Why lemmings have indoor plumbing in summer

Rudy Boonstra, Charles J. Krebs, and Alice Kenney

Abstract: The faeces 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 lemming (*Dicrostonyx groenlandicus*) burrows in 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 microtinés sont visibles à l'ultra-violet et les rapaces diurnes, tels le Faucon crécerelle (*Falco tinnunculus*) et la Buse pattue (*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 microtinés. Nous avons posé en hypothèse que, dans les zones de toundra arctique, en été, l'importante pression de prédation par les oiseaux et la végétation courte devraient favoriser un comportement propre à minimiser l'exposition aux rapaces chez les microtinés. Nous avons déterré les terriers de 62 Lemmings variables (*Dicrostonyx groenlandicus*) dans l'Arctique canadien et découvert que tous avaient des latrines intérieures. Les latrines ne sont pas cachées à l'intérieur en hiver, quand les lemmings vivent sous la neige, construisent leur nid au-dessus du sol et défèquent au-dessus du sol; cette situation ne se retrouve pas non plus chez les espèces de microtinés 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 iront se nourrir, mais également l'endroit où elles iront déféquer.
[Traduit par la Rédaction]

Introduction

Where animals decide to forage is under strong selection pressure 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 in a preference for cover that minimizes exposure to avian and mammalian predators (e.g., Brown and Morgan 1995; Hik 1995). 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 faeces and urine of voles (*Microtus agrestis*) 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, Tengmalm's owl, a nocturnal owl, could not "see" UV light in similar laboratory experiments (M. Koivula, E. Korpimäki, and J. Viitala, unpublished data). 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 population crashes in 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 faeces and urine to avoid detection. There is no evidence in voles (most species of which live in non-tundra 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 multi-annual vole fluctuations, particularly during the declines (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 in shaping vole 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 Norrdahl 1991; Hanski and Korpimäki 1995). Second, the vole runways, 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/m^2 (Whittaker 1975). Thus, voles give away their position to aerial predators for a rela-

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R. Boonstra.[1] Division of Life Sciences, Scarborough Campus, University of Toronto, 1265 Military Trail, Scarborough, ON M1C 1A4, Canada.
C.J. Krebs and A. Kenney. Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

[1] Author to whom all correspondence should be addressed (e-mail: boonstra@lake.scar.utoronto.ca).

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/m^2; Muc 1977; Svoboda 1977; 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 up over 62 lemming burrows at Pearce Point, 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 radiotelemetry (lactating females) (Krebs et al. 1995) or by a powdered slide technique (lemmings captured for breeding studies and transported to the University of Toronto) (Boonstra et al. 1992). We attempted to livetrap 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 made by others who have excavated burrows of lemmings of both genera (*Dicrostonyx* spp. and *Lemmus* spp.) throughout the arctic tundra regions of the northern hemisphere (Barkalow 1952; Chernyavskii 1969; Brooks and Banks 1973; Banfield 1974). Until now, no hypothesis has been put forward to explain this peculiar behaviour. Latrine 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 Viitala 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 where they defecate, 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 (hawks, 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 tundra 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., Boonstra and Craine 1986; Lambin 1994). Finally, at summer solstice at high latitudes, there is no night and lemmings are active at all hours. However, when periods of darkness occur again at the end of summer, lemmings rapidly shift their activity to these 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 (Artois 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 focussing on their waste appears to have been met by a counteradaptation 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 sacs of arctic lemmings by a nematode, *Pelodera strongyloides* (Cliff et al. 1978). This species is saprophagic, living particularly in decaying piles of faeces and vegetation. The immature form 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.

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