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

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

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

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ABSTRACT

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

INTRODUCTION

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

with changes in food availability on islands, small mammals evolve towards gigantism upon arrival to islands while larger species often display dwarfing (Lomolino, 2005; Lomolino et al., 2012). This pattern, observed across numerous archipelagos, contributes to the evolutionary trend called the "island rule" (Van Valen, 1973). Rodents have featured prominently in studies concerning the island rule, and the combination of increased body size with changes in behaviour and demography has been referred to as "island syndrome" in rodents (Adler & Levins, 1994). Although morphological and behavioural traits associated with island syndrome have been relatively well-characterized, few studies have focused on the effect of island life on stress physiology (but see Clinchy et al., 2004; Müller et al., 2007).

When an animal encounters a perceived stressor, its hypothalamic-pituitary-adrenal (HPA) axis is activated, resulting in increased secretion of glucocorticoid hormones (GCs; Sapolsky, Romero & Munck, 2000). Multiple environmental factors can influence GC levels, including predation (Clinchy et al., 2011; Sheriff, Krebs & Boonstra, 2011), food availability (Kitaysky, Wingfield & Piatt, 1999; Walker, Wingfield & Boersma, 2005), and population density (Dettmer et al., 2014; Blondel et al., 2016). Elevated GC levels are involved in preparation for future stressors by shifting resources from reproduction and digestion toward replenishing energy stores used during the initial stress response (Romero & Wingfield, 2016). Although short-term elevations of GCs are presumed to be adaptive, a sustained, chronic increase in GCs can result in allostatic and/or homeostatic overload, with negative health and fitness implications (McEwen & Wingfield, 2003).

In wildlife studies, stress has traditionally been evaluated by quantifying circulating GC levels from blood samples (Sapolsky, 1982; Wingfield, Smith & Farner, 1982). However, there is increasing interest in quantifying GCs from less-invasive alternative sources, including saliva, feces and hair (Sheriff et al., 2011). Importantly, combining measures of GC levels in different matrices allows for stress to be evaluated over different time scales (Mastromonaco et al., 2014). For example, while fecal GC metabolites provide an integrative biomarker of HPA activity over several hours prior to collection of fecal samples (Good, Khan & Lynch, 2003), hair GC concentrations provide a measure of GC levels over the time required for the sampled length of hair to grow, which may be weeks or months, depending on the species (Sheriff et al., 2011). Although concerns have been raised regarding interpretation of both fecal (Goymann, 2012) and hair GCs (Sharpley, Kauter & McFarlane, 2009; Keckeis et al., 2012; Stewart et al., 2018), a meta-analysis suggests they are useful metrics for quantifying an individual's response to environmental stressors (Dantzer et al., 2014).

Hair GC levels are influenced by both internal and external factors (Romero & Wingfield, 2016; Heimbürge, Kanitz & Otten, 2019). Hair GC levels vary within individuals between body regions (Macbeth et al., 2010; Acker, Mastromonaco & Schulte-Hostedde, 2018) and among individuals by age (Dettmer et al., 2014), body size (Waterhouse et al., 2017),

condition (Cattet et al., 2014), sex (Stewart et al., 2018), food availability (Cattet et al., 2014) and season (Martin & Réale, 2008). Further, a study of captive rhesus macaques showed that hair GC levels increased with population density (Dettmer et al., 2014). Fecal GC levels are also influenced by internal and external factors in wild mammals (Hayssen, Harper & DeFina, 2002; Smith et al., 2012; Mastromonaco et al., 2014). Although these factors were not primary focuses for our study, our analysis demonstrated interesting relationships between GC levels and several factors, which we will report in the interest of stimulating further research.

Many of the ecological factors shown to affect GC levels in wildlife (e.g., predation, competition, and resource availability) are also thought to account for island syndrome in rodents (see Adler & Levins, 1994). Therefore, we tested the hypothesis that island syndrome includes changes in stress physiology. To test this hypothesis, we compared corticosterone (the primary GC in mice and rats) in hair ($CORT_{hair}$), and its metabolites in feces ($CORT_{feces}$), of white-footed mice (*Peromyscus leucopus*) captured at multiple island and mainland locations in a near-shore archipelago; from sites in Thousand Islands National Park in Ontario, Canada. We predicted that if white-footed mice in the Thousand Islands were more abundant and larger than mainland mice (as expected by "island syndrome"), then island mice would also have lower $CORT_{hair}$ and $CORT_{feces}$ levels. Because aspects of island syndrome in rodents are affected by island area and distance from the mainland (Adler & Levins, 1994), we also predicted that white-footed mice would have lower GC levels on the smaller and more isolated islands in the archipelago. Finally, we evaluated how body mass affected CORT in white-footed mice, and whether CORT varied between seasons and with population density.

MATERIALS & METHODS

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

Study species and location

The white-footed mouse is a small, nocturnal rodent that inhabits deciduous and mixed forests in the eastern United States and southern edge of Canada, and is the most abundant small mammal in the Thousand Islands (Werden et al., 2014). All trapping locations were located in Thousand Islands National Park in Ontario, Canada (Figure 1). We trapped on 11 islands and at 5 mainland sites during two years (2015 and 2016). Mainland sites were located within 2 km of the St. Lawrence River (Figure 1). We targeted wooded areas as opposed to open fields both to maintain consistency and to increase trapping success. Island area and distance from the mainland were calculated using ArcMap (Version 10.4.1; see Table S1).

Small mammal trapping

We trapped during three periods: summer 2015 (July – August), spring 2016 (May-June) and summer 2016 (July – August). Sherman live-traps (H.B. Sherman Traps, Inc.,Tallahassee, FL, USA) were set 10 m apart in rectangular grids of varying size. The majority of grids were arranged in a 7 by 7 formation (49 traps in total), however some areas on small islands were limited by pedestrian paths, which necessitated using smaller grids (5 by 5), or in one case, transects (Mermaid Island). Hulled sunflower seeds were used as bait and natural cotton bedding was provided for warmth. Traps were set in the evening (ca. 1800 h) and checked in the morning (ca. 0700 h) to target the active period of white-footed mice. Trapping periods generally consisted of 2-4 nights of consecutive trapping.

Upon capture, white-footed mice were weighed (± 1 g) and a patch of hair (ca. 1 x 1 cm) was shaved from the rump of each individual, above the right-hind limb using an electric razor (Remington™ Model PG6025), collecting the entire length of each shaft from the skin to the distal end of the shaft. We standardized the shaving location because hair GC levels can vary among body regions (Macbeth et al., 2010; Acker, Mastromonaco & Schulte-Hostedde, 2018). Each white-footed mouse was ear-tagged to recognize recaptured individuals, and then released. The razor blades were cleaned with alcohol swabs between shaving each animal. Hair samples were stored in Fisherbrand™ Snap-Cap™ Flat-Top Microcentrifuge Tubes in the dark at ambient temperature (approx. 22°C) until hair hormone analysis (2-5 months later). Coat colour and stage was occasionally noted (grey, brown, reddish-brown or moulting) in 2015, and always noted in 2016. We excluded juveniles from analyses based on their grey pelage. In absence of field notes of pelage, we excluded individuals ≤14 g, following the age group classification used for *Peromyscus* (Adler & Tamarin, 1984), and also based on the body mass distributions of individuals of each coat color (N. Stewart, unpublished data).

White-footed mouse feces were collected from traps using forceps. Fecal samples were stored in Fisherbrand™ Snap-Cap™ Flat-Top Microcentrifuge Tubes and placed in a cooler with ice packs until they could be stored in a liquid nitrogen-cooled dry-shipper (within 6 h of collection). Soiled traps were cleaned with 70% ethanol between uses to ensure that the feces collected from each trap belonged to the animal caught in the trap that night. Samples were then transferred to a -80C freezer until hormone extraction (2-9 months in freezer).

Relative Abundance

As a proxy for the population density, we calculated relative abundance of white-footed mice at each site during each of the 3 trapping periods. Relative abundance was calculated as catch-per-unit-effort (CPUE), presented in number of white-footed mice captured per hundred trap-nights. We corrected for tripped traps following the correction factor equation (Nelson & Clark, 1973).

This approach has been widely used in other studies of small mammal ecology (Parker et al., 2016; Gill et al., 2018; Fauteux et al., 2018).

Hormone extraction and analysis

Hair corticosterone ($CORT_{hair}$) and fecal corticosterone metabolites ($CORT_{feces}$) were extracted with methanol (100% for hair, 80% for feces) following Mastromonaco et al. (2014) and Stewart et al. (2018). The supernatants from extracted hair and fecal samples were stored sealed at -20C for 1-9 months until they were evaporated and analyzed. Dried-down hair extracts (600 µl per sample) were reconstituted in 150 µl EIA buffer resulting in a 4-fold concentration. Dried-down fecal extracts (200 µl per sample) were reconstituted in 200 µl EIA buffer and diluted for a final 1:20 dilution.

To quantify hair CORT and fecal CORT metabolites, we used an enzyme immunoassay (EIA) following methods described by Baxter-Gilbert et al. (2014). In brief, antibody-coated microtitre plates (goat anti-rabbit IgG polyclonal antibody, 1:200,000 (Sigma-Aldrich, Mississauga, ON, Canada)) were loaded with corticosterone standard (Steraloids Q1550; 39–10,000 pg/ml), reconstituted extracts and controls, followed by horseradish peroxidase conjugate (1:1,000,000) and corticosterone antiserum (1:200,000) (C. Munro, University of California, Davis, CA, USA), all diluted in EIA buffer. The assay cross-reactivities are: corticosterone (100%), desoxycorticosterone (14.25%), and other GC metabolites (<3%) (Watson et al. 2013). Inter- and intra-assay CV's were 13.9% and 4.4%, respectively. Samples were run as duplicates, and only samples with < 10% CV were accepted. Because CORT is the dominant GC in white-footed mice, but is highly metabolized prior to excretion (Touma et al 2003), we refer to the values obtained from fecal analysis by EIA as fecal CORT metabolites. All hormone concentrations are described as ng of CORT / g of feces or hair.

Statistical analysis

We began by testing our predictions that island mice would show higher relative abundance and greater body mass than mainland mice. We then tested the predictions that $CORT_{hair}$ and $CORT_{feces}$ of mice would be lower on islands than on the mainland. We also evaluated whether island geography (island area and distance from the mainland) affected relative abundance, body mass and GC levels. For analyses of relative abundance, body mass, $CORT_{hair}$, and $CORT_{feces}$ data from the summers (July-August) of both 2015 and 2016 were included. Analyses of seasonal differences were performed using data for 2016 only, because we did not collect data in spring 2015. All corticosterone and body mass data were ln-transformed, and island area and distance to the mainland were $\log_{10}$ transformed in all analyses to improve the normality of model residuals. Any visibly pregnant females (n = 15) were excluded from all analyses, with the

exception of relative abundance. If an individual was captured more than once, only data from the first capture were used.

We used linear-mixed models to test our predictions. Depending on the specific analyses, fixed effects included habitat type (island or mainland), year (2015 or 2016), season (spring or summer), and sex. When evaluating factors potentially affecting GC levels, body mass, CPUE and, in the case of among island analyses, island size (ha) and distance from the mainland (m), were included as covariates. In island-mainland comparisons, sampling site (island or mainland location) was included as a random effect and nested within habitat type. In all analyses, two-way interactions were included in initial models for those variables that were determined to be relevant based on *a priori* knowledge and preliminary analysis, including habitat x sex, habitat x season, sex x season, and island size x distance from the mainland. To reduce model complexity, non-significant two-way interactions and fixed effects ($p > 0.05$) were dropped to test the variables of greatest interest. Two-way interactions were dropped first based on largest p-values, and then sequentially for other variables. Habitat type, sex, year, and island size and distance for the mainland (for among island analyses), were always retained, with the exception of testing seasonal variation. We present results from full models (not including interactions) if model reduction did not result in significance of main effects.

Analyses were conducted using RStudio (Version 0.99.484, RStudio, Inc). Linear-mixed effects models were fit with the lmer function of the "lme4" package using restricted maximum likelihood (REML). Results, including *p*-values, *t*-values, and Satterthwaite approximations to degrees of freedom, were obtained using the "summary" function of the "lmerTest" package (Kuznetsova, Brockhoff & Christensen, 2016). Goodness of fit was assessed using marginal $_{(M)}$ and conditional $_{(C)}$ pseudo R^2 values (R^2_{GLMM}; Nakagawa & Schielzeth, 2013) calculated with the "r.squaredGLMM" function in the "MuMIn" package (Bartoń, 2016). $R^2_{GLMM(M)}$ represents the proportion of the variation explained by the fixed effects alone, and $R^2_{GLMM(C)}$ represents the proportion of variation explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013). Correlations were tested using the "cor.test" function in R, which calculates a *p*-value based on Fisher's Z transformation.

RESULTS

We caught 408 individual white-footed mice during 2015-2016; 17 individuals were recaptured between trapping periods. Trapping success was highly variable across sampling sites, and there were no consistent trapping patterns between mainland and island sites. For example, based on overall CPUE, trapping was more successful on some islands than on the mainland (as would be predicted via the "island rule"); however, on some islands there were zero captures during some trapping periods while mainland sites always yielded captures (Table S1). More traps were tripped at island sites (mean ± SD; 38% ± 10.8%) than mainland sites (23% ± 12.8%), and it was

likely that trap disturbance contributed to the high degree of variation in trapping success across habitat types.

Relative abundance of mice did not differ between islands and the mainland

Contrary to expectations of the island rule, there was no difference in relative abundance of island and mainland white-footed mice (Habitat: $p = 0.667$, Table 1). Relative abundance differed between years; it was 44% higher in summer 2015 than in summer 2016 across both habitat types (Year: $p = 0.012$; Table 1). In 2016, in which we had data for both spring and summer, relative abundance was 74% higher in the summer than the spring (Season: $p = 0.033$; Table 1). Summer abundance of individual sampling sites was positively correlated between years (n = 11, r = 0.852, $t_9 = 4.87$, $p < 0.001$; Figure 2).

Focusing only on island sites, there was no effect of island area ($p = 0.603$, Table 1) nor distance from the mainland ($p = 0.442$) on relative abundance of white-footed mice. More individuals were captured on islands in 2015 than 2016 (Year: $p = 0.011$).

Body mass did not differ between island and mainland mice

Contrary to expectations of the island rule, white footed mice from the Thousand Islands (n = 209) were not heavier than on the mainland (n = 92; Habitat: $p = 0.804$; Table 2; Figure 3), nor did body mass differ between years (Year: $p = 0.875$). Male mice (n = 181; mean ± SD; 21.0 ± 3.7 g) were significantly heavier than females (n = 120; 20.2 ± 4.4 g) across habitat types (Sex: $p = 0.020$); however, the average difference was less than 1 g, and the model had little explanatory power ($R^2_{GLMM(M)} = 0.02$; $R^2_{GLMM(C)} = 0.04$; Table 2).

For island mice, there was no effect of island area ($p = 0.476$, Table 2) nor distance from the mainland ($p = 0.385$) on mass, and these two variables did not interact to affect body mass ($t_4 = 0.855$, $p = 0.436$). Again, males were heavier than females on islands (Sex: $p = 0.019$); however, this effect explained little variation in the model ($R^2_{GLMM(M)} = 0.04$; $R^2_{GLMM(C)} = 0.04$; Table 2).

Hair corticosterone did not differ between island and mainland mice, but increased with body mass

There was no difference between $CORT_{hair}$ of island (n = 188) and mainland (n = 82) white-footed mice (Habitat: $p = 0.408$; Table 3, Figure 3). Sex ($p = 0.961$), year of capture ($p = 0.516$), and relative abundance ($p = 0.384$) also had no effect on $CORT_{hair}$ (Table 3). However, $CORT_{hair}$ increased with body mass ($p < 0.01$; Table 3; Figure 4), suggesting possible condition-dependence. There was a small effect size for this model, and the higher conditional R^2_{GLMM} relative to the marginal R^2_{GLMM} indicates that the model had more explanatory power with the addition of the random effect (sampling site, nested within habitat) than with fixed effects alone

($R^2_{GLMM(M)}$ = 0.05, $R^2_{GLMM(C)}$ = 0.14; Table 3). This suggests that there was similarity among individuals from the same sampling sites that was not explained by the fixed effects in the model.

Focusing only on island mice, neither island area (p = 0.481, Table 3) nor distance from the mainland (p = 0.609) predicted $CORT_{hair}$ levels. However, body mass continued to be a significant predictor of $CORT_{hair}$ for the model testing only island mice ($p < 0.01$; Table 3).

Fecal corticosterone metabolites did not differ between island and mainland mice

There was no difference between $CORT_{feces}$ of island (n = 160) and mainland (n = 49) white-footed mice during the summer months (Habitat: p = 0.858; Table 4). Relative abundance also had no effect on $CORT_{feces}$ (t_{10} = 1.31, p = 0.218) and neither did body mass (t_{20} = - 0.511, p = - 0.610) so both terms were removed from the final model. The final (reduced) model for comparing $CORT_{feces}$ of island and mainland white-footed mice showed that male mice had lower $CORT_{feces}$ than females (p = 0.049; Table 4; Figure 3), and that $CORT_{feces}$ was higher in the summer of 2016 than summer 2015 ($p < 0.001$; Table 4).

There was no effect of either island area (p = 0.944, Table 4) nor distance from the mainland (p = 0.632) on $CORT_{feces}$ (Table 4). $CORT_{feces}$ levels were higher in 2016 than in 2015 (Year: $p < 0.001$), but unlike the model for the island-mainland comparison, there was no difference between sexes for $CORT_{feces}$ (p = 0.132; Table 4).

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

For $CORT_{hair}$ of white-footed mice collected in 2016 (n = 147), for which we had data from both spring and summer, there was a significant interaction between sex and season ($p < 0.01$, Table 5). Although males had on average higher $CORT_{hair}$ than females (Sex: $p < 0.001$), 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). Both sexes had lower $CORT_{feces}$ levels in spring than in summer ($p < 0.001$, 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 30.5-1239.8 ng/g, with a median of 335.4 ng/g. A simple correlational analysis suggests $CORT_{hair}$ and $CORT_{feces}$ of white-footed mice were significantly, although weakly, positively correlated ($r = 0.16$, $t_{178} = 2.196$, $p = 0.015$; Figure 6).

DISCUSSION

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

Despite the tendency for island wildlife to display morphological and physiological adaptations to insularity (Matson et al., 2014; Holding et al., 2014; Spencer et al., 2017), white-footed mice in the Thousand Islands did not differ in any of these characteristics from their mainland conspecifics. White-footed mice on islands did not display higher relative abundance than mainland mice in disagreement with the general prediction that rodents exhibit particularly high densities on islands (Adler & Levins, 1994; Crespin, Duplantier & Granjon, 2012; Cuthbert et al., 2016), which has been observed for other small vertebrates as well (Novosolov, Raia & Meiri, 2013; Sale & Arnould, 2013). These results also differ from Adler and Levins' (1994) description of island syndrome, and studies showing that island rodents are more stable, and less prone to cycling than mainland populations (Gliwicz, 1980; Herman & Scott, 1984; Tamarin & Sheridan, 1987). The stability of high population densities on oceanic islands has been partially attributed to marine resource subsidies and climate stability compared to continental systems (Stapp & Polis, 2003; Barrett et al., 2005; Sale & Arnould, 2013); which does not apply when comparing rodents on the near-shore Thousand Islands to the adjacent mainland.

Small mammals on islands often exhibit large body size (Lomolino et al., 2012; Sale & Arnould, 2013; Harper & Rutherford, 2016), however we could detect no difference in body mass between island and mainland white-footed mice in the Thousand Islands. This was surprising, because a high degree of isolation is not necessarily required for demographic (Adler, Wilson & Derosa, 1986) or body mass (Nupp & Swihart, 1996) differences among *Peromyscus* populations to occur. There was also no effect of island area or isolation on body mass of white-footed mice. These negative results regarding patterns between body size and island biogeography do not agree with results for other small mammals in the Thousand Islands. Lomolino (1984) found that the body size of meadow voles (*Microtus pennsylvanicus*) and short-tailed shrews (*Blarina brevicauda*) in the Thousand Islands increased as distance from the mainland increased. This pattern was attributed to the ability of larger individuals to cross greater distances on ice during the winter, and subsequent founder effects of large individuals reaching more distant islands (Lomolino, 1984). The islands sampled by Lomolino might have been better suited to investigating patterns related to isolation because they were less closely clustered

together than those that we sampled. The clustered nature of many of the islands in our study makes their true degree of isolation difficult to determine.

On average, we found that male white-footed mice in the Thousand Islands were heavier than females; consistent with data from laboratory raised white-footed mice (Dewsbury et al., 1980). Greater male body mass has also been found for deer mice collected in the field (Schulte-Hostedde, Millar & Hickling, 2001). Male-biased sexual size dimorphism is widespread in mammals (Isaac, 2005), and often explained by sexual selection favouring large male body size through competition between males for access to mates (Trivers, 1972).

No difference in CORT levels between island and mainland mice

We predicted that white-footed mice on islands would have lower $CORT_{hair}$ and $CORT_{feces}$ levels than mainland mice, however these predictions were not supported. There was also no effect of island size or distance from the mainland on CORT levels. This result may not be surprising, given that we found no evidence of island syndrome in white-footed mice. The lack of an island effect on any of these characteristics in the Thousand Islands suggests either that island white-footed mice experience similar stressors and pressures to mice on the mainland, or that there is a high degree of gene flow between island and mainland white-footed mice. Either of these explanations could be caused by the short distances between islands and from the islands to the mainland, and the freezing of the river in the winter.

High gene flow among islands and the mainland in the Thousand Islands could be attributed to the ability of white-footed mice to swim short distances or cross ice in the winter (Lomolino, 1989), and to disperse via transport onboard boats. Despite these dispersal mechanisms, genetic dissimilarity between *Peromyscus* populations can occur at short distances (< 500 m from mainland or large island) in other freshwater archipelagos (Landry & Lapointe, 2001; Vucetich et al., 2001). Genetic studies of white-footed mice in the Thousand Islands would provide greater understanding of the degree of similarity between separate populations in the archipelago.

Similar levels of competition and predation on islands

The proximity of these islands to the mainland, and to one another, may mean that insular white-footed mice experience similar levels of inter-specific competition to mainland mice. Although the diet of white-footed mice is based primarily on insects, they also forage heavily on seeds (Manson & Stiles, 1998). Release from competition with larger granivores, such as squirrel species (Sciuridae), could result in increased body size of *Peromyscus* (Nupp & Swihart, 1996). However, we caught red squirrels (*Tamiasciurus hudsonicus*) and flying squirrels (*Glaucomys* spp.) on near-shore islands (Constance and Georgina), and observed grey squirrels (*Sciurus carolinensis*) on more isolated islands (McDonald and Thwartway; N. Stewart, Personal

Observation). Although we did not catch eastern chipmunks on any islands, they have previously been caught on islands in the archipelago (Werden et al., 2014). Given the presence of other small mammal species, release from competition might not be a factor on these islands.

The proximity of these islands to shore might cause equal predation risk on the islands and the mainland. Small terrestrial predators, such as weasels (*Mustela* spp.), might occur in low numbers on some of the islands (Grenadier Island; Werden et al., 2014), however, avian predators can readily access islands to prey on mice. Coyotes (*Canis latrans*), red foxes (*Vulpes*), and raccoons (*Procyon lotor*) also inhabit or periodically forage on islands by crossing ice in the winter (Coleman, 1979).

Hair corticosterone increased with body mass

Body mass was a positive predictor of $CORT_{hair}$ in white-footed mice, but not $CORT_{feces}$. Body mass is positively correlated with age in *Peromyscus* (Chappell, 2003), and is often used to identify age classes in the field (Vandegrift, Raffel & Hudson, 2008). We suggest that the positive relationship between $CORT_{hair}$ and body mass indicates a relationship between moulting schedule and hormone deposition in hair. Moulting in *Peromyscus* occurs before or following energetically demanding time periods, such as breeding (Pierce & Vogt, 1993; Tabacaru, Millar & Longstaffe, 2011). Moulting is in part regulated by CORT, because steroid hormones have an inhibitory effect on moulting in *Peromyscus* (Garwood & Rose, 1995). As a result, hairs grown during complete moults might have relatively lower CORT concentrations, than replacement hairs grown during incomplete moults. This would result in heavier individuals (which are likely older and have increased in mass since their last moult) having higher $CORT_{hair}$ when compared with younger mice that have more recently grown their adult pelage.

In American pika (*Ochotona princeps*), hair CORT was strongly influenced by body size (measured by cranial diameter; Waterhouse et al., 2017), but in the opposite direction compared to white-footed mice. Larger American pikas had lower hair CORT, which the authors attributed to the negative relationship between mass-specific metabolic rate and GCs (Haase, Long & Gillooly, 2016). The conflicting directionalities of relationships between hair CORT and body size for small mammals demonstrate the need for more studies concerning internal factors affecting hair GCs.

Hair GC levels are an integrative measure of HPA activity, because they will reflect both an individual's phenotype related to their baseline GC levels (Fairbanks et al., 2011), but can also be influenced by an animal's exposure to stressors (Bryan et al., 2015; Scorrano et al., 2015). Because the two measures are representative of different time frames, it might not be surprising that CORT in hair and its related metabolites in feces are not correlated with the same measures (body mass and condition), and demonstrate different seasonal patterns. The correlation that we found between $CORT_{hair}$ and $CORT_{feces}$ ($n = 180$, $r = 0.16$, $p = 0.015$) was

similar to that reported for wild eastern chipmunks (n = 62, r = 0.25, $p = 0.055$; Mastromonaco et al., 2014). Such correlations presumably represent the influence of individuals' baseline GC levels on both $CORT_{hair}$ and $CORT_{feces}$, however, the relatively weak correlation may may reflect matrix-specific time-frames of GC secretion.

Sex-specific seasonal variation in corticosterone

Seasonal differences in GC levels are common among vertebrates (Romero, 2002). $CORT_{feces}$ levels of white-footed mice of both sexes were higher in the summer than the spring (Table 6, Figure 5B), in agreement with previous studies of *Peromyscus* (Harper & Austad, 2000, 2001). High summer $CORT_{feces}$ levels could be attributed to increased GC levels associated with reproduction (Harper & Austad, 2001), or perhaps could be caused by increased abundance of white-footed mice relative to the spring (Hayssen, Harper & DeFina, 2002).

In contrast to data for $CORT_{feces}$, only female white-footed mice showed seasonal variation in $CORT_{hair,}$, increasing from spring to summer (Table 5, Figure 5A). The contrasting sex-specific results between $CORT_{feces}$ and $CORT_{hair}$ patterns are likely the result of the two measures differing in their representative time-scales of CORT secretion (Mastromonaco et al., 2014). Sex differences in GC levels between seasons occur in other wild rodents and are attributed to interactions between GCs and sex hormones, and differences in parental behaviour (Romero et al., 2007; Schradin, 2008; Bauer et al., 2014). Seasonal differences could be attributed to decreased CORT during pregnancy in the spring, elevated CORT in response to lactation during the summer (Reeder & Kramer, 2005), and/or increased aggression among territorial females when population density increases during the summer (Wolff, 1993). Currently, we cannot distinguish these possibilities. However, the contrasting results between sexes shown for $CORT_{feces}$ and $CORT_{hair}$ emphasize the importance of considering the timeline represented by the sample material.

CONCLUSIONS

Local populations of white-footed mice in the Thousand Islands did not differ systematically in their abundance, body mass, or hair and fecal GC levels, compared with white-footed mice on the nearby mainland. We suggest this may be due to the relatively short distances between the islands and the mainland, the clustered nature of the islands, and that the St. Lawrence River freezes during the winter allowing for possible movement of mice and predators between islands and the mainland. Because we found no island-mainland differences in either body mass or GCs, our results leave open the possibility that on more isolated islands, where the community structure is distinctly different from mainland habitats, decreased interspecific competition and predation may cause changes in the stress physiology of rodents. However, such

studies would need to account for the many variables (temperature, precipitation, and day length) that differ between more distantly-spaced island and mainland habitats. Although our initial predictions were not supported, our incidental findings of a relationship between body mass and $CORT_{hair}$, and of that estimates of stress differed with sex, season, and matrix (hair or feces) emphasizes the complexity of inferring physiological state from hormonal profiles.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Nathan D. Stewart designed and conducted the field program, processed samples, analyzed the data, prepared the figures and tables, authored the drafts, and approved the final draft.
- Gabriela F. Mastromonaco supervised the hormone analyses, and reviewed the data and manuscript drafts, and approved the final draft.
- Gary Burness designed the experiments, edited drafts, and approved the final draft.

Animal Ethics

Animal ethics approvals were obtained by the Trent University Animal Care Committee (No. 23877 and 24341), and the Thousand Islands National Park via Parks Canada Research and Collection Permit (No. 22959).

Data Availability

Data are available for review.

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Table 1(on next page)

Factors predicting relative abundance of white-footed mice captured over two consecutive years.

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.

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

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	17 919	6584.56	22	2.72	0.012	0.23, 0.68
	Habitat (mainland)	2.60	5.90	13	0.44	0.667	
	Year	-8.88	3.27	22	-2.72	**0.012**	
	Season (summer)	7.16	3.15	22	2.27	**0.033**	
Island mice	Intercept	23945	8232.68	14	2.91	0.011	0.27, 0.76
	Year	-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	

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.

Table 2(on next page)

Factors predicting body mass of white-footed mice during summer (July-August) in two consecutive years.

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. Relative abundance was calculated as the number of individuals per hundred trap nights, corrected for trap disturbance.

Table 2. Factors predicting body mass of white-footed mice during summer (July-August) in two consecutive years.

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	10.208	45.75	292	0.22	0.824	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	-0.004	0.02	292	-0.16	0.875	
Island mice	Intercept	36.309	55.28	203	0.66	0.512	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	-0.017	0.03	203	-0.61	0.545	

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. Relative abundance was calculated as the number of individuals per hundred trap nights, corrected for trap disturbance.

Table 3(on next page)

Factors predicting hair corticosterone of white-footed mice during summer (July-August) in two consecutive years.

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.

Table 3. Factors predicting hair corticosterone of white-footed mice during summer (July-August) in two consecutive years.

Dataset	Fixed effects	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	-100.175	158.085	104	-0.63	0.528	0.05, 0.14
	Habitat (mainland)	-0.104	0.120	10	-0.86	0.408	
	CPUE (Corrected)	-0.004	0.004	20	-0.89	0.384	
	Sex (Male)	-0.003	0.064	261	-0.05	0.961	
	Year	0.051	0.078	104	0.65	0.516	
	Ln Body Mass	0.568	0.172	261	3.31	**< 0.01**	
Island mice	Intercept	-152.444	222.709	20	-0.68	0.502	0.07, 0.16
	Sex (Male)	-0.003	0.077	180	-0.04	0.971	
	CPUE (Corrected)	-0.002	0.005	6	-0.45	0.668	
	$\log_{10}$ Isl. Area	0.076	0.097	3	0.79	0.481	
	$\log_{10}$ Isl. Distance	-0.134	0.243	4	-0.55	0.609	
	Year	0.077	0.110	20	0.70	0.493	
	Ln Body Mass	0.631	0.211	179	3.00	**< 0.01**	

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.

Table 4(on next page)

Factors predicting fecal corticosterone metabolites of white-footed mice during summer (July-August) in two consecutive years.

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 reduced by removing all non-significant two-way interactions and ln-transformed body mass.

Table 4. Factors predicting fecal corticosterone metabolites of white-footed mice during summer (July-August) in two consecutive years.

Dataset	Fixed effect	β	se	df	t	p	R^2_{GLMM} (M), (C)
Island and mainland mice	Intercept	-1243.047	151.02	204	-8.23	< 0.001	0.25, 0.31
	Habitat (Mainland)	0.022	0.12	10	0.18	0.858	
	Sex (Male)	-0.136	0.07	201	-1.98	**0.049**	
	Year	0.620	0.07	204	8.27	**< 0.001**	
Island mice	Intercept	-1067.217	164.62	154	-6.48	< 0.001	0.25, 0.31
	Sex (Male)	-0.108	0.07	153	-1.52	0.132	
	Year	0.533	0.08	154	6.52	**< 0.001**	
	Log_{10} Isl. Area	-0.002	0.03	4	-0.07	0.944	
	Log_{10} Isl. Distance	-0.039	0.08	6	-0.50	0.632	

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 reduced by removing all non-significant two-way interactions and ln-transformed body mass.

Table 5(on next page)

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 model was reduced by removing all non-significant two-way interactions and the term for habitat (island or mainland).

Table 5. Factors predicting seasonal variation in hair corticosterone of white-footed mice 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	**< 0.001**	
Season (Summer)	0.472	0.119	137	3.96	**< 0.001**	
Ln Body Mass	0.891	0.186	136	4.78	**< 0.001**	
Sex x Season	-0.496	0.145	135	-3.41	**< 0.01**	

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 the term for habitat (island or mainland).

Table 6(on next page)

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 terms for habitat.

Table 6. Factors predicting seasonal variation in fecal corticosterone metabolites of white-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	< 0.001	0.30, 0.44
Sex (Male)	0.12	0.08	62	1.40	0.168	
Season (summer)	0.45	0.09	67	5.13	**< 0.001**	

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 terms for habitat.

Figure 1(on next page)

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

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.

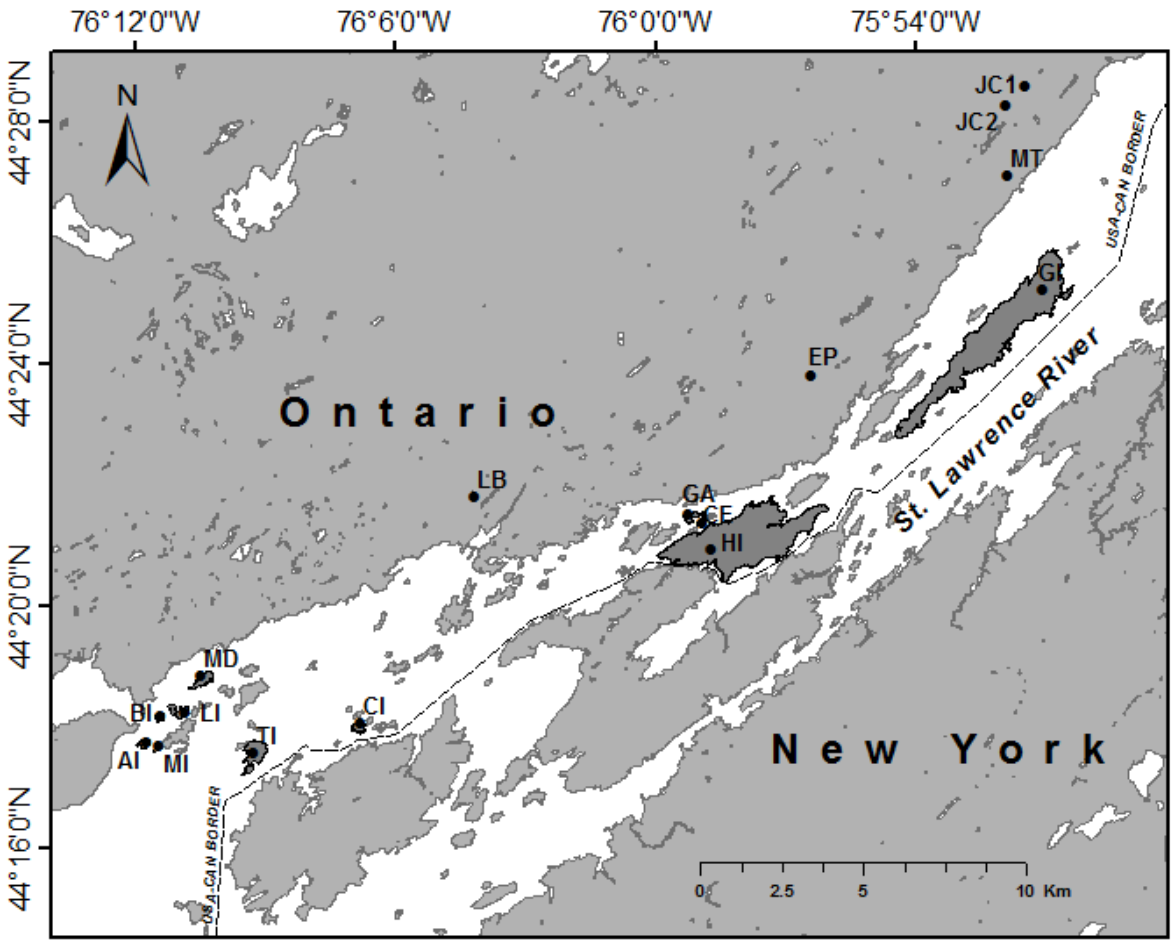

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Figure 2(on next page)

Correlation between years in abundance of white-footed mice at multiple trapping locations.

All trapping occurred in the 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. 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.

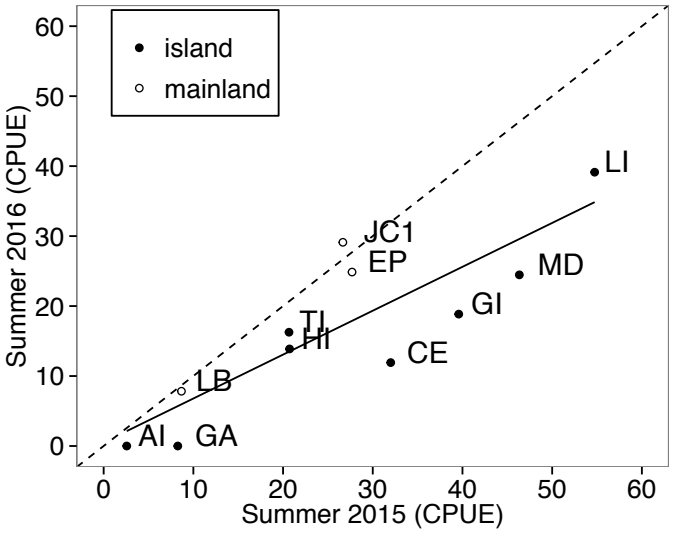

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Figure 3(on next page)

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

All data were ln-transformed

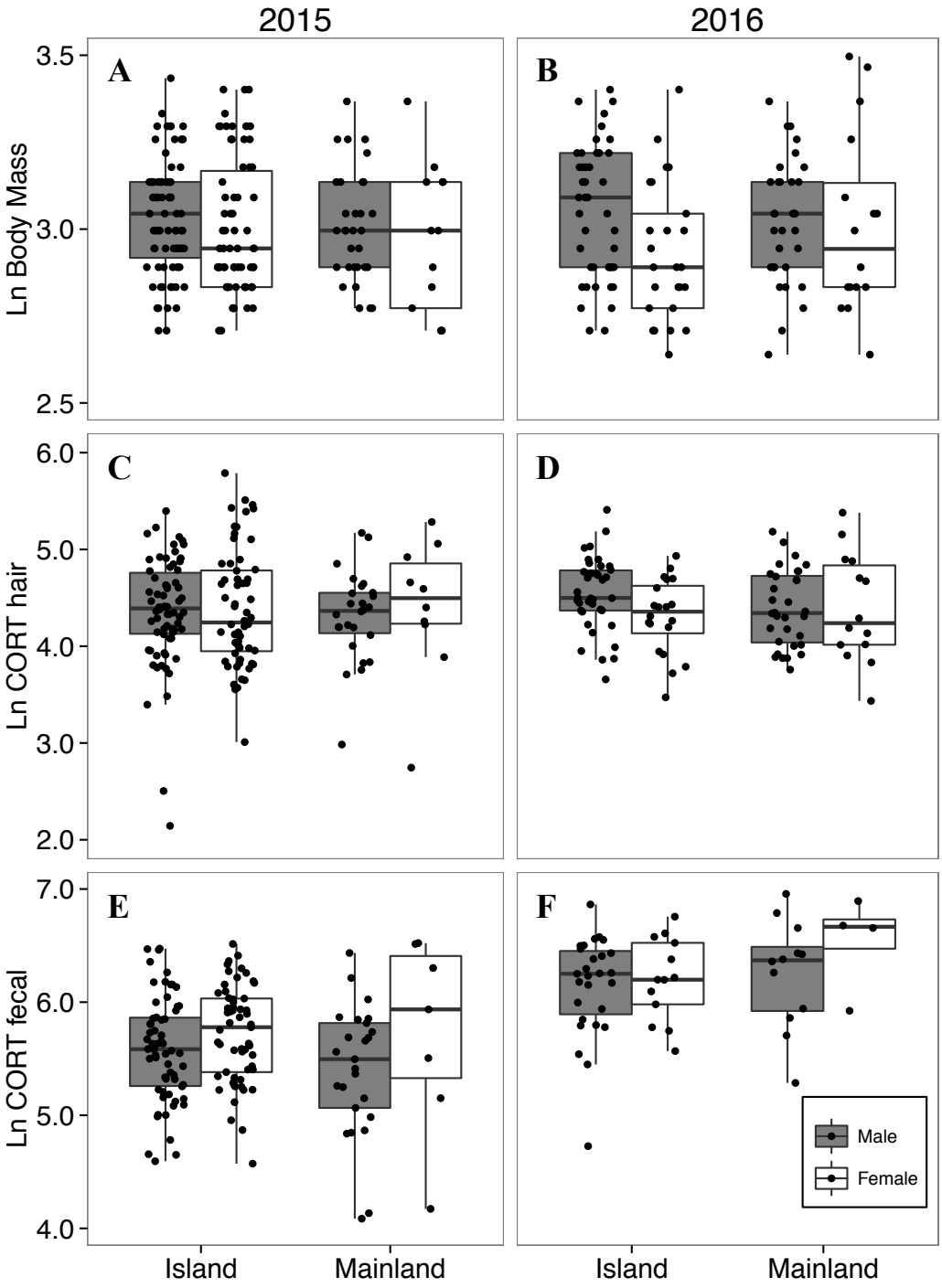

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Figure 4(on next page)

Hair corticosterone ($CORT_{hair}$) levels increased with body mass in white food mice captured over two years in the Thousand Islands National Park, Canada.

Data were ln transformed.

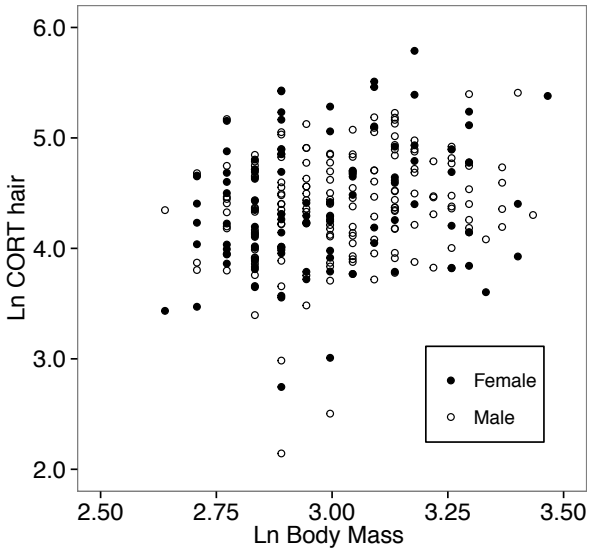

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Figure 5(on next page)

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; $p < 0.001$; A), while both sexes had lower fecal corticosterone metabolites in spring than summer ($p < 0.001$; B).

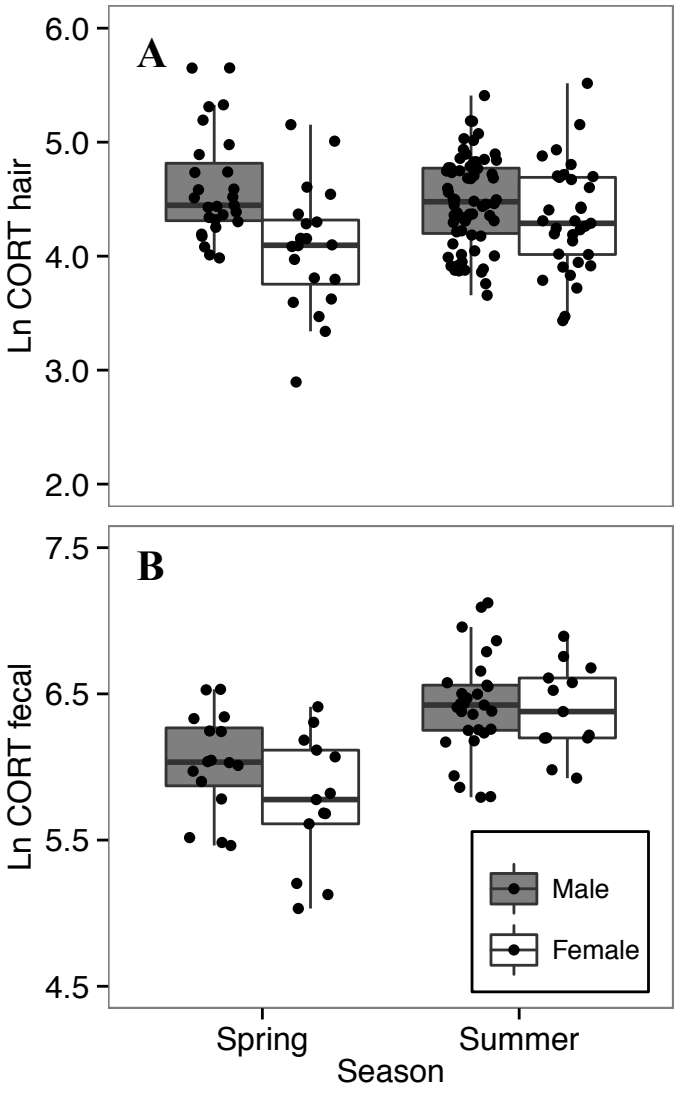

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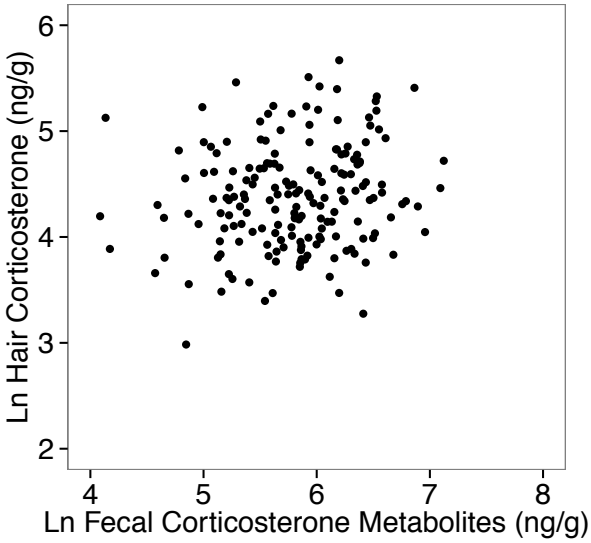
Figure 6(on next page)

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

Data were ln transformed



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