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Evaluation of a method to determine the breeding activity of lemmings in their winter nests

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Winter breeding under the snow is a critical ecological adaptation of lemmings and a key demographic process in their periodic multiannual fluctuations in abundance. However, logistic constraints limit our ability to quantify lemming winter reproduction. We evaluated a method to infer lemming reproduction based on the size distribution of feces found in their winter nests. We determined criteria allowing identification of reproduction from feces found in nests, using golden Syrian hamsters (*Mesocricetus auratus*) as a surrogate model. We found a large difference in individual mass of feces between juveniles at weaning and adults. Using bimodal distribution of feces size, mean size difference, and proportion of small feces, we showed that visual inspection of $\geq$30 feces was sufficient to infer hamster reproduction with an accuracy of $>$95%. We also applied the method to winter nests of collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) found in the Canadian Arctic. Because characteristics of feces found in lemming winter nests matched those found in hamster nests, we suggest that the method can be used to detect winter reproductive activity of lemmings.

Key words: fecal sample, lemming, method, nest, quantitative index, reproduction, small mammals, snow, winter

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Periodic multiannual fluctuations in lemming abundance are a major attribute of northern terrestrial ecosystems (Gruyer et al. 2008; Ims and Fuglei 2005; Krebs et al. 2002). Cyclic density fluctuations exhibited by northern rodent populations are related to some extent to the seasonality of their environment (Ostfeld and Tamarin 1986; Schmidt et al. 2008; Tkadlec 2000). In particular, winter breeding under the snow is an important feature of their population dynamics (Hansen et al. 1999; Millar 2001). Even though reproduction in the subnivean layer has been observed in most lemming species (Stenseth and Ims 1993), few studies have quantified this phenomenon because demographic studies typically are conducted during the summer months (Gruyer et al. 2010; Yoccoz et al. 1998). However, a full understanding of the factors driving lemming population cycles requires an accurate determination of demographic parameters, including during the winter period (Krebs et al. 1995; MacLean et al. 1974; Millar 2001).

Because of the inaccessibility of many northern field sites during the cold season, the winter reproductive activity of lemmings has been inferred mainly from summer population samples. Age structure of populations at the beginning of the summer has been used to describe winter breeding (Gruyer et al. 2010; Krebs et al. 1995). However, this approach could negatively bias estimates of winter reproduction if snowmelt is associated with high juvenile mortality, which can be as high as 65% (Millar 2001). Overwinter population change estimated by the difference between fall and spring abundance has been used to infer winter demography, but in this case reproduction and mortality are confounded (Aars and Ims 2002; Hansen et al. 1999; Reid and Krebs 1996).

Counts of placental scars in females captured in spring can be used to determine the number of litters and their size prior to snowmelt (Koshkina and Khalanski 1962). However, scars last for short and variable periods of time ranging from 3 to 7 weeks (Corthum 1967; Innes and Millar 1987; Martin et al. 1976). Moreover, this method requires sacrificing the animals. MacLean et al. (1974) inferred winter breeding from remains of young in lemming nests collected after snowmelt. However, this method would miss litters where all

young survived. Therefore, all of these methods present some drawbacks.

An alternative method to infer winter reproduction is to discriminate between adult and juvenile feces in nests used by lemmings during winter and recovered in spring. This approach was used in Greenland to estimate the winter breeding activity of lemmings (Sittler 1995), but the method never has been described formally or validated. We used this method to determine the occurrence of reproduction in collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) during the winter in the Canadian Arctic. Our overall objective was to develop criteria, based on the size of feces, that would allow discriminating between lemming winter nests where reproduction had occurred or not. In a 1st step we assessed the reliability of the method in correctly inferring reproduction by analyzing feces in nests of golden Syrian hamsters (*Mesocricetus auratus*) that produced litters in captivity. In a 2nd step we applied this method in the field to determine the occurrence of winter reproduction in lemmings.

Materials and Methods

Laboratory experiment.—We used 10 commercially bred pregnant golden Syrian hamsters that were housed in individual cages (20 × 30 × 40 cm). We used this species as a model because we could not obtain captive lemmings. Golden Syrian hamsters are closely related to lemmings but are heavier (mean body mass = 110 g) than lemmings (collared = 55 g, brown = 45 g—Gruyer et al. 2010). We conducted the experiment at the animal care facility of Université Laval from 2 October to 12 November 2007. Animals were fed ad libitum with formula food and sunflower seeds throughout the experiment, and cages were cleaned regularly. Nine females gave birth to a litter (mean litter size = 7; range 5–9) on average 13 days after the start of the experiment, but only 6 litters survived to weaning, which occurred 3 weeks later (3–9 November). At weaning we systematically scanned the 6 cages where litters had survived from front to back to collect fecal material accumulated over the previous 3 days. We then separated females from their litter and, after another 3 days, collected fecal material from juveniles and adults in their separate cages. This procedure generated 3 types of fecal samples: a mixture of adults with juveniles near weaning (6–9 November), juveniles alone (9–12 November), and adults alone (9–12 November). Feces were oven dried for 24 h at 45°C and then weighed individually (± 0.1 mg). All procedures were approved by the Université Laval Animal Care Committee (permit 2005-109-3) and followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Because of the large size difference found between juvenile and adult feces, we tested if a simple visual inspection of fecal samples could allow us to detect the presence of breeding activity. We performed blind trials to assess our ability to detect visually the presence of juvenile feces in hamster fecal samples. We used subsamples of 10, 20, 30, 40, 50, 60, 80, and 100 feces recovered through a systematic scan of the samples collected from either cages with only adults or reproductive cages (i.e., adult with their young). We did not include samples coming from cages with juveniles only because we considered this case not relevant to field situations. We visually examined each sample and assigned it as being from a cage with adult only or from a cage with reproduction (i.e., presence of juvenile feces) on the basis of criteria described in the results. The same observer repeated the experiment 10 times on all samples examined in random order, which allowed us to calculate an error rate in the assignment. The observer had no knowledge of the origin of the samples during the test.

Field observations.—We collected lemming winter nests during summer 2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73°08′N, 80°00′W; see Gruyer et al. [2008] for a description of the study area). Lemming nests are made of dead vegetation and are easy to recognize in the field. We sampled collared and brown lemming nests along 74 line transects (each 500 m long) distributed in equal proportion among 3 habitat types: wet tundra, mesic tundra, and along mesic streams. Starting points of these transects were selected randomly within the study area (156 km^2). Details of the sampling protocol are given in Duchesne (2009). All nests encountered along transects were collected, dried, and shipped to the laboratory for subsequent analyses. We performed a meticulous dissection of each nest to recover all fecal material. Collected feces were spread in a tray, and we performed a systematic scan to collect samples of 100 feces per nest. Feces were dried and weighed individually. Lemming species present in each nest were identified based on the distinctive specific shape of feces found; collared lemming feces are dark reddish, about 4–6 mm long, blunt at one end and rather pointed at the other end, whereas brown lemming feces are bright green, about 6–10 mm long, and rounded at both ends (MacLean et al. 1974).

Data analyses.—To determine if the mass of feces found in juvenile and adult hamster cages differed we used a Wilcoxon signed-rank test (Z). Juvenile and adult feces found in the same hamster cage or lemming nest represent a combination of 2 statistical distributions; that is, 1 for each age group, hereafter called a finite mixture distribution (Titterington et al. 1985). This distribution arises when samples include heterogeneous populations, each with a different probability density function. The multivariate normal distribution of feces mass can be represented by a probability density function of the form:

$$g(x) = \pi_j f_j(x) + \pi_a f_a(x) \quad (x \in X),$$

where the mass of individual feces, x, belongs to the finite mixture distribution X. Parameters π_j and π_a are, respectively, the proportion of juvenile and adult feces in the combined sample. The density functions of the 2 components of the mixture are defined by f_j and f_a. To estimate the value of unknown parameters (mixing proportions π_i, means μ_i, and standard deviation σ_i) we applied a maximum-likelihood estimation approach. Given that only the marginal distribution

of feces mass was available, maximum-likelihood estimations were computed iteratively using the Newton-type method in the maximization step of the expectation-maximization algorithm (procedure Rmix R 2.7—Dempster et al. 1977; Du 2002; R Development Core Team 2005). We used a chi-square test (χ^2) to determine if the finite mixture distribution improved model fit compared to the model with a single statistical distribution. Results are reported as mean ± *SE*.

Results

Laboratory experiment.—We collected 18 samples of 100 hamster feces: 6 from juvenile cages, 6 from adult cages, and 6 from reproductive cages (adult with juveniles). Mass of feces found in juvenile cages ranged from 0.6 to 15.7 mg, in adult cages from 15.2 to 66.6 mg, and in reproductive cages from 0.6 to 71.9 mg (Fig. 1). Average mass of juvenile feces at weaning was almost 5 times lower than that of adults (7.6 ± 2.2 mg versus 35.9 ± 10.8 mg, $Z_6 = 7.93$, $P < 0.001$). A finite mixture distribution model provided a better fit to the frequency distribution of the mass of feces found in reproductive cages than a model with a single statistical distribution ($\chi^2_3 = 295.42$, $P < 0.001$). The finite mixture distribution model estimated the mean mass of juvenile and adult hamster feces as 8.2 ± 0.2 mg and 28.9 ± 1.0 mg, respectively, and the proportion of juvenile feces was estimated as 0.36 ± 0.03.

Based on the previous analyses, we established the following criteria to determine if a fecal sample came from a cage where reproduction had occurred: a clear bimodal distribution of feces size, the smaller feces were 2–4 times smaller than the larger ones, and the smaller feces represented at least 33% of the sample. We used these criteria, hereafter called the reproduction criteria, as decisive tools to infer reproductive activity based on the visual inspection of fecal samples. We applied these criteria to the samples with variable number of feces coming either from adult or reproductive cages. We observed 30 detection errors in 960 trials, of which 4 were type I errors (reproduction assigned to a cage with adults only) and 26 were type II errors (no reproduction assigned to a cage with adults and juveniles). Type I errors were associated with the presence of some particularly small adult feces, whereas type II errors were associated with the presence of large juvenile feces and/or a small litter size. Nevertheless, the error rate decreased rapidly with the number of feces examined ($n = 10$ feces: error rate = 11%; $n = 20$: error rate = 6%; $n = 30$: error rate = 3%; $n \geq 40$: error rate $\leq$ 2%). Therefore, our laboratory experiment demonstrated that, on the basis of our simple criteria, reproductive activity of breeding hamsters in captivity could be inferred with >95% confidence by visually examining samples of ≥30 feces.

Field observations.—We collected and dissected 193 lemming nests and determined that 97 were used by collared lemmings, 50 by brown lemmings, and 46 by both species over the winter. Nests used by both species were excluded from the analyses because of the difficulty of reliably assigning juvenile feces to species when they were present.

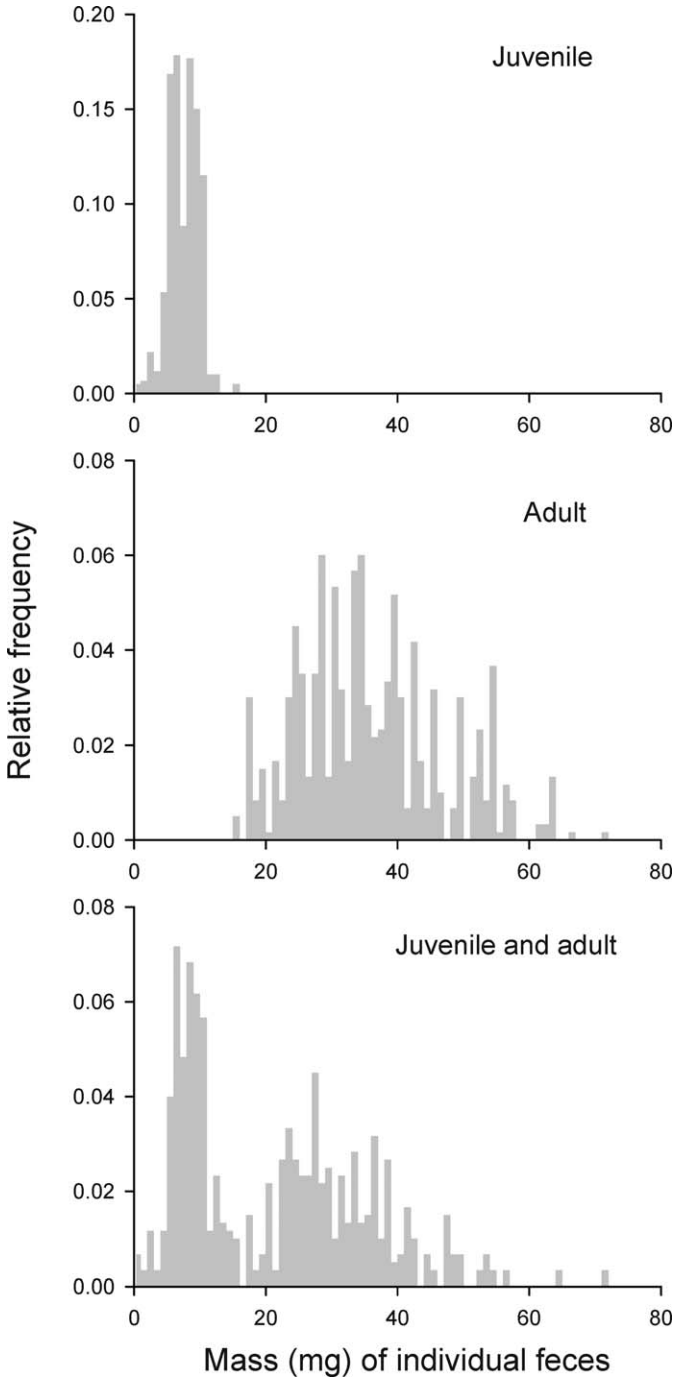

Fig. 1.—Relative frequency of hamster feces per mass category. Feces were collected in cages where juveniles only, adults only, or both juveniles and adults were present. Each graph is based on data from 6 cages with samples of 100 feces per cage.

On the basis of our reproduction criteria validated with hamsters we detected breeding activity in 39 collared and 9 brown lemming nests. Number of feces per nest ranged from 20 to >1,000, but we detected signs of reproductive activity only in nests with >100 feces.

We quantitatively analyzed fecal samples collected in a random sample of 39 lemming nests: 10 nests of each species without evidence of reproduction and 10 collared and 9 brown

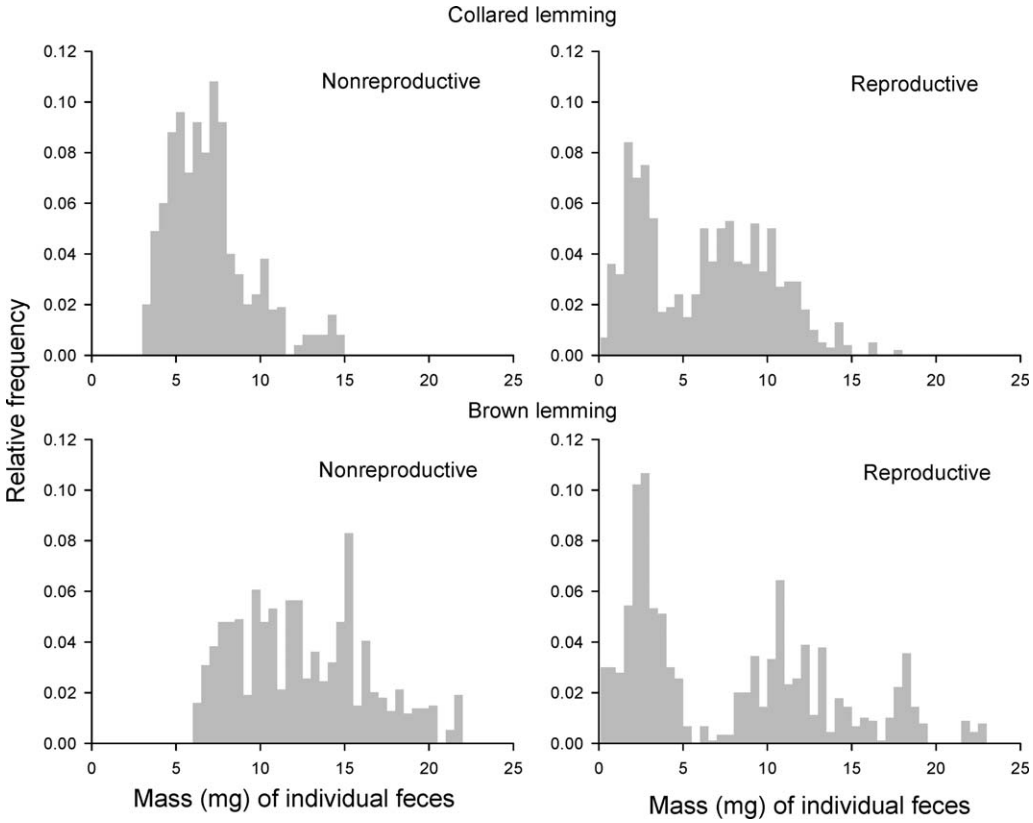

Fig. 2.—Relative frequency of lemming feces per mass category. Feces were collected from 10 nests of collared and brown lemmings without evidence of reproduction and 10 collared and 9 brown lemming nests with evidence of reproduction. One hundred feces from each nest were weighed. Nests were used by lemmings during winter 2006–2007 on south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada.

lemming nests with evidence of reproduction. Mass of feces found in nonreproductive collared and brown lemming nests ranged from 3.1 to 14.6 mg and 6.2 to 21.7 mg, respectively (Fig. 2). In contrast, mass of feces found in reproductive nests ranged from 0.4 to 17.7 mg and 0.7 to 22.6 mg, respectively. A finite mixture distribution model provided a much better fit to the frequency distribution of the mass of feces found in lemming nests with signs of reproduction compared to a model with a single statistical distribution (collared: $\chi^2_3 = 344.21$, $P < 0.001$; brown: $\chi^2_3 = 612.91$, $P < 0.001$). The finite mixture distribution models estimated the mean mass of juvenile collared and brown lemming feces at 2.2 ± 0.1 mg and 2.6 ± 0.1 mg and of adult feces at 8.4 ± 0.2 mg and 12.6 ± 0.2 mg, respectively. The proportion of juvenile collared and brown lemming feces in nests estimated by the model were, respectively, 0.35 ± 0.02 and 0.46 ± 0.02. These estimated parameters are consistent with the reproduction criteria developed with the surrogate hamster model.

Discussion

We demonstrated that feces of juveniles at the time of weaning and those of adults can be distinguished easily in the nests of a small mammal, the golden Syrian hamster, and that they can be used to infer reproduction. Under both controlled laboratory and field conditions juvenile feces were abundant in small mammal nests with reproduction, and a large difference in mass was found between the 2 types of feces. However, weighing a large number of individual feces (100 or more) is time consuming and difficult to apply under field conditions. This is why we developed simple visual criteria based on the relative size differences and the proportion of feces falling into the smaller size category to infer reproduction. Our blind trials show that this simple visual method can be used successfully (>95% confidence) to infer golden Syrian hamster reproduction when ≥30 feces are examined. Overall error rate in assigning reproductive status was low and mostly involved failure to detect reproduction when it had occurred, rendering the method conservative. Even though we validated our method in a species that weighs twice as much as lemmings, we note that individual adult feces represent a similar percentage of body mass in all 3 species (hamster: 0.026%, collared lemming: 0.015%, brown lemming: 0.028%). We conclude that visual inspection of feces found in lemming winter nests collected in spring is a simple, quick, and inexpensive method to detect winter reproduction of lemmings in their nests.

We must nonetheless recognize some limitations to the described method. First, reproduction is detected only if young are brought near the weaning stage. This approach will not detect litters where young die soon after birth because feces of

neonatal rodents are not solid and thus cannot be detected, as we observed with golden Syrian hamsters. Second, lemming feces are often concentrated outside the nest (MacLean et al. 1974). Therefore, the number of feces required and proportions suggested in this paper to infer breeding activity might not apply under all situations. However, we can expect feces of young to be proportionally more abundant than those of adults inside compared to outside of the nest, which would facilitate the detection of reproduction from feces recovered solely inside nests. Third, because juvenile feces are relatively small and sometimes difficult to detect, nest dissection needs to be conducted with care, and sampling of feces should be done systematically. Otherwise, type II errors (i.e., failure to detect reproduction when it occurred) can increase and lead to an underestimation of lemming reproductive activity. Fourth, the period with snow cover is long in northern latitudes (up to 9 months), and our method does not provide information on when reproduction occurred during winter (e.g., late fall, midwinter, or early spring). The timing of winter breeding could be important for the population dynamic of lemmings (Krebs et al. 1995). Fifth, the co-occurrence of several species of small mammals also could be a problem if many winter nests are used by more than 1 species. At our study site 24% of the nests were used by both lemming species, and when juvenile feces were detected, it was very difficult to determine which species had actually reproduced. The problem can be exacerbated in areas where *Microtus* species co-occur with lemmings, such as in western North America and Siberia. Finally, this method uses nests, not individuals, as the sampling unit, thus yielding an index of reproduction rather than a true reproductive rate. Therefore, one should use these data judiciously to study lemming population dynamics.

At the nest level a potential future development of this method would be to combine fecal counts with hormonal assays of adult feces. Pooled hormone concentration over time could be analyzed to detect reproductive activity, as suggested by Wildt et al. (1995). This combination would allow detection of reproductive activity even in nests where young died before weaning. However, because lemming feces in nests presumably are accumulated over a relatively long period, problems associated with sample decay due to microbial activity could arise (Hirata and Mori 1995; Yamauchi et al. 1999). At the population level combining nest analysis with placental scar dating or age structure determination in spring could add information about the timing of winter breeding activity and, in the case of placental scars, alleviate biases in inferring reproductive activity due to mortality of young before weaning. However, dating of placental scars requires adequate calibration (Corthum 1967).

Despite the limitations outlined above, the possibility of detecting lemming reproductive activity in their winter nests using objective criteria permits a greater understanding of the winter ecology of these species. Lemming reproduction in subnivean space is thought to be relatively common in collared lemmings but is still controversial in brown lemmings. Our results show that it occurs in this species on Bylot Island, as previously suggested by Gruyer et al. (2010). Intense winter breeding is considered by some an essential prerequisite for lemming populations to reach peak population size during the summer (MacLean et al. 1974; Millar 2001; Reid and Krebs 1996). However, this phenomenon remains poorly documented, and the method proposed in this paper offers a new approach to evaluate this hypothesis. Ultimately, the application of a robust method to measure the winter breeding activity of lemmings should advance our understanding of the demographic processes that drive their population cycles.

Résumé

La reproduction hivernale sous la neige est une adaptation écologique importante des lemmings et une composante démographique clé de leurs fluctuations périodiques d'abondance. Néanmoins, des contraintes logistiques limitent notre capacité à quantifier la reproduction hivernale des lemmings. Nous avons évalé une méthode permettant d'inférer l'occurrence de reproduction chez les lemmings basée sur la taille des fèces récupérées dans leurs nids d'hiver. Nous avons déterminé des critères permettant de détecter l'occurrence de reproduction à partir des fèces trouvées dans les nids de hamsters Syriens dorés (*Mesocricetus auratus*), un modèle substitut. Nous avons trouvé une grande différence dans la masse individuelle des fèces entre les juvéniles au sevrage et les adultes. En utilisant une distribution bimodale dans la taille des fèces, la différence moyenne de leur taille et la proportion de petites fèces comme critères, nous avons démontré qu'une inspection visuelle de $\geq$30 fèces était suffisante pour inférer l'occurrence de reproduction chez le hamster avec une exactitude de $>$95%. Nous avons aussi appliqué cette méthode aux nids d'hiver de lemmings variables (*Dicrostonyx groenlandicus*) et bruns (*Lemmus trimucronatus*) récupérés dans l'Arctique canadien. Considérant que les caractéristiques des fèces trouvées dans les nids d'hiver de lemmings concordaient avec celles observées dans les nids de hamsters, nous suggérons que cette méthode peut être utilisée pour détecter l'activité reproductrice hivernale des lemmings.

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