Ontario, Canada
144   (Figure 1). Selection of trapping locations was limited to locations within Thousand Islands
145   National Park, and those islands that were large enough to place trapping grids. These islands are
146   also visited by visitors to the National Park, so traps had to be placed away from walking paths
147   and campsites. We trapped on 11 islands and at 5 mainland sites during two years (2015 and
148   2016). Mainland sites were located within 2 km of the St. Lawrence River (Figure 1). We

149 targeted wooded areas as opposed to open fields so that relative abundance could be compared
150 between locations and to increase trapping success. Island area and distance from the mainland
151 were calculated using ArcMap (Version 10.4.1; see Table S1).
152

153 **Small mammal trapping**
154 We trapped during three periods: summer 2015 (July – August), spring 2016 (May-June) and
155 summer 2016 (July – August). Efforts were made to alternate between trapping on islands and
156 mainland sites; however, weather conditions occasionally dictated access to island sites (trapping
157 dates are provided in Table S1). Sherman live-traps (H.B. Sherman Traps, Inc.,Tallahassee, FL,
158 USA) were set 10 m apart in rectangular grids of varying size. The majority of grids were
159 arranged in a 7 by 7 formation (49 traps in total), however some areas on small islands were
160 limited by pedestrian paths, which necessitated using smaller grids (5 by 5), or in one case,
161 transects (Mermaid Island). Hulled sunflower seeds were used as bait and natural cotton bedding
162 was provided for warmth. Traps were set in the evening (ca. 1800 h) and checked in the morning
163 (ca. 0700 h) to target the active period of white-footed mice. Trapping periods generally
164 consisted of 2-4 nights of consecutive trapping.
165 Upon capture, white-footed mice were weighed (± 1 g) and a patch of hair (ca. 1 x 1 cm)
166 was shaved from the rump of each individual, above the right-hind limb using an electric razor
167 (Remington™ Model PG6025), collecting the entire length of each shaft from the skin to the
168 distal end of the shaft. We standardized the shaving location because hair GC levels can vary
169 among body regions (Macbeth et al., 2010; Acker, Mastromonaco & Schulte-Hostedde, 2018).
170 Each white-footed mouse was ear-tagged to recognize recaptured individuals, and then released.
171 The razor blades were cleaned with alcohol swabs between shaving each animal. Hair samples
172 were stored in Fisherbrand™ Snap-Cap™ Flat-Top Microcentrifuge Tubes in the dark at
173 ambient temperature (approx. 22°C) until hair hormone analysis (2-5 months later). Coat colour
174 and body mass were used to exclude juveniles from our analyses. Coat colour and stage were
175 occasionally noted (grey, brown, reddish-brown or moulting) in 2015, and always noted in 2016.
176 We identified juveniles by their grey pelage and in the absence of coat colour data, individuals
177 ≤14 g were excluded (Wolff, 1984).
178 White-footed mouse feces were collected from traps using forceps. Fecal samples were
179 stored in Fisherbrand™ Snap-Cap™ Flat-Top Microcentrifuge Tubes and placed in a cooler with
180 ice packs until they could be stored in a liquid nitrogen-cooled dry-shipper (within 6 h of
181 collection). Fecal glucocorticoid metabolites are stable over the timeframe of our sample
182 collection. For example, fecal samples maintained for 5-hours at room temperatures had similar
183 levels as samples immediately frozen following collection (Dantzer et al., 2010). At ambient
184 temperature, metabolites are reported to be stable for up to 48-hrs (Parnell et al., 2015). Soiled
185 traps were cleaned with 70% ethanol between uses to ensure that the feces collected from each

186   trap belonged to the animal caught in the trap that night. Samples were then transferred to a -80C
187   freezer until hormone extraction (2-9 months in freezer). At sub-zero temperatures, fecal
188   glucocorticoid metabolites are stable for at least a year (Beehner and Whitten, 2004).
189
190   **Relative Abundance**
191   As a proxy for the population density, we calculated relative abundance of white-footed mice at
192   each site during each of the 3 trapping periods. Relative abundance was calculated as catch-per-
193   unit-effort (CPUE), presented in number of white-footed mice captured per hundred trap-nights.
194   We corrected for tripped traps following the correction factor equation (Nelson & Clark, 1973):
195                                    $$CPUE = A \times 100/(TU - S/2)$$
196 $$TU = P \times N$$
197   where A = number of white-footed mice caught; TU = trapping units, calculated as total number
198   of trap nights per site session; P = number of nights in each trapping session; N = number of
199   traps set each night; and S = total sprung traps. This approach has been widely used in other
200   studies of small mammal ecology (Parker et al., 2016; Gill et al., 2018; Fauteux et al., 2018).
201
202   **Hormone extraction and analysis**
203   The use of fecal CORT metabolites and hair CORT have been validated as measures of
204   stress in laboratory mice (*Mus musculus;* Daniszová et al., 2017; Erickson, Browne & Lucki,
205   2017). Hair corticosterone ($CORT_{hair}$) and fecal corticosterone metabolites ($CORT_{feces}$) were
206   extracted with methanol (100% for hair, 80% for feces) following Mastromonaco et al. (2014)
207   and Stewart et al. (2018). Hair samples were cut into 5 mm pieces and weighed into 7 ml glass
208   scintillation vials. The samples were washed with 100% methanol by vortexing for 10 s followed
209   by immediate removal of the methanol. Immediately thereafter, 100% methanol was added to the
210   samples at a ratio of 0.005g/ml. Samples were vortexed for 10 s and mixed for 24 h on a plate
211   shaker. After 24 h, the vials were centrifuged for 10 min at 2400 g and the supernatants were
212   transferred into clean glass vials. Fecal samples were thawed and weighed into 7 ml glass
213   scintillation vials to which 80% methanol in water (v:v) was added at a ratio of 0.05g/ml. The
214   samples were vortexed for 10 s and mixed overnight on a plate shaker. The vials were then
215   centrifuged for 10 min at 2400 g and the supernatants were transferred into clean glass vials. The
216   supernatants from extracted hair and fecal samples were stored sealed at -20 °C for 1-9 months
217   until they were evaporated and analyzed. Dried-down hair extracts (600 µl per sample) were
218   reconstituted in 150 µl EIA buffer (0.1 mM sodium phosphate buffer, pH 7.0, containing 9 g of
219   NaCl and 1 g of bovine serum albumin per litre) resulting in a 4-fold concentration. Dried-down
220   fecal extracts (200 µl per sample) were reconstituted in 200 µl EIA buffer and diluted for a final
221   1:20 dilution.

222   To quantify $CORT_{hair}$ and $CORT_{feces}$, we used an enzyme immunoassay (EIA) following

223 methods described by Baxter-Gilbert et al. (2014). Microtitre plates were coated with 0.25

224 µg/well goat anti-rabbit IgG polyclonal antibody (Sigma-Aldrich, Mississauga, ON, Canada;

225 1:200,000 in coating buffer, 50 mM bicarbonate buffer, pH 9.6) and incubated overnight at room

226 temperature. Plates were washed with 0.05% Tween 20, 0.15M NaCl solution and blocked with

227 250 µl EIA buffer for 1 hr at room temperature. Plates were then loaded with 50 µl

228 corticosterone standard (Steraloids Q1550; 39–10,000 pg/ml), reconstituted extracts and controls,

229 followed by 100 µl horseradish peroxidase conjugate (1:1,000,000) and 100 µl corticosterone

230 antiserum (1:200,000) (antibody lot: CJM006; C. Munro, University of California, Davis, CA,

231 USA), all diluted in EIA buffer. Plates were incubated overnight at room temperature, and then

232 washed and loaded with 200 µl of substrate solution (0.5 ml of 4 mg/ml tetramethylbenzidine in

233 dimethylsulphoxide and 0.1 ml of 0.176 M H_2O_2 diluted in 22 ml of 0.01 M sodium acetate

234 trihydrate $[C_2H_3NaO_2 \cdot 3H_2O]$, pH 5.0). After 30 minute incubation, colour reaction was stopped

235 with 50 µl H_2SO_4 (1.8M) and absorbance was measured at 450 nm using a spectrophotometer

236 (MRX^e microplate reader, Dynex Technologies, Chantilly, VA. The assay cross-reactivities are:

237 corticosterone (100%), desoxycorticosterone (14.25%), and other GC metabolites (<3%)

238 (Watson et al. 2013). Inter- and intra-assay CV's were 13.9% and 4.4%, respectively, with 25

239 plates being run in total. Samples were run as duplicates, and only samples with < 10% CV were

240 accepted (if CV > 10%, the sample was re-run). Because CORT is the dominant GC in white-

241 footed mice, but is highly metabolized prior to excretion (Touma et al 2003), we refer to the

242 values obtained from fecal analysis by EIA as fecal CORT metabolites. All hormone

243 concentrations are described as ng of CORT / g of feces or hair. Serial dilutions of pooled hair

244 and fecal extract showed parallel displacement with the corticosterone standard curve (hair: r =

245 0.997, $p < 0.01$; fecal: r = 0.996, $p < 0.01$; Figure S1). The recovery of known concentrations of

246 corticosterone from mouse hair and fecal extracts were $102.7 \pm 4.3\%$ and $83.5 \pm 5.4\%$,

247 respectively. The measured hormone concentrations in the spiked samples correlated with the

248 expected concentrations (hair r = 0.999, p < 0.01; fecal r = 0.998, p < 0.01).

249

250 **Statistical analysis**

251   We tested all of our predictions using linear-mixed effects models, with sampling site

252 (specific island or mainland location) as a random effect that was nested within habitat type

253 (whether the site was on an island or on the mainland) for island-mainland comparisons. Our

254 analyses can be broken down into three groups: island-mainland comparisons, among-island

255 comparisons, and seasonal analyses. With the exception of our analysis of relative abundance,

256 island-mainland comparisons were made using only summer data (July-August captures) for

257 2015 and 2016 (spring 2016 data were excluded). For among-island comparisons, only island

258 capture data from summer months were used and island size and isolation were added as

259   covariates. For seasonal analyses, only 2016 data were used because we had both spring and
260   summer data for that year. Habitat type (island-mainland) and island size and isolation were
261   dropped from testing for seasonal effects on morphological and physiological parameters. All
262   corticosterone and body mass data were ln-transformed, and island area and distance to the
263   mainland were $\log_{10}$ transformed in all analyses to improve the normality of model residuals.
264   Any visibly pregnant females (n = 15; Millar, Wille & Iverson, 1979) were excluded from all
265   analyses (Novikov & Moshkin, 1998; Young et al., 2006), with the exception of relative
266   abundance. If an individual was captured more than once, only data from the first capture were
267   used.
268   In all analyses, two-way interactions were included in initial models for those variables
269   that were expected to be biologically relevant (sex and season) and pertinent to our hypotheses
270   (habitat type and island measurements). Sampling site was retained as a random effect in all
271   models and nested within habitat type for island-mainland comparisons. The full model for the
272   island-mainland comparison of relative abundance included habitat type, year and season with all
273   two-way interactions. The full model for comparing relative abundance among islands included
274   year and season with their interaction, and covariates for island size and isolation with their
275   interaction. The full model for the island-mainland comparison of body mass included habitat
276   type, sex and year with all two-way interactions. The full model for comparing body mass
277   among islands included sex and year with their interaction, and covariates for island size and
278   isolation with their interaction. The full models for the island-mainland comparisons of both
279   CORT$_{hair}$ and CORT$_{feces}$ included habitat type, sex and year with all two-way interactions, and
280   covariates for relative abundance and body mass. The full models for comparing CORT$_{hair}$ and
281   CORT$_{feces}$ among islands included sex and year with their interaction, covariates for body mass,
282   relative abundance, and island size and isolation, and the interaction between island size and
283   isolation. The full model for comparing CORT$_{hair}$ and CORT$_{feces}$ between seasons included sex
284   and season with their interaction, and body mass as a covariate.
285   To reduce model complexity, non-significant two-way interactions ($p > 0.05$) were
286   dropped to test the variables of greatest interest (habitat type, sex, and season). Two-way
287   interactions were dropped in order of largest p-value, and then remaining fixed effects were also
288   dropped in that order. Habitat type, sex, year and island size and distance to the mainland (for
289   among island analyses), were always retained, with the exception of testing seasonal variation.
290   Full models (not including two-way interactions) were presented if model reduction did not
291   result in significance of main effects.
292   Analyses were conducted using RStudio (Version 0.99.484, RStudio, Inc). Linear-mixed
293   effects models were fit with the lmer function of the "lme4" package (Version 1.1.7) using
294   restricted maximum likelihood (REML) and non-standardized variables. Results, including p-
295   values, t-values, and Satterthwaite approximations to degrees of freedom, were obtained using

296   the "summary" function of the "lmerTest" package (Version 2.0.20; Kuznetsova, Brockhoff &
297   Christensen, 2016). Goodness of fit was assessed using marginal $_{(M)}$ and conditional $_{(C)}$ pseudo
298   R^2 values (R^2_{GLMM}; Nakagawa & Schielzeth, 2013) calculated with the "r.squaredGLMM"
299   function in the "MuMIn" package (Version 1.13.4; Bartoń, 2016). $R^2_{GLMM(M)}$ represents the
300   proportion of the variation explained by the fixed effects alone, and $R^2_{GLMM(C)}$ represents the
301   proportion of variation explained by both the fixed and random effects (Nakagawa & Schielzeth,
302   2013). Correlations were tested using the "cor.test" function in R, which calculates a p-value
303   based on Fisher's Z transformation.
304
305   **RESULTS**
306   We caught 408 individual white-footed mice during 2015-2016; 17 individuals were recaptured
307   between trapping periods. Trapping success was highly variable across sampling sites, and there
308   were no consistent trapping patterns between mainland and island sites. For example, based on
309   overall CPUE, trapping was more successful on some islands than on the mainland (as would be
310   predicted via the "island rule"); however, on some islands there were zero captures during some
311   trapping periods while mainland sites always yielded captures (Table S2). More traps were
312   tripped at island sites (mean ± SD; 38% ± 10.8%) than mainland sites (23% ± 12.8%), and it was
313   likely that trap disturbance contributed to the high degree of variation in trapping success across
314   habitat types. Although trapping effort varied among sites due to some sites only being trapped
315   during one sampling period, trapping effort was approximately equal between the two habitat
316   types. Mainland sites received an average of 288 ± 151.1 trap nights across the entire sampling
317   program, and island sites received an average of 264 ± 147.6 trap nights (Table S1)
318
319   **Relative abundance of mice did not differ between islands and the mainland**
320   The final model for the island-mainland comparison of relative abundance of white-
321   footed mice was reduced from the full model by removing two-way interactions. Contrary to
322   expectations of the island rule, there was no difference in relative abundance of island and
323   mainland white-footed mice (p = 0.667, Table 1). Relative abundance differed between years; it
324   was 44% higher in summer 2015 than in summer 2016 (p =0.012; Table 1). In 2016, in which we
325   had data for both spring and summer, relative abundance was 74% higher in the summer than the
326   spring (p = 0.033; Table 1). The final model for the among-islands comparison of relative
327   abundance of white-footed mice was reduced from the full model by removing two-way
328   interactions. CPUE decreased on all islands between 2015 and 2016 (p = 0.011). There was no
329   effect of island area (p = 0.603) nor distance from the mainland (p = 0.442, Table 1) on relative
330   abundance of white-footed mice.
331   Summer abundance of white-footed mice from individual sampling sites was positively
332   correlated between years (11 sites, r = 0.852, t_9 = 4.87, p = 0.0009; Figure 2). Although there was

333   a general decrease in relative abundance between years across habitat types, CPUE was nearly
334   equal between years for the three mainland sites that were trapped during both summers (Figure
335   2). This is demonstrated in Figure 2, where CPUE values for mainland sites fall close to the
336   dotted line which represents the relationship if abundances were equal between years. All
337   resampled island sites fall below that line, showing a decrease in abundance between years for
338   island mice (Figure 2).
339

340   **Body mass did not differ between island and mainland mice**
341   The final model for the island-mainland comparison of body mass of white-footed mice was
342   reduced from the full model by removing two-way interactions. Contrary to expectations of the
343   island rule, white footed mice from the Thousand Islands (n = 209) were not heavier than on the
344   mainland (n = 92; $p = 0.804$; Table 2; Figure 3), nor did body mass differ between years ($p =$
345   0.875). Male mice (n = 181; mean ± SD; 21.0 ± 3.7 g) were significantly heavier than females (n
346   = 120; 20.2 ± 4.4 g) across habitat types ($p = 0.020$); however, the average difference was less
347   than 1 g, and the model had little explanatory power ($R^2_{GLMM(M)} = 0.02$; $R^2_{GLMM(C)} = 0.04$; Table
348   2).
349   The final model for the among-islands comparison of body mass of white-footed mice
350   was reduced from the full model by removing two-way interactions. For island mice, there was
351   no effect of island area ($p = 0.476$, Table 2) nor distance from the mainland ($p = 0.385$) on body
352   mass. Again, males were heavier than females on islands ($p = 0.019$); however, this effect
353   explained little variation overall ($R^2_{GLMM(M)} = 0.04$; $R^2_{GLMM(C)} = 0.04$; Table 2).
354

355   **Hair corticosterone did not differ between island and mainland mice, but increased with**
356   **body mass**
357   The final model for the island-mainland comparison of $CORT_{hair}$ of white-footed mice was
358   reduced from the full model by removing two-way interactions. There was no difference between
359   $CORT_{hair}$ of island (n = 188) and mainland (n = 82) white-footed mice ($p = 0.4080$; Table 3,
360   Figure 3). Sex ($p = 0.9611$), year of capture ($p = 0.5159$) and relative abundance ($p = 0.3837$)
361   also had no effect on $CORT_{hair}$ (Table 3). However, $CORT_{hair}$ increased with body mass ($p =$
362   0.0011; Table 3; Figure 4). There was a small effect size for this model ($R^2_{GLMM(M)} = 0.05$,
363   $R^2_{GLMM(C)} = 0.14$; Table 3).
364   The final model for the among-islands comparison $CORT_{hair}$ of white-footed mice was
365   reduced from the full model by removing two-way interactions. Focusing only on island mice,
366   neither island area ($p = 0.4807$, Table 3) nor distance from the mainland ($p = 0.6092$) predicted
367   $CORT_{hair}$ levels. However, body mass continued to be a significant predictor of $CORT_{hair}$ for the
368   model testing of only island mice ($p < 0.0031$; Table 3).
369

Fecal corticosterone metabolites did not differ between island and mainland mice

The final model for the island-mainland comparison of $CORT_{feces}$ of white-footed mice was reduced from the full model by removing two-way interactions, relative abundance and ln-transformed body mass, each of which had no significant effect. There was no difference between $CORT_{feces}$ of island (n = 160) and mainland (n = 49) white-footed mice during the summer months ($p = 0.8578$; Table 4). Male mice had lower $CORT_{feces}$ than females ($p = 0.0492$; Table 4; Figure 3) and $CORT_{feces}$ was higher in the summer of 2016 than summer 2015 ($p < 0.0001$; Table 4).

The final model for the among-islands comparison $CORT_{feces}$ of white-footed mice was reduced from the full model by removing two-way interactions, relative abundance and ln-transformed body mass, each of which had no significant effect. There was no effect of either island area ($p = 0.9440$, Table 4) nor distance from the mainland ($p = 0.6320$) on $CORT_{feces}$ (Table 4). $CORT_{feces}$ levels were higher in 2016 than in 2015 ($p < 0.0001$), but unlike the model for the island-mainland comparison, there was no difference between sexes for $CORT_{feces}$ ($p = 0.1320$; Table 4).

Hair corticosterone levels were lower in spring than summer for females, but not for males

The full model was retained for comparing $CORT_{hair}$ of white-footed mice between seasons. For $CORT_{hair}$ of white-footed mice collected in 2016 (n = 147), when we had data from both spring and summer, there was a significant interaction between sex and season ($p = 0.0009$, Table 5). Female $CORT_{hair}$ was lower in spring than in summer, while male $CORT_{hair}$ did not differ between seasons (Figure 5). This model had a greater effect size than other models of factors affecting $CORT_{hair}$ ($R^2_{GLMM(M)} = 0.22$, $R^2_{GLMM(M)} = 0.35$; Table 5), indicating a relatively strong effect of season on $CORT_{hair}$ for female white-footed mice.

Fecal corticosterone metabolites of both sexes were lower in spring than summer

To explore seasonal effects on $CORT_{feces}$ we focused on 2016, for which we had data from both spring and summer (n = 71). The final model for comparing $CORT_{feces}$ levels between seasons was reduced from the full model by removing two-way interactions and ln-transformed body mass. Both sexes had lower $CORT_{feces}$ levels in spring than in summer ($p < 0.0001$, Table 6), but there was no difference between sexes ($p = 0.168$; Table 6). The interaction between sex and season, that had influenced $CORT_{hair}$ levels, did not influence $CORT_{feces}$ levels ($t_{63} = -1.423$, $p = 0.160$) so it was dropped from the model.

Corticosterone in hair and related metabolites in feces were positively correlated

$CORT_{hair}$ values from all collected samples (n = 333) ranged from 5.1-398.6 ng/g, with a median level of 79.8 ng/g. Values for $CORT_{feces}$ from all collected samples (n = 303) ranged from 30.5-

407   1239.8 ng/g, with a median of 335.4 ng/g. A simple correlational analysis suggests $CORT_{hair}$ and

408    $CORT_{feces}$ of white-footed mice were significantly, although weakly, positively correlated (r =

409   0.16, t_{178} = 2.196, p = 0.015; Figure 6).

410

411   **DISCUSSION**

412   **White-footed mice do not display island syndrome in the Thousand Islands**

413   Despite the tendency for island wildlife to display morphological and physiological adaptations

414   to insularity (Matson et al., 2014; Holding et al., 2014; Spencer et al., 2017), white-footed mice

415   in the Thousand Islands did not differ in any of these characteristics from their mainland

416   conspecifics. White-footed mice on islands did not display higher relative abundance than

417   mainland mice in disagreement with the general prediction that rodents exhibit particularly high

418   densities on islands (Adler & Levins, 1994; Crespin, Duplantier & Granjon, 2012; Cuthbert et

419   al., 2016), which has been observed for other small vertebrates as well (Novosolov, Raia &

420   Meiri, 2013; Sale & Arnould, 2013). Additionally, island sites showed a trend toward a greater

421   decrease in relative abundance compared to mainland sites for the two years that we sampled

422   (Figure 2). This trend may not have resulted in a significant interaction effect between habitat

423   type and year due to the small number of mainland sites that were sampled during both summers.

424   Although this trend only represents two years of data, these results differ from Adler and Levins'

425   (1994) description of island syndrome, and studies showing that island rodents are more stable,

426   and less prone to drastic changes in abundance than mainland populations (Gliwicz, 1980;

427   Herman & Scott, 1984; Tamarin & Sheridan, 1987). The stability of high population densities on

428   oceanic islands has been partially attributed to marine resource subsidies and climate stability

429   compared to continental systems (Stapp & Polis, 2003; Barrett et al., 2005; Sale & Arnould,

430   2013); factors that do not apply when comparing rodents on the near-shore Thousand Islands to

431   the adjacent mainland.

432   Small mammals on islands often exhibit large body size (Lomolino et al., 2012; Sale &

433   Arnould, 2013; Harper & Rutherford, 2016); however, we did not detect a difference in body

434   mass between island and mainland white-footed mice in the Thousand Islands. This was

435   surprising, because a high degree of isolation is not necessarily required for demographic or

436   body mass differences among *Peromyscus* populations to occur. Adler, Wilson & Derosa (1986)

437   detected a relationship between population density and island isolation of white-footed mice on

438   coastal islands located between 16 – 1,046 m from shore (by comparison, we had large samples

439   of mice from Thwartway and Grenadier islands, which were 2,837 and 1,038 m from the

440   mainland, respectively; Table S1). Deer mice on Anaho Island in Pyramid Lake, Nevada

441   (approximately 1,000 m from the mainland) have significantly greater body length than mainland

442   mice (Kuhn, Gienger & Tracy, 2016).

443   We also found no effect of island area or isolation on body mass of white-footed mice.

444   These negative results regarding patterns between body size and island biogeography do not
445   agree with results for other small mammals in the Thousand Islands. Lomolino (1984) found that
446   the body size of meadow voles (*Microtus pennsylvanicus*) and short-tailed shrews (*Blarina*
447   *brevicauda*) in the Thousand Islands increased as distance from the mainland increased. This
448   pattern was attributed to the ability of larger individuals to cross greater distances on ice during
449   the winter, and subsequent founder effects of large individuals reaching more distant islands
450   (Lomolino, 1984). The islands sampled by Lomolino might have been better suited to
451   investigating patterns related to isolation because they were less closely clustered together than
452   those that we sampled. The clustered nature of many of the islands in our study makes their true
453   degree of isolation difficult to determine.
454   On average, we found that male white-footed mice were heavier than females for both
455   island and mainland habitats. This result is consistent with data from laboratory raised white-
456   footed mice (Dewsbury et al., 1980). Greater male body mass has also been found for deer mice
457   collected in the field (Schulte-Hostedde, Millar & Hickling, 2001). Male-biased sexual size
458   dimorphism is widespread in mammals (Isaac, 2005), and often explained by sexual selection
459   favouring large male body size through competition between males for access to mates (Trivers,
460   1972).
461
462   **No difference in CORT levels between island and mainland mice**
463   We predicted that white-footed mice on islands would have lower $CORT_{hair}$ and
464   $CORT_{feces}$ levels than mainland mice, however these predictions were not supported. There was
465   also no effect of island size or distance from the mainland on CORT levels. This result may not
466   be surprising, given that we found no evidence of island syndrome. The lack of an island effect
467   on any of these characteristics in the Thousand Islands suggests either that island white-footed
468   mice experience similar stressors and pressures to mice on the mainland, or that there is a high
469   degree of gene flow between island and mainland white-footed mice. Either of these
470   explanations could be caused by the short distances between islands and from the islands to the
471   mainland, and the freezing of the river in the winter.
472   The proximity of these islands to the mainland, and to one another, may mean that insular
473   white-footed mice experience similar levels of inter-specific competition to mainland mice.
474   Although the diet of white-footed mice is based primarily on insects, they also forage heavily on
475   seeds (Manson & Stiles, 1998). Release from competition with larger granivores, such as squirrel
476   species (Sciuridae), could result in increased body size of *Peromyscus* (Nupp & Swihart, 1996).
477   However, we caught red squirrels (*Tamiasciurus hudsonicus*) and flying squirrels (*Glaucomys*
478   spp.) on near-shore islands (Constance and Georgina), and observed grey squirrels (*Sciurus*
479   *carolinensis*) on more isolated islands (McDonald and Thwartway; N. Stewart, Personal
480   Observation). Although we did not catch eastern chipmunks on any islands, they have previously

481   been caught on islands in the archipelago (Werden et al., 2014). Given the presence of other

482   small mammal species, release from competition might not be a factor on these islands.

483   The proximity of these islands to shore might cause equal predation risk on the islands

484   and the mainland. Small terrestrial predators, such as weasels (*Mustela* spp.), might occur in low

485   numbers on some of the islands (Grenadier Island; Werden et al., 2014). however, avian

486   predators can readily access islands to prey on mice. Coyotes (*Canis latrans*), red foxes (*Vulpes*

487   *vulpes*), and raccoons (*Procyon lotor*) also inhabit or periodically forage on islands by crossing

488   ice in the winter (Coleman, 1979). We experienced somewhat higher numbers of tripped traps on

489   islands than at mainland trapping sites. We visually observed raccoons on a number of the

490   islands, and attribute much of the disturbance to raccoons instead of missed white-footed mice,

491   given that traps were often wide open and moved from their original set point (Grant, 1976).

492   Racoons might have been more likely to find traps within the boundaries of islands than

493   mainland expanses, given the small size of most the islands in this study compared to typical

494   raccoon home range size (100-300 ha; Kaufmann 1982).

495   High gene flow among islands and the mainland in the Thousand Islands could be

496   attributed to the ability of white-footed mice to swim short distances or cross ice in the winter

497   (Lomolino, 1989), and to disperse via transport onboard boats. Despite these dispersal

498   mechanisms, genetic dissimilarity between *Peromyscus* populations can occur at short distances

499   (< 500 m from mainland or large island) in other freshwater archipelagos (Landry & Lapointe,

500   2001; Vucetich et al., 2001). Genetic studies of white-footed mice in the Thousand Islands would

501   provide greater understanding of the degree of similarity between separate populations in the

502   archipelago.

503   Studies of the island rule attribute a range of factors to the degree to which body size of

504   small mammals on islands differs from their mainland relative, including island isolation,

505   latitude, and marine subsidies (foraging on aquatic prey; Lomolino et al., 2012). Rainfall has also

506   been attributed to increased body size of small mammals, and used as evidence of the island rule

507   being more of a "resource rule" (McNab, 2010). It is because of this range of explanations for

508   observed island-mainland differences that we were drawn to study island rodents in a near-shore

509   archipelago, where climatic and ecological variation is limited between island and mainland

510   sites. However, based on our results, a significant degree of ecological isolation may be required

511   for island syndrome to be detectable across an archipelago.

512

513   **Hair corticosterone increased with body mass**

514   Body mass was a positive predictor of $CORT_{hair}$ in white-footed mice, but not $CORT_{feces}$,

515   which suggests this might be a hair-specific CORT observation, as opposed to representative of

516   baseline CORT levels. Because body mass is positively correlated with age in *Peromyscus*

517   (Chappell, 2003), the positive relationship between $CORT_{hair}$ and body mass might be indicative

518   of a relationship between mouse age, moulting, and CORT$_{hair}$ levels. Moulting in *Peromyscus*
519   occurs before or following energetically demanding time periods, such as breeding (Pierce &
520   Vogt, 1993), although some hair replacement likely occurs year-round outside of complete
521   moults as in deer mice (Tabacaru, Millar & Longstaffe, 2011). Moulting is in part regulated by
522   CORT, because steroid hormones have an inhibitory effect on moulting in *Peromyscus*
523   (Garwood & Rose, 1995). As a result, hairs grown during complete moults might have relatively
524   lower CORT concentrations than replacement hairs grown following a complete moult. This
525   would result in heavier individuals (which are likely older and have increased in mass since their
526   last moult) having higher CORT$_{hair}$ when compared with younger mice that have more recently
527   grown their adult pelage. Testing this relationship would require more specific knowledge
528   concerning the exact age of each mouse, and time since their last moults.
529   In American pika (*Ochotona princeps*), hair CORT was strongly influenced by body size
530   (measured by cranial diameter; Waterhouse et al., 2017), but in the opposite direction compared
531   to white-footed mice. Larger American pikas had lower hair CORT, which the authors attributed
532   to the negative relationship between mass-specific metabolic rate and GCs (Haase, Long &
533   Gillooly, 2016). The conflicting directionalities of relationships between hair CORT and body
534   size for small mammals demonstrate the need for more studies concerning internal factors
535   affecting hair GCs.
536   Hair GC levels are an integrative measure of HPA activity, because they will reflect both
537   an individual's phenotype related to their baseline GC levels (Fairbanks et al., 2011), but can
538   also be influenced by an animal's exposure to stressors (Bryan et al., 2015; Scorrano et al.,
539   2015). Because the two measures are representative of different time frames, it might not be
540   surprising that CORT in hair and its related metabolites in feces are not correlated with the same
541   measures (body mass and condition), and demonstrate different seasonal patterns. We did find,
542   however, that CORT$_{hair}$ and CORT$_{feces}$ were positively correlated for white-footed mice. Such
543   correlations presumably represent the influence of individuals' baseline GC levels on both
544   CORT$_{hair}$ and CORT$_{feces}$, however, the relatively weak correlation may reflect matrix-specific
545   time-frames of GC secretion.
546
547   **Sex-specific seasonal variation in corticosterone**
548   Seasonal differences in GC levels are common among vertebrates (Romero, 2002).
549   CORT$_{feces}$ levels of white-footed mice of both sexes were higher in the summer than the spring
550   (Table 6, Figure 5B), in agreement with previous studies of *Peromyscus* (Harper & Austad,
551   2000, 2001). High summer CORT$_{feces}$ levels could be attributed to increased GC levels
552   associated with reproduction (Harper & Austad, 2001); however, breeding occurs in white-
553   footed mice during early spring and lasts throughout the summer months (Pierce & Vogt, 1993).
554   Alternatively, high summer CORT$_{feces}$ levels could be caused by increased abundance of white-

555   footed mice compared to the spring (Hayssen, Harper & DeFina, 2002), which is consistent with
556   our finding that abundance was higher in the summer than the spring in the Thousand Islands.
557   Although we did not find a relationship between CORT and relative abundance across sites,
558   CORT and population density may be correlated within areas as densities change during annual
559   cycles.
560   In contrast to data for $CORT_{feces}$, only female white-footed mice showed seasonal
561   variation in $CORT_{hair,}$, increasing from spring to summer (Table 5, Figure 5A). Male $CORT_{hair}$
562   did not differ between seasons. The contrasting sex-specific results between $CORT_{feces}$ and
563   $CORT_{hair}$ patterns might be the result of the two measures differing in their representative time-
564   scales of CORT secretion (Mastromonaco et al., 2014). Similar to our proposed explanation of
565   the relationship between $CORT_{hair}$ and body mass, it is important to consider the effect that
566   CORT has on hair growth. Female deer mice have been observed developing seasonal moults
567   during pregnancy; however, moulting ceased following the birth of their young (Collins, 1923).
568   If hair growth in in adult female white-footed mice occurs during pregnancy (similar to deer
569   mice), our observation of low $CORT_{hair}$ in females may represent low CORT levels during spring
570   pregnancies. Low CORT during pregnancy occurs in laboratory rodents and it has been
571   suggested that attenuation of the HPA axis during pregnancy protects fetuses from adverse
572   effects of high GCs (Reeder & Kramer, 2005; Brunton, Russell & Douglas, 2008). Although we
573   did not assess the influence of reproductive condition on $CORT_{hair}$, a study focused on the
574   relationship between reproductive condition and $CORT_{hair}$ in wild rodents would be useful.
575   Sex differences in GC levels between seasons occur in other wild rodents and are
576   attributed to interactions between GCs and sex hormones, and differences in parental behaviour
577   (Romero et al., 2007; Schradin, 2008; Bauer et al., 2014). In addition to reproductive influences
578   on $CORT_{hair}$, higher female $CORT_{hair}$ levels could be attributed to increased aggression among
579   territorial females when population density increases during the summer (Wolff, 1993). The
580   significant interaction that we observed between sex and season on $CORT_{hair}$ raises the question
581   of why males did not differ as much as females. The contrasting results between sexes shown for
582   $CORT_{feces}$ and $CORT_{hair}$ emphasize the importance of considering the timeline represented by the
583   sample material.
584
585
CONCLUSIONS
586
587   The two aims of our study were: 1. To test if white-footed mice in the Thousand Islands
588   display characteristics of island syndrome, including greater body mass and higher relative
589   abundance than their mainland counterparts, and 2. To test if there were also differences in stress
590   physiology between island and mainland mice. Local populations of white-footed mice in the
591   Thousand Islands did not differ systematically in their abundance, body mass, or hair and fecal

592   GC levels, compared with white-footed mice on the nearby mainland. We suggest this may be
593   due to the relatively short distances between the islands and the mainland, the clustered nature of
594   the islands, and that the St. Lawrence River freezes during the winter allowing for possible
595   movement of mice and predators between islands and the mainland. Because we found no island-
596   mainland differences in either body mass or GCs, our results leave open the possibility that on
597   more isolated islands, where the community structure is distinctly different from mainland
598   habitats, decreased interspecific competition and predation may cause changes in the stress
599   physiology of rodents. However, such studies would need to account for the many variables
600   (temperature, precipitation, and day length) that differ between more distantly-spaced island and
601   mainland habitats. Although our initial predictions were not supported, our incidental findings of
602   a relationship between body mass and $CORT_{hair}$, and that measures of stress differed with sex,
603   season, and matrix (hair or feces) emphasizes the complexity of inferring physiological state
604   from hormonal profiles.
605
606

607   ## ACKNOWLEDGEMENTS
608   We thank Chantelle Penny, Tess Ward and Don Stewart for assistance with field work, Christine
609   Gillman and Stephanie Matteer for assistance with hormone analysis, Gabriel Huebsch for
610   guidance with spatial analysis and map-making, and Aaron Shafer, Jeff Bowman, Jim Schaefer,
611   and three anonymous referees for comments on previous drafts of the manuscript.
612

613   ## ADDITIONAL INFORMATION AND DECLARATIONS
614
615

616   **Author Contributions**
617   - Nathan D. Stewart designed and conducted the field program, processed samples,
618   analyzed the data, prepared the figures and tables, authored the drafts, and approved the
619   final draft.
620   - Gabriela F. Mastromonaco supervised the hormone analyses, and reviewed the data and
621   manuscript drafts, and approved the final draft.
622   - Gary Burness designed the experiments, edited drafts, and approved the final draft.
623

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Factors predicting relative abundance of white-footed mice captured over two years, for two separate models (island- mainland comparison, and among-islands comparison).

Linear-mixed effects models were used for analysis (random effect: sampling site, nested within habitat type) of variation between island and mainland sites, and among islands in response to geographic variables. Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Models were reduced by removing all non-significant two-way interactions.

1 **Table 1. Factors predicting relative abundance of white-footed mice captured over two**

2 **years, for two separate models (island- mainland comparison, and among-islands**

3 **comparison).**

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	16 640	4.801	34	3.47	0.001	0.23, 0.68
	Habitat (mainland)	2.60	5.90	13	0.44	0.667	
	Year (2016)	-8.88	3.27	22	-2.72	**0.012**	
	Season (summer)	7.16	3.15	22	2.27	**0.033**	
Island mice	Intercept	40.00	32.05	8	1.248	0.244	0.27, 0.76
	Year (2016)	-11.86	4.08	14	-2.91	**0.011**	
	Season (summer)	7.48	4.05	14	1.85	0.085	
	Log_{10} (Area)	2.72	5.03	7	0.54	0.603	
	Log_{10} (Distance)	-8.86	11.00	8	-0.81	0.442	

4 Linear-mixed effects models were used for analysis (random effect: sampling site, nested within

5 habitat type) of variation between island and mainland sites, and among islands in response to

6 geographic variables. Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are

7 provided. Models were reduced by removing all non-significant two-way interactions.

Factors predicting body mass of white-footed mice during summer (July-August) in two years, for two separate models (island-mainland comparison, and among-islands comparison).

Linear-mixed effects models were used for analysis (random effect: sampling site, nested within habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Models were reduced by removing all non-significant two-way interactions.

1   **Table 2. Factors predicting body mass of white-footed mice during summer (July-August)**

2   **in two years, for two separate models (island-mainland comparison, and among-islands**

3   **comparison).**

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	2.985	0.02	17	133.04	< 0.0001	0.02, 0.04
	Habitat (Mainland)	-0.008	0.03	9	-0.25	0.804	
	Sex (Male)	0.052	0.02	295	2.34	**0.020**	
	Year (2016)	-0.004	0.02	292	-0.16	0.875	
Island mice	Intercept	2.826	0.14	8	19.6	< 0.0001	0.04, 0.04
	Sex (Male)	0.061	0.03	203	2.37	**0.019**	
	Log_{10} (Area)	0.014	0.02	5	0.76	0.476	
	Log_{10} (Distance)	0.048	0.05	8	0.91	0.385	
	Year (2016)	-0.017	0.03	203	-0.61	0.545	

4   Linear-mixed effects models were used for analysis (random effect: sampling site, nested within

5   habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Models

6   were reduced by removing all non-significant two-way interactions.

Factors predicting hair corticosterone of white-footed mice during summer (July-August) in two years, for two separate models (island- mainland comparison, and among-islands comparison).

Linear-mixed effects models were used for analysis (random effect: sampling site, nested

within habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided.

Models were reduced by removing all non-significant two-way interactions.

1 **Table 3. Factors predicting hair corticosterone of white-footed mice during summer (July-**

2 **August) in two years, for two separate models (island- mainland comparison, and among-**

3 **islands comparison).**

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	2.812	0.539	253	5.216	< 0.0001	0.05, 0.14
	Habitat (mainland)	-0.104	0.120	10	-0.86	0.4080	
	CPUE (Corrected)	-0.004	0.004	20	-0.89	0.3837	
	Sex (Male)	-0.003	0.064	261	-0.05	0.9611	
	Year (2016)	0.051	0.078	104	0.65	0.5159	
	Ln Body Mass	0.568	0.172	261	3.31	**0.0011**	
Island mice	Intercept	2.824	0.923	15	3.06	0.0075	0.07, 0.16
	Sex (Male)	-0.003	0.077	179	-0.04	0.9713	
	CPUE (Corrected)	-0.002	0.005	6	-0.45	0.6675	
	$\log_{10}$ Isl. Area	0.076	0.097	3	0.79	0.4807	
	$\log_{10}$ Isl. Distance	-0.134	0.243	4	-0.55	0.6092	
	Year (2016)	0.077	0.110	19	0.70	0.4934	
	Ln Body Mass	0.631	0.211	179	3.00	**0.0031**	

4 Linear-mixed effects models were used for analysis (random effect: sampling site, nested within

5 habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Models

6 were reduced by removing all non-significant two-way interactions.

Factors predicting fecal corticosterone metabolites of white-footed mice during summer (July-August) in two years, for two separate models (island- mainland comparison, and among-islands comparison).

Linear-mixed effects models were used for analysis (random effect: sampling site, nested within habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Both models were reduced by removing all non-significant two-way interactions, relative abundance, and ln-transformed body mass.

1   **Table 4. Factors predicting fecal corticosterone metabolites of white-footed mice during**

2   **summer (July-August) in two years, for two separate models (island- mainland**

3   **comparison, and among-islands comparison).**

Dataset	Fixed effect	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	5.695	0.779	12	73.13	< 0.0001	0.25, 0.31
	Habitat (Mainland)	0.022	0.12	10	0.18	0.8578	
	Sex (Male)	-0.136	0.07	201	-1.98	**0.0492**	
	Year (2016)	0.620	0.07	204	8.27	**< 0.0001**	
Island mice	Intercept	5.960	0.489	7	12.18	< 0.0001	0.21, 0.25
	Sex (Male)	-0.108	0.07	153	-1.52	0.1320	
	Year (2016)	0.533	0.08	154	6.52	**< 0.0001**	
	Log_{10} Isl. Area	-0.002	0.03	4	-0.07	0.9440	
	Log_{10} Isl. Distance	-0.039	0.08	6	-0.50	0.6320	

4   Linear-mixed effects models were used for analysis (random effect: sampling site, nested within

5   habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. Both

6   models were reduced by removing all non-significant two-way interactions, relative abundance,

7   and ln-transformed body mass.

Factors predicting seasonal variation in hair corticosterone of white-footed mice captured in spring (May-June) and summer (July-August) 2016.

A linear-mixed effects model was used for analysis (random effect: sampling site, nested within habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. The results from the full model are presented.

2 **Table 5. Factors predicting seasonal variation in hair corticosterone of white-footed mice**

3 **captured in spring (May-June) and summer (July-August) 2016.**

Fixed effect	β	se	df	t	p	R^2_{GLMM} (M), (C)
Intercept	1.258	0.596	138	2.11	0.037	0.22, 0.35
Sex (Male)	0.553	0.117	136	4.73	**< 0.0001**	
Season (Summer)	0.472	0.119	137	3.96	**0.0001**	
Ln Body Mass	0.891	0.186	136	4.78	**< 0.0001**	
Sex x Season	-0.496	0.145	135	-3.41	**0.0009**	

4 A linear-mixed effects model was used for analysis (random effect: sampling site, nested within

5 habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. The

6 results from the full model are presented.

Factors predicting seasonal variation in fecal corticosterone metabolites of white-footed mice captured during spring (May-June) and summer (July-August) 2016.

A linear-mixed effects model was used for analysis (random effect: sampling site, nested within habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. The model was reduced by removing all non-significant two-way interactions and ln-transformed body mass.

2 Table 6. Factors predicting seasonal variation in fecal corticosterone metabolites of white-

3 footed mice captured during spring (May-June) and summer (July-August) 2016.

Fixed effect	β	se	df	t	p	R^2_{GLMM} (M), (C)
Intercept	5.90	0.09	39	64.75	< 0.0001	0.30, 0.44
Sex (Male)	0.12	0.08	62	1.40	0.168	
Season (Summer)	0.45	0.09	67	5.13	**< 0.0001**	

4 A linear-mixed effects model was used for analysis (random effect: sampling site, nested within

5 habitat type). Marginal (M) and conditional (C) pseudo R^2 (R^2_{GLMM}) values are provided. The

6 model was reduced by removing all non-significant two-way interactions and ln-transformed

7 body mass.

Figure 1

Trapping locations of white-footed mice (*Peromyscus leucopus*) in Thousand Islands National Park, Ontario, Canada (USGS, 2016).

Islands on which trapping occurred are shaded in dark grey. Abbreviations: AI – Aubrey Island, BI – Beau Rivage Island, CE – Constance Island, CI – Camelot Island, EP – Escot Property, GA – Georgina Island, GI – Grenadier Island, HI – Hill Island, JC1 - Jones Creek 1, JC2 – Jones Creek 2, LB – Landon Bay, LI – Lindsay Island, MD – McDonald Island, MI – Mermaid Island, MT – Mallorytown, and TI – Thwartway Island.
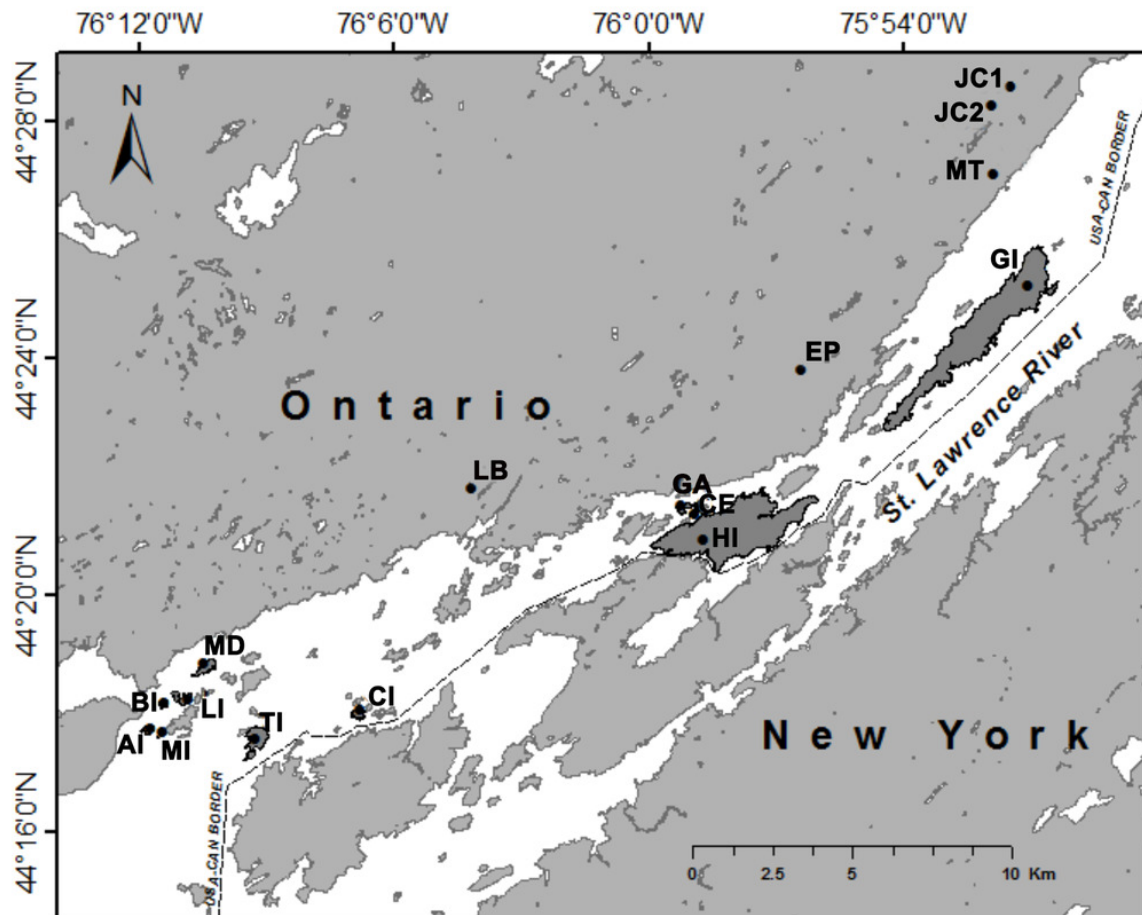
Figure 2

Correlation between years in abundance of white-footed mouse (*Peromyscus leucopus*) at multiple trapping locations.

All trapping occurred in Thousand Islands National Park, Canada. The solid black line represents the linear relationship in abundance between the two years and the dashed line represents the predicted line if abundances were equal between years. Points that fall on the dotted line represent sites where abundance was nearly equal for white-footed mice between the two years. Abundance was measured in catch-per-unit-effort (CPUE, captures per 100 trap nights), which was corrected for tripped traps. Abbreviations represent individual sampling locations and correspond with those in Figure 1.
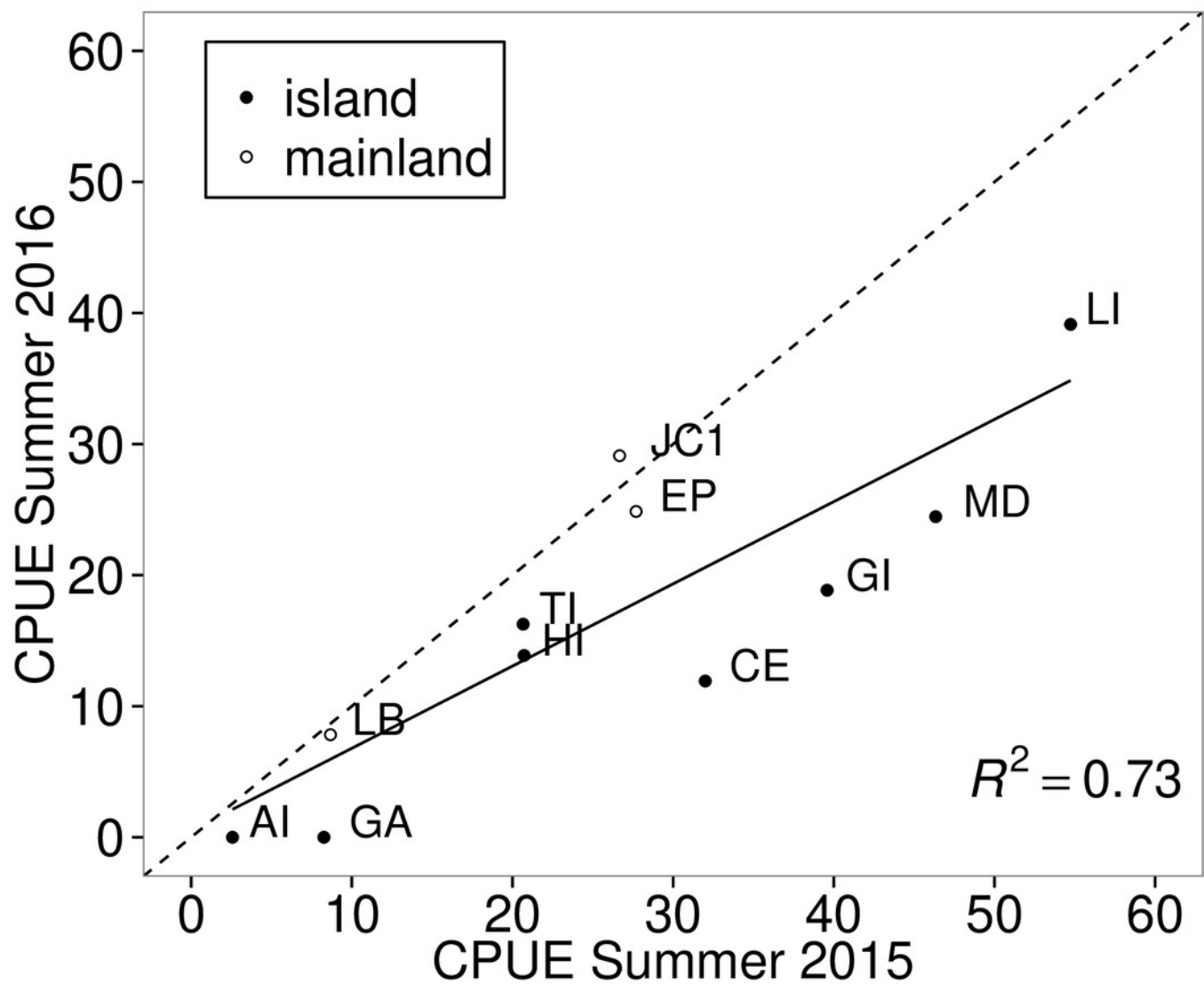
Figure 3

Body mass (A), hair corticosterone (B), and fecal corticosterone metabolites (C) of white-footed mice captured during the summer (July-August) in two consecutive years.

Body mass was measured in grams, and both measures of CORT were measured in ng/g. All response variables were ln-transformed.
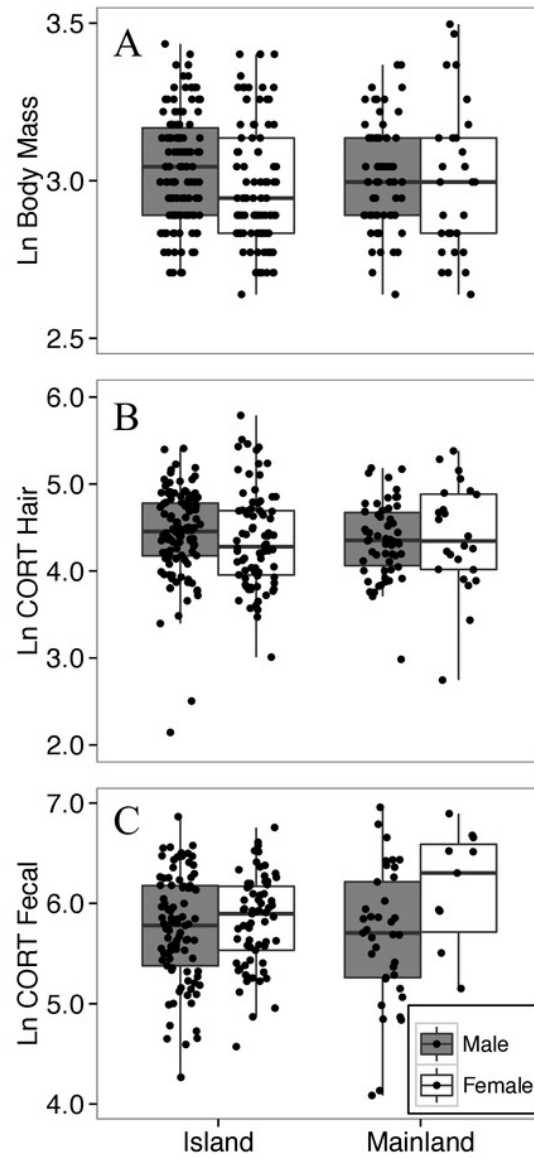
Figure 4

Hair corticosterone (CORT$_{hair}$; measured in ng/g and ln-transformed) levels increased with body mass in white food mice captured over two years in the Thousand Islands National Park, Canada.

The solid line shows a simple regression line; however, the relationship was tested within a linear mixed effects model. Body mass was measured in grams, and CORT$_{hair}$ was measured in ng/g. Both measures were ln-transformed.
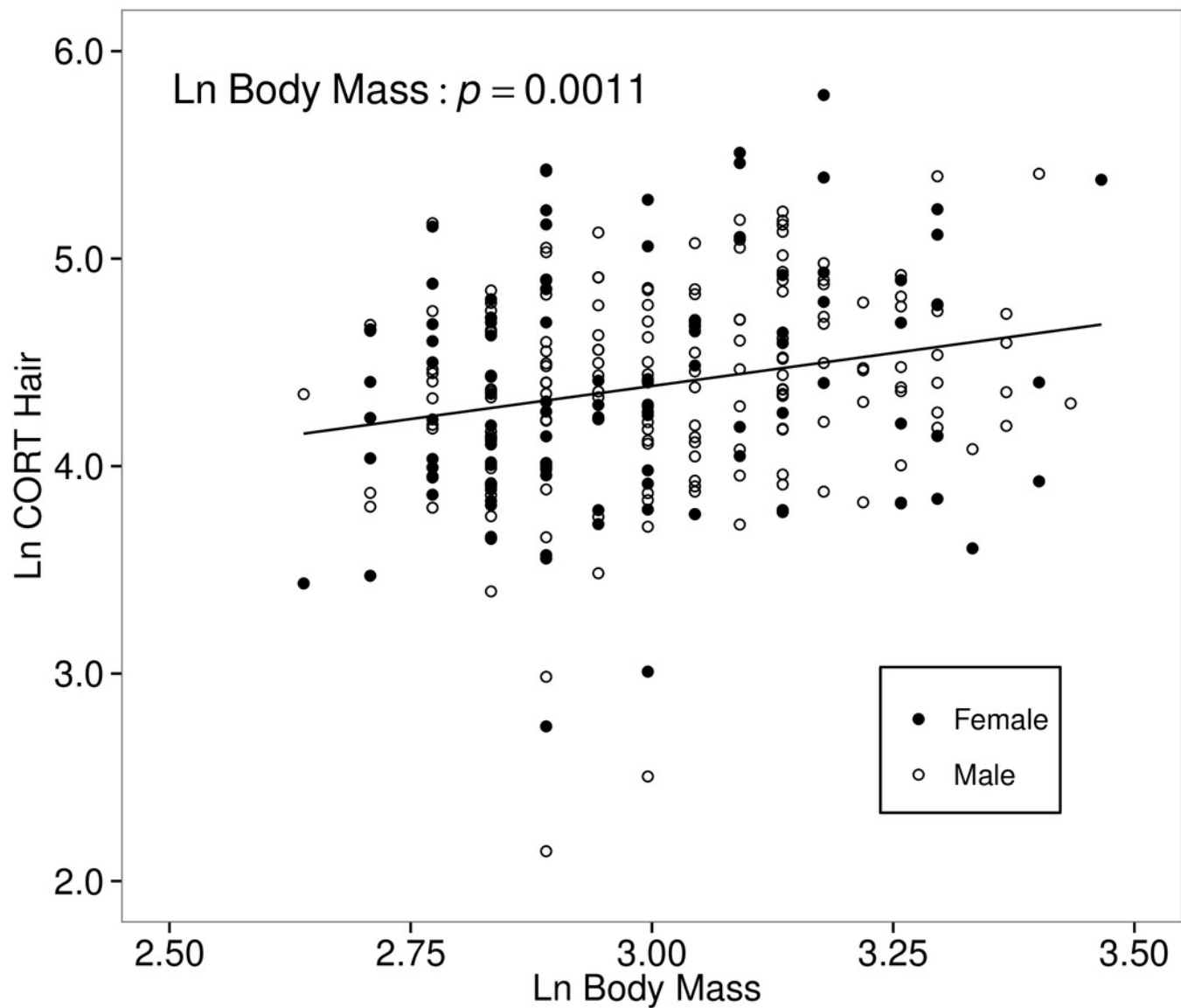
Figure 5

Seasonal variation in (A) hair corticosterone ($CORT_{hair}$), and (B) fecal corticosterone metabolites ($CORT_{fecal}$) from white-footed mice captured in spring and summer, 2016.

Females had lower hair corticosterone levels in the spring (May-June) than in the summer (July-August) (sex*season interaction; $p < 0.0009$; A), while both sexes had lower fecal corticosterone metabolites in spring than summer ($p < 0.0001$; B). Both CORT measures were quantified in ng/g and ln-transformed.
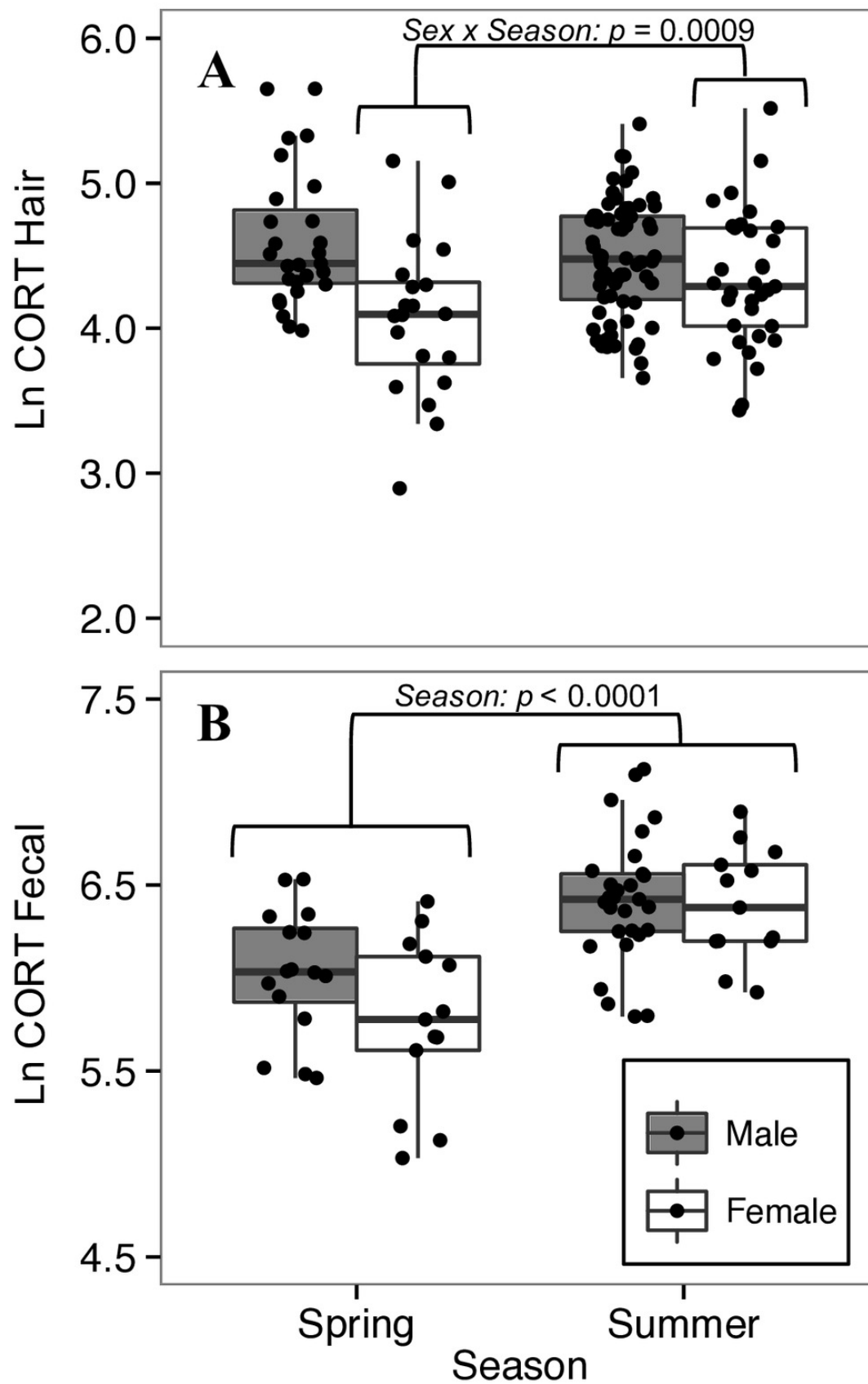
Figure 6

Correlation between hair corticosterone levels and fecal corticosterone metabolites for white-footed mice (n = 180) captured in the Thousand Islands National Park, Canada.

Both CORT measures were quantified in ng/g and ln-transformed.