The form *radnensis* in the upper second molar in isolated subpopulations of the root vole (*Alexandromys oeconomus arenicola*) in the Netherlands

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Abstract: During a preliminary study of unsorted barn owl pellets from Texel, the Netherlands, twelve out of 140 upper second molars (M^2) of the root vole (*Alexandromys* (*Microtus*) *oeconomus arenicola*) were identified as the form *radnensis*. Besides the regular or normal form (N), four different stages of *radnensis* are recognized, which show a progressive incision of the lingual field: V_1, V_2, V_3, and V_4. The aim of this study is to determine the frequencies of the prevalence of the form *radnensis* of M^2 in the known subpopulations of the root vole in the Netherlands, to establish whether or not these frequencies differ from each other and, if so, whether this can be explained by the age structure of the root vole subpopulation. We analysed the skulls of root voles from owl pellets from all the known subpopulations in the Netherlands. The subpopulation of Texel shows 12.5% *radnensis,* significantly higher than all the other subpopulations. No link was found with age. It is concluded that the prevalence of the form *radnensis* is unevenly distributed over the subpopulations of root voles in the Netherlands.

Keywords: *Alexandromys oeconomus arenicola*, form *radnensis* M^2, genetic drift, *Microtus*, Netherlands, root vole, Texel, upper second molar.

Introduction

The root vole (*Alexandromys oeconomus arenicola*) is an endemic subspecies in the Netherlands and is considered an ice age relict (van Laar 2018). Under the criteria mentioned in the proposal for a revised Red List for Mammals of the Netherlands, the root vole's status remains 'vulnerable' (van Norren et al. 2020). In the past many areas became unsuitable habitats for the root vole, leading to the development of isolated subpopulations. Small populations are more prone to genetic drift, a greater chance of minor physical alterations and, potentially, of local extinctions. As such it is important to monitor seemingly minor alterations as these changes to the phenotype could indicate a genetic impoverishment of this vulnerable endemic subspecies.

During a preliminary study of unsorted barn owl pellets from Texel, the Netherlands, the presence of a number of variants that can be described as an inverted omega (Ω) at the lingual side of the upper second molar (M^2) in the root vole (*Alexandromys* (*Microtus*) *oeconomus arenicola*) was immediately obvious (Figure 1). Twelve out of 140 M^2s appeared to be of this specific form, also known as the form *radnensis* (Ruprecht 1967). Within this subset, eight were on the left side and four on the right side.

Angermann (1984) reported the occurrence of different stages of the form *radnensis* of M^2 of the root vole from 30 localities from all over its circumpolar distribution in Central and Northern Europe, Central Asia and Beringean. The highest prevalence of *radnensis*

Figure 1. The omega shaped indentation of the left second upper molar (M^2) of the root vole (*Alexandromys oeconomus arenicola*) described as the form *radnensis* (V_2). *Photo: J.P. Bekker*.

(10.5%) was found in a sample of 124 M^2s from specimens from St. Lawrence Island, USA and from 145 M^2s from the Netherlands (locations not specified), which was the second highest percentage (7.6%).

Ruprecht (1967) studied 610 skulls of the root vole from the Kujawy area, Poland, and discovered, for the first time, a specimen with a remarkable feature: the triangle in the second field of M^2 was completely divided (the form *radnensis*). Ten other specimens, also from this area, had M^2s with a partial division. Besides the regular or normal form (N), Ruprecht (1967) recognized four stages in the form *radnensis* : V_1, V_2, V_3, and V_4, representing progressive incision of the lingual field (Figure 2).

Van Laar's study (2018) on the origin and distribution history of the root vole in the Netherlands, identifies at least five subpopulations. These historically-based subpopulations are: 1. the island of Texel; 2. Friesland and the adjacent IJsseldelta; 3. the moorlands of Noord-Holland; 4. the moorlands of Zuid-Holland and adjacent parts of Utrecht; 5. the estuaries of the rivers Rhine and Meuse (almost always referred to as the 'Delta') and (maybe) 5a. the Biesbosch. Van den Brink et al. (2011) made a study of differences of skull shape (geometric morphometrics) and slightly altered this classification; recognizing the same subpopulations for the island of Texel, Friesland and the IJsseldelta, unifying the moorlands of Noord-Holland, Zuid-Holland and adjacent Utrecht. In addition to the Delta these authors identified the area around the Vlaardingse Vlietlanden, north of the Nieuwe Waterweg, as having a separate relict population. Based on the distribution of the root vole in the Netherlands and its recent discontinuities, this led to reclassification of the five subpopulations: 1. Texel; 2. Friesland; 3. the moorlands of Noord-Holland; 4. the moorlands of Zuid-Holland; 5. the Delta (Koelman & Bekker 2016, especially the map on page 128).

The origin of the term *radnensis* derives from the description by Éhik (1942) of a new species of snow vole, described by the author as *Microtus* (*Chionomys*) *radnensis*, collected in the Rodna mountains (German: Radnaer Gebirge) in the north of Romania. In the described specimen the second field of the M^2 was partly divided and could be classified as stage V_2 under Ruprecht's classification (1967) (see photograph opposite to page 30 in Éhik (1942)). In this photograph it is also clear that the form *radnensis* is present at both sides. Tast (1982) regarded this snow vole, *M. nivalis radnensis*, as a subspecies, although this subspecies is no longer mentioned in the Handbook of the Mammals of the World (Wilson et al. 2017).

In addition to the snow vole, *Chionomys nivalis radnensis*, and the root vole, the form *radnensis* is also described in recent specimens of Savi's pine vole (*M. savii*) (Contoli 1992). Malez & Rabeder (1984) described special shapes of occlusal views of different *Microtus* specimens from an Early Pleistocene fissure filling of Podumci 1 in Croatia. In their

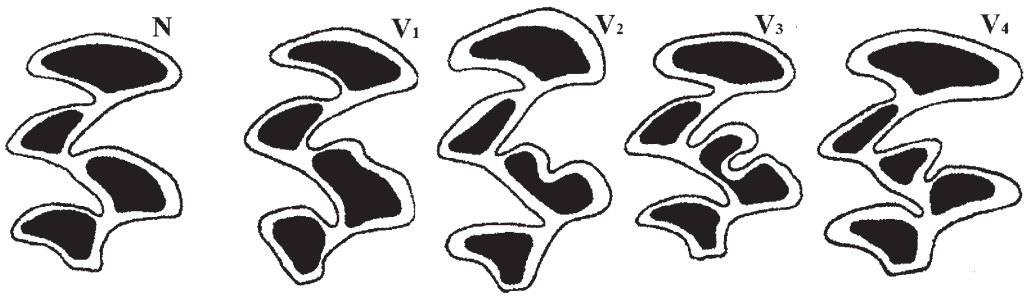

Figure 2. The regular right second upper molar (N) and the different stages of M^2 in the form *radnensis* (V_1, V_2, V_3, and V_4) of the root vole (adapted from Ruprecht 1967).

study another form of a left M^2 is depicted and described as *praeradnensis*, without further comments on frequencies. Malez & Rabeder (1984) also describe a left M^1, with a "*radnensis*"-wrinkle at the mesial side of the lobus anterior.

The aim of this study is to determine the frequencies of the prevalence of *radnensis* of M^2 in the known subpopulations of the root vole in the Netherlands and to establish whether the frequencies differ significantly from each other. In the samples studies by Ruprecht (1967) and Jorga (1973), there was not an even distribution of the different stages (V_1-V_4) of the form *radnensis* which was higher among the lower stages than the higher ones (Table 1). However the limited number of unsorted skulls from Texel showed equal numbers of both V_1 and V_4, raising the question of whether this skewed distribution of the form *radnensis* would be found in a larger set of observations from the total population in the Netherlands. In voles the molar patterns of opposing molar pairs suggest a transient role for the second upper and lower molars. While the early developmental architecture of such traits is masked by later stages of growth, it may still be deciphered from the adult phenotype, if careful attention is paid to the relevant features (Labonne et al. 2014). Assessing ontogenetic changes in molar complexity during the process of tooth wear in the narrow-headed vole (*Microtis gregalis*), closely related to the root vole, suggested that morphotype dental patterns could not be clearly established in half-month old animals due to presence of juvenile characteristics and for animals of one month and older, age differences in morphotype dental patterns were insignificant (Markova et al. 2013). If an inverse relation (i.e. decreasing numbers from V_1 to V_4) could be demonstrated, this raises the question as to whether the age structure of the root vole population could be the explanation of this skewed distribution.

Table 1. Frequencies of the stages of the form *radnensis* in M^2 of root voles in a preliminary and two regular studies.

Author / form of *radnensis*	N	V_1	V_2	V_3	V_4
Unsorted skulls Texel	140	6			6
Ruprecht 1967	610	11	6	2	1
Jorga 1973	251	21		1	1
Total	861	38	6	3	8

Material and methods

This study analyses owl pellets that were collected from known localities on the island of Texel, between 2015 and 2020, together with the available skulls of root voles from owl pellets, collected between 1994-2020 from all over the Netherlands, which were provided by the Dutch Mammal Society (Zoogdiervereniging). Additional root vole skulls from owl pellets from Schouwen-Duiveland, mainly

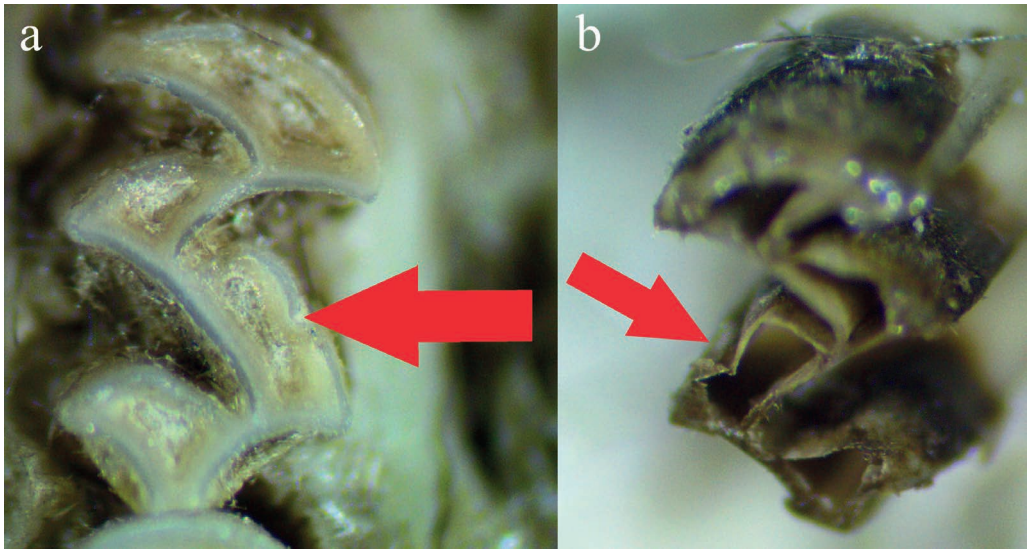

Figure 3. Occlusal view (a) and root rim view (b) of M^2 with form *radnensis* V_1; the indentation of the occlusal view is hardly visible, while the indentation of the root rim view is obvious. *Photos: J.P. Bekker*.

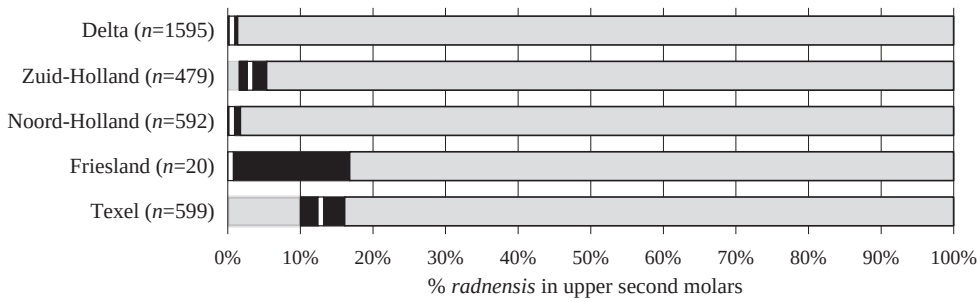

Figure 4. Percentages of the form *radnensis* in upper second molars, with limits of confidence (black), of root voles in subpopulations in the Netherlands.

collected during the years 1998-2003, completed the sample. The skulls with M^2s were sorted by the collection site and used to determine the frequencies of the form *radnensis* in the subpopulations. The following numbers of available skulls, with M^2s present on one or two sides were counted: 303 from Texel, 315 from the moorlands of Noord Holland, 253 from the moorlands of Zuid Holland and 853 from the Delta, and 10 from Friesland.

Based on the drawings and detailed descriptions of Ruprecht (1967) and Jorga (1973) the definitions of the regular form (N), and the stages V_1, V_2, V_3, and V_4 of the form *radnensis* can be described as follows. The regular form N can be characterized as the lingual line of the second field of the upper second molar (M^2) being slightly convex till plane and showing no concavity. It may show a slight concavity outside of the centre of the lingual enamel ridge; a form that is also assigned to the regular form N. The form V_1 shows an indentation rather than a concavity in the middle of the oral line, which is less than the thickness of the enamel ridge. The concavity in the form V_2 is deeper than the enamel ridge oral line, but does not reach the middle of the breadth of the triangle of the second field. The concavity in the form V_3 reaches deeper than half of the breadth of the triangle, but not to

the enamel ridge of the opposing side of the triangle. In the form V_4 the concavity is even deeper, so that both opposing enamel ridges touch or coalesce. In some cases it may be difficult to assign a specific molar into the right category, e.g. the difference between a form N with a slight concavity, outside the centre of the lingual enamel ridge or form V_1 (Figure 3a); in such cases it is helpful to observe the root side of this molar (Figure 3b).

Two types of analysis were conducted in order to determine whether the distribution of the stages of the form *radnensis* is determined by the age structure of the investigated subpopulations of root voles or by another cause: age dependent factors and a comparison of the left and right M^2s from the same skull (which by definition were of the same age).

Markowski (1980) proposed ten skull measurements for root voles but in this study we only use the upper molar row length, measured from the anterior margin of the alveolar of M^1 to the posterior margin of the alveolar of M^3. This is because this measurement has the fewest drop-outs as vole skulls in owl pellets are often broken. The values of the age categories in root voles are derived from Markowski (1980) and presented in boxplots using the mean values and twice the standard error. The upper molar row lengths of the four stages V_1, V_2, V_3 and V_4 *radnensis*, are also presented in boxplots for comparison.

M^2s from the same individuals were compared by determining the correlation of the presence of the stages V_1, V_2, V_3 and V_4 between the left and the right sides. Frequencies (including 95% confidence intervals) of the form *radnensis* are presented as percentages of the total numbers of the observed upper second molars (M^2). The 95% confidence interval is calculated around the measured difference in percentages (Wilson's formula, RIVM 2020; see also Bekker 2020) to determine whether the two percentages differ. The probability of the true value of the difference falling within the interval is 95% (Rothman & Greenland 1998). In the case of zero observations, the upper limit of the 95% confidence interval is calculated using the Byar formula (RIVM 2020).

The chi-square test was used to determine whether or not there is a significant association between two categorical variables. The pairwise differences in left/right presence were tested with confidence interval tables (Diem & Lentner 1968).

Results

The percentages of the form *radnensis* in the second upper molars of root vole skull material in the different subpopulations in the Netherlands is presented in Figure 4. The subpopulation of Texel shows 12.5% *radnensis*, which is higher than in the other subpopulations and, with the 5% confidence limit, is well above the 95% limits of confidence, except the percentage from Friesland (=0%), which is based upon a very limited number of M^2s (n=20). The subpopulation of the moorlands of Zuid-Holland shows 2.7% *radnensis,* much lower than the percentage from Texel, but higher than the percentages of subpopulations of the moorlands of Noord-Holland (0.17%) and the Delta (0.19%). There was no discernible difference between the percentages of the subpopulations of the Delta and the moorlands of Noord-Holland. The sample size of M^2s from Friesland was low (n=20) and because of this it is difficult to draw any conclusions regarding this subpopulation.

Table 2 shows the total numbers of the forms *radnensis* stages V_1, V_2, V_3, and V_4 in the second upper molars of root vole skull material in all the subpopulations in the Netherlands. The totals are not evenly distributed, but there are fewer cases of the higher forms.

The five coloured boxes in Figure 5 represent different age categories. The mean values ('x') of the upper molar row length indicate an upward pattern for the five age categories (coloured boxes, age classes accord-

Table 2. Upper second molars of root voles in the Netherlands, rated according to the form *radnensis* V_1, V_2, V_3, and V_4 (chi square test: $P<<0.01$).

	V_1	V_2	V_3	V_4
Expected M^2s with *radnensis*	23	23	23	23
Established M^2s with *radnensis*	36	31	18	7

Table 3. The presence of N and f. *radnensis* stages V_1-V_4 in left and right M^2s, with symmetrical presence (including unsorted skulls from Texel; skulls with missing M^2s on one side were excluded).

	Left	Right
N	1503	1504
V_1	16	20
V_2	19	11
V_3	8	10
V_4	3	4
Total	1549	1549

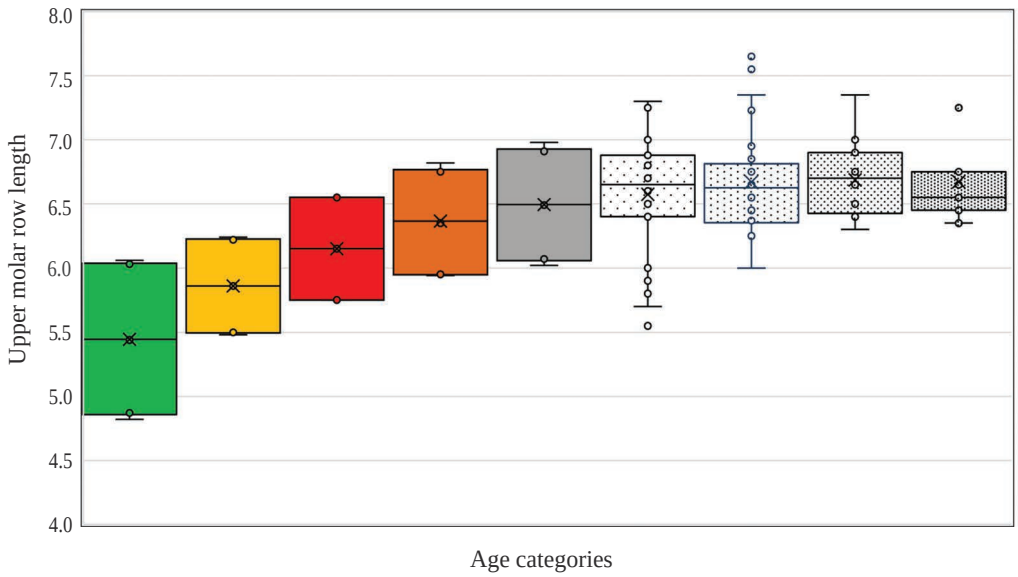

Figure 5. Boxplots of upper molar row lengths in mm (left axis) by age categories I (< 1 month: green), II (1 month - 6 weeks: orange), III (6 weeks - 3 months: red), IV (4-7 months: brown) and V (> 7 months: grey) (age classes derived from Markowski (1980) and the stages of the form *radnensis* (dotted boxes V_1, V_2, V_3 and V_4, from left to right).

ing to Markowski 1980). The upper molar row lengths of all the available skulls (including 'unsorted' material from Texel) were determined for the presence of *radnensis* V_1-V_4 M^2. A comparison of the four dotted boxes (V_1, V_2, V_3 and V_4) with the coloured boxes in Figure 5, shows an upward pattern, suggesting that there is no relationship between the form *radnensis* (stage V_1-V_4) and age and that the presence of the different types of M^2s with *radnensis* is not linked to age.

The distribution of the four stages of *radnensis* from specimens with M^2s present on both left and right side (n=1549) is presented in Table 3. These results do not show a tendency for the form *radnensis* stages (in any of its stages) to appear on either the left or right M^2s among any of the subpopulations of root vole in the Netherlands (chi-square test: P=0.16).

Discussion

The prevalence of the form *radnensis* is unevenly distributed over the subpopulations of root voles in the Netherlands. The subpopulation on the island of Texel has by far the highest percentage (12.5%) followed by the moorlands of Zuid-Holland (2.7%). The occurrence of *radnensis* is very limited in the subpopulations of the Delta (0.3%) and the moorlands of Noord-Holland (0.2%). The number of M^2s from Friesland was too small (20) to draw any conclusions.

Until the 1980s the root vole was the only vole on the island of Texel. In 1985 the first remnants of a field vole (*M. agrestis*), in an owl pellet, was reported by Lange (1986), and field vole specimens were trapped close to that owl pellet four years later (van Apeldoorn et al. 1991). One possible explanation of the high prevalence of the form *radnensis* in root voles on Texel is the island's lengthy isolation (almost 5000 years) from the mainland (Fries-Drents Plateau) (van Laar 2018). During this period, genetic drift may have caused a higher prevalence of *radnensis* than is found in the other subpopulations in the Netherlands. Superficially the situation on Texel is similar to other islands (e.g. Schouwen-Duiveland, the Delta), where root voles have also expanded their ecological niche due to the absence of field voles. However Texel is more isolated from the mainland than other islands, such as Schouwen-Duiveland. So the longer and more emphatic isolation on Texel, rather than the broader ecological niche, might have been the factor influencing the prevalence of the form *radnensis* on Texel. It is also possible that this extra enamel loop provided by this form enables more efficient grinding of vegetable matter.

The percentage of M^2s in root voles with the form *radnensis* found on Texel is slightly higher (12.5%) than that (10.5%) found on St. Lawrence Island (Angermann 1984). The latter island, west of mainland Alaska in the Bering Sea, south of the Bering Strait, is thought to be one of the last exposed portions of the land bridge that once joined Asia with North America during the Pleistocene, ca. 25,000 years ago (Anonymous 1979). Although both islands are considered to be continental islands, their isolation from the nearest mainland (and thereby from neighbouring populations of root voles) probably causes the high percentages of the form *radnensis*. These figures can be compared with findings by Angermann (1984), who examined 70 M^2s from an island in Germany (Riems) and found no presence of the form *radnensis*. This is probably due to this island's close proximity to the mainland (ca. 500 metres), to which it is connected by a dam since the early 1970s.

The results of this study do not suggest any correlation between the upper molar row lengths in the ordinal ranked stages of *radnensis* forms with age. A more precise, direct comparison of upper molar row length stages of *radnensis* forms with the upper molar row lengths in different age categories is not possible as the age class specimens are retrieved from other work by Markowski (1980), conducted in East Poland (*A. o. stimmingi*), while the *radnensis* form specimens are present in a different subspecies (*A. o. arenicola*).

There was no evidence of a prevalence of the form *radnensis* V_1, V_2, V_3 and V_4 in the left or right M^2 of root voles in any of the subpopulations of root vole in the Netherlands.

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Samenvatting

Verschillen in frequentie van de vorm radnensis M^2 tussen geïsoleerde subpopulaties van de noordse woelmuis

(*Alexandromys oeconomus arenicola*) in Nederland

Bij een analyse van ongesorteerde kerkuilbraakballen uit Texel bleken twaalf van de 140 bovenste tweede kiezen (M^2) van de noordse woelmuis (*Alexandromys* (*Microtus*) *oeconomus arenicola*) de vorm *radnensis* te vertonen: deze manifesteert zich als een omgekeerde omega (Ω) aan het driehoekje aan de tongzijde. Naast de reguliere of normale vorm (N) wordt de vorm *radnensis* in vier stadia ingedeeld: V_1, V_2, V_3 en V_4, waarbij V_1 het minst en V_4 het sterkst is ingesneden. Het doel van dit onderzoek is om de frequenties van het voorkomen van de vorm *radnensis* van M^2 in de bekende subpopulaties van de noordse woelmuis in Nederland te bepalen en vast te stellen of er verschillen zijn tussen de subpopulaties. In andere studies wijzen de totalen van de gevonden vormen van de stadia V_1-V_4 op hogere totalen in de lagere stadia. Het is de vraag of de leeftijdsopbouw van de noordse woelmuizenpopulatie de verklaring zou kunnen zijn voor deze scheve verdeling. Naast materiaal van Texel zijn ook alle beschikbare schedels van noordse woelmuizen uit heel Nederland onderzocht. Het betreft schedels afkomstig van: Texel (*n*=303), Noord-Hollandse laagveengebieden (315), Zuid-Hollandse laagveengebieden (253) en de Delta (853); het aantal schedels afkomstig uit Friesland was relatief laag (10). Om de relatie met de leeftijdsopbouw te onderzoeken is van beschikbare exemplaren van de M^2 de stagering van de vorm *radnensis* bepaald en is van dezelfde schedels de lengte van de bovenste tandenrij gemeten. De subpopulatie van Texel toont het hoogste aandeel *radnensis*, 12,5%, gevolgd door de subpopulatie van de laagveengebieden van Zuid-Holland met 2,7%. De percentages *radnensis* binnen de andere subpopulaties zijn lager. Een mogelijke verklaring voor de hoge prevalentie van *radnensis* op Texel is de langdurige isolatie (>4000 jaar) van het eiland, waardoor het aandeel *radnensis* (als gevolg van genetic drift) kon toenemen. Metingen van de bovenste kiezenrijlengtes waar minimaal één *radnensis* aanwezig was, laten stijgende waarden zien bij toenemende leeftijd. Een positieve relatie tussen de bovenste kiezenrijlengte van de vormen *radnensis* V_1-V_4 met de vijf leeftijdscategorieën kon echter niet worden bevestigd. Ook een verschil in frequentie van de vorm *radnensis* V_1, V_2, V_3 en V_4 tussen linker en rechter M^2s van noordse woelmuizen in alle subpopulaties in Nederland kon niet worden aangetoond.

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