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POPULATION ECOLOGY – ORIGINAL RESEARCH

High Arctic lemmings remain reproductively active under predator-induced elevated stress

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Abstract

Non-consumptive effects of predation have rarely been assessed in wildlife populations even though their impact could be as important as lethal effects. Reproduction of individuals is one of the most important demographic parameters that could be affected by predator-induced stress, which in turn can have important consequences on population dynamics. We studied non-consumptive effects of predation on the reproductive activity (i.e., mating and fertilization) of a cyclic population of brown lemmings exposed to intense summer predation in the Canadian High Arctic. Lemmings were live-trapped, their reproductive activity (i.e., testes visible in males, pregnancy/lactation in females) assessed, and predators were monitored during the summers of 2014 and 2015 within a 9 ha predator-reduction exclosure delimited by a fence and covered by a net, and on an 11 ha control area. Stress levels were quantified non-invasively with fecal corticosterone metabolites (FCM). We found that FCM levels of lemmings captured outside the predator exclosure ($n = 50$) were 1.6 times higher than inside ($n = 51$). The proportion of pregnant/lactating adult females did not differ between the two areas, nor did the proportion of adult scrotal males. We found that lemmings showed physiological stress reactions due to high predation risk, but had no sign of reduced mating activity or fertility. Thus, our results do not support the hypothesis of reproductive suppression by predator-induced stress.

Keywords Cyclic populations · Top-down limitation · Glucocorticoids · Population regulation · Reproduction suppression

Introduction

Indirect effects of environmental factors on population dynamics have been the subject of a renewed interest since Christian's (1950) pioneering review. Individual responses to external stressors may scale up to the population level through their effects on reproduction or survival (McDonald et al. 1981; Sheriff et al. 2009) and could persist through maternal programming (Boonstra et al. 1998a; Inchausti and Ginzburg 2009; Sheriff and Love 2013). Predation and food limitation have often been identified as the most important factors affecting growth and declines in fluctuating vertebrate populations (Sinclair and Krebs 2002). Although lethal effects may be sufficient to explain population fluctuations (Gilg et al. 2003), non-consumptive effects, mediated through physiology and behavior, could also significantly affect survival and reproduction (Boonstra et al. 1998a; Bian et al. 2015).

The interaction of glucocorticoids (i.e., stress hormones) with biological processes such as immune function, growth, and survival has been shown in clinical studies of rodents

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and suggests potential trade-offs between these processes (Sapolsky et al. 2000; Whirledge and Cidlowski 2013). Repeated exposure to stressors may induce chronic stress, which can disrupt homeostasis and suppress reproduction (Takahashi et al. 1990; Boonstra et al. 1998a; Herod et al. 2010). Such suppression may be maladaptive in the short-term but may ultimately increase individual fitness through a reallocation of energy to survival (Lima 1986; Wingfield and Sapolsky 2003; Rogovin et al. 2008). For example, delayed reproduction could be favored when the chance of having offspring is maximized by investing in survival mechanisms during high predation periods (Kokko and Ranta 1996). In contrast, some studies found that chronically stressed rodents responded with increased reproductive activity or faster development of juveniles (Boonstra et al. 2001b; Dantzer et al. 2013).

A suppressive effect of stress hormones on reproduction has a strong potential to affect the population dynamics of mammals in natural settings (Sheriff et al. 2009; Bian et al. 2015). Mechanisms of reproductive suppression can be behavioral (e.g., fear and avoidance of copulation) or physiological (e.g., inhibition of reproductive hormones, poor body condition; Lima 1986; Wingfield and Sapolsky 2003). There is evidence that reproductive activity and recruitment were reduced in female snowshoe hares (*Lepus americanus*) and voles when exposed to stressful environments (Charbonnel et al. 2008; Sheriff et al. 2009; Bian et al. 2015). These studies further showed that stress experienced by females can have important consequences on subsequent generations through maternal effects, which could eventually impact population growth. Although some field studies have reported reduced reproduction in small mammals when exposed to high predation (Korpimaki et al. 1994; Jochym and Halle 2012), evidence that this effect was induced by elevated stress hormones is still scant.

Small rodents are prey to a vast spectrum of predators (Krebs 2011; Legagneux et al. 2012) and typically have elevated stress responses (i.e., elevated cortisol or corticosterone levels, change in behavior) in face of danger, which makes them ideal for studying non-consumptive effects of predation (Fletcher and Boonstra 2006; Romero et al. 2008; Monclús et al. 2009; Bosson et al. 2013). In the Arctic, cyclic lemming populations are exposed to highly fluctuating predation risk that reaches peak intensity during summer, every 3–5 years (Gilg et al. 2006; Therrien et al. 2014). Brown lemming (*Lemmus trimucronatus*) populations, for instance, can be decimated by predation within a few months during the peak summer phase (Fauteux et al. 2015). We used a large (9-ha) predator reduction exclosure, where lemmings were protected from both mammalian and avian predators to determine experimentally whether predation induces elevated stress levels in lemmings and ultimately reduces their reproductive activity. Here, reproductive activity is defined as the proportion of individuals being fertile and showing physiological signs of being reproductively active (i.e., males with testes in scrotum, lactating/pregnant females).

We collected fecal samples to measure stress levels non-invasively and monitored reproductive activity for 2 years during which lemmings were at peak density and predators were abundant. Based on the stress-induced reproduction suppression hypothesis, we predicted that: (1) lemmings in the predator-reduction area would have lower stress hormone concentrations than those on the control area exposed to natural predators; and (2) a higher proportion of reproductively active individuals would be found in the exclosure compared to the control. Alternatively, if high population density is the primary source of stress for lemmings, predictions of this hypothesis are opposite to those of the predator-induced stress hypothesis because population density will be higher in the predator-reduction grid than the control.

Materials and methods

Study area

Our study was conducted in the Qarlikturvik valley (50 km^2) of the Sirmilik National Park on Bylot Island, Nunavut, Canada (73°08′N; 80°00′W), where two rodent species coexist: brown lemmings and collared lemmings (*Dicrostonyx groenlandicus*), the latter species being less abundant. Both species fluctuate regularly in abundance but brown lemmings have much higher amplitude cycles, which can be up to 100-fold between low and high abundance years (Fauteux et al. 2015). Lemmings are also exposed to highly fluctuating predation pressure that is driven by their own abundance (Gilg et al. 2003; Therrien et al. 2014). During summer, the main predators of lemmings are the arctic fox (*Vulpes lagopus*), ermine (*Mustela erminea*), snowy owl (*Bubo scandiacus*), long-tailed jaeger (*Stercorarius longicaudus*), and rough-legged hawk (*Buteo lagopus*). In winter, only foxes and ermine reside on the island.

Both lemmings occupy the two main habitats of the valley (Duchesne et al. 2011). The wet habitat is characterized by a mosaic of tundra polygons, ponds, and thaw lakes and is found mainly in the valley bottom. Sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*) mainly compose the vegetation of the wet meadows. Mesic habitats cover higher grounds in the valley and the surrounding slopes and hills due to better drainage. The mesic habitat is the most abundant and is primarily composed of prostrate shrubs (*Salix* spp., *Cassiope tetragona*), grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs

(*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such as *Polytrichum swartzii*).

Experimental design and lemming trapping

We used two live-trapping grids for this study. Both have been monitored since 2008 and are located in mesic habitat. In 2012–2013, we built an 8.6-ha predator-reduction exclosure around one grid and left the other as the control. The exclosure was made of a 1.2 km fence made of chicken wire (1-inch mesh) that was 1.4 m high (2.0 m when crossing snow drift areas), which allowed movements of lemmings in and out of the predator exclosure. The chicken wire was attached to T-shaped steel bars around the experimental grid to exclude mammalian predators. The exclosure was covered with a net made of criss-crossing fishing lines (40 lb test) 0.5 m apart to exclude avian predators.

Lemming density was monitored monthly from June through August with primary capture sessions spanning 3 consecutive days using capture-mark-recapture methods (Fauteux et al. 2015). We refer to this sampling as the abundance sampling scheme. The control grid had 144 trapping stations (12×12 stations, 10.9 ha) and the grid inside the exclosure had 96 stations (8×12, 6.9 ha). Each station was spaced at 30 m in each grid and consisted of one Longworth trap. Independence of trapping grids was ensured by separating them by ~ 600 m, a distance much longer than typical lemming home range radii (Banks et al. 1975).

In 2014 and 2015, we used an additional trapping scheme to collect lemming feces on each grid, referred to as the feces collection scheme, which differed from the one described above to assess density. Fecal pellets were collected between late June and early August during three trapping sessions in 2014 and 2015 in the exclosure and six in 2014 and four in 2015 on the control. More sessions were conducted on the control, where lemmings were less abundant, to obtain similar sample sizes in both grids. A feces collection occasion consisted of setting the traps in the morning (~ 10:00) and visiting them every 2 h until their closure at 18:00 in both grids. Collecting feces from animals that had stayed < 2 h in traps was essential to ensure that FCM concentrations represented baseline levels (Touma et al. 2004; Fauteux et al. 2017). We used a subset of 36 trapping stations among those used during the abundance sampling scheme. Trapping stations were selected based on the results from the previous trapping occasion to maximize the number of individual lemmings captured for feces collection. A minimum of 3 days separated feces collection sessions from the abundance sampling sessions to avoid potentially confounding effects of stress induced by previous captures (Rogovin and Naidenko 2010; Fauteux et al. 2017). Each captured lemming was identified to species, sexed, weighed, and its reproductive condition noted. Only feces from adults (males: ≥ 30 g; females: ≥ 28 g; Fauteux et al. 2015) were kept for the analyses to eliminate potential confounding age effects. Feces from individuals recaptured during the feces collection scheme were not collected to avoid artificially elevated stress levels due to previous captures (Fauteux et al. 2017).

We assessed the reproductive status of all animals captured. As for the stress hormone hypotheses, juveniles were excluded from this analysis because they were generally more abundant in the predator exclosure (Fauteux et al. 2016) and this may have biased the proportion of non-reproductive individuals. Males were classified as abdominal (i.e., testes retracted in the abdomen) or scrotal (i.e., testes in the scrotum). Females were classified as lactating or pregnant. Adult lemmings classified as adults based on body mass but showing no signs of reproduction (i.e., males with an inconspicuous scrotum and females being neither pregnant nor lactating) were classified as non-reproductive adults. All captured lemmings were tagged, either with passive integrated transponders injected in the nape of the neck (PIT, AVID®; Avid Identification Systems, Inc., Norco, CA, USA) or ear tags (1005-1 Monel, National Band & Tag Company, Newport, KY, USA) in both grids. Field manipulations were conducted in a similar fashion in both trapping grids and were approved by the Animal Welfare Committee of Université Laval (2014-061) and Parks Canada (SIR-2013-13953).

To quantify predation risk, we conducted observations of predator activity at trapping grids every 2–3 days during the summers (June–August) of 2014 and 2015. Over the two summers, we cumulated 127 h of observations at the predator exclosure and 143 h at the control grid (methodological details can be found in Fauteux et al. 2016). In 2015, we increased our effort to monitor predator activity inside the exclosure with a passive method by deploying seven artificial nests made of four quail eggs in the predator exclosure ($n = 7$), whereas 40 similar nests had been deployed outside as part of a long-term monitoring of predation risk for shorebirds nesting in the area (McKinnon et al. 2014). Predators of artificial nests of birds are the same as those of lemmings at our study area (McKinnon et al. 2014).

Sampling pellets and quantifying fecal corticosterone metabolites

Fecal samples were collected directly from the anus of captured lemmings when possible or in the traps and placed in small plastic tubes (1.5 ml). Contamination by urine was prevented by placing a small elevated floor made of welded wire in the Longworth traps to retain pellets above the bottom of the trap. All wet pellets were discarded. We collected pellets with surgical gloves and flat-tipped forceps that were pre-sterilized with benzalkonium chloride. Feces were placed in 1.5 ml plastic vials and stored at − 20 °C within 15 min after collection until analysis. In the laboratory, fecal corticosterone metabolites (FCM) were quantified with the 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA) adapted for brown lemmings (Touma et al. 2003; validated by Fauteux et al. 2017).

Briefly, fecal samples were freeze-dried ≥ 12 h prior to crushing with a mortar and pestle and liquid nitrogen. Each crushed sample was weighed up to 30 ± 5 mg and transferred in a separate 1.5 ml plastic tube in which we added 1 ml of an 80% methanol solution. The suspended samples were vortexed (1500 rpm) for 30 min and centrifuged (2500*g*) for 15 min (Palme et al. 2013), then 0.7 ml of the supernatant were transferred into a new 1.5 ml plastic tube and stored at − 20 °C for later analysis with the 5α-pregnane-3β,11β,21-triol-20-one EIA (Touma et al. 2003).

Statistical analyses

We first compared FCM levels of captured lemmings between the control and experimental trapping grids. Because reproductive condition can affect FCM levels (Fauteux et al. 2017), we developed seven candidate models to test the treatment effect (i.e., predator reduction) while controlling for potential effects of: reproductive condition, sex, and additive or interactive effects of treatment and reproductive condition (two models), and treatment and sex (two models), on FCM concentrations. Reproductive condition and sex were placed in different models due to partial redundancy between these two variables (i.e., reproductive condition differed between males and females). The model selection procedure allowed testing of the treatment effect while controlling for endogenous effects. Linear mixed-effects models with a Gaussian distribution were used with month nested in year as random variables to control for potential seasonal or annual variability related to the phase of the population cycle (Boonstra et al. 2001a; Romero et al. 2008; Sheriff et al. 2009).

We quantified the effects of the exclosure on the reproductive activity by comparing frequencies of each reproductive category between trapping grids. For this analysis, we used lemmings captured during the abundance sampling scheme to maximize our sample size. For each sex, we modeled the frequencies of reproductive and non-reproductive individuals with a single generalized linear mixed-effects model with a Poisson distribution. We modeled the interaction between trapping grids and reproductive conditions as fixed effects and year as a random effect. We pooled lemmings captured at all sessions but eliminated recaptures within primary sessions.

All statistical analyses were run with R software. We used Cook's distance (Cook 1977) to measure the influence of a few extreme FCM values. Data points with a high Cook's value were considered highly influential if their Cook's distance (D_i) was high ($D_\mathrm{i} > 4 \times (n - k)^{-1}$; where n is the number of lemmings and k the number of parameters included in the model) and excluding them changed the statistical significance. We used the package "nlme" for estimating coefficients in linear mixed-effects models (Pinheiro et al. 2017) and "lme4" in mixed-effects Poisson models (Bates et al. 2015). Model selection was based on AICc and we model averaged on models with reasonable statistical support (ΔAICc < 4; Burnham and Anderson 2002). Model-averaging was conducted with the package "AICcmodavg" (Mazerolle 2017) and both marginal (i.e., fixed-effects only) and conditional R^2 adapted for mixed-effects models were estimated according to the methods of Nakagawa and Schielzeth (2013). All estimates reported in the results are given with their 95% confidence intervals (CI). When necessary, response variables were log-transformed to meet normality for Gaussian distributions and Poisson mixed-effects models were corrected for overdispersion ($\hat{c} \geq 2$) if necessary.

Results

During the feces collection scheme, we captured 68 adults in 2014 (control grid: 33; exclosure: 35) and 34 in 2015 (control grid: 18; exclosure: 16). Numbers were similar in each grid because we adjusted our trapping effort accordingly (see methods). During the abundance sampling scheme, we captured 215 adult individuals in 2014 (106 control grid, 109 experimental grid) and 98 in 2015 (49 control grid, 49 experimental grid). In 2014, lemming densities including juveniles were, on average, 8.2 ind ha^{-1} (CI = [6.9, 9.5]) in the predator exclosure and 3.9 ind ha^{-1} (CI = [3.2, 4.6]) on the control. In 2015, densities were 4.6 ind ha^{-1} (CI = [3.8, 5.5]) in the exclosure and 2.8 ind ha^{-1} (CI = [2.2, 3.4]) on the control (for more details of lemming densities, see Fauteux et al. 2016).

All species of predators except parasitic jaegers were observed more often around or on the control grid than around the predator-exclusion grid. Overall, we observed 3.4 times more predators around the control than around the predator-exclusion grid (N predators observed 100 h^{-1}: control: 133 (2014) and 99 (2015); predator exclosure: 24 (2014) and 79 (2015); Online Resource A, Table A1). However, ermines were never observed in both years. We found no indication that predators entered the experimental grid during the experiment except in one instance in spring 2015, when a fox entered the exclosure by digging under the fence (Fauteux et al. 2016). The hole was quickly blocked and the fence reinforced. All 40 artificial shorebird nests outside the exclosure were depredated within 72 h, while all nests located inside the predator exclosure remained intact after 48 days.

Effects of predator reduction on FCM

Modeling of the effects between FCM concentrations and treatment and endogenous effects revealed that one value had high influence on the relationship (i.e., high Cook's distance). We present results with and without this influential value in Table 1. The most parsimonious model included an additive effect of both predator reduction and sex-specific reproductive condition on FCM concentrations (Table 1; Online Resource B, Table B1). However, the model including only sex-specific reproductive condition also had high statistical support (ΔAICc < 2), suggesting both models are plausible. In general, lemming FCM concentrations were 1.6 times lower in the predator exclosure (without influential value: 746 ng/g, CI = [582, 954], *n* = 50; with influential value: 823 ng/g, CI = [618, 1097], *n* = 51) compared to the control (1189 ng/g, CI = [945, 1497], *n* = 51; Fig. 1a). Abdominal and scrotal males generally had the highest FCM concentrations, whereas non-reproductive individuals had the lowest (Fig. 1b). Scrotal and abdominal males had similar FCM concentrations and lactating and pregnant females had similar FCM concentrations (Table 1).

Table 1 Model-averaged coefficient estimates of the effect of predator reduction and reproductive condition on fecal corticosterone metabolite concentration of adult lemmings

Parameter	Without influential value			With influential value		
	Coefficient	Low CI	High CI	Coefficient	Low CI	High CI
Exclosure	**– 0.277**	**– 0.551**	**– 0.003**	– 0.232	– 0.509	0.045
Repro						
Abdominal	**1.309**	**0.823**	**1.795**	**1.425**	**0.942**	**1.909**
Scrotal	**1.371**	**0.998**	**1.744**	**1.371**	**0.991**	**1.752**
Lactating	**0.537**	**0.125**	**0.948**	**0.525**	**0.108**	**0.943**
Pregnant	**0.563**	**0.047**	**1.078**	**0.537**	**0.017**	**1.057**

Month nested in year were used as random factors

Coefficients in bold indicate that the 95% confidence intervals (CI) exclude 0

Model selection results are presented in Table B1

Exclosure = grid effect (predator reduction vs control, which was the reference level); Repro = reproductive condition (scrotal males, abdominal males, pregnant females, lactating females, and non-reproductive individuals of both sexes; the latter category was the reference condition)

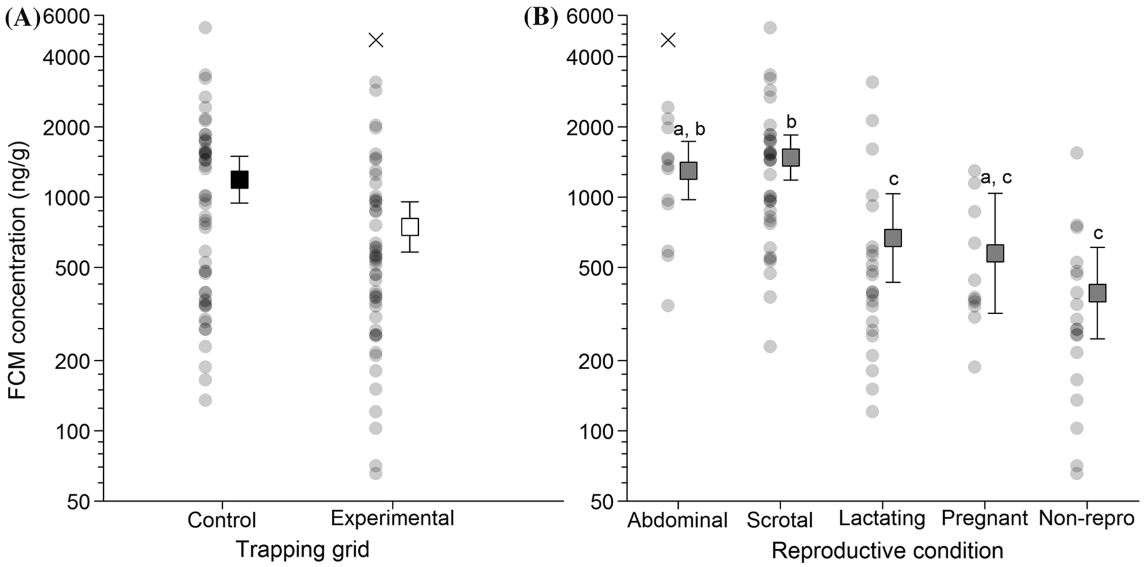

Fig. 1 Average fecal corticosterone metabolite concentrations (FCM) of adult lemmings with 95% confidence intervals in the control (normal predation; black square) and experimental grid (predator reduction; white square (**a**) and according to the reproductive condition of each sex (**b**). Individual data points are shown in gray and crosses indicate influential values. Non-repro = non-reproductive adult males and females. The 95% confidence intervals were calculated without the influential value and the small letters indicate Tukey's multiple comparison statistical similarity or difference conducted on the top model (i.e., no model averaging). Sample sizes in **a**: $n_{\mathrm{control}} = 51$ and $n_{\mathrm{experimental}} = 50$. Sample sizes in **b**: $n_{\mathrm{abdominal}} = 13$, $n_{\mathrm{scrotal}} = 36$, $n_{\mathrm{lactating}} = 23$, $n_{\mathrm{pregnant}} = 11$, $n_{\mathrm{non\text{-}repro}} = 19$

Effects of predator reduction on reproductive activity

The proportion of adult males that were scrotal ($\beta = -0.84$, CI = [− 1.91, 0.24], $R_m^2 = 0.42$, $R_c^2 = 0.72$; Fig. 2) and the proportion that were abdominal were similar on both grids ($\beta = -0.04$, CI = [− 0.81, 0.72]). The proportions of pregnant ($\beta = 0.15$, CI = [− 0.65, 0.94], $R_m^2 = 0.43$, $R_c^2 = 0.83$) and lactating females ($\beta = 0.08$, CI = [− 0.61, 0.76]) were also similar on both grids. The proportion of non-reproductive males and females was not affected by trapping grid (Fig. 2). Sample size used to calculate proportions in Fig. 2 are reported in Online Resource C, Table C1.

Discussion

Our results confirm that lemmings responded physiologically to an experimental reduction of predation risk by having lower levels of stress hormones when protected by a predator exclosure compared with those under natural predation pressure. Our results are conservative (i.e., difference in stress hormone levels could be larger) because lemming densities were higher in the predator exclosure, which could have contributed to elevate stress hormone levels (Boonstra and Boag 1992; Creel et al. 2013). However, although lemmings had 37% lower FCM levels within the exclosure than on the control, the proportions of reproductively active adults were similar in both males and females. Thus, our results suggest that even though lemmings were sensitive to high predation risk as indicated by their high FCM levels, we found no evidence that this effect modified their reproductive activity.

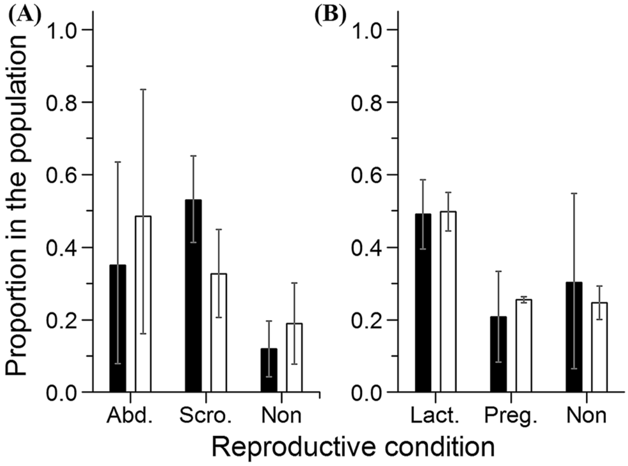

Fig. 2 Average proportions of each reproductive categories among adult male (**a**) and female (**b**) lemmings captured during the abundance sampling scheme (see methods) for 2014 ($n = 215$) and 2015 ($n = 98$) in the control (black bars) and experimental (white bars) grids. Proportions of males and females were calculated separately. Estimates are presented with their 95% confidence intervals. Sample sizes are presented in Online Resources C. *Abd.* abdominal, *Scro.* scrotal, *Non* non-reproductive, *Lact.* lactating, *Preg.* pregnant

Effects of predation on reproduction

Predator-reduction experiments generally increase population size and survival of northern small rodents (Norrdahl and Korpimäki 1995; Reid et al. 1995; Wilson et al. 1999). In accordance with those results, lemmings in our study were on average 2.2 times (up to 4.8 times in June 2014) more abundant and survival of both adults and juveniles were between 1.4 and 1.6 times higher within the exclosure than on the control (Fauteux et al. 2016). In contrast, there are inconsistencies among studies that assessed the relationship between predation risk and reproduction in small rodents. Predator-reduction experiments did not affect the reproductive condition of lemmings in the Canadian low Arctic (Wilson et al. 1999) and voles in Fennoscandia (Huitu et al. 2003). These results contrast with other semi-natural experimental studies that reported lower reproductive activity in voles under high predation risk (Korpimaki et al. 1994; Jochym and Halle 2012). Charbonnel et al. (2008) speculated that high FCM levels could impair reproduction of voles during declines but our results show that small mammals can remain reproductively active under elevated FCM levels. Therefore, the lower reproductive activity observed during the peak and decline phases in some lemming and vole populations (Korpimaki et al. 1994; Erlinge et al. 2000) may have been caused by factors not related to stress hormones. For example, Ylönen et al. (2006) found that voles exposed to olfactory cues of predators modified their foraging behavior without showing elevations in FCM concentrations.

Physiological and behavioral effects of stress

Impairment of reproductive activity (e.g., interruption of ovulation, hormonal inhibition, and disruptive behaviors) is one of the most commonly reported pathologies related to chronic stress in laboratory experiments (Bethea et al. 2008; Chrousos 2009). However, recent studies have questioned the occurrence of this effect in wild populations because continued breeding under chronic stress has now been reported in several species (Boonstra et al. 2001b; Dantzer et al. 2013). Evidence suggests that species with relatively short generation time generally show no reproductive suppression when exposed to persistent stressors (McDonald et al. 1988; Boonstra and Boag 1992). In arctic ground squirrels, breeding males showed more signs of chronic stress compared to non-breeding males due to their low maximal cortisol binding capacity for free glucocorticoids (Boonstra et al. 2001b). The consequence of chronic stress for breeding squirrels was a less-efficient immune response, which could compromise their survival. In this case, the trade-off for keeping high reproductive activity was a lower survival probability.

Brown lemmings typically live less than 12 months (only 0.8% of marked lemmings were recaptured in the following year, $n = 1330$; Fauteux et al. 2018) and can reproduce during both the summer and winter periods with a possible interruption during the snow-melt period in early June (Gruyer et al. 2010; Fauteux et al. 2015). The high proportion of reproductively active males and females in the control grid during the summer indicates that the elevated stress hormone levels experienced by lemmings due to high predation were still insufficient to interrupt ovulation, fetal development or inhibition of reproductive hormones. In a related paper (Fauteux et al. 2016), we found that the survival of lemmings was 1.6 times higher in the exclosure compared to those captured in the control area during two summers. The absence of effect of predation on brown lemming reproductive activity supports the hypothesis that the physiological trade-off forced by chronic stress may favor reproduction over survival through resistance of the gonadal axis in short-lived species (Wingfield and Sapolsky 2003).

Limitations of the study and future directions

As is often the case with large-scale experiments (Carpenter et al. 1995), we had no replication of the predator-reduction exclosure. Indeed, we favored the construction of a single large exclosure over several smaller ones to increase the number of lemmings with their complete home range enclosed inside the protected area and minimize the risk that some would move out and become exposed to predation. A large exclosure also reduced the perimeter to area ratio and thus edge effects such as potential detection by lemmings (e.g., olfactory or visual) of terrestrial predators passing near the fence. It allowed us to trap a large number of different individuals over a large area, avoiding the need to resample the same individuals. Building more than one large exclosure was impossible due to the prohibitive cost of working in the High Arctic. Two other large-scale predator-reduction experiments conducted built to protect collared lemmings in the Canadian low Arctic (only one exclosure built in each case) also reported no effect of predation on lemming reproduction (Reid et al. 1995; Wilson et al. 1999). Thus, we are confident that our predator-reduction experiment was successful and that our ability to reduce perceived predation risk was robust.

Our 2-year study did not cover all phases of the lemming cycle. Indeed, brown lemmings can reach extremely low densities during low phases as indicated by a total absence of captures in 2013 despite 3500 trap nights in our study area (Fauteux et al. 2015). Moreover, we could not capture lemmings during the harsh Arctic winter. In our study, we measured the impact of predation on lemming stress during the summer of peak years, which is the time when predator density is at its highest (Legagneux et al. 2012; Therrien et al. 2014). As a result, predation should have the highest direct and indirect effects on lemmings during this phase. However, we acknowledge that predator-induced stress could have lasting effects over several generations due to maternal effects, and it remains unknown if there are carryover effects on lemming fecundity during winter (Boonstra et al. 1998b).

This study focused on the effects of predator-induced stress on the reproductive condition of individuals. In their meta-analysis of predator manipulation experiments, Salo et al. (2010) reported higher reproduction in populations protected from predators. However, their definition of reproduction was very broad and included the proportion of juveniles in the population, which was also higher within our exclosure than the control (Fauteux et al. 2016). Because proportion of juveniles is affected by early survival after birth and dispersal (Boonstra 1985; Reid et al. 1995), it may be a poor index of reproduction per se. Selective predation may favor less mobile individuals (Norrdahl and Korpimäki 1998; but see Banks 2000), such as non-reproductive males and pregnant or lactating females concentrating their activities around their burrow (Predavec and Krebs 2000). We do not have data to test whether the survival of reproductive individuals differed from that of non-reproductive ones in the control area. However, if selective predation was strong, differences in reproductive activity between the exclosure and the control should have been observed due to those mortalities, which was not the case.

The higher density of lemmings recorded in the predator exclosure could have been a source of stress in itself due to increasing social interactions or resource competition (Huck and Banks 1982; Creel et al. 2013; Dantzer et al. 2013). However, if this had been the dominant source of stress for lemmings, we should have recorded lower FCM levels in the less densely populated control grid than the predator-reduction grid, which is opposite to what we found. Thus, even though high population density may have been a source of stress for lemmings, it was apparently insufficient to override the decrease in stress induced by a reduced predation risk in our experimental grid.

Conclusion

Our study shows that high predation risk elevates stress hormones in cyclic brown lemmings in the High Arctic, but that this response is insufficient to cause population-wide suppression of reproductive activity. It is important to remember, however, that our study was not designed to determine a threshold at which stress hormone levels become pathological, but was instead aimed at measuring the effects of natural predation pressure levels on stress levels and their possible demographic consequences. Our results support the hypothesis that stress responses in natural conditions do not necessarily cause a suppression of reproductive activity as observed in laboratory conditions unless it has a positive long-term impact on the fitness of individuals (Boonstra 2013). Since our predator-reduction experiment revealed lower survival (Fauteux et al. 2016) but no change in reproductive activity under high predation risk (this study), we further hypothesize that highly vulnerable species with short generation time and relying on rapid population growth (*r*-selected species) such as cyclic lemmings and voles favor the maintenance of high reproductive activity over survival mechanisms (Crespi et al. 2013).

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