The role of predation in mass mortality of wood lemmings (Myopus schisticolor)

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Abstract

The wood lemming (*Myopus schisticolor*) is known for its skewed sex-ratio and unpredictable population outbreaks followed by mass mortality. Both mammalian and avian predators include the wood lemming in their diet, but the role of predation in the population dynamics and mass mortality of wood lemmings is unclear. To test the predation hypothesis, I dissected 158 wood lemmings found-dead during population outbreaks in 2014 and 2017 in the county of Värmland, Sweden, and looked for injuries and haemorrhages. For comparison, I also included 55 wood lemmings that were snap-trapped in 1995 - 2014 in Sweden. The most common injury in found-dead specimens was large holes and the most common location of injuries was the chest and the head. Predators killed 40 % of the wood lemmings examined and injured 33 % after their death. The male ratio before and during the outbreaks varied from 10 - 36 %. It must be stated that it is possible that an unknown number were predated and completely consumed and therefore not included in this study. Of the wood lemmings found and killed by predators in 2014 and 2017 combined, 87 % were females and 13 % males. Among the wood lemmings snap-trapped in 1995 - 2014 there were 73 % females and 27 % males. Further analyses suggest that predators did not select for larger wood lemmings and that predation varied temporally. Predation increased from July until September and most predation occurred from late July until early August, a trend that coincided with the increase in found-dead wood lemmings.

Since 60 % of wood lemmings did not die from predation, predation can be refuted as the main cause of mass mortality. Future studies should therefore focus on testing alternative hypotheses of the mass mortality of wood lemmings including the disease, stress and food shortage hypotheses. Even though predation was not the cause of mass mortality, it affected a high proportion of wood lemmings. A future study should therefore aim to identify which predators that kill wood lemmings.

Keywords: wood lemming, *Myopus schisticolor*, outbreak, predation, predator, mass mortality

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Introduction

Population cycles and mass mortality

Some populations of small rodents undergo large fluctuations in density throughout time (Krebs & Myers, 1974). According to the same authors there can be plenty of animals during some years while in other years the rodents can be almost absent from the same area. For some populations, these peak and low phases in density occur with a regular interval, also known as a cycle, but in other populations the cycles might be completely absent (Krebs & Myers, 1974). Hanski *et al.* (1991) reported that the cycles increase from around three years in length in the south-central parts of Fennoscandia up to four years in the northern parts.

The drivers behind these cycles are not fully understood but several hypotheses have been developed to explain the enigma of population cycles. Krebs & Myers (1974) list several factors that could potentially influence the existence of these cycles including food, predation, weather, stress, behaviour and genetics. Further, Elton (1931) mentioned diseases as a factor regulating the numbers of wild animals. These factors can be categorized as extrinsic (food, predation and weather) and intrinsic (stress, behaviour and genetics) (Hansson & Henttonen, 1985). Microparasites such as viruses and bacteria can be seen as extrinsic factors (Hansson & Henttonen, 1988). If it's the extrinsic, intrinsic or a combination of these factors that drive vole cycles is still being discussed. Turchin & Hanski (2001) suggest that predation, food and maternal effects are more likely to explain these cycles with predation being the most likely out of the three.

According to Fey *et al.* (2015) events causing mass mortality are made up of demographic catastrophes able to affect all life stages at the same time and can quickly remove a large part of a population which occurs over a

short time period compared to the generation time of the organism. One example of a mass mortality event (MME) occurred in Kazakhstan in 2015 where over 200,000 saiga antelopes (*Saiga tatarica tatarica*) died during a time period of three weeks (Kock *et al.*, 2018). According to the same authors the cause of death was haemorrhagic septicemia caused by the bacteria *Pasteurella multocida* type B. It was also found that there was unusually high relative humidity and temperature in the days before the MME and that this unusual humidity and temperature could have contributed to the MME (Kock *et al.*, 2018). Based on this information the drivers of this MME seem to be a combination of two extrinsic factors, weather and disease (Kock *et al.*, 2018). Another example of an MME occurred on Kinkazan Island in northern Japan in 1984 where carcasses of 293 sika deer (*Cervus nippon*) were found from late March until mid April, comprising 43 % of the population (Takatsuki *et al.*, 1994). According to the same authors the drivers of this MME seem to be a combination of two extrinsic factors, weather and food. The winter preceding this mass mortality was unusually cold with deep snow which made the deer lose their fat reserves when moving through it. Then they gathered in high density at lower altitude with less deep snow, consumed the most nutritious food, were upon depletion forced to forage on less nutritional items, and therefore suffered from malnutrition before dying (Takatsuki *et al.*, 1994). A third and final example of an MME affected Swainson's hawks (*Buteo swainsoni*) in Argentina between 1995 and 1996 (Goldstein *et al.*, 1999). According to the same authors farmers used an insecticide called monocrotophos to protect their crops and the hawks were affected when feeding on grasshoppers and caterpillars in these fields. Monocrotophos was responsible for the death of over 4,000 hawks (Goldstein *et al.*, 1999). As demonstrated by these three examples, mass mortality events seem mostly caused by extrinsic factors, usually a combination of several factors such as weather and food or weather and disease.

The predation hypothesis assumes predators cause population cycles (Krebs, 1996). Further, the mere risk of predation can affect the behaviour of the prey by altering for example sociality, mating and foraging (Lima, 1998). These behavioural changes can be seen as a defensive trait, also known as a "trait-mediated interaction", which can be adopted in the presence of a predator (Preisser *et al.*, 2005). Predators can be divided into two groups. There are generalist predators which change their preferred prey species depending on what they can find and there are specialist predators which are relying more on a specific group of animals or even a

specific species (Hansson, 1987). Besides the preferred kind of prey, predators can further be divided by their mobility in search of prey; nomadic and resident predators where nomadic predators can leave areas in search for prey and resident predators stay in a certain area (Andersson & Erlinge, 1977). Based on these groups, predators can be divided into resident specialists, resident generalists and nomadic specialists (Andersson & Erlinge, 1977). Predators specific for small rodents in the boreal zone were summarized into these categories by Hanski *et al.* (2001). According to the same authors the least weasel (*Mustela nivalis*) and the stout (*Mustela erminea*) are resident specialists. Furthermore, representatives of resident generalists include red fox (*Vulpes vulpes*), badger (*Meles meles*), domestic cat (*Felis catus*), polecat (*Mustela putorius*), pine marten (*Martes martes*), common buzzard (*Buteo buteo*) and tawny owl (*Strix aluco*). Finally, nomadic specialists include short-eared owls (*Asio flammeus*), long-eared owls (*Asio otus*), hawk owls (*Surnia ulula*), Tengmalm's owls (*Aegolius funereus*), kestrels (*Falco tinnunculus*), rough-legged hawks (*Buteo lagopus*) and long- tailed skuas (*Stercorarius longicaudus*) (Hanski *et al.*, 2001). Hanski *et al.* (1991) report that the number of generalist predators and avian predators are higher in the southern parts of Fennoscandia than in the northern parts. Besides predators there is a possibility that small insectivores, like the common shrew (*Sorex araneus*), would seize the opportunity and predate on the young of wood lemmings if found unattended and there is a lack of other food items. For example common shrews may be predators of the pups of bank voles (*Myodes glareolus*) and during periods of low food availability they can be aggressive towards the pups (Lisenjohann *et al.*, 2011).

The wood lemming

The wood lemming (*Myopus schisticolor*) belongs to the order Rodentia (Fedorov *et al.*, 1995) and the family Cricetidae (Henttonen, 2016). The geographical range of the wood lemming stretches from Norway in the west all the way to Kamchatka in the east and includes the majority of the coniferous forest zone of Eurasia (Fedorov *et al.*, 1995). Wood lemmings prefer spruce forests with a thick layer of mosses (Eskelinen, 2002). One reason for the preferred choice of habitat of the wood lemming is likely its specific diet. Unlike other small rodents, the wood lemming feeds primarily on mosses (Eskelinen, 2002). According to the same author, wood lemmings prefer the mosses *Dicranum* spp. and *Polytrichum* spp. Furthermore, a small degree of grass can occasionally be included in the

diet and also stems and leaves from for example European bilberry (*Vaccinium myrtillus*) (Eskelinen, 2002).

Wood lemmings have been reported to migrate (Eskelinen, 1997). These migrations occur when there are plenty of lemmings and they can then be found in areas that do not include their preferred habitat (Eskelinen, 1997). According to the same author, migrations in Finland in 1989 started in early August and stopped in late September or early October. The wood lemming undergoes cyclic changes in density in some areas. In eastern Finland Eskelinen *et al.* (2004) found that the cycle has a time interval of three years. The cycle of the field vole (*Microtus agrestis*) was synchronized with the cycle of the wood lemmings in eastern Finland (Eskelinen *et al.*, 2004). Despite these findings in eastern Finland, no cycle was found among wood lemmings in western Finland (Eskelinen *et al.*, 2004).

The wood lemming has an average gestation period of 25 days (Ilmén & Lahti, 1968). Females have been observed to reach sexual maturity as early as 22 days of age, but males reach it later, earliest after 44 days (Ilmén & Lahti, 1968). The average litter size in captivity is three offspring (Cheprakov, 2000) but there is evidence that some females have up to seven young (Ilmén & Lahti, 1968). Wood lemmings can reach up to 49.7 g, which was recorded for a male individual raised in captivity by Ilmén & Lahti (1968). Andreassen & Bondrup-Nielsen (1991) used radio telemetry to measure the home range size of wood lemmings in Norway. They found that males have a significantly larger home range size than females. The mean home range size for males was 2,144 m^2, with the largest home range being 4,247 m^2, and for females it was 285 m^2, with the largest home range being 635 m^2 (Andreassen & Bondrup-Nielsen, 1991). Further, the same authors also found that males are more active than females. The mean distance moved during a day for a male wood lemming was 217 m and the same distance for a female wood lemming was 21 m (Andreassen & Bondrup-Nielsen, 1991). Mironov *et al.* (2003) studied the budget of daily activity in four captive wood lemmings in Russia. The results showed that wood lemmings spend the majority of the day (42.5 %) sleeping, followed by spending time in shelters (18.9 %), running in running wheels (18.2 %), other activity (13.0 %) and feeding (7.3 %).

Wood lemmings constantly posses a skewed sex-ratio where there are more females than males (Fredga *et al.*, 1977). For example, Eskelinen (2004) found that in one Finnish population the proportion of males varied

between 15 - 29 %. This skewed sex-ratio can be linked to a genetic mutation on the female chromosomes. According to Fredga *et al.* (1977) there are three types of female sex chromosomes: XX, X*Y and X*X where X* carries the mutation. Females with XX have an offspring ratio of 1:1. Females with X*X have an offspring ratio of 3:1 where daughters are in majority and XY females produce no sons (Fredga *et al.*, 1977).

There is a variety of predators that include wood lemmings in their diet. Pulliainen & Ollinmäki (1996) studied the winter food niche of the pine marten (*Martes martes*) in northern Finland. Between the winter of 1986/87 and 1991/92 the remnants of wood lemmings were found in 10 % of the scats although the numbers varied among years depending on the availability of animals (Pulliainen & Ollimäki, 1996). Obuch & Bangjord (2016) studied the diet of the Eurasian eagle owl (*Bubo bubo*) in Central Norway. The same authors analyzed the scats of the Eurasian eagle owl and found remnants of 25 wood lemmings in the mountainous area of Central Norway during a period of eight years. Støvern (2012) studied the diet of the Eurasian kestrel (*Falco tinnunculus*) in south eastern Norway. The same author used video monitoring at the nests of six breeding pairs to see what prey species were delivered to the nests. Støvern (2012) found 32 wood lemmings delivered to the nests in the breeding season of 2011, which made them the second most common species delivered, outnumbered only by field voles. Nybo & Sonerud (1990) found remnants of wood lemmings in the scats of hawk owls (*Surnia ulula*) in south eastern Norway.

Aim of project

Based on the information that predators do include wood lemmings in their diet my project focused on the predation-hypothesis, i.e. that predation causes mass mortality of wood lemmings. The first and main aim was to investigate to which extent wood lemmings during outbreak years are attacked by predators and if predation varies among sexes of wood lemmings. Specifically, I tested if predators are the main cause of death or if they take wood lemmings after their death.

Secondly, I tested if there is a difference in weight between injured and non-injured wood lemmings for both sexes combined and each sex separately. Thirdly, I studied temporal differences in predation with focus on differences among months as well as differences among days. Fourth, I compared the sex-ratio between outbreak and non-outbreak years as well as

the sex-ratio for snap-trapped specimens. Fifth, since the sex ratio of wood lemmings in outbreak years is biased towards females, I also tested if the sex-ratio of predator-killed wood lemmings followed the same trend. Due to the larger home range of males compared to females, males could be more vulnerable to predation if moving more in open terrain within this home area, which would result in a comparatively high proportion of predator-killed males. Finally, I tried to identify the predators involved, by studying the position of damage on the body and the shape of damage.

Material & Methods

Sampling and trapping of wood lemmings

A total of 213 wood lemmings (*Myopus schisticolor*) were included in my study. Of these 30 were snap-trapped in the Vindeln area, county of Västerbotten, during 1995 - 2014. The remaining 183 specimens were found on a number of locations in the county of Värmland in 2014 and 2017. Of these, 158 were found-dead and 25 were snap-trapped. Specimens were found in July, August and September in 2014 and only in September in 2017. In 2014, 59 of the specimens were found in Gustavsfors, on the border between county of Värmland and county of Västra Götaland. The remaining specimens in 2014 were all found in the county of Värmland but in different areas. Most were found in the municipality of Torsby followed by the municipality of Filipstad and Hagfors. In 2017, 75 of the specimens were found near Lennartsfors, county of Värmland, close to the Norwegian border. The remaining eight specimens in 2017 were found in Glaskogens nature reserve, county of Värmland.

The specimens from the Vindeln area were included in the project to investigate if the sex-ratio differed in specimens during outbreak and non-outbreak years. Based on the areas where specimens were found a map was made using QGIS to visualize the sites on a national scale (Fig. 1a). Since the position of the found specimens were recorded with the x and y co-ordinates, these specific sites could be visualized on a more locally produced map in this case including the county of Värmland (Fig. 1b).
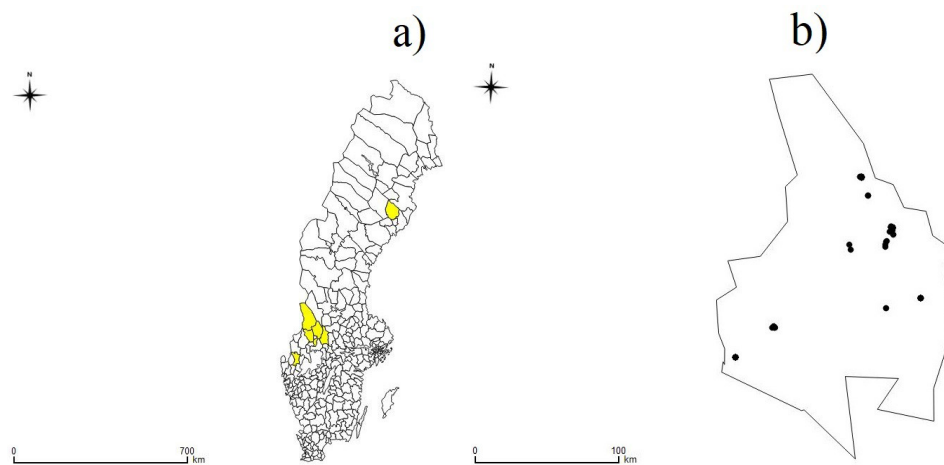
Fig. 1. Geographic location of the sampling sites a) in municipalities included in the study (yellow polygons) and b) in the county of Värmland where wood lemmings were found-dead during population outbreaks in 2014 and 2017 (black dots).

Dissections

After sampling, all wood lemmings in this study were stored in -20 °C freezers. Before dissection, the specimens were taken out of the freezer to thaw in room temperature for about one hour depending on the size of the specimens. Once defrosted the limbs of the animals were stretched perpendicular to the body axis and the feet were fixed with needles on a linoleum to simplify the work. The linoleum was put in a fume hood for the entire process to avoid possible pathogen transmission. Lab coats and rubber gloves were used during the process for safety reasons.

When in place, another student started to open the stomach using tweezers, scalpel and scissors. After opening the specimen, all organs were taken out including the heart, lungs, kidney, adrenal gland and spleen. The intestines were also removed. When this was done, I started to look for signs of predation. Within a different initial project, the specimens from 2014 had their heads separated from the bodies. For the other specimens, the heads were removed with scissors to simplify the process. When looking at the body, the chest was usually removed from the back part by breaking of the spine with tweezers. Then the two body parts were dragged out and removed from the skin to make it easier to detect any possible injuries. The skin, body and head were thoroughly searched for signs of injury. Any deviations from the normal state, such as bleedings, marks, scars, cracks and holes were photographed and added to the dissection protocol. The protocol included the ID for each specimen, the date for the dissection, weight, sex, a code for the position of the injuries on the body (head, upper or lower chest and back), a sketch depicting the exact position of the injury

if present, the side of the body on which the injury was found and the shape of the injury. Further, it was recorded if there were any haemorrhages found, photograph ID and comments on the injuries. I also recorded if a specimen was found dead or trapped, year, month and date when found, name of locality, coordinates, comments on the place found and name of the person who found the specimen. After completion, all body parts belonging to the specimen were again stored in the freezer. For disinfection, the tools used were put in a Virkon^{TM} solution overnight, then burned off with a candle and washed with soap and water before being used for another specimen.

Data selection

To test the hypotheses that wood lemmings are attacked and/or killed by predators during outbreak years, I excluded all specimens that had been snap-trapped in the Värmland dataset. For found-dead specimens, I applied three categories depending on if the lemmings had no injuries "N", if they had injuries and haemorrhages and therefore were taken by predators "P" or if they had injuries but no haemorrhages which implied that they were injured by predators after their death "NP".

To test the hypothesis regarding difference in weight between injured and non-injured specimens I excluded all the specimens with unknown sex as well as specimens that had been snap-trapped. Finally, specimens that were missing their head or any other significant body part were excluded because this would negatively affect the weight. Following these exclusions, the dataset consisted of 131 specimens from Värmland, including both sexes. The category "P" includes specimens killed by predators and the category "N" includes specimens that died from other reasons than predation.

Regarding the hypothesis of temporal differences in predation I excluded all specimens with unknown sex and specimens that had been snap-trapped in the Värmland dataset. This resulted in a dataset containing 148 specimens. To easier detect differences in the proportion of animals suffering from predation, each month was investigated separately in the two outbreak years.

To test the hypothesis regarding sex differences in predation rate I excluded all specimens with unknown sex as well as all snap-trapped specimens. The rate of predation was determined for September 2017 including a) both

sexes, b) females only, c) males only, September 2014 including d) both sexes, e) females only, f) males only, August 2014 including g) both sexes, h) females only, i) males only and finally July 2014 including j) both sexes, k) females only and l) males only.

To test the hypothesis that the sex-ratio differs between outbreak and non-outbreak years, I excluded all specimens with unknown sex. The sex-ratio was determined a) across all years combined, b) 2014 only, c) 2017 only, d) for specimens that died from others reasons than predation 2014 and 2017 combined, e) 2014 only, f) 2017 only), g) that died from predation in 2014 and 2017 combined, h) 2014 only, i) 2017 only, j) that had been snap-trapped in 1995- 2014, k) 2014 only and l) 1995 - 2007 in the Vindeln area.

To investigate the hypothesis regarding difference in predation over time in days across years, I excluded all snap-trapped specimens in the Värmland dataset. This resulted in a dataset of 82 specimens in 2017 and 76 specimens in 2014.

To test the hypothesis regarding the proportion of damage per shape and per position, I excluded all specimens that had not been killed by predators or that had been taken by predators after their death. This resulted in a dataset of 63 specimens for 2014 and 2017 combined. The shapes were divided into point-shaped holes, larger holes, cracks, crushed parts, broken parts or missing parts as well as blood stains. The positions were divided into: head, upper chest, lower chest, upper back and lower back.

Statistical analysis

To test if wood lemmings were killed by predators or if lemmings were taken after their death a non-parametric Pearson's chi-square test for count data was used. The same test was also used to test if the predation differed between months for both years combined and for both sexes combined. A chi-square test was used to test if wood lemmings were killed by predation or died for other reasons for each month during both years. Further, the same test was used to look at the proportion of damage per shape and the proportion of damage per position on the wood lemming. A Mann-Whitney U test was used to test if wood lemmings killed and not killed by predators differed in weight for both sexes combined and each sex separately, respectively.

All data from the dissection protocol was stored in a file in Microsoft Excel. The analyses were done using the statistical software R and R-studio (R Core Team, 2018). Graphs produced in R were partly modified using Adobe Acrobat Pro DC (Adobe Acrobat Pro DC, 2018).

Results

Predation as cause of mass mortality

For 2014 and 2017 combined 63 (40 %) wood lemmings were killed by predators, 52 (33 %) animals were injured by predators after their death and 43 (27 %) had no injuries (Fig. 2a). For each of the separate years, predators killed 40 % (30 in 2014 and 23 in 2017) of the wood lemmings. In 2014, the number of animals injured by predators after their death was 23 (30 %; Fig. 2b) and the number of animals without injuries was also 23 (30 %; Fig. 2b). In 2017 a total of 29 (36 %) animals were injured by predators after their death and 20 (24 %) had no injuries (Fig. 2c). Significantly more wood lemmings were killed by other causes than by predators for the years combined (χ^2 = 6.48, p <0.05).
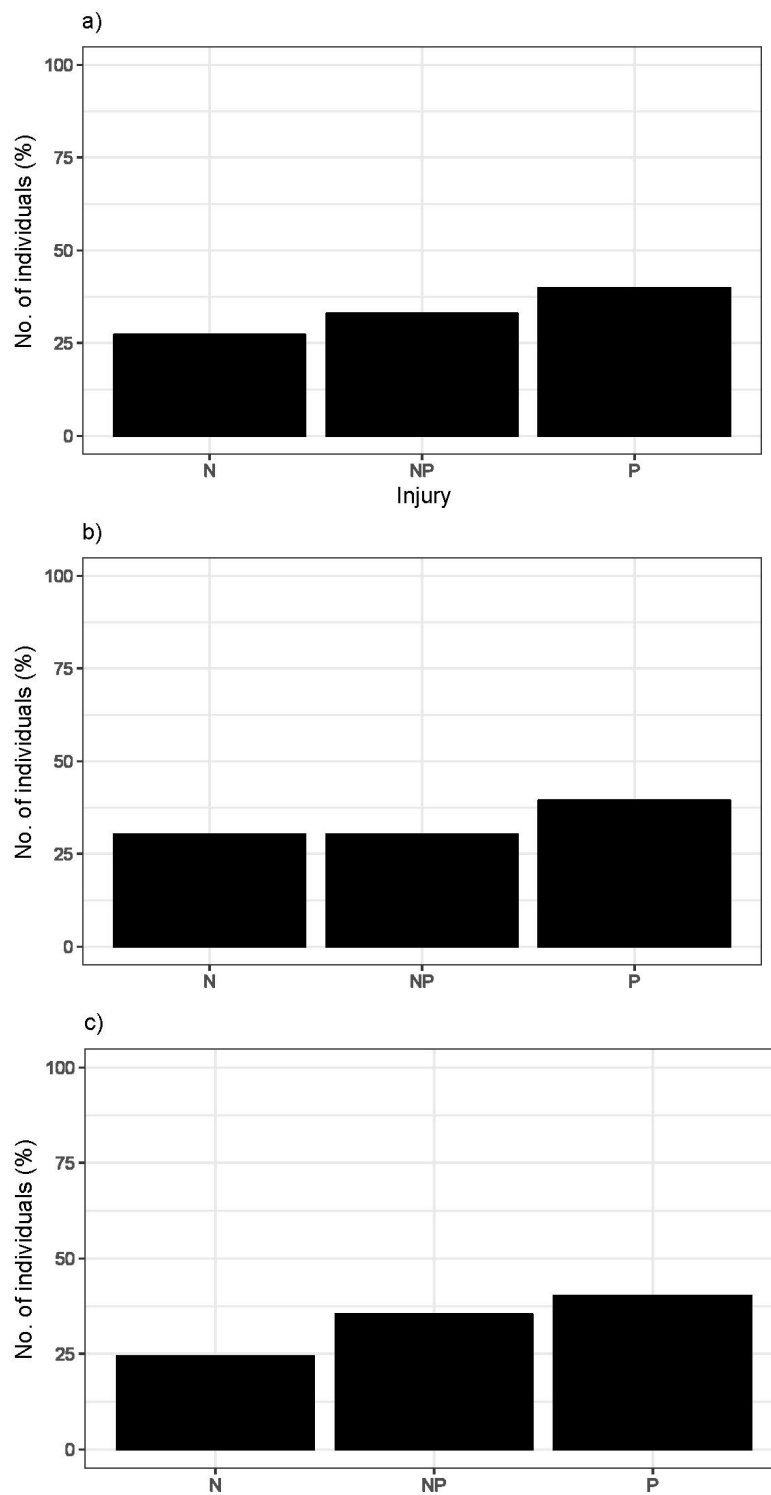
Fig. 2. Number of *Myopus schisticolor* specimens (%) without injury (N), injured by predators after their death (NP) or killed by predators (P) in a) 2014 and 2017 combined (n = 158), b) 2014 (n = 76) and c) 2017 (n = 82).

Specimens from 2014 were found in July, August and September. In September, a total of three specimens were found of which one died from

predation and two of other causes. There was no significant difference between wood lemmings killed by predators and those that died from other causes than predation (χ^2 = 0.33, p >0.05) (Fig. 3a). In August, a total of 47 specimens were found, 18 (38 %) died from predation and 29 (62 %) from other causes. There was no significant difference between wood lemmings killed by predators and those that died from other causes than predation (χ^2 = 2.57, p >0.05) (Fig. 3b). In July, a total of 18 specimens were found, 10 (56 %) died from predation and eight (44 %) from other causes. In this month, there was no significant difference between wood lemmings killed by predators and those that died by other causes than predation (χ^2 = 0.22, p >0.05) (Fig. 3c).

All 80 specimens from 2017 were found in September. Of these, 33 (41 %) died from predation and 47 (59 %) of other causes. In September, there was no significant difference between wood lemmings killed by predators and those that died from other causes than predation (χ^2 = 2.45, p >0.05) (Fig. 3d).
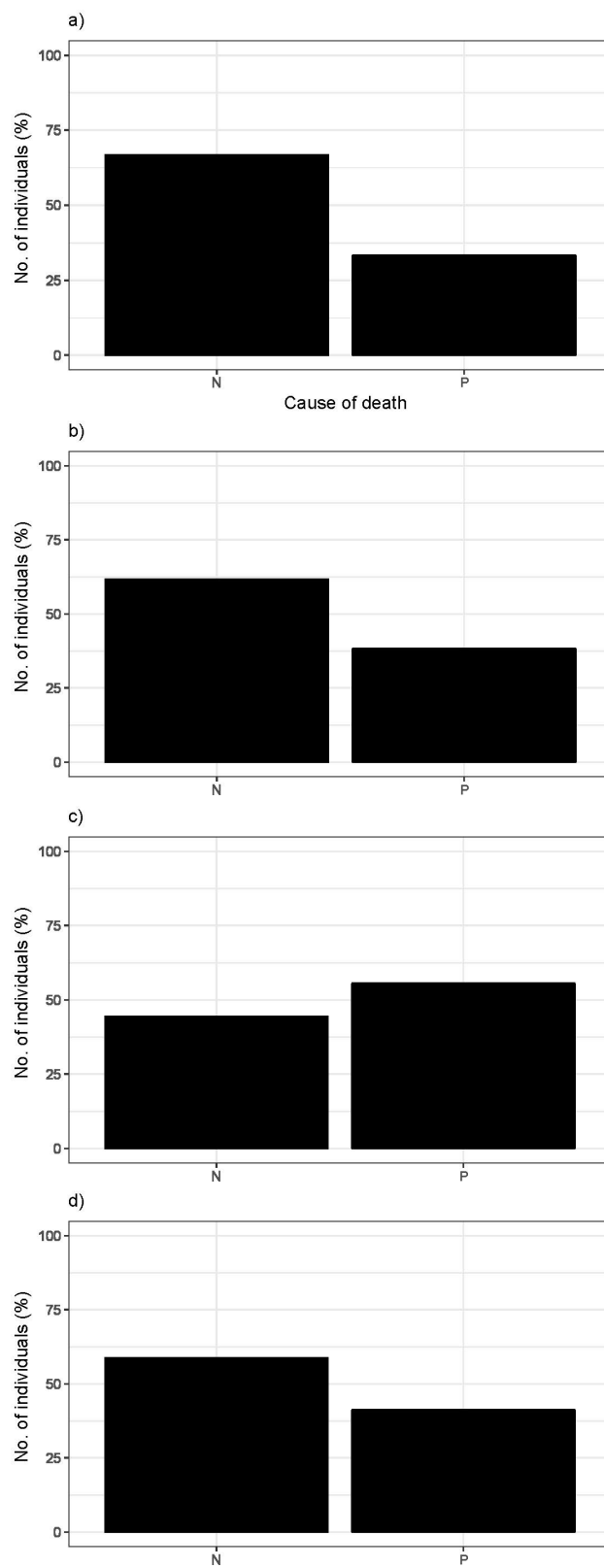
Fig. 3. Number of *Myopus schisticolor* specimens (%) killed by predation (P) or that died from other causes than predation (N) including both sexes in a) September 2014 (n = 3), b) August 2014 (n = 47), c) July 2014 (n = 18) and d) September 2017 (n = 80).

Weight of injured and non-injured specimens

Wood lemmings killed and not killed, respectively, by predators did not differ in weight (median weight, killed = 16.95g, median weight, not killed = 16.90g, U = 2117, p >0.05) when combining both sexes (Fig. 4a). Female wood lemmings killed and not killed, respectively, by predators did not differ in weight (median weight, killed = 16.70g, median weight, not killed = 17.35g, U = 1647, p >0.05; Fig. 4b). Male wood lemmings killed and not killed, respectively, by predators did not differ in weight either (median weight, killed = 17.3g, median weight, not killed = 16.2g, U = 22.5, p >0.05; Fig. 4c).
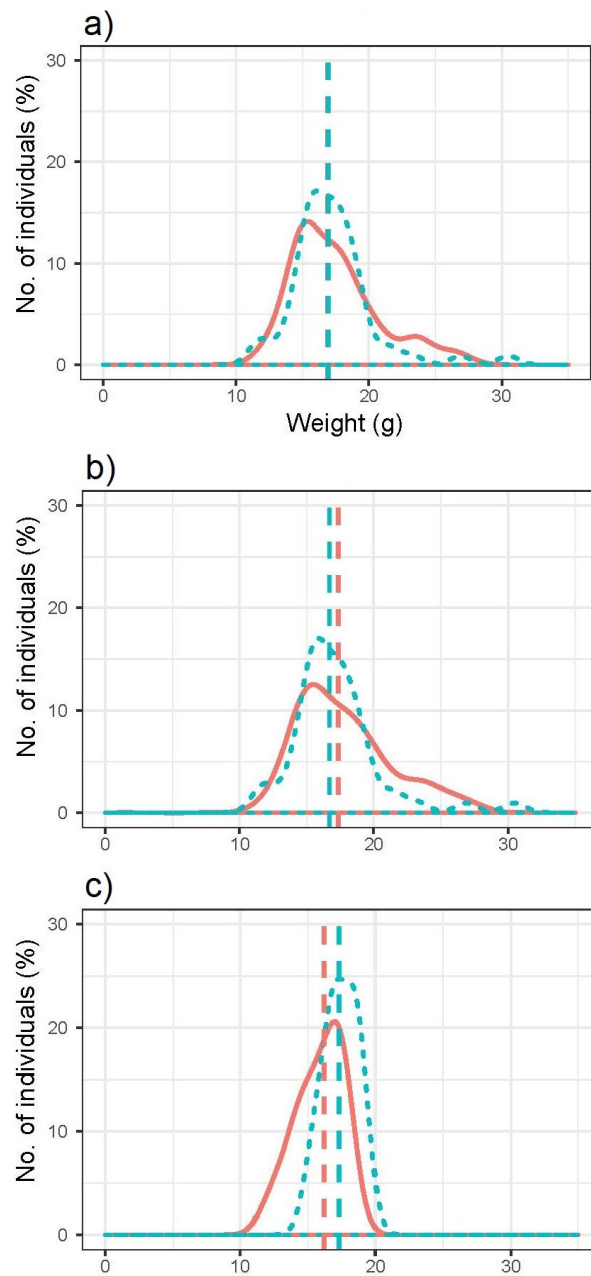
Fig. 4. Weight distribution of *Myopus schisticolor* specimens found-dead in Värmland in 2014 and 2017 and killed by predators (red solid line) and not killed by predators (blue dashed line), respectively, for a) both sexes (n = 131), b) females (n = 111) and c) males (n = 20). The dashed vertical lines of each colour represent the median weight of each category.

Sex differences in predation

In September 2017, there were 69 females of which 28 (41 %) died from predation and 41 (59 %) of other causes (Fig. 5a). In the same period there were 11 males of which five (45 %) died from predation and six (55 %) of other causes (Fig. 5b). In September 2014, there were two females of which one died from predation and one of other causes (Fig. 5c). In the same period, there was one male and that one died from other causes than predation (Fig. 5d).

In August 2014, there were 38 females of which 16 (42 %) died from predation and 22 (58 %) from other causes (Fig. 5e). In the same period there were nine males of which two (22 %) died from predation and seven (78 %) from other causes (Fig. 5f). In July 2014, there were 16 females of which nine (56 %) died from predation and seven (44 %) from other causes (Fig. 5g). In the same period there were two males of which one died from predation and one from other causes (Fig. 5h).
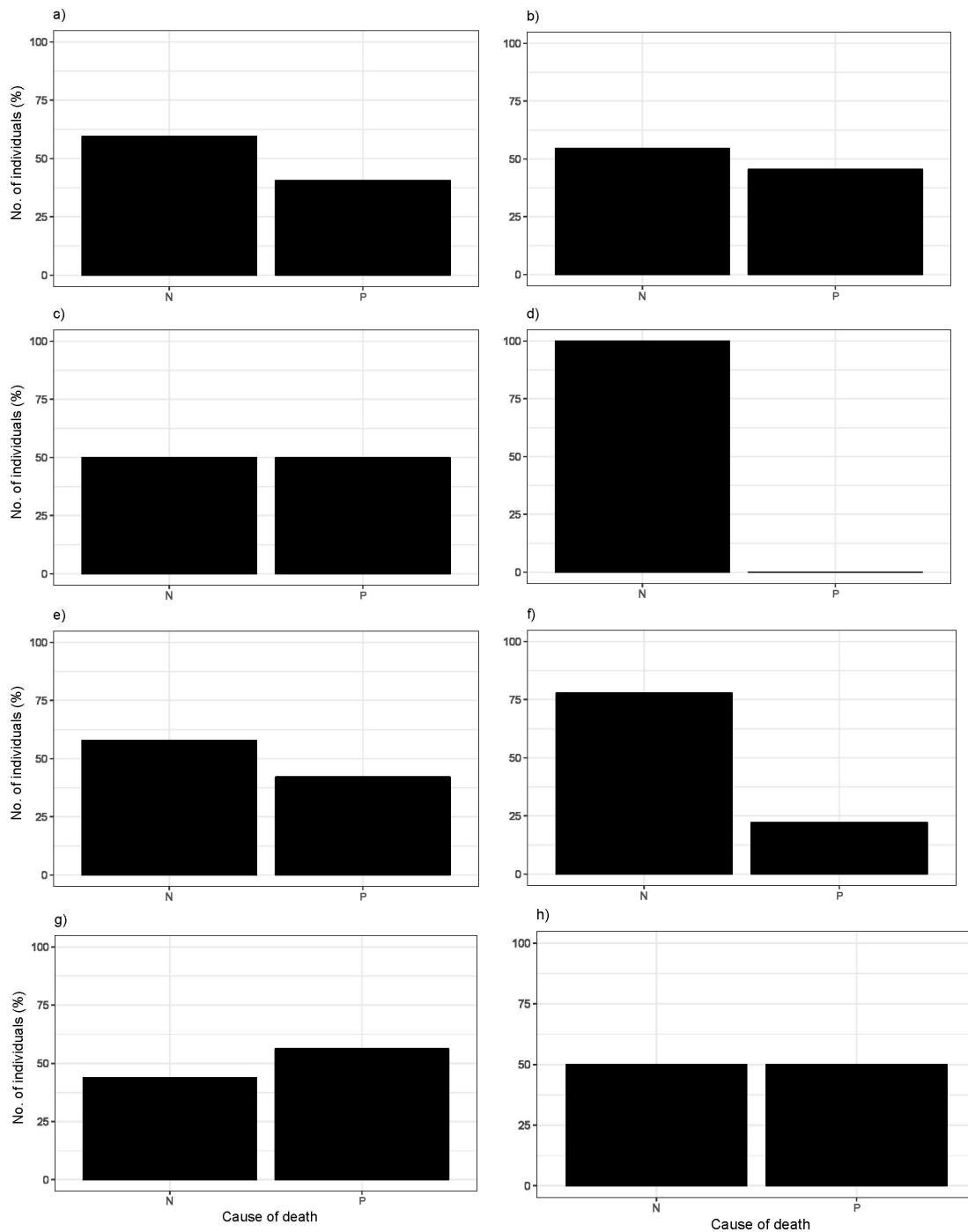
Fig. 5. Number of *Myopus schisticolor* specimens (%) found-dead and killed by predation (P) or that died from other causes than predation (N). September 2017 includes a) females, only (n = 69) and b) males, only (n = 11). September 2014 includes c) females, only (n = 2) and d) males, only (n = 1). August 2014 includes e) females, only (n = 38) and f) males, only (n = 9). July 2014 includes g) females, only (n = 16) and h) males, only (n = 2).

Sex-ratio in outbreak and non-outbreak years

In total, there were 174 specimens found-dead and snap-trapped in 2014 and 2017 combined of which 143 (82 %) were females and 31 (18 %) males (Fig. 6a). In 2014, there were 94 specimens of which 74 (79 %) were females and 20 (21 %) males (Fig. 6b). In 2017, there were 80 specimens of which 69 (86 %) were females and 11 (14 %) males (Fig. 6c).

Of the 113 specimens that died from other causes than predation in 2014 and 2017, 90 (80 %) were females and 23 (20 %) males (Fig. 6d). In 2014, of the 66 specimens that died from other causes than predation, 49 (74 %) were females and 17 (26 %) males (Fig. 6e). Of the 47 specimens found-dead in 2017 and that died from other causes than predation, 41 (87 %) were females and six (13 %) males (Fig. 6f).

Of the 62 specimens that died from predation in 2014 and 2017 combined, 54 (87 %) were females and eight (13 %) males (Fig. 6g). In 2014, there were 29 specimens that died from predation and of these 26 (90 %) were females and three (10 %) males (Fig. 6h). In 2017, there were 33 specimens that died from predation and of these 28 (85 %) were females and five (15 %) males (Fig. 6i).

Of the 55 specimens that were snap-trapped in 1995 – 2014 in Värmland and Vindeln combined, 40 (73 %) were females and 15 (27 %) males (Fig. 6j). In 2014, there were 25 animals that had been snap-trapped in Värmland and Vindeln combined and of these 16 (64 %) were females and nine (36 %) males (Fig. 6k). In 1995 – 2007 there were 30 animals that had been snap-trapped in Vindeln with 24 (80 %) being females and six (20 %) males (Fig. 6l). There was no significant difference between the sex-ratio of specimens snap-trapped in the outbreak year of 2014 and those snap-trapped during the non-outbreak years of 1995 - 2007 (χ^2 = 1.04, p >0.05).
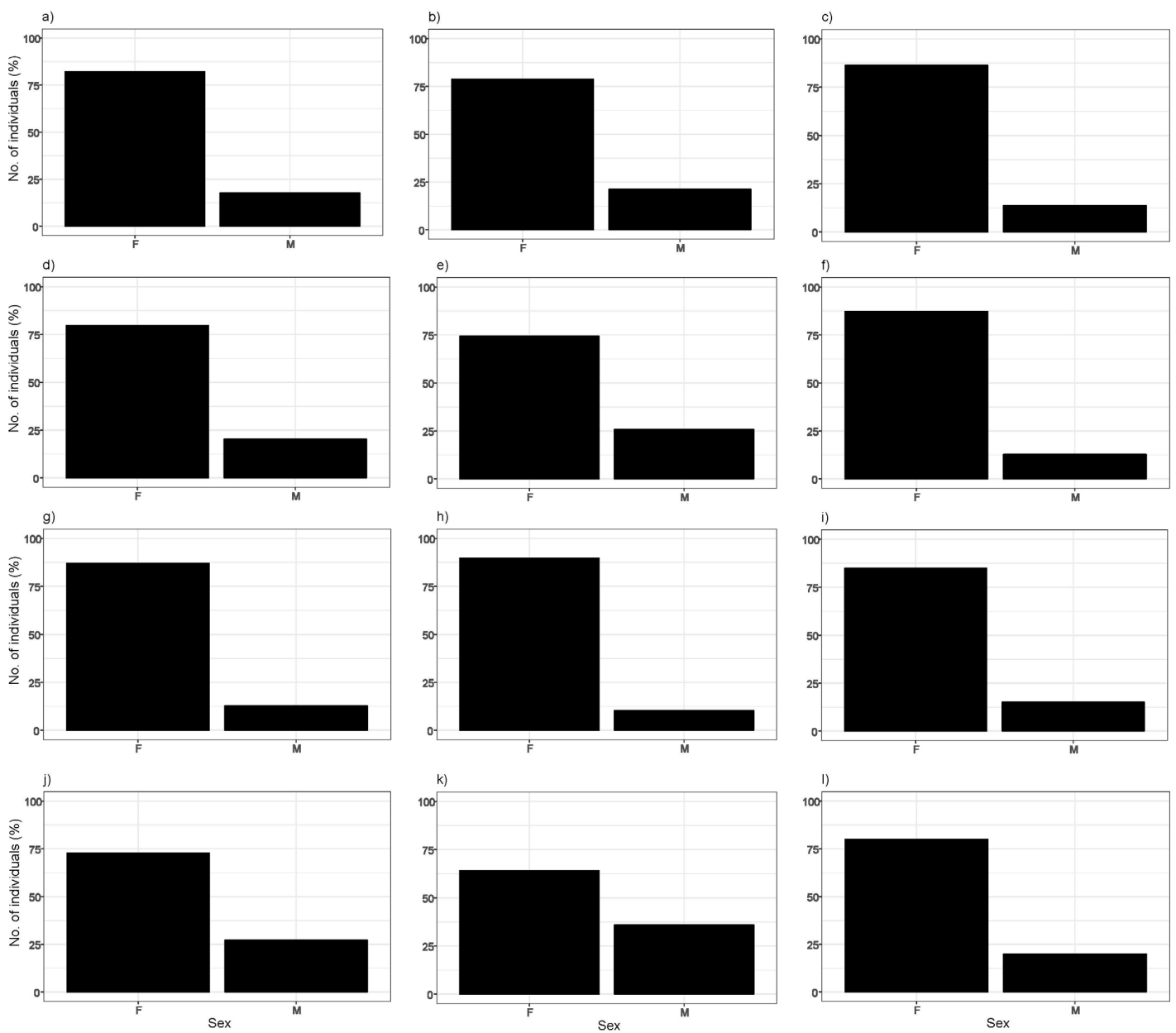
Fig. 6. Number of *Myopus schisticolor* specimens (%) divided by females (F) and males (M) in a) 2014 and 2017 combined (n = 174), b) 2014 (n = 94), c) 2017 (n = 80), that died from other reasons than predation in d) 2014 and 2017 combined (n = 113), e) 2014 (n = 66), f) 2017 (n = 47), that died from predation in g) 2014 and 2017 combined (n = 62), h) 2014 (n = 29), i) 2017 (n = 33), that had been snap-trapped in j) 1995 – 2014 (n = 55), k) 2014 (n = 25) and l) 1995 – 2007 (n = 30).

Temporal differences in predation

In 2014 and 2017 combined and including both sexes, July generated the lowest number of predator-killed wood lemmings (10; 7 %), September the highest (34; 23 %) with August in between (18; 12 %). I observed the same trend for animals that died from other causes than predation, with July

including eight (5 %), August 29 (20 %) and September 49 animals (33 %). The number of predator-killed specimens and specimens that died due to other reasons than predation did not differ among months (χ^2 = 1.66, p >0.05; Fig. 7a).

At the sex level, there were in total 125 females found-dead. July generated the lowest number of predator-killed female wood lemmings (9; 7 %), September the highest (29; 23 %) with August in between (16; 12 %). The same trend was true for animals that died from other causes than predation, with July including seven (6 %), August 22 (18 %) and September 42 animals (34 %) (Fig. 7b). In the same period there were 23 males. July generated the lowest number of predator-killed male wood lemmings (1; 4%), September the highest (5; 23 %) with August in between (2; 9 %). The same trend was true for animals that died from other causes than predation, with July including one (4 %), August seven (30 %) and September seven animals (30 %) (Fig. 7c).
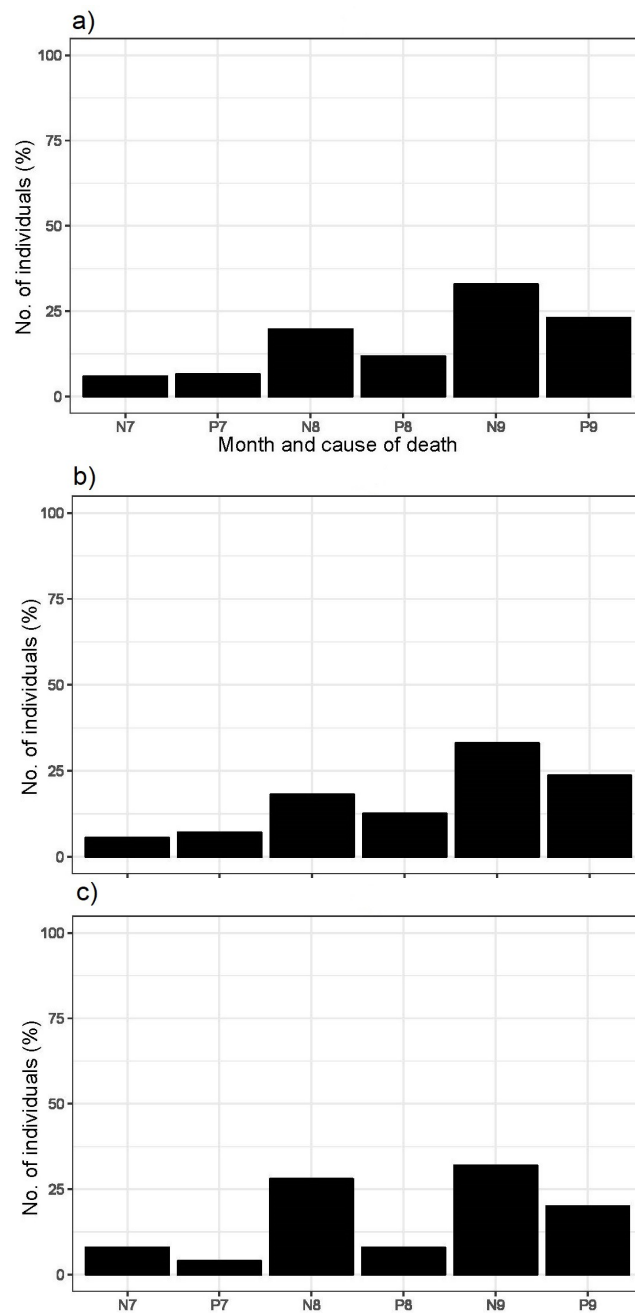
Fig. 7. Number of *Myopus schisticolor* specimens (%) found-dead and killed by predators (P) and those that died from other causes (N) in July (7), August (8) and September (9) including a) both sexes (n = 148), b) females (n = 125) and c) males (n = 23).

In 2017 all specimens were found in September and predation peaked in the second half of the month. There were 82 specimens found during this time

(Fig. 8a). In 2014, specimens were found in July, August and September and there was a peak in predation in early August. There were 76 specimens found during this time (Fig. 8b).

Fig. 8. Number of *Myopus schisticolor* specimens (%) found-dead without injury (white bar), killed by predators (black bar) and injured by predators after their death (grey bar), respectively, across days in a) September 2017 (n = 82) and b) 2014 (n = 76). In 2014, days 1 – 31 are in July, days 32 – 62 in August and days 63 – 92 in September.

Type and position of predator damage

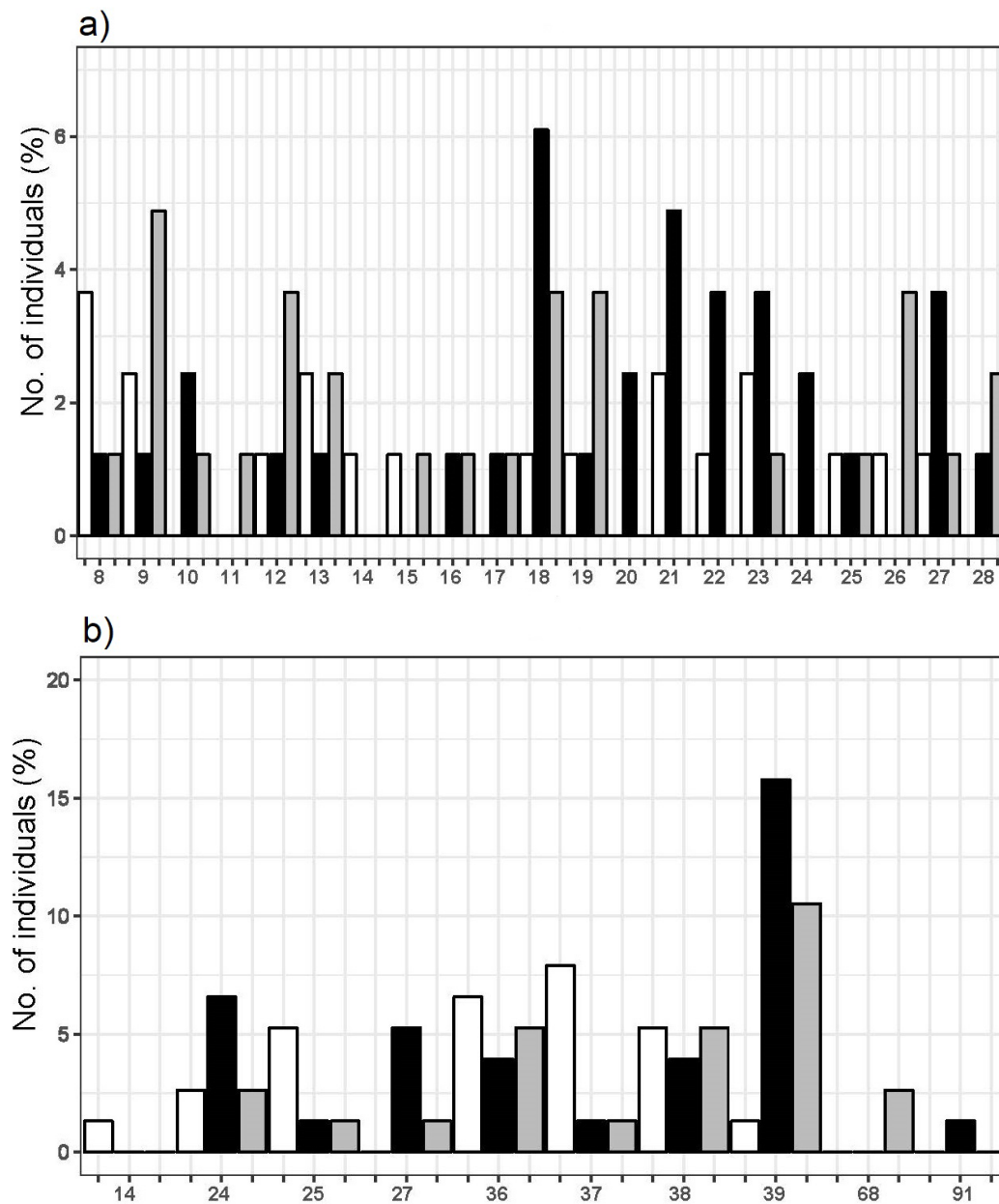Of the found-dead specimens, there were 22 (35 %) with holes, 18 (29 %) with a stain, 17 (27 %) with a broken body part, 10 (16 %) with a crushed head, nine (14 %) with a crack in the head, seven (11 %) with a missing body part and five (8 %) with point shaped holes (Fig. 9). The total number of specimens included here (n = 63) is exceeded by the total number of injuries (88) because the specimens could have several different kinds of injuries. There was a significant difference in the number of observed shapes of injuries caused by predators (χ^2 = 19.55, p <0.05).
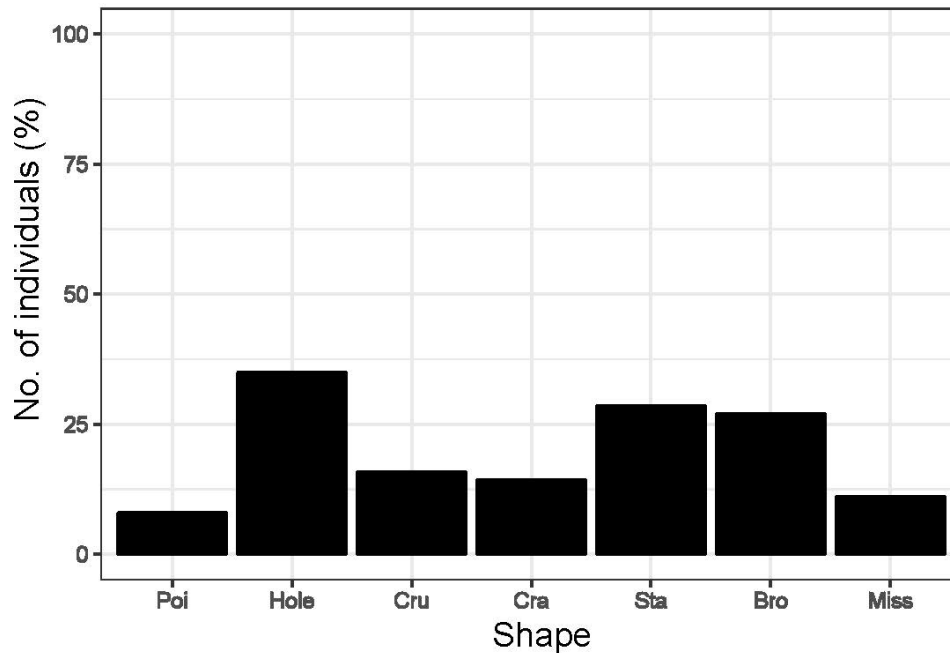
Fig. 9. Number of predator-killed (n = 63) *Myopus schisticolor* specimens (%) found-dead in 2014 and 2017 with type of shape of injury including point (Poi), hole (Hole), crushed (Cru), cracked (Cra), stain (Sta), broken (Bro) and missing (Miss).

There were 46 (73 %) specimens with injuries on the ventral side of the dorsal plane and on the cranial side of the transverse plane, 39 (62 %) with injuries on the dorsal side of the dorsal plane and on the cranial side of the transverse plane, 38 (60 %) with injuries on the head, five (8 %) with injuries on the ventral side of the dorsal plane and on the caudal side of the transverse plane and finally there were four (6 %) with injuries on the dorsal side of the dorsal plane and on the caudal side of the transverse plane (Fig. 10). The total number of specimens included here (n = 63) is exceeded by the total number of injuries (132) because the specimens partly had multiple injuries on different positions. There was a significant difference

between the different positions of the injuries caused by predators (χ^2 = 62.02, p <0.05).
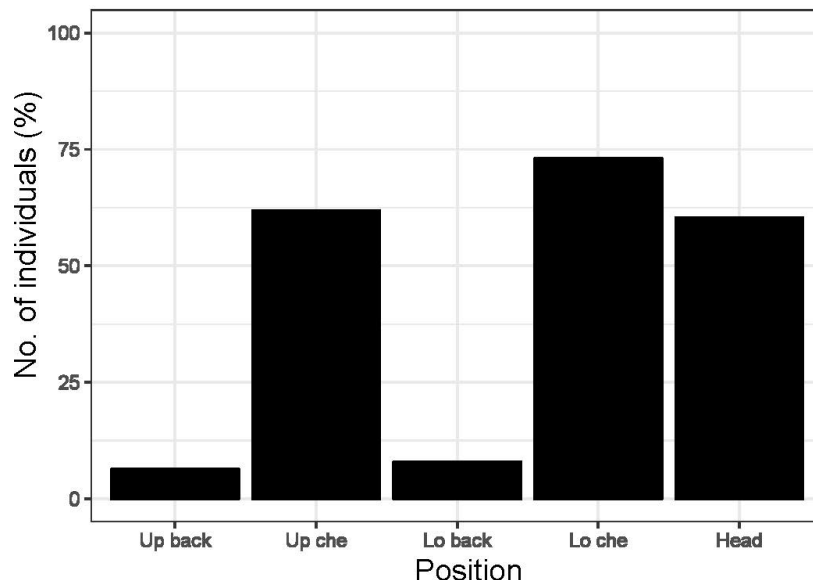
Fig. 10. Number of predator-killed (n = 63) *Myopus schisticolor* specimens (%) found-dead in 2014 and 2017 showing the position of injuries including upper back (Up back), upper chest (Up che), lower back (Lo back), lower chest (Lo che) and head.

Discussion

Predation as cause of mass mortality

In the two outbreak years that I studied, 40 % of the wood lemmings were killed by predators. Hence, I refute the hypothesis that predation is the main cause of mass mortality in wood lemmings. Although predation was not the main cause of mass mortality in the study area included in this thesis it could still have a large impact in other areas. This is the first study, to my knowledge, that sheds light on potential causes of mass mortality of wood lemmings.

Several avian and mammalian species predate on wood lemmings including pine martens (Pulliainen & Ollimäki, 1996), hawk owls (Nybo & Sonerud, 1990), Eurasian eagle owls (Obuch & Bangjord, 2016) and Eurasian kestrels (Støvern, 2012). Besides these documented cases, it is likely that other predators include wood lemmings in their diet as well. For example, resident specialists like weasels and stouts, resident generalists as red foxes and nomadic specialists as Tengmalm's owls. The fact that I did not find more dietary studies of predators including wood lemmings could be due to

several factors. One explanation could be that there are no dietary studies of other predators carried out in areas that occupy wood lemmings or these studies took place in years with very low densities of wood lemmings. Predators do eat wood lemmings but consume them instantly or hide them where we cannot find them. Finally, predators do not include wood lemmings in their diet and prefer other prey species. This last assumption seems to be true for most owl species. According to Eskelinen *et al.* (2004), wood lemmings are an alternative prey species for all owls residing in areas where wood lemmings can be found. However, I still found evidence that owls do include wood lemmings in their diet (Nybo & Sonerud, 1990; Obuch & Bangjord, 2016). Perhaps this is more a question of availability, it there are plenty of wood lemmings easily accessible owls will predate on them even if it's not their preferred prey species. Nybo & Sonerud (1990) found that roughly 5 % of all prey items consumed by hawk owls in June were wood lemmings and Obuch & Bangjord (2016) found 25 (0.06 %) wood lemmings in the diet of the Eurasian eagle owl. In the same studies the percentage of field voles was 80 % (Nybo & Sonerud, 1990) and 41 % (Obuch & Bangjord, 2016), respectively, which suggests that field voles seem to be preferred over wood lemmings for these two predators. Had there been a lower amount of field voles available perhaps the predators would have switched and focused more on alternative species such as wood lemmings instead. This is not always possible since wood lemmings are very rare, except in outbreak years. This becomes obvious when looking at the number of wood lemmings collected in the Vindeln area during 1979 - 2017 within the National Monitoring Programme of small rodents. In this period there were a total of 394 wood lemmings collected compared to over 14,000 bank voles (Ecke & Hörnfeldt, 2018). Although wood lemmings are not a dominating part of the diet of hawk owls and Eurasian eagle owls, their predation can have large effects on the population of wood lemmings, especially if its male specimens being killed considering the already skewed sex-ratio.

The fact that 40 % of the wood lemmings in this study were killed by predators could be explained by the amount of predators in the study area and which species of predators residing in the study area. Weasels for example are specialist predators preying mainly upon rodents (Erlinge, 1975). When there are many rodents in an area there are also many weasels (Erlinge, 1974). This means that during the outbreak years of 2014 and 2017 when there were many wood lemmings, there could also have been many weasels in the area which could have caused the higher percentage of predation. Other predators are classified as generalists and therefore not dependent on rodent prey alone to reproduce. Some of these include foxes and martens. These can also prey upon rodents when easily found

(Andersson & Erlinge, 1977). Since martens are known to include wood lemmings in their diet (Pulliainen & Ollinmäki, 1996) this could also have contributed to the predation percentage in my thesis. There are also nomadic species which leave their area if there is not enough food resources (Andersson & Erlinge, 1977). If such nomads were to settle in an area with more food abundance this could increase the predation on the prey species residing in that area. This could mean that if more nomads entered the study area in 2014 and 2017 when wood lemmings were plentiful, this could also have caused increased predation. To be able to know the density of predators in an area a proper census needs to be conducted. This was not done within this thesis. It would be meaningful to study predators and their numerical responses to wood lemming outbreaks.

The second aim of this thesis was to investigate if predators are the cause of death or if they take wood lemmings after their death. As seen before, 63 (40 %) specimens could be classified as killed by predators and 52 (33 %) were injured by predators after their death. So there seems to be a trend towards that predators do actually kill wood lemmings rather than taking them after their death. It is likely that the actual number of wood lemmings killed by predators is much higher since some predators probably consume their prey instantly or move them somewhere else where we cannot find them.

The third aim of my thesis was to investigate if predation is that common that it might be the main cause of death. In this case predators killed 40 % of the wood lemmings and 60 % (33 % injured after death and 27 % without injuries) have died from other reasons. This implies that predation is not the main cause of death in this case. The National Veterinary Institute in Sweden (SVA) performed a necropsy on 25 found-dead wood lemmings in July and August 2014 to find out the cause of death (Bröjer *et al.*, 2014). They did not find any sign of disease and the cause of death was trauma caused by bite wounds from predators (Bröjer *et al.*, 2014).

Other possible causes of death could be disease, stress or starvation. Skarén (1981) kept 19 wood lemmings in an enclosure of which 17 died from *Listeria monocytogenes*. Another disease that could have a lethal effect on small rodents is the Borna disease virus (BDV) where infection can be fatal for animals due to a chronic progressive meningoencephalomyelitis (Kinnunen *et al.*, 2007). The same authors detected antibodies in one tundra vole or root vole (*Microtus oeconomus*) and two bank voles in Finland. If antibodies are detected in small rodents in Finland it is possible that the virus is present in Sweden as well and could have a lethal effect on wood lemmings.

Due to the very specific diet of the wood lemmings, there might be a shortage of food when densities are high. Under such conditions they might suffer from malnutrition, impairing their condition and therefore increasing susceptibility for both disease and predation. When there is a shortage of food there might be more intra-specific competition for the remaining food resources, possibly leading to aggressive interactions and injuries that could get infected or make them easier targets for predators. Wood lemmings might also migrate in search of food as reported by Eskelinen (1997). When doing so they might end up in habitats without their preferred food leading to starvation. They might also cross roads and get hit by cars and trains. Further, when migrating they can fall from bridges and into canals and die (Eskelinen, 1997). Another reason for these migrations, a part from lack of food, might be lack of space (Eskelinen, 1997). Home areas of wood lemmings are small with an average male home area being 2,144 m^2 and the females being 285 m^2 (Andreassen & Bondrup-Nielsen, 1991) but in high densities large areas are required to satisfy all the specimens. Further, migrating wood lemmings could be at greater risk of predation. There might not be as many hiding spots in the new areas and moving in open habitats could increase the risk of avian predation. Metzgar (1967) tested the predation from screech owls (*Otus asio*) on white-footed mice (*Peromyscus leucopus*). One group of the mice were accustomed to the environment and the other were new. The owls caught 13 mice in total and 11 of these were from the group of mice not accustomed to the area (Metzgar, 1967). The results could possibly be the same for wood lemmings, that they suffer a higher risk of predation when migrating into new habitats. Stress can also be a source of starvation. The presence of a predator is stressful for prey species like wood lemmings. Ylönen *et al.* (2006) showed that the odour of weasels affected the foraging behaviour of bank voles where foraging was significantly lower for bank voles subjected to the odour. If there is plenty of predators in an area, wood lemmings might be too scared to forage and therefore starve.

Weight of injured and non-injured specimens

The average weight of the specimens included in this study was under 17 g which can be seen as low considering that adults may reach a weight of almost 50 g (Ilmén & Lahti, 1968). This low weight could be an indication that there were mostly juveniles found dead. If there were mostly juveniles killed in the study this can be linked to the kind of predators residing in the study area. If juveniles spend most time in nests and burrows they should not be attacked by avian predators. Other predators like the weasel can enter nests and therefore take juveniles there (Andersson & Erlinge, 1977). Foxes can dig up burrows and therefore gain access to the juveniles

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residing in there (Andersson & Erlinge, 1977). If there were a lot of weasels and foxes in the study area this could be one explanation why there were many juvenile and likely dispersing wood lemmings found dead. Since foxes are larger than weasels they also need to consume more prey (Andersson & Erlinge, 1977). If they learn that juvenile wood lemmings are an easily accessible food source they might focus on this when plentiful as in an outbreak year.

Another explanation for the low weight of the specimens can be due to the density of wood lemmings. More wood lemmings implies less food and more competition implies that some might starve and therefore not grow normally therefore having a lower weight than normal for their age. It is also a possibility that the specimens were infected with a disease making them weaker and therefore not foraging in a normal way and making them an easier target for predators. Juvenile specimens might also be an easier target for predators due to lack of experience. Adults might be more vigilant when moving in open areas while juveniles might not realize the danger.

Temporal differences in predation

The total amount of wood lemmings killed by predators increased from July to September. The higher number of predator-killed wood lemmings in September could be explained by several factors. The amount of wood lemmings found-dead increased from July to September. If there are more prey available generalist predators may use this food source more. There is also a possibility that more nomadic predators entered the area during this time due to the increasing amount of available prey (Andersson & Erlinge, 1977). The number of weasels is related to the number of rodents (Erlinge, 1974). Hence, as the amount of wood lemmings increased so could the amount of weasels and therefore also predation.

However, the amount of wood lemmings that died from other causes than predation also increased from July to September. This could be due to increased competition over limited food resources followed by malnutrition and starvation. There is also the possibility of an outbreak of a disease killing specimens.

Sex differences in predation

In 2017 a higher percentage of males died from predation than females. One reason for this slightly higher male predation could be due to the males' mobility. According to Andreassen & Bondrup-Nielsen (1991) male

wood lemmings move on average 217 m during a day compared to females 21 m. Because of their higher mobility, they are more likely to suffer more from avian predation (Andersson & Erlinge, 1977). In September 2014, the results were the opposite with more females being killed than males, however based on low sample size (two females and one male). Low sample size in September 2014 could have been caused by predation in earlier months reducing the density of wood lemmings and because of the lower density, generalist predators might have switched to other more common prey and nomadic predators might have left the area in search of other food sources.

In August 2014 more females died from predation than males. There were more wood lemmings found-dead in August 2014 compared to September 2014 and because of the skewed sex-ratio there were also more females available for predators than males thus explaining the results. Predation in 2014 peaked in August, therefore reducing the total number of specimens left for predators in September when there were not many wood lemmings killed by predators. In July 2014 the trend was the same as in August and September with more females being killed by predators than males. There were less specimens found-dead in July than in August possibly meaning that the population was still growing and there were not that many predators in the area. When the population increased even more in August, more predators could have switched to wood lemmings and then switched to other prey in September when numbers went down again. The fact that the predation decreased from August 2014 until September 2014 could be due to nomadic predators leaving the area as the amount of wood lemmings decreased or that the amount of weasels decreased with decreasing number of wood lemmings. Another explanation for the low number of wood lemmings found-dead in September 2014 could be migration. When densities are high, wood lemmings might leave their home range in search of food. Eskelinen (1997) found that the migration of wood lemmings in Finland started in the first half of August and peaking in the end of August or the beginning of September. If the wood lemmings in the study area engaged in the same behavior, this could explain the low number of specimens found-dead in September 2014.

Sex-ratio in outbreak and non-outbreak years

Eskelinen (2004) found that the ratio of males in a population varied between 15 - 29 %. Overall, this seems to be the case in my thesis as well (10 - 36 %) apart from specimens killed by predation in 2014 (10 % males) and for specimens snap-trapped in 2014 (36 % males). The low number of males taken by predators in 2014 could again partly be explained by the

skewed sex-ratio (54 females and eight males). Traps do not select for sex and since males are more mobile Andreassen & Bondrup-Nielsen (1991) suggested a bias from snap-traps on the sex-ratio of males where they would expect a higher proportion of males in snap-traps. My results support their suggestion with (36 % males snap-trapped 1995 - 2014) compared to the sex-ratio of males found-dead (18 % in 2014 and 2017 combined).

Andreassen & Bondrup-Nielsen (1991) found that the sex-ratio of wood lemmings caught in traps were 67 % females and 33 % males. This was slightly more skewed than in the overall result here for all years with snap-trapped specimens. In the outbreak year of 2014 the sex-ratio of snap-trapped wood lemmings was 64 % females and 36 % males. In the non-outbreak years of 1995 - 2007 the sex-ratio was 80 % females and 20 % males. This means that the sex-ratio was less skewed in outbreaks years compared to non-outbreak years of wood lemmings caught in snap-traps. This might seem a bit controversial since the skewed sex-ratio might be the reason for the high number of wood lemmings in outbreak years but it was not significant when I tested it so it only gives indication of this pattern.

Difference in predation over time in days across years

In 2017 predation was stable at a low level and peaked in mid September. After this peak there were multiple dates with high rates of predation. The reason for this could be that one or several nomadic predators entered the area at that time. The pattern in 2014 where predation increased in late July and early August could be related to the total number of wood lemmings found then. It would appear that the population was building up in July (18 specimens found-dead), peaking in August (47) and then declining in September (3). Most predation occurred within a period of 2.5 weeks in 2014 (24th of July - 9th of August) although there was one case in late September as well. As mentioned before this could be due to weasel numbers following the numbers of wood lemmings as well as nomadic predators entering the area at high wood lemming numbers and leaving when numbers decreased.

Type and position of predator damage

The most common type of injury was larger holes and the least common was point-shaped holes. Point-shaped holes are likely caused by different predatory birds grabbing their prey with their talons and therefore I interpret the results as if predation from avian species were not common for the wood lemmings in my thesis due to the low amount of point-shaped holes. The larger holes are more likely caused by mammalian predators

such as weasels, stouts and foxes. Since there are photographs and descriptions of all the injuries identified here it would be interesting to compare these to the usual types of injuries inflicted by a specific kind of predator to try to identify which predator caused which type of injury. Unfortunately, there was not enough resources to include this aspect in my thesis. This could be an interesting idea for future projects within this topic since there is evidence that both mammalian and avian predators include wood lemmings in their diet (Pulliainen & Ollinmäki, 1996; Støvern, 2012; Nybo & Sonerud, 1990; Obuch & Bangjord, 2016). One helpful tool to identify the predators involved could be to use environmental DNA (eDNA). Nichols *et al.* (2012) used eDNA to identify which species of herbivores that had been browsing at plants. If predator saliva is found at the wood lemmings this method might unveil which predators are involved in the predation.

Injuries on both sides of the chest was most common, closely followed by the head with a large gap to both sides of the back. This makes sense since the chest contains many vital organs and it would be easy to cause lethal injuries in this area as well as on the head. Based on the most common locations of the injuries, one could infer which predator killed the specimens. Allen (1938) observed a New York weasel (*Mustela frenata noveboracensis*) attacking a chipmunk (*Tamias striatus*). The weasel bit the chipmunk at the back of the head and bit through the skull (Allen, 1938). Byrne *et al.* (1978) observed the long-tailed weasel (*Mustela frenata*) killing Richardson's ground squirrels (*Citellus richardsoni*) and observed that the weasel used two different killing techniques. The first one was biting the neck and the second one was biting the throat and thus suffocating the prey (Byrne *et al.*, 1978). Heidt (1972) states that the least weasel kills its prey by biting the neck and biting through the skull or the throat thus resembling the techniques used by the other subspecies of weasels mentioned here.

Avian predators have different hunting techniques than mammalian predators. Ogden (1974) states that the short-tailed hawk (*Buteo brachyurus*) strike their prey from above with their talons. Csermely *et al.* (1998) observed Eurasian kestrels catching mice and rats. The kestrels landed on the preys back and held them down with their talons. After gripping, the kestrel usually struck the prey with its beak on the head. Although rare, some prey had talon wounds. These were very small holes in skin and not considered as serious. The biting killed some of the mice but the main cause of death was suffocation when the kestrel was holding the prey with its talons (Csermely *et al.*, 1998). This information could explain why point-shaped holes was the least common type of injury since the

talons do not seem to cause serious injury. Grabbing the prey from above should inflict damage to the back, but since the talons seem to be delicate this could also explain why there was not much damage located to the back of the wood lemmings. That head injuries were almost the most common location could be explained by the hunting techniques by the least weasel and the Eurasian kestrel both targeting the head of their prey.

Conclusions

My study refutes predation as the main cause of observed mass mortality in wood lemmings. About 40 % of the specimens had injuries indicating that they had been killed by predators meaning that 60 % of the wood lemming died from other reasons than predation. Found-dead wood lemmings had a low weight indicating that there were mostly juveniles found-dead. This could be explained by lack of food or disease. The shape of injuries in the found-dead wood lemmings indicates involvement of least weasel and/or Eurasian kestrel. The wood lemming is known for its skewed sex-ratio and the male ratio in this study varied from 10 - 36 % which is similar to previous studies about the sex-ratio.

Since predation was not the main cause of death in this study it would be interesting to investigate other possible reasons for the mass mortality of wood lemmings recorded here. Some potential causes include disease, stress and starvation due to intraspecific competition in years when numbers are high. In future studies it would also be interesting to try to identify which predators that are most commonly including wood lemmings in their diet.

Acknowledgements

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