Differences in behavior help to explain lemming coexistence

Douglas W. Morris,* Angélique Dupuch, MaryJane Moses, Kaylee Busniuk, and Helen Otterman

Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada (DWM)
Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, Ripon, Québec J0V 1V0, Canada (AD)
Ontario Ministry of Environment, Conservation and Parks, Thunder Bay, Ontario P7E 6S7, Canada (MJM)
Cognitive and Behavioural Ecology Graduate Program, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada (KB)
Faculty of Health Sciences, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada (HO)

* Correspondent: douglas.morris@lakeheadu.ca

Collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings coexist in tundra habitats across much of the middle and lower Canadian arctic. Their coexistence, and response to predation risk, appears mediated by behavior. We analyzed field-collected videos of open-field tests to assess potential differences in innate behaviors between the two species. Collared lemmings were less active and exhibited less exploratory behavior than did brown lemmings, which were more active under cover than in the open. Similar behaviors scaling along axes of activity and curiosity were revealed by principal components analysis. Each axis defined different aspects of brown lemming personality, but repeated testing of the same individuals yielded a striking dependence of their behavioral response on open-field treatments. Even so, the differences between species in behavior correlate well with their habitat preferences that resolve competition and govern their coexistence.

Key words: arctic, behavior, competition, *Dicrostonyx*, *Lemmus*, personality, predation risk

Despite nearly a century of research and contemplation, the dynamics and coexistence of arctic lemmings remain ecological enigmas (Oksanen et al. 2008, 2009; Gauthier et al. 2009; Ims et al. 2011; Krebs 2011, 2013). Field experiments, which consistently report population dynamic and demographic differences between control and predator exclusion treatments (Reid et al. 1995; Wilson et al. 1999; Fauteux et al. 2016), implicate a role for predation. Other controlled experiments (e.g., Hambäck et al. 2004; Aunapuu et al. 2008; Hoset et al. 2017) document that top-down forces on lemming population dynamics depend on productivity, as predicted by exploitation ecosystems theory (Oksanen et al. 1981; Oksanen and Oksanen 2000). Both perspectives include a role for predator control of arctic food webs, but they do not typically address how predation, or its absence, can act as a mechanism explaining the coexistence of two or more species of herbivorous arctic microtines.

When coexistence between arctic lemmings has been examined, it appears to be mediated by differential habitat selection (Morris et al. 2000; Ale et al. 2011), and its interaction with stochastic dynamics (Morris et al. 2000, 2012). When densities are low, each species tends to retreat into its preferred habitat. The species that recovers most quickly expands into less-preferred habitat and uses that advantage to dominate abundance during the next period of high densities (Morris et al. 2000). Differential habitat selection between lemmings occurs even as habitats change (Morris et al. 2011; Morris and Dupuch 2012) but appears immune to experimental reduction in predation (Dupuch et al. 2014a).

The apparent impotence of predators to influence habitat selection by lemmings mirrors small-scale experiments that monitored lemming behavior in open versus covered patches safeguarding lemmings from predators (Dupuch et al. 2014b). Both collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings preferred covered patches, but occupation was independent of their respective choice of upland hummock versus mesic meadow habitat (Dupuch et al. 2014b). The type of patch also had no effect on vigilance, which was greater in *Dicrostonyx* than in *Lemmus*. Notably, however, each species increased vigilance when sharing a patch with its competitor.

It thus appears that any effective synthesis of lemming dynamics and coexistence will only be possible if it identifies a common link that unites predation risk, interspecific competition, and habitat selection with spatial variation in productivity.

Adaptive behavior operating at different scales in time, space, and organization may be such a link. Before promulgating that view, we must first test whether coexisting lemming species possess similar or divergent behaviors that might influence their interactions with predators and with one another.

With these points in mind, we searched for similarities and differences in behavior between the two species with modified open-field tests. We complemented these tests by evaluating whether lemmings can be characterized by behavioral types (Sih et al. 2004a, 2004b—typically represented by axes of behavior that scale from one extreme to another). We begin with a brief overview of animal personalities and behavioral types, and their potential connection to ecological processes. We set the stage for our research with a short description of our study system, then describe how we conducted open-field tests in the tundra, their statistical analysis, and their somewhat surprising results. We conclude by revisiting how differences in innate behaviors reflect potential differences between species in dealing with predation risk and how those differences can promote species coexistence.

Animal Personalities and Behavioral Types

Animal personality, the repeated expression of differences in behavior among individuals through time and contexts (e.g., Réale et al. 2007; Dingemanse et al. 2010; Roche et al. 2016), is usually used to explore how different individuals respond to common stressors. The within-population variation in behavior represented by personalities (e.g., Dall and Griffith 2014) has, nevertheless, major implications to ecological interactions and eco-evolutionary dynamics (Bolnick et al. 2011; Wolf and Weissing 2012). Many, but by no means all, of these effects emerge through differences in behavioral types such as averages along active versus inactive, bold versus shy, or aggressive versus docile behavioral syndromes (Sih et al. 2012). Much less attention has been devoted to the consequences of these and other behavioral differences among coexisting species. Differences among prey species in their behavior toward shared predators, for example, can enhance species coexistence by reducing vulnerability, or yield a wide variety of possible negative (apparent competition) and positive (mutualistic) interactions (Holt 1977; Holt and Kotler 1987; Holt and Bonsall 2017; Morris et al. 2017). It is within this context that we seek to compare similarities and differences in behavior between lemming species. Our data are insufficient to assess personalities of both species, but they do enable us to explore whether there are repeatable differences of behavior among individual *Lemmus*.

Materials and Methods

Some basics of lemming biology.—Field biologists familiar with both species will know that some individuals of *D. groenlandicus* engage in aggressive defensive postures and vocalizations that distinguish them from relatively docile *L. trimucronatus*. Regardless of this obvious difference, we do not currently know whether other behaviors correlate with morphological and physiological differences between the two lemming species, or whether those behaviors are more-or-less stereotyped by the species' convergent evolution to a shared environment (Oksanen et al. 2008).

Although both species are well adapted to life in the arctic, *Dicrostonyx* is arguably more prototypical of a tundra specialist than is *Lemmus*. The more northerly distribution of *Dicrostonyx* coincides with its stockier build, shorter appendages, and photoperiod-induced changes in pelage and cornification of its "snowshovel" digits (e.g., Weil et al. 2006). The preference of *Dicrostonyx* for drier upland tundra reflects its dicot diet of forbs and small shrubs (e.g., *Salix*, *Dryas*). *Lemmus*, by comparison, builds and uses runways in moist habitats where its main diet consists of grasses, sedges, and moss (Batzli 1993).

Study system and field protocols.—We livetrapped lemmings, and collected behavioral videos, during June from 2015 to 2017. All data were collected from 12 small (60 m × 60 m) permanent sampling grids (Morris et al. 2000, 2012) and on the site of a large former exclosure (270 m × 270 m—Dupuch et al. 2014a) at Walker Bay on the Kent Peninsula, Nunavut, Canada (68°21′N; 108°05′′W—habitat descriptions and sampling protocols are detailed in Morris et al. 2000 and Dupuch et al. 2014a). A prolonged blizzard limited our activities in 2016 such that we trapped lemmings and collected videos on only the exclosure site and six of the smaller grids. The two lemming species are the only small rodents at Walker Bay (small colonies of arctic ground squirrels, *Urocitellus parryii*, are restricted to rock-strewn dry moraines that are not part of the ~ 10-km^2 study area).

We video-recorded behaviors of a subset of animals at their capture location in a modified open-field box (52 cm × 34 cm × 24 cm tall) that we carried with us. Open-field and hole-board tests are commonly used to assay behaviors such as activity, exploration, and fear responses of wild rodents (Martin and Réale 2008; Lantová et al. 2011; Herde and Eccard 2013; Gracceva et al. 2014; Schuster et al. 2017). The box consisted of a clear plastic "tote" inserted into a slightly larger white-plastic opaque tote. We marked a 3 × 5 grid of equal-sized squares underneath the floor of the clear tote with black electrical tape that was clearly visible on the other side (Fig. 1). We then fitted two 30-mm diameter holes with short black ABS (acrylonitrile butadiene styrene) piping equidistant from the box's interior walls. The dead-end piping extended approximately 5 mm above and 6 cm below the floor. Lemmings of both species could enter and exit the pipes.

We attached a video camera (GoPro Hero 3) above the open-field box such that its field of view encompassed all but the top lip of the tote (Fig. 1). We released lemmings one at a time into the center of the box, moved away, and video-recorded their behavior. The area of our arena (1,836 cm^2), though much smaller than the approximately 8,000- to 10,000-cm^2 arenas often used to assess behaviors of herbivorous voles (e.g., Demas et al. 1999; Eccard and Herde 2013; Herde and Eccard 2013; Maiti et al. 2018), is nevertheless comparable to the smaller-sized open-field arenas used by others to evaluate
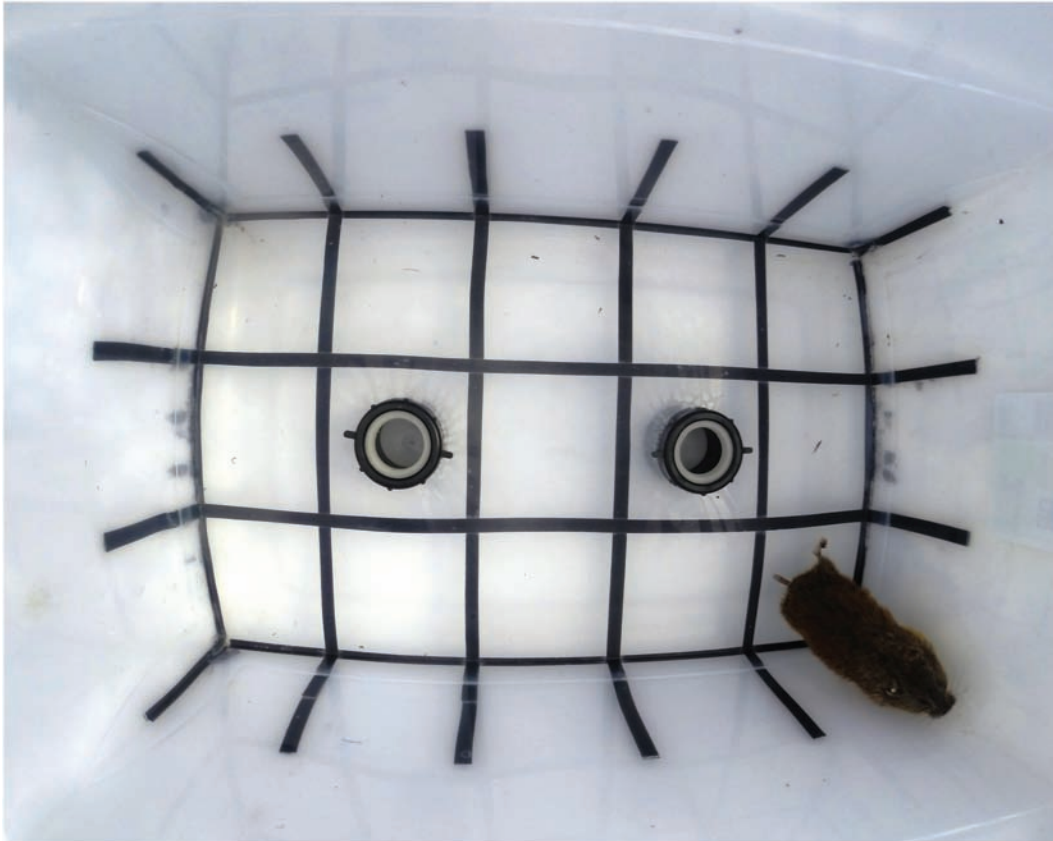
Fig. 1.—GoPro photograph of an adult *Lemmus trimucronatus* (rearing) in the modified open-field arena.

vole behavior (e.g., 1,962 cm² by Zadubrovskiy et al. 2017; 3,600 cm² by Vogel et al. 2018; and 2,400 cm² by Eilam 2003), and to that used by Martin and Réale (2008; 3,200 cm²) on much more mobile eastern chipmunks. Eilam's experiments are particularly relevant because they documented a remarkable stability of vole behavior across a 44-fold increase in arena area. Although we acknowledge that lemmings might display quantitative differences in behavioral metrics in larger arenas, our goal was simply to acquire comparable behaviors of the two species monitored identically while being exposed to the same conditions.

In 2015, we recorded behavior for 5 continuous minutes, placed a novel object (empty 12-gauge rubber-bullet shotgun shell expended during one of several grizzly-bear encounters) in the corner most distal to the lemming's position, and continued recording for an additional 5-min period. We released the animal, then washed, and sanitized the arena and shell casing with a dilute bleach solution before moving to the next capture location.

We modified our protocol in 2016 and 2017 to include an initial 5-min observation period while the box and camera were covered with "mossy oak" camouflage netting (total of 15 min of video-recording). The leaf cutouts in the netting mimicked cover similar to that provided by interspersed upright shrubs (*Salix richardsonii*) at our field site. We removed the netting after 5 min and continued with the 2015 10-min video protocol. We initiated each video session with netting to ensure

that the novel object was always placed into an uncovered open-field arena. Doing so yielded data from the final 10 min of observations in 2016 and 2017 comparable with the 10-min observations from 2015.

We partitioned our four- to five-member field crews into permanent capture and video-recording teams to ensure that all animals were handled and video-recorded by the same personnel each year. We video-recorded animals only during the approximately 2- to 3-h time periods required for us to process and release all captured animals on the grids. We processed a subset of animals because we captured and released lemmings far more quickly than other team members could video-record their behavior. When possible, in 2016 and 2017, we video-recorded animals twice (typically on successive days). All research on live animals followed ASM guidelines (Sikes et al. 2016) and was approved by Lakehead University's Animal Care Committee.

Behavioral assays.—We observed the videos on a computer monitor to quantify behaviors used to discriminate rodent personality (e.g., Gracceva et al. 2014), and that should be related to the relative abilities of the two lemming species to evade predators (Table 1). Data included estimates of activity–exploratory behavior (e.g., number of perimeter lines crossed, time spent walking and running, time spent inspecting holes), use of risky areas (e.g., thigmotaxis; number of interior lines crossed), data gathering (time spent sniffing and scanning), and boldness (number of encounters, and time spent in contact with a

Table 1.—List of 14 variables from open-field tests used to quantify behavioral types of two coexisting lemming species in the central Canadian arctic.

Variable name	Description
Walk	Number of seconds spent walking during a 5-min observation period
Run	Number of seconds spent running during a 5-min observation period
Sniff	Number of seconds spent sniffing during a 5-min observation period
Scan	Number of seconds spent scanning during a 5-min observation period
Autogroom	Number of seconds spent grooming during a 5-min observation period
Still	Number of seconds with no movement during a 5-min observation period
Inspect	Number of seconds inspecting holes during a 5-min observation period
Rear	Number of seconds with front paws raised off the floor during a 5-min observation period
Dip	Combined number of times the animal stuck its head into one of two holes
Perimeter	Number of perimeter lines crossed during a 5-min observation period
Interior	Number of interior lines crossed during a 5-min observation period
Jump	Number of jumps recorded during a 5-min observation period
Encounters[a]	Number of encounters with the novel object during a 5-min observation period
Contact[a]	Number of seconds of sustained contact with the novel object during a 5-min observation period

[a]Novel object variables that were not used in the conditional logistic regressions and personality assays (2016 and 2017 data, phases 2 and 3).

novel object). Meristic variables (e.g., number of jumps) were tabulated manually. Timed data were recorded either with a stop-watch (2015 data only, 1-s accuracy) or with the aid of BORIS (Friard and Gamba 2016) software (all subsequent data). We controlled potential observer bias by ensuring that all timed variables were mutually exclusive, and by training observers (KB and HO) on pre-existing video data.

We quantified behavioral variables during two time intervals; the first minute of our 5-min observation periods, then for the remaining 4 min. The values for these two intervals were highly correlated, so we merged them for each respective 5-min observation period (5-min uncovered open-field observation, 5-min novel object observation in 2015; 5-min under cover, 5-min uncovered, 5-min novel object observations in 2016 and 2017).

Statistical analyses.—We analyzed lemming behavior in three phases. The first phase comprised an assessment of which open-field behavioral metrics differed between the two lemming species (Forward LR Binary Logistic Regression). We evaluated the model's predictive power by calculating the number of individuals that were correctly classified to species and determined model fit with Tjur's coefficient of discrimination (D—Tjur, 2009). We used only data from first videos collected in 2015 (n = 25 *Dicrostonyx* videos and 12 *Lemmus* videos; all 10-min videos without cover) to ensure independent and identically collected samples. We used this analysis to provide insights into whether significantly different

open-field behaviors corresponded with our previous adaptive explanations of species' differences in vigilance and predation risk (Dupuch et al. 2014b). We repeated the analysis within species to evaluate possible differences between sexes. We restricted the analyses of sexual differences to homogeneous and independent subsets of open-treatment data collected in identical ways (2015 for *Dicrostonyx*, 2016 and 2017 for *Lemmus*). We acknowledge that reproductive state might also influence behavior, but our samples are insufficient for such a detailed analysis.

The second phase used Stepwise Forward LR Conditional (Case–Control) Logistic Regression to assess differences in open-field behavior between covered and open treatments (first videos collected in 2016 and 2017 when animals were exposed to both cover and open arenas; *Lemmus*, n = 50; *Dicrostonyx*, n = 11). We did not include novel object data in these analyses (or in phase 3) because exposure to the novel object occurred only once, whereas all other variables were quantified separately for covered and uncovered treatments.

The third phase searched for repeatable personality traits among animals tested on two different occasions. First, we summarized correlated behavioral traits with principal components analysis (PCA with varimax rotation, scores calculated with the Anderson-Rubin method). We used all videos recorded for both species in 2016 and 2017 (these videos included both covered and uncovered treatments) to create composite lemming behavioral types (PCs). We repeated the PCA with data excluding *Dicrostonyx* to confirm that the two-species behavioral PCs were appropriate for an assessment of repeatable *Lemmus* behavior. We used stepwise logistic regression to confirm our earlier assessment of differences between species conducted with the 2015 data. We then evaluated whether *Lemmus* behavior (PCs) differed between videos while controlling for covered and uncovered treatments with a doubly multivariate repeated-measures General Linear Model (GLM). We did not repeat the analysis for collared lemmings because low *Dicrostonyx* abundance in 2016 and 2017 yielded only five individuals with two complete videos.

Our next analysis evaluated the repeatability (personality) of *Lemmus*' PC scores between first and second videos by calculating intraclass correlation coefficients in two-way mixed effects models (n = 31; again, we had insufficient replicates for a similar analysis on *Dicrostonyx*, n = 5). We aimed to evaluate whether our assessments of differences between species truly represented differences among individuals (avoids the "individual gambit"—Niemelä and Dingemanse 2018), not to document behavioral reaction norms that typically require much larger samples (Martin et al. 2011). We conducted all analyses with IBM SPSS Statistics 25 (P to enter = 0.05; P to remove = 0.1 for all stepwise procedures).

RESULTS

The abundance of lemmings, and thus the number of videos, varied among years. We recorded 25 *Dicrostonyx* videos in 2015 versus 18 in 2016 and only one in 2017 (battery failure

caused one *Dicrostonyx* video from 2016 to be comprised only of the covered treatment). We recorded 12 *Lemmus* videos in 2015, but many more in 2016 and 2017 (33 and 50, respectively) when brown lemmings were more abundant than were collared lemmings. Of the total, 36 represented second videos of the same animal (31 *Lemmus* and five *Dicrostonyx*). Sex ratios of video-recorded animals were equal for *Dicrostonyx* (22 of each sex) but biased toward males (59 versus 36) in *Lemmus*. Independent juveniles comprised a small fraction of the total videos (*Dicrostonyx*: five of 44; *Lemmus*: three of 95).

Differences in behavior.—The two lemming species exhibited dramatically different behaviors ($\chi^2_3 = 34.6$, $P < 0.001$). *Dicrostonyx* was far less active, spent more time grooming, and was less likely to explore the center of the arena than was *Lemmus* (Table 2). Separation along these three variables correctly classified all but one *Dicrostonyx* and one *Lemmus* (95% success). There were no significant differences in behavior between male and female *Dicrostonyx* but male *Lemmus*, on average, spent less time running, and more time scanning, than did females ($\chi^2_2 = 16.5$, $P < 0.001$; Table 2; 39 of 50 animals in the analysis classified correctly [78%]).

There were highly significant differences in lemming behavior between covered and open treatments, but the pattern differed between species. *Lemmus* spent less time walking, and more time scanning, when in the open than when under cover ($\chi^2_2 = 33.5$, $P < 0.001$; Table 2). *Dicrostonyx* was much more active (crossed many more perimeter lines) while under cover than in the open ($\chi^2_1 = 8.4$, $P = 0.004$; Table 2).

Behavioral types.—Two principal components accounted for slightly more than 49% of the common variation among the

Table 2.—Significant differences in open-field behavior between *Dicrostonyx groenlandicus* and *Lemmus trimucronatus* in the central Canadian arctic (data from 2015, Forward LR Binary Logistic Regression Analysis of 14 potential predictors, $\chi^2_3 = 34.6$, $P < 0.001$, $D = 0.78$), between sexes (2016 and 2017, *Lemmus* only, $\chi^2_2 = 16.5$, $P < 0.001$, $D = 0.33$), and between covered and open treatments (Conditional Logistic Regression, 12 potential predictors, 2016 and 2017, *Lemmus*, $\chi^2_2 = 33.5$, $P < 0.001$; *Dicrostonyx*, $\chi^2_1 = 8.4$, $P = 0.004$).

Variable	Mean	SD
Dicrostonyx groenlandicus		
Total time running (seconds)	1.6	2.25
Total time auto grooming (seconds)	7.3	4.64
Interior lines crossed	30.9	22.82
Lemmus trimucronatus		
Total time running (seconds)	17.2	16.60
Total time auto grooming (seconds)	3.2	3.14
Interior lines crossed	76.5	27.86
Male versus female *Lemmus*		
Total time running (seconds)	1.49 (4.0)	1.60 (7.78)
Total time scanning (seconds)	59.7 (35.2)	32.09 (21.4)
Lemmus under cover		
Total time walking (seconds)	91.4	23.44
Total time scanning (seconds)	27.3	16.28
Lemmus in the open		
Total time walking (seconds)	65.2	28.05
Total time scanning (seconds)	50.4	30.70
Dicrostonyx under cover		
Perimeter lines crossed	92.1	49.07
Dicrostonyx in the open		
Perimeter lines crossed	35.2	33.78

12 variables retained for the behavioral type and personality repeatability analyses (2016 and 2017 data; Table 3). The PCs corresponded roughly with the behavioral differences observed between species and cover treatments. PC1 was best associated with "activity," scaling from nearly sedentary to hyper-active individuals. PC2 ("curiosity") represented a cline from animals allocating much of their time exploring the holes to others that were less mobile and "introspective."

Our PCA excluding *Dicrostonyx* revealed virtually identical behavioral types to that of the two-species solution ($n = 166$; the same sets, signs, and similar magnitudes of loadings were associated with each PC). The summed eigenvalues were somewhat lower, however (5.66 versus 5.91), so we retained the two-species solution for further analyses. As expected from its association with activity, only PC1 was significantly different between species ($\chi^2_1 = 5.3$, $P = 0.021$; *Dicrostonyx* less active, mean $= -0.82$ [$SD = 0.91$]; *Lemmus* mean $= -0.13$ [$SD = 0.98$]).

The analysis assessing differences in PCs for *Lemmus* between videos (31 animals; Table 4) was more complex. The multivariate analysis revealed a significant video number × cover interaction ($F_{2,29} = 4.77$, $P = 0.016$). The univariate analysis was similar (video number × cover interaction; PC1, $F_{1,30} = 3.66$, $P = 0.065$; PC2, $F_{1,30} = 6.66$, $P = 0.015$). *Lemmus* were more active under cover in video 1 than they were in the open (mean PC1 $= 0.59$ versus -0.13; $SE = 0.18$ versus 0.17), but were not differentially active in video 2 (mean PC1 $= -0.003$ versus -0.15; $SE = 0.15$ versus 0.16; Fig. 2, PC1). The opposite trend applied to PC2. *Lemmus* exhibited no difference in curiosity in video 1 (mean PC2 $= -0.013$ versus -0.015; $SE = 0.15$ versus 0.19), but achieved a much higher curiosity score in video 2 (mean $= 0.52$ under cover versus -0.095 in the open; $SE = 0.18$ versus 0.16; Fig. 2, PC2).

Lemmus personality.—The effects of the video number × cover interaction were mirrored in our assessments of repeatable *Lemmus* behaviors. Intraclass correlations for PC1 suggested among-individual differences in *Lemmus* activity, but only under cover (cover: ICC $= 0.237$, $P = 0.06$; open: ICC $= 0.086$, $P = 0.32$). There was clear evidence for individual differences in curiosity, but the ICC was statistically significant

Table 3.—Loadings and eigenvalues of a principal components analysis (varimax rotation) assessing behavioral types of lemmings in covered versus uncovered open-field tests in the central Canadian arctic ($n = 203$; bold text identifies the most influential variables contributing to each principal component).

Variable	PC1	PC2
Perimeter	**0.883**	0.158
Walk	**0.761**	0.361
Interior	**0.746**	0.387
Jump	**0.721**	−0.207
Still	**−0.699**	−0.421
Rear	**0.666**	−0.197
Run	**0.384**	0.075
Autogroom	**−0.330**	0.084
Scan	**−0.171**	−0.027
Inspect	−0.043	**0.887**
Dip	−0.012	**0.865**
Sniff	0.078	**0.370**
Eigenvalue	3.951	1.958

Table 4.—Summary of a doubly multivariate repeated-measures GLM assessing differences in two principal components summarizing behavioral types of 31 *Lemmus trimucronatus* individuals assessed twice in covered versus uncovered open-field tests in the central Canadian arctic (effect size = ηp^2 [partial eta squared]; video = video number [first versus second]).

Multivariate analysis				
Source	*F*	*d.f.*	*P*	ηp^2
Video	2.87	2, 29	0.073	0.165
Cover	8.45	2, 29	< 0.001	0.368
Video × cover	4.77	2, 29	0.016	0.247

Univariate analysis					
Source	Measure	*F*	*d.f.*	*P*	ηp^2
Video	PC1	4.18	1, 30	0.05	0.122
	PC2	2.2	1, 30	0.15	0.068
Cover	PC1	11.27	1, 30	0.002	0.273
	PC2	6.22	1, 30	0.018	0.172
Video × cover	PC1	3.66	1, 30	0.065	0.109
	PC2	6.66	1, 30	0.015	0.182

only under cover (PC2, cover: ICC = 0.37, *CI* = 0.038–0.633, *P* = 0.007; open: ICC = 0.266, *P* = 0.075).

DISCUSSION

Collared and brown lemmings expressed distinctively different behaviors. *Lemmus* were more active and inquisitive than were *Dicrostonyx*. There was tantalizing evidence that those differences might be linked to sex (no difference in *Dicrostonyx*; different in *Lemmus*, but with relatively low predictive power).

Regardless, the behavioral differences between species were similar to those reported in dyadic encounters of male lemmings by Batzli and Jung (1980). *Lemmus* was more likely to initiate an encounter, but also most likely to retreat. *Dicrostonyx* was less likely to initiate encounters, but rarely retreated (Batzli and Jung 1980). Similar results and interpretations emerged from an earlier study on captive males, concluding that "more assertive" and "investigatory" *Lemmus* was more likely to initiate contact, whereas *Dicrostonyx* was more likely to attack (Banks et al. 1979). Once attacked, however, *Lemmus* was more persistent than *Dicrostonyx*. Both studies add credence to interpretations from field research on habitat selection. Those studies point toward interference as the main form of competition expressed by coexisting lemmings (Morris et al. 2000; Ale et al. 2011).

An alternative, and not mutually exclusive, interpretation is that the behaviors promote coexistence through differential susceptibility to predation. Active *Lemmus* might be more likely to encounter predators, then rely on escape to evade them. Less active and "introspective" *Dicrostonyx* may use enhanced vigilance to encounter predators less frequently, then fight or frighten predators with their stereotyped aggressive postures and vocalizations. Both behaviors might thus be adaptive to lemmings that share a precarious existence with both specialized and opportunistic predators.

Other behaviors also appear directed toward reducing predation risk. The two species were characterized by behavioral

types varying along clines of activity and curiosity. Both were more active under protective cover than in the open, a behavior that reflects their preference for protective cover in the field (Dupuch et al. 2014b). Both species also expressed vigilant behavior that is highest in *Dicrostonyx*, and heightened in both species when they confront competing individuals (Dupuch et al. 2014b). Vigilance in snowshoe hares (*Lepus americanus*), another quintessentially fearful prey species (e.g., Krebs 2011; Krebs et al. 2018), is also highest in patches where they are likely to encounter both predators and competing individuals (Morris and Vijayan 2018; Morris 2019). Risk management by snowshoe hares, and that of lemmings, thus appears to be another example of apparent predation risk (Morris 2009; Halliday and Morris 2013) whereby interference competition within and among species yields behavioral responses usually attributed to predation.

The interaction between video number (first versus second repeated video for individual lemmings) and cover was unexpected. In order to be classified as a "personality," behavior must be repeatable through time and across contexts (Réale et al. 2007). Assessments of animal personality thus minimally require repeated observations of individuals at different times, and most studies of rodent personalities include observations additional to those obtained from open-field tests (e.g., Martin and Réale 2008; Herde and Eccard 2013; Gracceva et al. 2014). Our repeated measures in modified open-field tests were designed to assess interindividual differences in behavior, not to reveal the panoply of lemming personalities. Be that as it may, short-term re-assessments, especially when using a fixed order of treatments as we did here, maximize the likelihood of carryover effects. Carryover effects can yield spurious correlations that create false negative or false positive interpretations of personality (Bell 2013). Similar biases can arise whenever behavior varies through time (Biro and Stamps 2015). We caution readers to view our repeatability estimates as demonstrating only that individuals express different behavioral types: they should not be used as absolute values for those differences.

It is nevertheless instructive to ask what is responsible for the interaction between video number and cover that we observed in *Lemmus*. One likely possibility is that the animals, having learned that escape was improbable, altered their behavior during the first 5-min observation period in the second video (the covered treatment) toward other options. Our fixed order of treatments, and the relatively short time frame between videos, dictates that we cannot unambiguously assign differences through time to differences in treatment (cover; the same is true for the effects of treatment on *Dicrostonyx* behavior). We knew that this would be a complication, but elected to use a fixed order to ensure that each subject possessed the same experience as all others (Bell 2013). Regardless of cause, *Lemmus* altered their behavior between videos, and both species changed behavior when we removed cover. Our results should thus give pause to anyone contemplating predictable repeated patterns of behavior in response to experimental manipulations.

Although plastic within species, it is clear that lemming behavior differs between *Lemmus* and *Dicrostonyx* in ways that
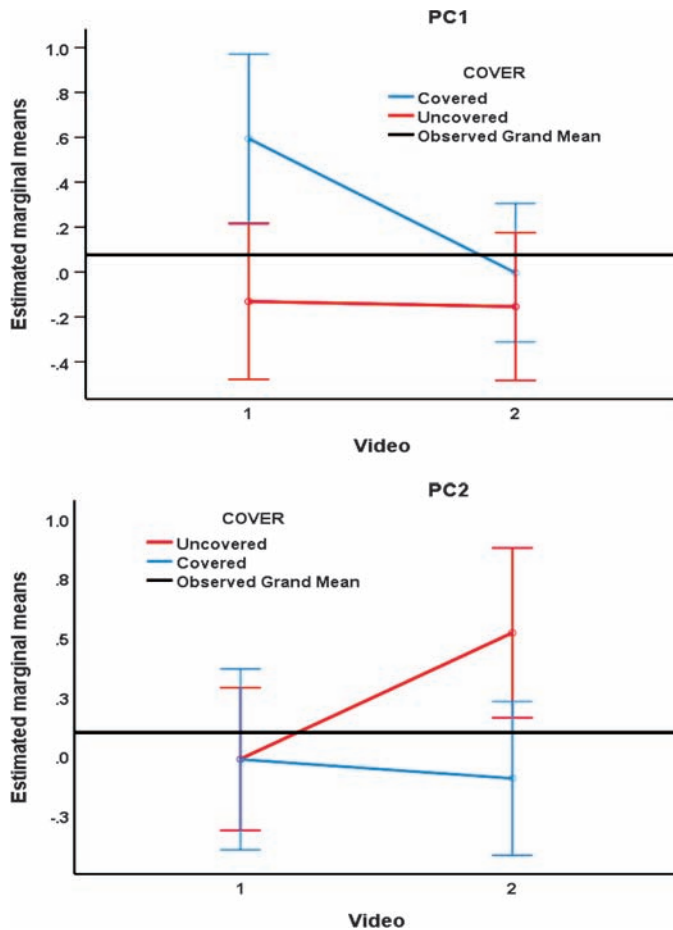
Fig. 2.—Profile plots illustrating the significant interaction between video number (1 versus 2) and cover (covered versus uncovered) emerging from an analysis of two principal components (top = PC1; bottom = PC2) summarizing lemming behavioral types in covered versus uncovered open-field tests in the central Canadian arctic.

are likely to impinge on their dynamics and coexistence. The more active and exploratory behaviors exhibited by *Lemmus* correlate well with their occupation of open moist habitats where they use runways to evade and escape from predators and competing individuals. Relatively inactive and "combative" *Dicrostonyx* typically occupy a more rugose habitat of shrub-covered hummocks that reduce sight lines and thus provide less opportunity to avoid direct interactions with predators and other lemmings. The differential behaviors, reminiscent of avian studies on asymmetric competition (e.g., Morse 1974; Robinson and Terborgh 1995), are consistent with the earlier interpretation (Morris et al. 2000) that lemming coexistence invokes a ghost of competition (Rosenzweig 1974, 1979) driven by interference and pre-emptive habitat selection (Pulliam 1988; Pulliam and Danielson 1991). The species nevertheless share common axes of activity and curiosity that appear to represent shared behavioral repertoires reflective of lemming morphology and lifestyle.

Differences in behavior, as well as habitat preference, suggest significant influences of habitat-dependent competition and predation risk on lemming dynamics and coexistence.

Those dynamics are similarly influenced by shared predators that typically display type III functional responses for both collared (Reid et al. 1997; Gilg et al. 2006) and brown lemmings (Therrien et al. 2014). Avian predators, at least those at Bylot Island, preferentially consume collared lemmings at low lemming densities, then switch their preference toward abundant brown lemmings at higher population sizes (Therrien et al. 2014). This pattern is consistent with our interpretation of habitat-dependent species interactions. When brown lemming density is high in wet habitat, their cumulative competition limits *Dicrostonyx* density in that habitat (Morris et al. 2000). Assuming that avian predators are more effective at catching prey in wet habitat, intense competition from brown lemmings force *Dicrostonyx* into drier habitat and facilitates relatively higher survival.

Differential predation, in concert with habitat occupancy and behavior, might thus help to explain the peculiar "lagomorphed" dynamics (Morris et al. 2000) proposed for the two lemming species at Walker Bay. When populations collapse, stochastic differences in reproduction and survival during recovery can favor a community dominated by either brown or collared lemmings. If brown lemming populations recover first, then they will occupy both habitats and limit population growth by *Dicrostonyx*. In the absence of predators, *Dicrostonyx* is likely to remain sparse. When predators are present in sufficient numbers, their preference for abundant brown lemmings might then facilitate a habitat-dependent increase in the *Dicrostonyx* population. If, on the other hand, collared lemmings recover first, then their preference for upland hummocks spills over into moist meadows and inhibits population growth by *Lemmus*. If predators nevertheless prefer *Lemmus* in wet habitat, then predation can reinforce the stochastically induced numerical dominance of collared lemmings.

It is unclear whether clines of lemming behavioral types, such as we report here, act to destabilize (e.g., Chitty 1960; Krebs 1978 [includes a prescient insight into "rapid evolution"]; Voipio 1988) or stabilize (e.g., Stenseth and Ims 1993) population dynamics. We will not have a clear answer on this point until we know whether lemming behavioral types vary consistently through time and with population density. But even if they do, it is unlikely that we will easily disentangle cause from effect in the absence of controls for habitat. The dependence of behavior on cover, for example, suggests an important and possibly over-riding role for habitat in lemming behavior. Those behaviors, and any effect that they might have on population dynamics, are undoubtedly embedded in the wonderful density- and frequency-dependent evolutionary games of habitat selection that explain lemming coexistence, and underlie their keystone (Krebs 2011) role in northern ecosystems.

Literature Cited

Ale, S. B., D. W. Morris, A. Dupuch, and D. E. Moore. 2011. Habitat selection and the scale of ghostly coexistence among Arctic rodents. Oikos 120:1191–1200.

Aunapuu, M., et al. 2008. Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). The American Naturalist 171:249–262.

Banks, E. M., U. W. Huck, and N. J. Mankovich. 1979. Interspecific aggression in captive male lemmings. Animal Behaviour 27:1014–1021.

Batzli, G. O. 1993. Food selection by lemmings. Pp. 281–301 in The biology of lemmings (N. C. Stenseth and R. A. Ims, eds.). Published for The Linnean Society of London by Academic Press, London, United Kingdom.

Batzli, G. O., and H.-J. G. Jung. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. Arctic and Alpine Research 12:483–499.

Bell, A. 2013. Randomized or fixed order for studies of behavioral syndromes? Behavioral Ecology 24:16–20.

Biro, P. A., and J. A. Stamps. 2015. Using repeatability to study physiological and behavioural traits: ignore time-related change at your peril. Animal Behaviour 105:223–230.

Bolnick, D. I., et al. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Chitty, D. 1960. Population processes in the vole and the relevance to general theory. Canadian Journal of Zoology 38:99–113.

Dall, S. R. X., and S. C. Griffith. 2014. An empiricist guide to animal personality variation in ecology and evolution. Frontiers in Ecology and Evolution 2:1–7.

Demas, G. E., C. A. Moffatt, D. L. Drazen, and R. J. Nelson. 1999. Castration does not inhibit aggressive behavior in adult male prairie voles (*Microtus ochrogaster*). Physiology & Behavior 66:59–62.

Dingemanse, N. J., A. J. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution 25:81–89.

Dupuch, A., D. W. Morris, S. B. Ale, D. J. Wilson, and D. E. Moore. 2014a. Landscapes of fear or competition? Predation did not alter habitat choice by arctic rodents. Oecologia 174:403–412.

Dupuch, A., D. W. Morris, and W. D. Halliday. 2014b. Patch use and vigilance by sympatric lemmings in predator and competitor-driven landscapes of fear. Behavioral Ecology and Sociobiology 68:299–308.

Eccard, J. A., and A. Herde. 2013. Seasonal variation in the behaviour of a short-lived rodent. BMC Ecology 13:43.

Eilam, D. 2003. Open-field behavior withstands drastic changes in arena size. Behavioural Brain Research 142:53–62.

Fauteux, D., G. Gauthier, and D. Berteaux. 2016. Top-down limitation of lemmings revealed by experimental reduction of predators. Ecology 97:3231–3241.

Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7:1325–1330.

Gauthier, G., D. Berteaux, C. J. Krebs, and D. Reid. 2009. Arctic lemmings are not simply food limited—a comment on Oksanen et al. Evolutionary Ecology Research 11:483–484.

Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre, and I Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos 113:193–216.

Gracceva, G., A. Herde, T. G. G. Groothuis, J. M. Koolhaas, R. Palme, and J. A. Eccard. 2014. Turning shy on a winter's day: effects of season on personality and stress response in *Microtus arvalis*. Ethology 120:753–767.

Halliday, W. D., and D. W. Morris. 2013. Safety from predators or competitors? Interference competition leads to apparent predation risk. Journal of Mammalogy 94:1380–1392.

Hambäck, P. A., L. Oksanen, P. Ekerholm, Å. Lindgren, T. Oksanen, and M. Schneider. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. Oikos 106:85–92.

Herde, A., and J. A. Eccard. 2013. Consistency in boldness, activity and exploration at different stages of life. BMC Ecology 13:49.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–129.

Holt, R. D., and M. B. Bonsall. 2017. Apparent competition. Annual Review of Ecology, Evolution, and Systematics 48:447–471.

Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. American Naturalist 130:412–430.

Hoset, K. S., et al. 2017. Changes in the spatial configuration and strength of trophic control across a productivity gradient during a massive rodent outbreak. Ecosystems 20:1421–1435.

Ims, R. A., N. G. Yoccuoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. Proceedings of the National Academy of Sciences of the USA 108:1970–1974.

Krebs, C. J. 1978. A review of the Chitty hypothesis of population regulation. Canadian Journal of Zoology 56:2463–2480.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society of London, Series B 278:481–489.

Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.

Krebs, C. J., R. Boonstra, and S. Boutin. 2018. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. The Journal of Animal Ecology 87:87–100.

Lantová, P., K. Zub, E. Koskela, K. Šíchová, and Z. Borowski. 2011. Is there a linkage between metabolism and personality in

small mammals? The root vole (*Microtus oeconomus*) example. Physiology & Behavior 104:378–383.

MAITI, U., E. T. SADOWSKA, K. M. CHRZĄŚCIK, AND P. KOTEJA. 2018. Experimental evolution of personality traits: open-field exploration in bank voles from a multidirectional selection experiment. Current Zoology 2018:1–10.

MARTIN, J. G. A., D. H. NUSSEY, A. J. WILSON, AND D. RÉALE. 2011. Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. Methods in Ecology and Evolution 2:362–374.

MARTIN, J. G. A., AND D. RÉALE. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. Animal Behaviour 75:309–318.

MORRIS, D. W. 2009. Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition. Evolutionary Ecology Research 11:209–225.

MORRIS, D. W. 2019. Contingent strategies of risk management by snowshoe hares. Facets in press. doi:10.1139/facets-2018-0048.

MORRIS, D. W., D. L. DAVIDSON, AND C. J. KREBS. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the coexistence and dynamics of lemmings. Evolutionary Ecology Research 2:41–67.

MORRIS, D. W., AND A. DUPUCH. 2012. Habitat change and the scale of habitat selection: shifting gradients used by coexisting Arctic rodents. Oikos 121:975–984.

MORRIS, D. W., A. DUPUCH, AND W. D. HALLIDAY. 2012. Climate induced habitat selection predicts future evolutionary strategies of lemmings. Evolutionary Ecology Research 14:689–705.

MORRIS, D. W., R. D. HOLT, AND B. P. KOTLER. 2017. Apparent competition. In Reference module in life sciences. Elsevier. doi:10.1016/B978-0-12-809633-8.12264-2

MORRIS, D. W., D. E. MOORE, S. B. ALE, AND A. DUPUCH. 2011. Forecasting ecological and evolutionary strategies to global change: an example from habitat selection by lemmings. Global Change Biology 17:1266–1276.

MORRIS, D. W., AND S. VIJAYAN. 2018. Trade-offs between sight lines and escape habitat determine spatial strategies of risk management by a keystone herbivore. Facets 3:338–357.

MORSE, D. H. 1974. Niche breadth as a function of social dominance. American Naturalist 108:818–830.

NIEMELÄ, P. T., AND N. J. DINGEMANSE. 2018. On the usage of single measurements in behavioural ecology research on individual differences. Animal Behaviour 145:99–105.

OKSANEN, L., S. D. FRETWELL, J. ARRUDA, AND P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

OKSANEN, L., AND T. OKSANEN. 2000. The logic and realism of the hypothesis of exploitation ecosystems. The American Naturalist 155:703–723.

OKSANEN, T., L. OKSANEN, J. DAHLGREN, AND J. OLOFSSON. 2008. Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. Evolutionary Ecology Research 10:415–434.

OKSANEN, T., L. OKSANEN, J. DAHLGREN, J. OLOFSSON, AND K. KYRÖ. 2009. On the implications of currently available data on population fluctuations of arctic lemmings—reply to Gauthier et al. Evolutionary Ecology Research 11:485–487.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:S50–S66.

RÉALE, D., S. M. READER, D. SOL, P. T. MCDOUGALL, AND N. J. DINGEMANSE. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews of the Cambridge Philosophical Society 82:291–318.

REID, D. G., C. J. KREBS, AND A. KENNEY. 1995. Limitation of collared lemming population growth at low densities by predation mortality. Oikos 73:387–398.

REID, D. G., C. J. KREBS, AND A. KENNEY. 1997. Patterns of predation on noncyclic lemmings. Ecological Monographs 67:89–108.

ROBINSON, S. K., AND J. TERBORGH. 1995. Interspecific aggression and habitat selection by Amazonian birds. Journal of Animal Ecology 64:1–11.

ROCHE, D. G., V. CAREAU, AND S. A. BINNING. 2016. Demystifying animal 'personality' (or not): why individual variation matters to experimental biologists. The Journal of Experimental Biology 219(Pt 24):3832–3843.

ROSENZWEIG, M. L. 1974. On the evolution of habitat selection. Pp. 401–404 in Proceedings of the First International Congress of Ecology. Centre for Agricultural Publishing, Wageningen.

ROSENZWEIG, M. L. 1979. Optimal habitat selection in two-species competitive systems. Pp. 283–293 in Population ecology (U. Halbach and J. Jaobs, eds.). Gustav Fischer Verlag, Stuttgart, Germany.

SCHUSTER, A. C., T. CARL, AND K. FOERSTER. 2017. Repeatability and consistency of individual behaviour in juvenile and adult Eurasian harvest mice. Die Naturwissenschaften 104:10.

SIH, A., A. BELL, AND J. C. JOHNSON. 2004a. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19:372–378.

SIH, A., A. M. BELL, J. C. JOHNSON, AND R. E. ZIEMBA. 2004b. Behavioral syndromes: an integrative overview. The Quarterly Review of Biology 79:241–277.

SIH, A., J. COTE, M. EVANS, S. FOGARTY, AND J. PRUITT. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

STENSETH, N. C., AND R. A. IMS. 1993. Population dynamics of lemmings: temporal and spatial variation—an introduction. Pp. 61–96 in The biology of lemmings (N. C. Stenseth and R. A. Ims, eds.). Published for The Linnean Society of London by Academic Press, London, United Kingdom.

THERRIEN, J. F., G. GAUTHIER, E. KORPIMÄKI, AND J. BÊTY. 2014. Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian arctic. Ecology 95:56–67.

TJUR, T. 2009. Coefficients of determination in logistic regression models—a new proposal: the coefficient of discrimination. The American Statistician 63:366–372.

VOGEL, A. R., H. B. PATISAUL, S. E. ARAMBULA, F. TIEZZI, AND L. A. MCGRAW. 2018. Individual variation in social behaviours of male lab-reared prairie voles (*Microtus ochrogaster*) is non-heritable and weakly associated with V1aR density. Scientific Reports 8:1396.

Voipio, P. 1988. Comments on the implication of genetic ingredients in animal population dynamics. Annales Zoologici Fennici 25:321–333.

Weil, Z. M., L. B. Martin, 2nd, and R. J. Nelson. 2006. Photoperiod differentially affects immune function and reproduction in collared lemmings (*Dicrostonyx groenlandicus*). Journal of Biological Rhythms 21:384–393.

Wilson, D. J., C. J. Krebs, and A. R. E. Sinclair. 1999. Limitation of collared lemming populations during a population cycle. Oikos 87:382–398.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution 27:452–461.

Zadubrovskiy, P. A., A. V. Stepanova, N. V. Lopatina, and Y. N. Litvinov. 2017. Behavior of subadult mountain voles of two species (*Alticola strelzowi* and *A. tuvinicus*) in the open field test. Contemporary Problems of Ecology 10:224–229.