Why lemmings have indoor plumbing in summer

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Abstract: The faces and urine of microtine rodents are visible in ultraviolet light, and diurnal raptors, such as European kestrels (Falco tinnunculus) and rough-legged buzzards (Buteo lagopus), have the ability to see in ultraviolet light. It has been reported that in Fennoscandia, these raptors use this ability to concentrate their hunting activity in spring on areas where microtines are abundant. We hypothesized that in arctic tundra areas in summer, intense avian predation pressure and short vegetation should select for microtine behaviour that would minimize their exposure to these raptors. We dug up 62 collared lemmings (Dicrostonyx groenlandicus) near the Canadian Arctic and all had underground latrines. Latrines are not hidden underground in winter, when lemmings live under the snow, build nests above ground, and defecate above ground, nor does this occur in microtine species living in temperate areas, where summer vegetation growth is greater. Thus, high predation risk may influence not only where prey forage but also where they defecate.

Résumé: Les fèces et l'urine des rongeurs microtinaux sont visibles à l'ultra-bleu et les rapaces diurnes, tels le Faucon crécerelle (Falco tinnunculus) et la Buée pâute (Buteo lagopus), sont capables de voir à la lumière ultraviolette. En Fennoscandie, au printemps, on rapporte que ces rapaces utilisent cette propriété visuelle et peuvent concentrer leurs efforts de chasse dans les zones d'abondance des microtines. Nous avons posté en hypothèse que, dans les zones de toundra arctique, en été, l'importante pression de prédation par les oiseaux et la végétation courte devaient favoriser un comportement propre à minimiser l'exposition aux rapaces chez ces microtines. Nous avons détéré les terriers de 62 Lemmings variétés (Dicrostonyx groenlandicus) dans l'Antarctique canadien et découvrir que tous avaient des latrines intérieures. Les latrines ne sont pas cachées à l'intérieur ni hiver, quand les lemmings vivent sous la neige, construisent leur nid au-dessus du sol et déposent au-dessus du sol, cette situation ne se retrouve pas non plus chez les espèces de microtines qui vivent en zone tempérée où la végétation d'été et plus touffue. Les risques élevés de prédation n'influencent donc pas seulement l'endroit où les proies ioni se nourrir, mais également l'endroit où elles ioni se déféquer. [Traduit par la Rédaction]

Introduction

Where animals decide to forage is under strong selection pressures that involves a trade-off between predation risk and food intake (e.g., McNamara and Houston 1987; Ludwig and Rowe 1990, Matsuda and Abrams 1994). In rodents and lagomorphs this generally results a preference for cover that minimizes exposure to avian and mammalian predators (e.g., Brown and Morgan 1995; Hik 1993). In the same way, where animals choose to defecate and urinate may also be under strong selection pressure, particularly if their presence influences the hunting location and effort of their predators. Viitala et al. (1995) report that the faces and urine of voles (Microtus oeconomus) are visible in ultraviolet (UV) light and that European kestrels (Falco tinnunculus) and rough-legged buzzards (Buteo lagopus), both diurnal raptors, can "see" UV light. In contrast, "englemann's owl, a nocturnal owl, could not "see" UV light in similar laboratory experiments (M. Koivula, E. Korpimäki, and J. Viitala, unpublished data).

Received February 23, 1996. Accepted May 30, 1996. 
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Diurnal raptors use this ability to concentrate their hunting in areas where voles are abundant. Viitala et al. (1995) argue that in Fennoscandia, this ability of diurnal raptors permits them to scan large areas in a short time, especially after popula
tion crashes is the voles cause the raptors to disperse widely. If the ability to detect UV light is shared by all diurnal raptors, there may be strong selection pressure on microtines (lemmings and voles) to "hide" their faces and urine to avoid detection. There is no evidence in voles (most species of which live in nonarctic regions of the world) that this occurs at any time in Fennoscandia or elsewhere, and there may be two reasons for this. First, mammalian predators are thought to be the major agent influencing microtine outbreaks, particularly during the drought (e.g., Henttonen et al. 1987; Korpimäki et al. 1994; Hanski and Korpimäki 1995), and thus mammalian predators would likely have a greater evolutionary impact on shaping voles adaptations than avian predators. In contrast, because of their ability to move rapidly over wide areas, raptors appear to have a stabilizing influence on microtine fluctuations (Korpimäki and Nordrha 1991; Hanski and Korpimäki 1993). Second, the voles run
ways, in which the urine and faeces are deposited, are most evident from the air for only a short period after snowmelt in spring but before growth of vegetation (Viitala et al. 1995). At all other times in the growing season, dense vegetation may serve to limit visibility of waste products at ground level. In general, net primary productivity in north-temperate areas is relatively high, 400-800 g/m² (Whitaker 1975). Thus, voles give away their position to aerial predators for a rela
tively short window of time and selection pressure to deal with the avian threat may be less than that to deal with the mammalian threat. In contrast, in arctic tundra areas, vegetation grows little during the summer, is always relatively short, as net productivity is low (40–55 g/m²; Mue 1977; Svaoboda 1974; Reid 1995), and the ground is readily visible from the air throughout the growing season in most habitats. In addition, predation pressure from a number of avian predators, some of which appear to be obligate lemming predators (Pitelka et al. 1955; Reid et al. 1995), may make the threat from avian predators in summer more similar to that from mammalian predators. In this paper we report on a behaviour of the collared lemming, the building of underground summer latrines, which is consistent with the argument for the significance of the intensity of avian predation risk in the Arctic and which has defied explanation till now.

Materials and methods
From 1987 to 1989, we dug to over 62 lemming burrows at Fauce Poire, N.W.T., Canada (69°48’N, 122°40’W), to capture both adult and juvenile collared lemmings (Dicrostonyx groenlandicus). Active burrows were located either by radio telemetry (Pitale and Kebu 1985) or by a powder dust side technique (lemmings captured for breeding studies and transported to the University of Toronto) (Boostra et al. 1992). We attempted to live-trap the lemmings first, but if we were unsuccessful we excavated the burrow.

Results and discussion
All active burrows had small side chambers (latrines) full of faeces, and faeces were not noticed above ground. Similar observations have been recorded (Boostra and Banks 1973) for lemming burrows in the central forest region of the northern hemisphere (Barklow 1952; Chernysheva 1966; Brooks and Banks 1973; Barfield 1974). Until now, no hypothesis has been put forward to explain this peculiar behaviour. Lattice building does not occur in winter, when lemmings live under the snow, build nests above ground, and defecate above ground.

Given the evidence provided by Viiuala et al. (1995), the most plausible explanation for this phenomenon is that lemmings hide their faeces in latrines underground to avoid detection by aerial predators. We do not know if collared lemmings also urinate in their tunnels, but given their behaviour, we predict that they do.

The following evidence indicates that predation pressure by raptors may be extremely intense in the Arctic. First, a large diversity of raptors (scaws, jaegers, diurnal owls) prey on lemmings in the Arctic summer (Pitelka et al. 1955). Second, the elimination of aerial predation by using monofilament lines strung above the area has recently been shown to significantly improve lemming survival (Reid et al. 1995). Third, radiotelemetry studies indicate that lemmings spend up to 95% of their time in burrows in summer (Brooks 1993). This behaviour is likely to be energetically very expensive, as the burrows must be near 0°C, given that the permafrost is within 30 cm of the surface over much of the Arctic (note that microtines in temperate latitudes often nest above ground in summer; e.g., Boostra and Craine 1986; Larinville 1994). Finally, at summer solstice at high latitudes, there is no light and lemmings are active at all hours. However, when periods of darkness occur again at the end of summer, lemmings rapidly shift their activity periods, presumably to minimize predation risk from diurnal aerial predators (Peterson and Batzli 1975). In addition, underground latrines may possibly increase predation in summer by mammalian carnivores such as foxes because latrines will concentrate lemming odour and foxes have an extremely good sense of smell (Arquilla 1989). This suggests that any additional predation cost to lemmings from mammalian carnivores because of the concentration of their waste in underground latrines is outweighed by the benefits. Thus, the remarkable adaptation of diurnal raptors to detect microtines by focusing on their waste appears to have been met by a counteradaption of arctic lemmings to avoid detection by hiding their faeces and urine.

The building of underground latrines may also explain the high frequency (up to 92%) of infection in the conjunctival sac of arctic lemmings by a nematode, Pseudolaimus pseudolaimus (Cliff et al. 1978). This species is saproxylic, living particularly in decaying piles of faeces and vegetation. The immaturity of this species can be found swimming over the eyes of lemmings (personal observation), but apparently causes no harmful effects to the lemmings and simply uses them as a dispersal vehicle.

Acknowledgements
We thank M. Kanter and J. Serenius for field assistance in the Arctic, J. Orchick and D. Sherstone of the Science Institute of the Northwest Territories and the Polar Continental Shelf Project of the Department of Energy, Mines and Resources of Canada for their field support, the Inuvialuit Land Administration for permission to work on their land, and the Natural Sciences and Engineering Research Council of Canada for financial support.

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