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Demographic structure of long-distance dispersers in the bank vole *Clethrionomys glareolus*: Choosing the optimal age categorization

Oleg V. Tolkachev

ABSTRACT. This study analyzes the demographic composition of bank voles *Clethrionomys glareolus* (Schreber, 1780) dispersing over distances exceeding one kilometer. This process plays a key role in maintaining the metapopulation structure of species and recolonizing habitats, especially in fragmented landscapes. Despite numerous studies, data on long-distance movements and demographic characteristics of dispersers remain limited. The research was conducted from 2014 to 2018 in the Southwestern Forest Park of Yekaterinburg, Russia. Dispersers were identified using group marking with tetracycline and rhodamine B, followed by trapping animals at various distances (1–3 km) from the marking points. A total of 818 individuals were captured, of which 343 dispersed over a kilometer. Bank voles were found to disperse as far as 3100 m — the longest distance ever recorded for this species. Age was determined based on body weight, reproductive system condition, and tooth root formation stages. The study found that most long-distance movements in the surveyed bank vole population were natal dispersal, primarily involving immature underyearlings of both sexes aged 35–55 days. Breeding dispersal is less common and involves primarily overwintered individuals of both sexes, with females potentially being more active. The lowest dispersal probability was observed in mature underyearlings, many of which likely either started breeding near their birthplace or had matured after dispersal but prior to being captured. Analysis of different age-classification approaches demonstrated that using four categories (immature underyearlings under 30 days, immature underyearlings over 30 days, mature underyearlings, and overwintered individuals) is optimal for studying bank vole dispersal.

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Демографическая структура рыжих полёвок *Clethrionomys glareolus*, при дисперсии на большие расстояния: выбор оптимальной возрастной категоризации

О.В. Толкачёв

РЕЗЮМЕ. В данном исследовании анализируется демографический состав рыжих полёвок *Clethrionomys glareolus* (Schreber, 1780), совершающих перемещения на расстояния, превышающие один километр. Этот процесс играет ключевую роль в поддержании метапопуляционной структуры вида и повторном заселении местообитаний, особенно в фрагментированных ландшафтах. Несмотря на многочисленные исследования, данные о дальних перемещениях и демографических характеристиках расселяющихся или переселяющихся животных остаются ограниченными. Работа была проведена с 2014 по 2018 год на территории Юго-Западного лесного парка г. Екатеринбурга (Россия). Мигрантов выявляли с помощью метода группового мечения тетрациклином и родамином В с последующим отловом зверьков на различных расстояниях (1–3 км) от точек мечения. Использованы данные по 818 особям, из которых 343 переместились на расстояние более километра. Было установлено, что рыжие полёвки способны расселяться на расстояние до 3100 м, что является максимальным зарегистрированным показателем для данного вида. Возраст зверьков определяли на основе массы тела, состояния репродуктивной системы и стадии формирования корней зубов. В ходе исследования было выявлено, что большинство дальних перемещений в изученной популяции рыжих полёвок представляет собой первичное расселение от места рождения, в котором участвуют преимущественно неполовозрелые сеголетки обоих полов в возрасте 35–55 дней. Репродуктивное переселение встречается реже и включает в основном перезимовавших зверьков обоих по-

лов, при этом самки, возможно, проявляют более высокую активность. Наименьшая вероятность расселения была отмечена у половозрелых сеголетков, многие из которых, вероятно, начинали размножаться вблизи места рождения или созревали до выявления дисперсии. Анализ различных подходов к возрастной классификации показал, что для изучения дисперсии рыжих полёвок оптимальным является использование четырёх категорий: неполовозрелые сеголетки младше 30 дней, неполовозрелые сеголетки старше 30 дней, половозрелые сеголетки и перезимовавшие особи.

КЛЮЧЕВЫЕ СЛОВА: дальняя дисперсия, первичное расселение, репродуктивное переселение, рыжая полёвка, демография.

Introduction

Dispersal is the foundation of the metapopulation structure in mouse-sized mammal species (Hanski & Gilpin, 1991). It ensures connectivity among local populations and the recolonisation of habitats, many of which experience regular local extinctions (especially during winter in temperate zones). The practical significance of this type of movement increases as landscape fragmentation intensifies. Understanding the specifics of dispersal is important both for the conservation of endangered small mammal species and for managing invasive species (King *et al.*, 2011; Stolen *et al.*, 2014).

To date, a large body of literature has accumulated, providing examples where dispersal includes movements of small mammals ranging from tens of metres to kilometres (Shchipanov *et al.*, 1997; Andreassen & Ims, 2001; Shchipanov, 2003; Smith & Batzli, 2006; Gaillard *et al.*, 2012; Kalinin & Kupriyanova, 2015; Mukhacheva & Tolkachev, 2022; Grigorkina *et al.*, 2024). Clearly, the latter are of greatest interest, as they occur on a landscape scale and are critical for maintaining genetic diversity and population resilience (Shchipanov, 2003, 2019; Shchipanov & Kuptsov, 2004; Le Galliard *et al.*, 2012). However, due to the lifestyle of mouse-sized rodents and the associated methodological challenges, most publications focus on movements spanning tens to hundreds of metres. The data obtained in such cases can be difficult to interpret, since short-distance movements may include activity types other than dispersal — for example, shifts in home range boundaries or exploratory excursions (Bovet, 1992; Stenseth & Lidicker, 1992; Tolkachev, 2023; Tolkachev *et al.*, 2023).

One of the most important parameters of dispersal is the demographic composition of dispersing animals, here defined as the ratio of sex-age groups. This information is used to infer the immediate triggers, effectiveness, and adaptive significance of dispersal (Greenwood, 1980; Stenseth & Lidicker, 1992; Sutherland *et al.*, 2000). It also determines the mode of population functioning — either controlling or reestablishing (sensu Shchipanov, 2002). Knowledge of the demographic composition of dispersers is fundamental for determining its type — natal or breeding dispersal (sensu Greenwood, 1980). The first type involves the initial dispersal of young animals from their birthplace, while the second involves the change of home range by sexually mature individuals between breeding episodes. These types of dispersal can have different meanings in the life of species (Selonen & Wistbacka, 2017 and references therein). However, data on the sex and age structure of small mammal dispersers remain scarce. Even for a widespread and well-studied species like the bank vole *Clethrionomys glareolus* (Schreber, 1780), most available data concern short-distance movements (Ylönen *et al.*, 1988; Dickman & Doncaster, 1989; Rajska-Jurgiel, 1992). Some studies based on long-term depopulation in experimental plots provide demographic data on dispersers, classified as all immigrants, but lack information on the distances they travelled (Kozakiewicz, 1976; Gliwicz, 1988, 1989). The linear dimensions of a bank vole's home range typically remain within 100 m (Mazurkiewicz & Rajska, 1998). The maximum distance of exploratory excursions is not known precisely but is likely to reach several hundred metres (Tolkachev, 2023; Tolkachev *et al.*, 2023). Therefore, movements of voles over distances of up to 1000 m could be attributed to either dispersal or exploratory excursions. Only a few studies describe bank vole dispersal over distances exceeding one kilometre (Bolshakov & Bazhenov, 1988; Szacki & Liro, 1991; Tolkachev, 2016). None of them include an analysis of the demographic characteristics of dispersers. Meanwhile, long-distance movements are common for bank voles, as evidenced by the rapid shift in their range boundaries (2.5 km/year) in Ireland, where the species is invasive (White *et al.*, 2012). Within the species' primary range, long-distance movements of the bank vole can reach up to 2 km and are also not considered uncommon (Tolkachev, 2016). Individuals of a closely related species, the northern red-backed vole *Clethrionomys rutilus* (Pallas, 1779), have been recaptured multiple times at distances greater than 9 km from their original marking site (Grigorkina & Olenev, 2018).

An additional challenge is the use of different approaches to age determination, complicating the comparison of results across studies. Various categorisations may be used: mature/immature, juvenile/subadult/adult, juvenile/adult, overwintered/young of different cohorts (Watts, 1970; Dickman & Doncaster, 1989; Gliwicz, 1989; Kozakiewicz *et al.*, 2007). The choice of age criteria depends on field methods, research objectives, data volume, and possibly personal preferences. It remains unclear which approach is most suitable for studying small mammal dispersal.

The aim of this study was to analyse the demographic composition of bank voles that dispersed at

landscape scale. An additional objective was to compare results obtained using different age determination approaches.

Material and methods

Experimental design. The study was conducted from 2014 to 2018 in the Southwestern Forest Park of Yekaterinburg, Russia. To study the demographic composition of dispersers in line with the research objectives, a sufficiently large sample of animals captured at distances exceeding 1 km is required. However, the probability of recapturing marked individuals decreases rapidly with increasing distance from the marking plot. Consequently, despite its advantages, the traditional CMR (Capture-Mark-Recapture) method is not the best option in this case, as it entails prolonged and labour-intensive work at the marking plots. Furthermore, the accuracy of determining the age and reproductive status of individuals when working with live animals may be insufficient. To identify dispersers and resident animals, group marking with tetracycline (TC) and rhodamine B (RB) administered in bait was used (Crier, 1970; Fisher, 1995; Tolkachev, 2019a). All animals that consume the bait receive a mark. This approach enables the easy marking of all or nearly all rodents that either inhabit the marking plot or pass through it while the bait remains available. This, in turn, allows research efforts to be concentrated primarily on trapping dispersers at various points located far from the original marking plot. Both biomarkers can be transferred to juveniles through breast milk, marking them before they leave the nest (Lobkov, 1984; Tolkachev & Bespamyatnykh, 2019). This is particularly valuable for marking potential natal dispersers, as it increases the chance of identifying young animals that disperse soon after first emergence — a period when capture probability is low. However, marking via milk is only possible if the mother consumes the bait containing the marker during the lactation period.

The bait consisted of oat flakes mixed with either tetracycline hydrochloride or rhodamine B at a concentration of 800 mg/kg. After mixing, boiling water was added, and the mixture was stirred again. The resulting «porridge» was spread evenly on a flat surface, cut into ~2×2 cm pieces, and dried at 80°C for 24 hours. Immediately before use, the bait was sprayed with unrefined sunflower oil, which partially protected it from moisture and served as an attractant for small mammals. The bait was applied at a rate of 4.2 kg/ha across two marking plots, each covering 1.44 ha (Fig. 1). I aimed to distribute the bait evenly across the plots (approximately in a grid pattern with 5 m intervals). Marking was conducted three times each year at 6–8-day intervals (avoiding rainy periods). The total duration of group marking via bait was 21 days during the latter half of June in each year of the study. Tetracycline was used from 2014 to 2018 (marking plot at point 4), while rhodamine B was used from 2016 to 2018 (marking plot at point 1). Rhodamine marking was added after a convenient and reliable method for its detection became available; field testing of this method was conducted by me in parallel with the work on small mammal dispersal. I employed two biomarkers to potentially double the number of marked animals for the same trapping effort. Furthermore, to obtain large sample sizes, the study was conducted during a period of high seasonal vole abundance in the region (mid-June to late July). Three weeks after marking began, animals were captured using all-metal snap traps with a hook mechanism triggered when an animal pulled the bait (Tolkachev, 2019b). Trapping was carried out at 14 locations (excluding those where dispersing bank voles were not caught): points 1–11, 13, and 14 in 2014–2018; point 17 in 2016–2018 (Fig. 1). From 2014 to 2018, trapping was not simultaneous across all points but occurred in three stages over three weeks. At each point, I set up a trap-line of 25 snap traps spaced 5 m apart, which remained active for five nights. Traps were checked every morning. Captured animals were transported to the laboratory for mark detection and dissection. Methods for detecting marks have been described previously (Tolkachev *et al.*, 2017; Tolkachev, 2019a; Tolkachev & Bespamyatnykh, 2019). In brief, tetracycline marks rodent incisors, yielding yellow UV-induced fluorescence. Rhodamine B marks hair and claws, producing yellow fluorescence under green light (observed through an orange filter). Mark persistence is ~50 days for tetracycline and ≥6 months for rhodamine B. Movement distance was calculated as the shortest distance from the perimeter of the individual's original marking plot (TC or RB) to the trap-line where it was recaptured. Individuals marked with TC or RB and captured at least 1 km away from their marking plot were classified as long-distance dispersers. The maximum possible movement distance was 3100 m (from point 1 to point 11 via point 4 in Fig. 1, which would require an individual to carry both rhodamine and tetracycline marks). In contrast, marked voles captured within their original marking plot were considered residents. Dissections were performed to determine age and maturity more accurately, using the following criteria: body weight, reproductive system data (thymus development, right testis weight, or uterine condition), and stages of tooth root formation (after Olenev, 2009). Three schemes were used to classify reproductive age categories: 1) immature underyearlings (stages of tooth root formation 1–4), mature underyearlings (stages of tooth root formation 3–6), overwintered individuals (stage 7); 2) mature (mature underyearlings and overwintered individuals) and immature; and 3) seven groups based on tooth root formation stages.

Ethics approval. The use of lethal trapping methods was absolutely necessary for the following reasons:

1. The need to determine the reproductive status of animals accurately, which requires dissection (in accordance with the study's aim);
2. The need to determine the age of individuals precisely based on the degree of tooth root development (in accordance with the study's aim);

3. Tetracycline marks can only be detected in extracted rodent incisors;
4. To increase the sample size of marked individuals (dispersers and residents), which is important for statistical analysis.

Data from captured animals not included in the results presented here will be used in other studies. This study followed all applicable international, national, and institutional guidelines for the care and use of animals. Field methods were approved by the Bioethics Commission of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (protocol #14/2023).

Data analysis. A total of 1114 bank voles were captured (Table 1). To refine the subsequent "unknown movement status" reference group, marked individuals recaptured within 1 km of their original site were excluded from the analysis. This reduced the sample to 818 individuals. This exclusion was necessary because such individuals could represent either short-distance dispersers or animals engaged in exploratory movements. Thus, the "unknown movement status" reference group includes only individuals without marks that were not recorded making long-distance movements. To assess the potential impact of indiscriminate lethal trapping of small mammals on interannual population dynamics and dispersal, I used data from snap-trap captures in the Southwestern Forest Park from 2011 to 2019. To determine sex- and age-related characteristics of dispersers, generalized linear models (GLMs) were used. The response variable in all models was the binary variable "dispersal" (0 = non-disperser, 1 = disperser). The link function was logit. The reference group (non-dispersers) included either only residents or residents plus voles of unknown status. Predictors included sex, age (three levels), maturity (mature/immature), or seven age categories based on tooth development, along with their interactions (where applicable). Mul-



Fig. 1. Map of the study area showing the locations of marking plots and trap-lines. Numbers refer to trap-line identifiers (IDs). RB — rhodamine B; TC — tetracycline.

Table 1. Structure of bank vole dispersal data and collection methods.

	Dispersal distance, m	Number of dispersers or residents	Voles captured & (percentage of dispersers or residents)	Trapping effort, trap-nights	Trap-line ID* & (mark type)
Dispersal	1000	1	47 (2%)	375	6 (RB)
	1040	8	48 (17%)	375	4 (RB)
	1100	57	132 (43%)	1250	1 (TC), 3 (TC)
	1150	4	47 (9%)	375	6 (TC+RB)
	1200	64	143 (45%)	1250	2 (TC), 7 (TC)
	1250	1	46 (2%)	375	5 (RB)
	1430	2	32 (6%)	375	14 (RB)
	1440	55	138 (40%)	1250	8 (TC), 10 (TC)
	1450	15	35 (43%)	375	17 (TC)
	1480	3	35 (9%)	375	17 (TC+RB)
	1500	1	46 (2%)	375	5 (TC+RB)
	1620	24	64 (38%)	625	9 (TC)
	1700	3	66 (5%)	750	2 (TC+RB), 3 (TC+RB)
	2030	16	48 (33%)	625	11 (TC)
	2400	8	63 (13%)	375	7 (TC+RB)
	2480	3	54 (6%)	375	8 (RB)
	2500	12	43 (28%)	625	14 (TC)
	2530	8	32 (25%)	375	14 (TC+RB)
	2540	4	54 (7%)	375	8 (TC+RB)
	2650	10	45 (22%)	375	10 (RB), 10 (TC+RB)
	2780	17	48 (35%)	375	9 (RB), 9 (TC+RB)
	3000	16	37 (43%)	625	13 (TC)
	3030	4	30 (13%)	375	11 (RB)
	3100	7	30 (23%)	375	11 (TC+RB)
Residency	NA	66	76(87%)	625	4 (TC) in 2014–2018
	NA	23	46(50%)	375	1 (RB) in 2016–2018
Total		343 dispersers, 89 residents	818** (dispersers — 42%, residents — 11%)	9875**	

* — The position of all trap-lines is shown in Figure 1; RB = rhodamine B; TC = tetracycline; TC+RB — individuals with both marks that visited two marking plots

** — Not the sum of the previous lines due to the parallel use of two markers. For example, trap-line 11 appears in the table three times: individuals with only the TC mark (distance from the corresponding marking plot: 2030 m; total of 48 individuals, marked and unmarked, captured over 625 trap-nights during 2014–2018, when tetracycline was used), individuals with only the RB mark (distance: 3030 m; total of 30 individuals, marked and unmarked, captured over 375 trap-nights during 2016–2018, when rhodamine was used), and individuals with both markers (distance: 3100 m; 30 individuals, marked and unmarked, captured over 375 trap-nights during 2016–2018, when both tetracycline and rhodamine were used). However, the total number of voles captured on this line is 48, not 48+30+30. The same applies to the calculation of trapping effort. The actual number of voles captured is 818 individuals over 9875 trap-nights. Where distances to different lines coincided, the data for them were combined. NA — not available.

ticollinearity was assessed using the generalized variance inflation factor (GVIF) for GLMs (critical value: GVIF^(1/(2*Df)) > 2 or VIF > 5). Overdispersion was checked (critical value: residual deviance/Df > 1.25). When overdispersion was detected, the findings were tested in a quasi-binomial model. Likelihood ratio tests were used for all models to assess overall fit and determine the necessity of including interaction terms. Differences in body weight among four reproductive age groups (identified during the analysis) were assessed

using ANOVA. All statistical analyses were performed in R 4.4.3 (R Core Team, 2025). The ggeffects package (Lüdecke, 2018) was used to visualise dispersal probabilities derived from the models.

Results

The bank vole dominated the community (42% of all animals captured over 5 years). Snap-trapping over several years during the seasonal peak in abundance did not lead to a consistent decline in the abundance of either the bank vole or the entire small mammal community (Fig. 2). The study utilised data from 818 bank voles, of which 89 were residents on one of the two marking plots, 386 had an undetermined status, and 343 were dispersers (Table 1). Seven bank voles — one overwintered female, three immature underyearlings, and three sexually mature underyearling males — were captured 3100 m from the marking plots. The sex ratio in the overall population, as well as among dispersers, was 1:1.3 in favour of males. Among dispersers, the most numerous group was immature males, while the smallest group was mature male underyearlings (Table 2). For females, the predominant group was mature underyearlings, whereas for males, it was immature underyearlings.

Table 2. Ratio of reproductive-age groups among dispersers of different sexes.

Sex-age group	Individuals (%)
Immature males	101 (29%)
Mature underyearling females	63 (18%)
Overwintering males	54 (16%)
Overwintering females	45 (13%)
Immature females	43 (13%)
Mature underyearling males	37 (11%)
Total	343 (100%)

The first model included sex and age (three categories) as factors. The interaction of factors was not included due to multicollinearity. Only animals with a mark that were captured on the corresponding marking plot were classified as

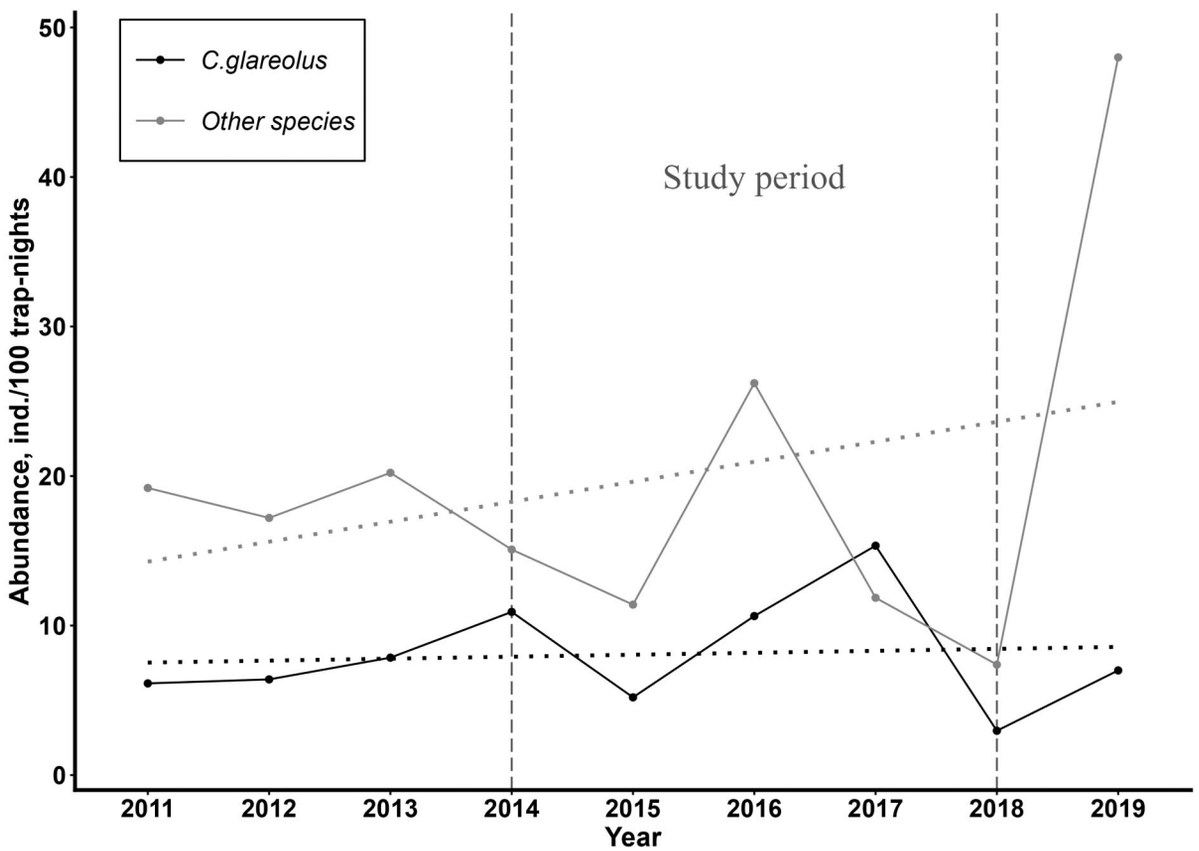


Fig. 2. Small mammal abundance in Yekaterinburg's Southwest Forest Park (2011–2019) according to snap-trap captures. The other species include: *Apodemus uralensis* (Pallas, 1811), *A. agrarius* (Pallas, 1771), *Microtus arvalis* sensu lato, *M. agrestis* (Linnaeus, 1761), *Alexandromys oeconomus* (Pallas, 1776), *Sicista betulina* (Pallas, 1779), *Sorex araneus* (Linnaeus, 1758), *S. minutus* (Linnaeus, 1766), *S. caecutiens* (Laxmann, 1788).

residents. Only the age factor was found to be significant (Table 3). The probability of dispersal was approximately the same for immature underyearlings and overwintered individuals (Fig. 3A). No sex differences were detected.

Based on the ratio of age groups for both sexes, animals of undetermined status were closer to resident individuals than to dispersers (Fig. 4). Therefore, I attempted to include these individuals in the analysis as

Table 3. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and age group (animals of undetermined status were excluded). Reference group — immature female underyearlings.

Term	Estimate	Std. error	z-statistic	*p*-value
(Intercept)	1.817	0.290	6.269	<0.001
Age group:				
Mature underyearlings	–1.204	0.306	–3.935	<0.001
Overwinterings	–0.294	0.348	–0.846	0.398
Sex (MALE)	0.236	0.255	0.925	0.355

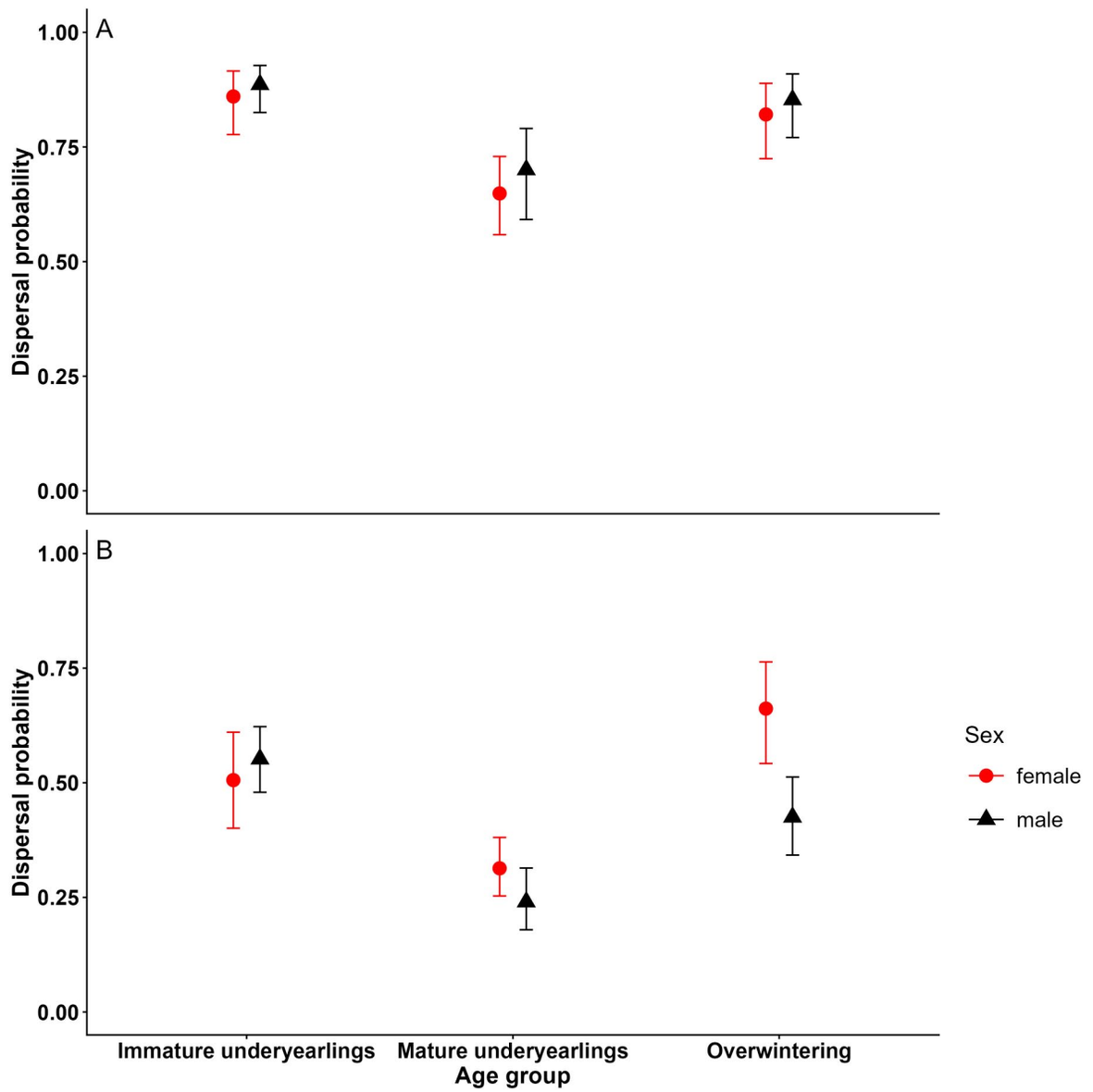


Fig. 3. Probability of dispersal for males and females of different reproductive-age groups (whiskers — 95% CI). A — individuals of undetermined status were excluded from the analysis; B — included in the analysis.

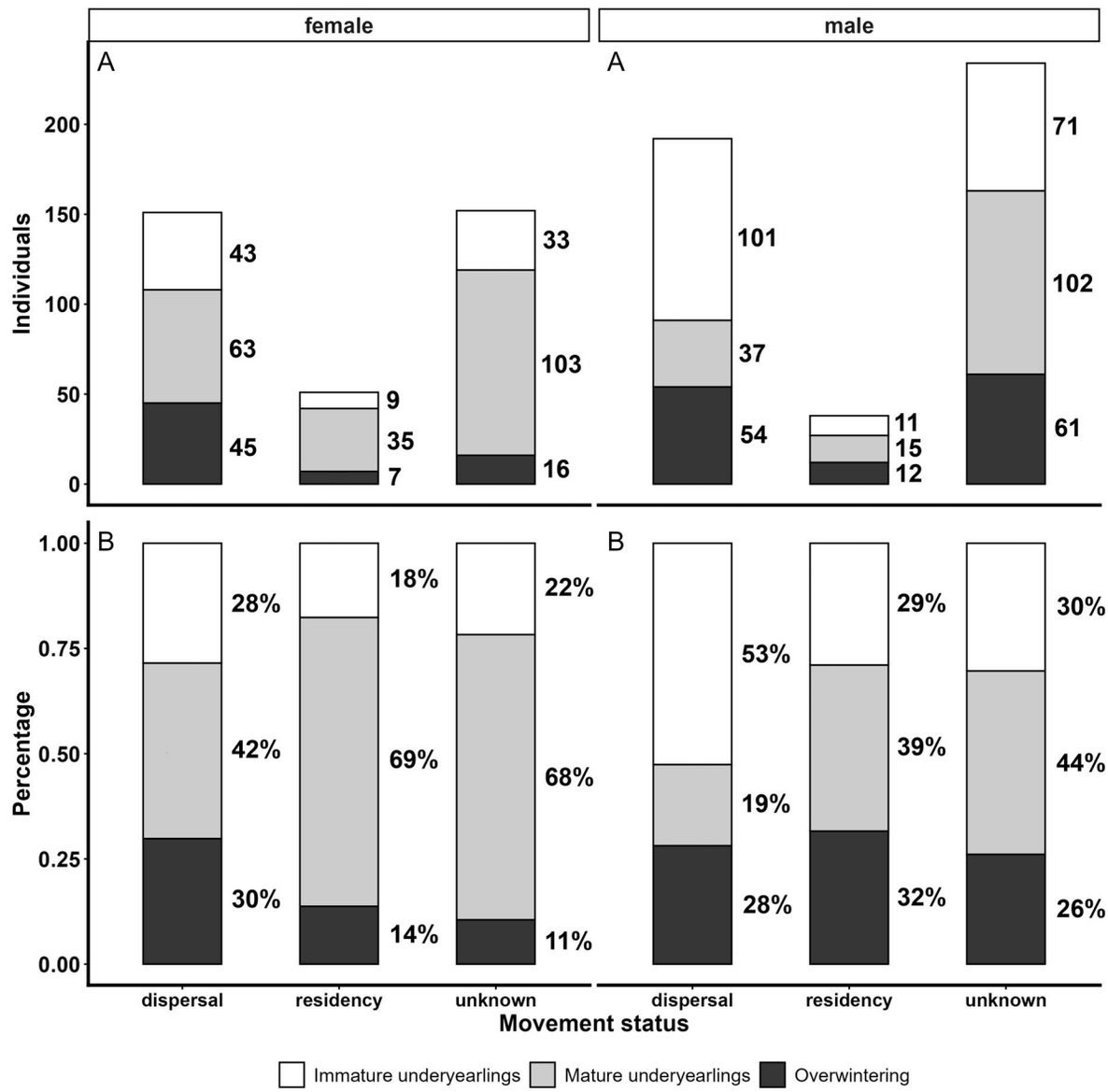


Fig. 4. Ratio of reproductive-age groups in males and females with different movement statuses: A — by individuals; B — in percentages.

Table 4. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex, age group, and their interaction (animals of undetermined status were included in the model as residents). Reference group — immature female underyearlings.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	0.024	0.217	0.108	0.914
Age group:				
Mature underyearlings	–0.808	0.265	–3.049	<0.01
Overwinterings	0.648	0.336	1.929	0.054
Sex (MALE)	0.185	0.263	0.703	0.482
Age group & Sex:				
Mature underyearling males	–0.552	0.358	–1.544	0.123
Overwintering males	–1.158	0.409	–2.832	<0.01

residents to increase the sample size. In this case, the model included age, sex, and their interaction. The age factor and the interaction between age and sex were significant (Table 4). The probability of dispersal remained low for mature underyearlings of both sexes and high for immature underyearlings, but among overwintered individuals, the rate was significantly higher in females than in males (Fig. 3B).

To assess the effect of maturity *per se* and verify the adequacy of the analysis using only two age categories, two additional models were constructed. In the first model, animals of undetermined status were excluded. Only the maturity factor was significant — the probability of dispersal was higher in immature individuals regardless of sex (Table 5, Fig. 5A). Including animals of undetermined status as residents did not fundamentally change the result (Table 6, Fig. 5B).

To test how the results would change with a different approach to age categorisation, models were constructed that included age assessment based on tooth root development stages (7 stages). The conservative approach, which considered only marked individuals recaptured at the marking plot as residents, did not yield significant predictors (Table 7). In the approach that included animals of undetermined status as residents, root formation stage was significant, but sex was not (Table 8).

This result aligns well with that obtained using three age categories (Fig. 3). The highest probability of dispersal was found for age groups with root formation stages 2 and 3, most of which belong to the group of immature underyearlings (Fig. 6). Dispersal probability was also high for animals of age group 7. This category almost entirely overlaps with the overwintered group. Dispersal probability was low in age groups 5 and 6. Nearly all these voles were mature underyearlings. Individuals in group 4 had an intermediate dispersal probability, as they included comparable numbers of mature and immature animals. Animals of age 1 (less than 30 days) had a low dispersal probability, although most belonged to the immature underyearling group (Fig. 6).

Thus, when studying bank vole dispersal, it is advisable to distinguish four age categories: immature underyearlings younger than 30 days, immature underyearlings older than 30 days, mature underyearlings, and overwintered individuals. Their dispersal probabilities are presented in the figure (Fig. 7).

In the conservative approach, where animals of undetermined status were excluded, only the age-related predictor approached significance, although the formal threshold was not reached (p=0.06; Table 9). In the expanded sample model, both age and sex were significant — males were less prone to dispersal (Table 10, Fig. 7B).

Capture–mark–recapture (CMR) is a widely employed method in studies of small mammal dispersal, providing basic data on sex, maturity, and body weight. Therefore, I decided to test whether these data were sufficient to classify animals into four reproductive-age categories (Fig. 8). It was found that both males and females from different groups significantly differed in average body weight (females: F value = 279.2, df = 3, $p < 0.001$; males: F value = 543.7, df = 3, $p < 0.001$). However, the subgroups largely overlapped, and precise categorisation based on sex, maturity, and body weight was impossible.

Discussion

As already described in the Methods section, the use of lethal trapping was absolutely necessary for this study. Despite several years of removal trapping, no downward trend in abundance was observed, contrary to what might have been anticipated. (Fig. 2). The reason for this is likely that trapping was conducted during the season of high abundance, but before the end of the small mammal breeding period, when there is a large surplus of animals in the populations capable of compensating for the removal of individuals, which occurred locally across an area of approximately 5 km². It is known that animal removal can lead to the formation of a local "ecological vacuum" that is filled within 3–4 weeks (Bol'shakov *et al.*, 1973). Potentially, this could have influenced animal movements. Although experimental studies on the bank vole have demonstrated that vacant areas are recolonized through long-distance dispersal, trapping itself does not appear to induce immigration (Shchipanov & Lyapina, 2011). In this study, trapping began 3–5 weeks after the start of marking, by which time most dispersal movements had already occurred.

The documented dispersal of voles over a distance of 3100 m represents the maximum dispersal distance documented for the species. The probability of detecting such long-distance movements may have been increased in this study due to the "channeling" of movements within a forest tract surrounded by urban development and the "migrant trap" effect (Tolkachev, 2016; Kalinin, 2022). However, I do not think that landscape features could have influenced the dispersal probability of specific individuals, as prior to the onset of this process, they have a very limited understanding of the properties of the entire habitat.

All sex and age groups were represented among dispersers (Table 2). This has been previously observed in various small mammal species (Dickman & Doncaster, 1989; Rajska-Jurgiel, 1992; Shchipanov & Lyapina, 2011; Kalinin & Kupriyanova, 2015; Shchipanov, 2019). In small rodents, dispersal is often biased toward young individuals, particularly males (Fairbairn, 1978; Krohne & Miner, 1985; Wolton & Flowerdew, 1985; Stenseth & Gustafsson, 1985). Most studies on bank vole dispersal have concluded a male bias (Brown, 1956; Rajska-Jurgiel, 1992; Kozakiewicz *et al.*, 2007). In this study, immature males were indeed the most numerous group among dispersers, but this is because males outnumbered females by 30% in the overall population. Cases of male predominance in bank vole populations have also been reported by other authors (Rajska-Jurgiel, 2000; Kozakiewicz *et al.*, 2007). Re-

Table 5. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and maturity (animals of undetermined status were excluded). Reference group — immature female.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	1.734	0.284	6.100	<0.001
Maturity (MATURE)	–0.829	0.283	–2.932	<0.01
Sex (MALE)	0.368	0.248	1.486	0.137

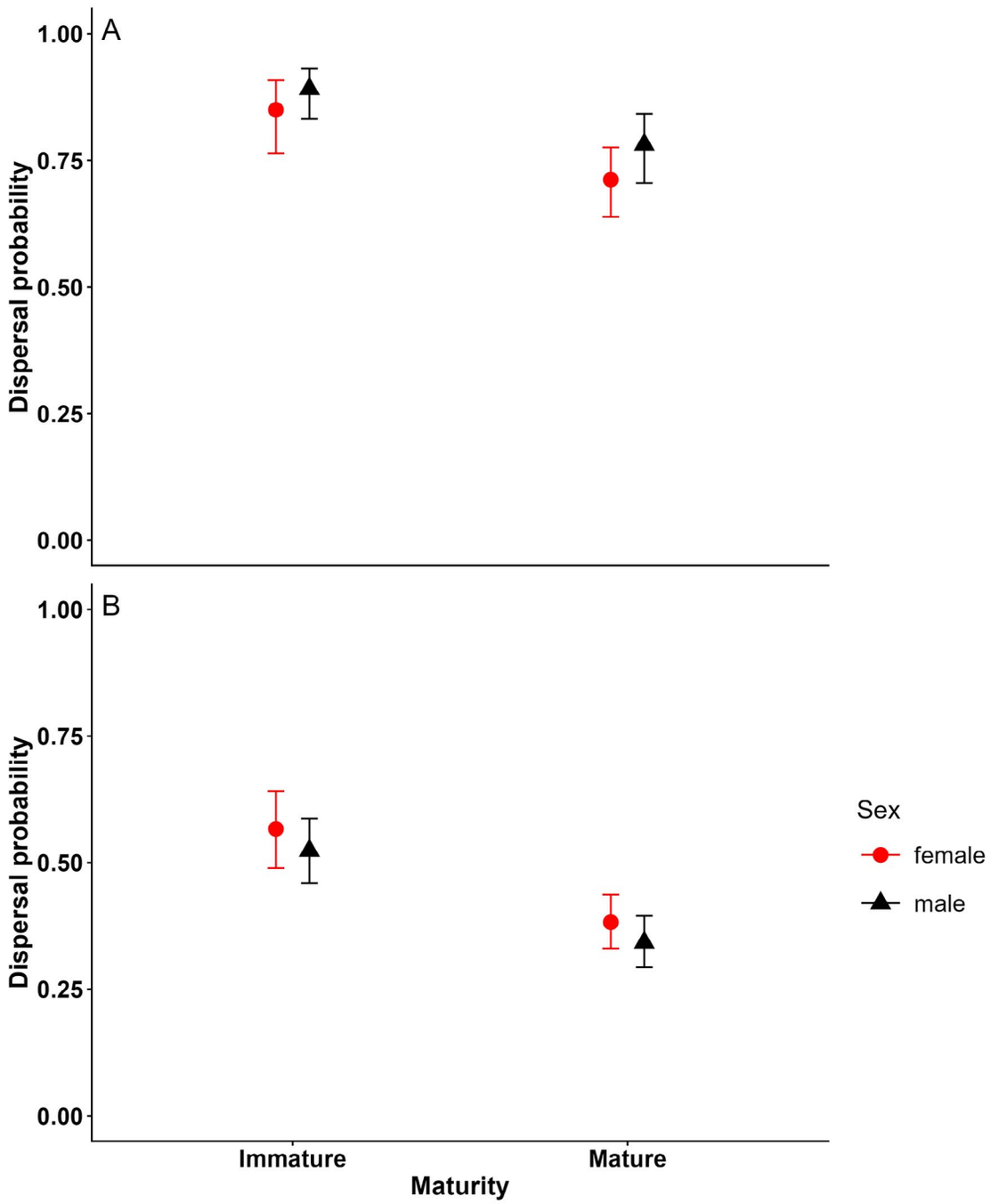


Fig. 5. Probability of dispersal for mature and immature bank voles (whiskers — 95% CI). A — individuals of undetermined status were excluded from the analysis; B — individuals included in the analysis.

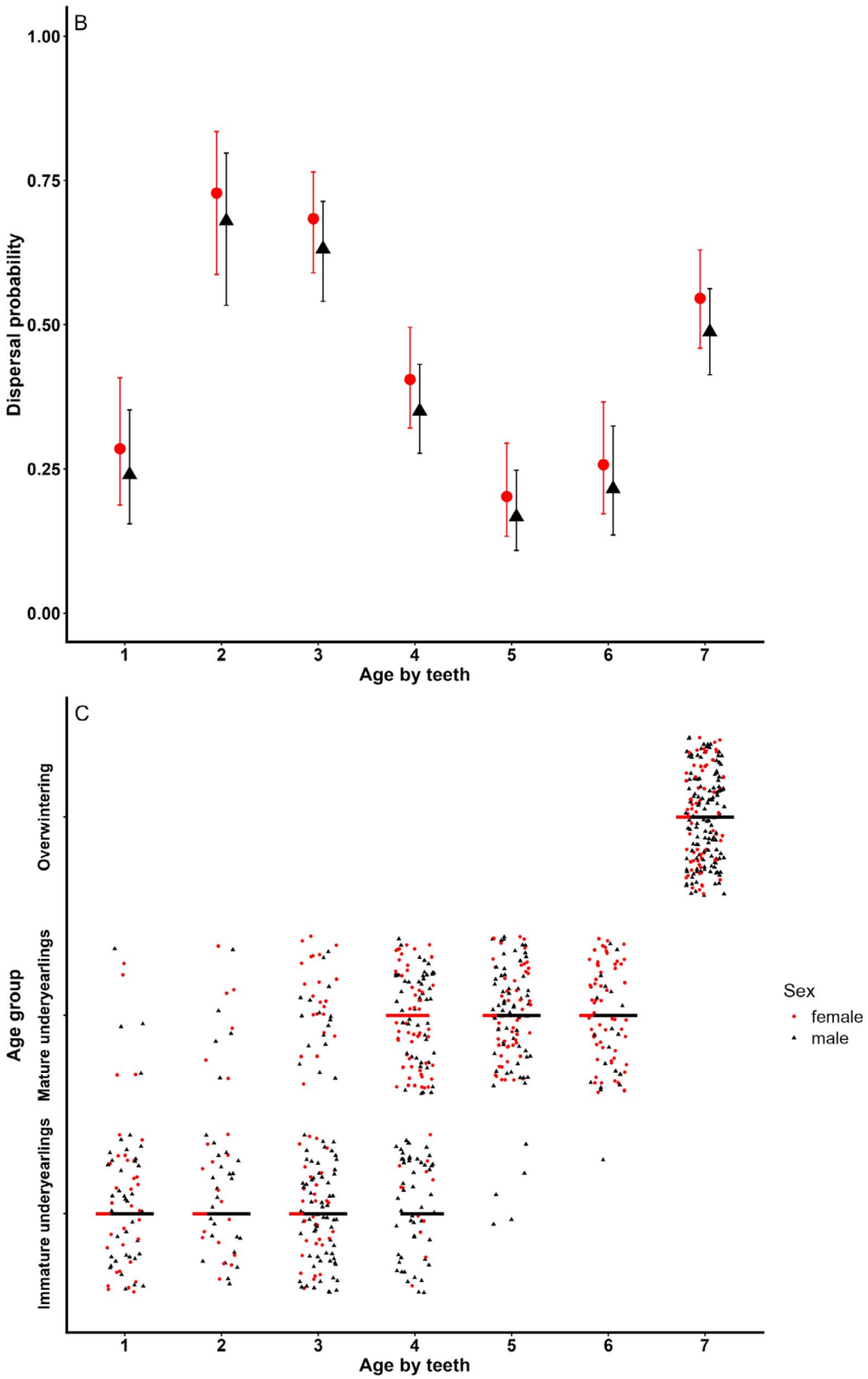


Fig. 6. A — probability of dispersal for voles of different ages determined by teeth (animals of undetermined status were included in the model as residents), B — distribution of individuals across age groups identified using two different approaches. Horizontal lines — modal values.

Table 6. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and maturity (animals of undetermined status were included in the model as residents). Reference group — immature female.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	0.268	0.159	1.688	0.091
Maturity (MATURE)	–0.748	0.154	–4.862	<0.001
Sex (MALE)	–0.173	0.147	–1.177	0.239

Table 7. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and age assessed by teeth (animals of undetermined status were excluded). Reference group — female stage 1.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	0.734	0.467	1.573	0.116
Age by teeth				
STAGE 2	0.796	0.628	1.268	0.205
STAGE 3	1.064	0.548	1.941	0.052
STAGE 4	0.018	0.508	0.036	0.971
STAGE 5	–0.528	0.565	–0.935	0.350
STAGE 6	–0.007	0.609	–0.012	0.991
STAGE 7	0.683	0.511	1.337	0.181
Sex (MALE)	0.447	0.251	1.778	0.075

Table 8. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and age assessed by teeth (animals of undetermined status were included in the model as residents). Reference group — female stage 1.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	–0.920	0.279	–3.292	<0.01
Age by teeth:				
STAGE 2	1.905	0.409	4.662	<0.001
STAGE 3	1.691	0.324	5.215	<0.001
STAGE 4	0.535	0.312	1.713	0.087
STAGE 5	–0.453	0.360	–1.259	0.208
STAGE 6	–0.140	0.374	–0.375	0.708
STAGE 7	1.103	0.304	3.629	<0.001
Sex (MALE)	–0.234	0.158	–1.479	0.139

Table 9. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and membership in one of four reproductive-age categories (animals of undetermined status were excluded). Reference group — immature female underyearlings younger than 30 days.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	1.001	0.494	2.025	<0.05
Age group:				
Immature underyearlings >30 days	1.026	0.547	1.875	0.061
Mature underyearlings	–0.411	0.505	–0.813	0.416
Overwintering	0.519	0.532	0.975	0.329
Sex (MALE)	0.243	0.256	0.948	0.343

Table 10. Summary of the regression model analyzing the frequency of bank vole dispersal depending on sex and membership in one of four reproductive-age categories (animals of undetermined status were included in the model as residents). Reference group — immature female underyearlings younger than 30 days.

Term	Estimate	Std.error	z-statistic	*p*-value
(Intercept)	–0.674	0.286	–2.361	<0.05
Age group:				
Immature underyearlings >30 days	1.460	0.312	4.672	<0.001
Mature underyearlings	–0.099	0.299	–0.330	0.741
Overwintering	0.962	0.310	3.101	<0.01
Sex (MALE)	–0.393	0.158	–2.483	<0.05

garding the age of dispersers, direct comparison with literature data is impossible due to methodological differences in age determination. However, most studies report a higher proportion of «young» dispersers (Gliwicz, 1988, 1989; Dickman & Doncaster, 1989; Rajska-Jurgiel, 2000), though exceptions exist (Ylönen *et al.*, 1988; Kozakiewicz *et al.*, 2007).

In terms of probability, immature underyearlings of both sexes were equally likely to disperse — 0.5–0.8 by various estimates (Fig. 3). In reality, the probability might have been even higher. Since six weeks elapsed between the first marking session and the end of trapping, some immature underyearlings may have reached maturity after dispersal. Therefore, the number and

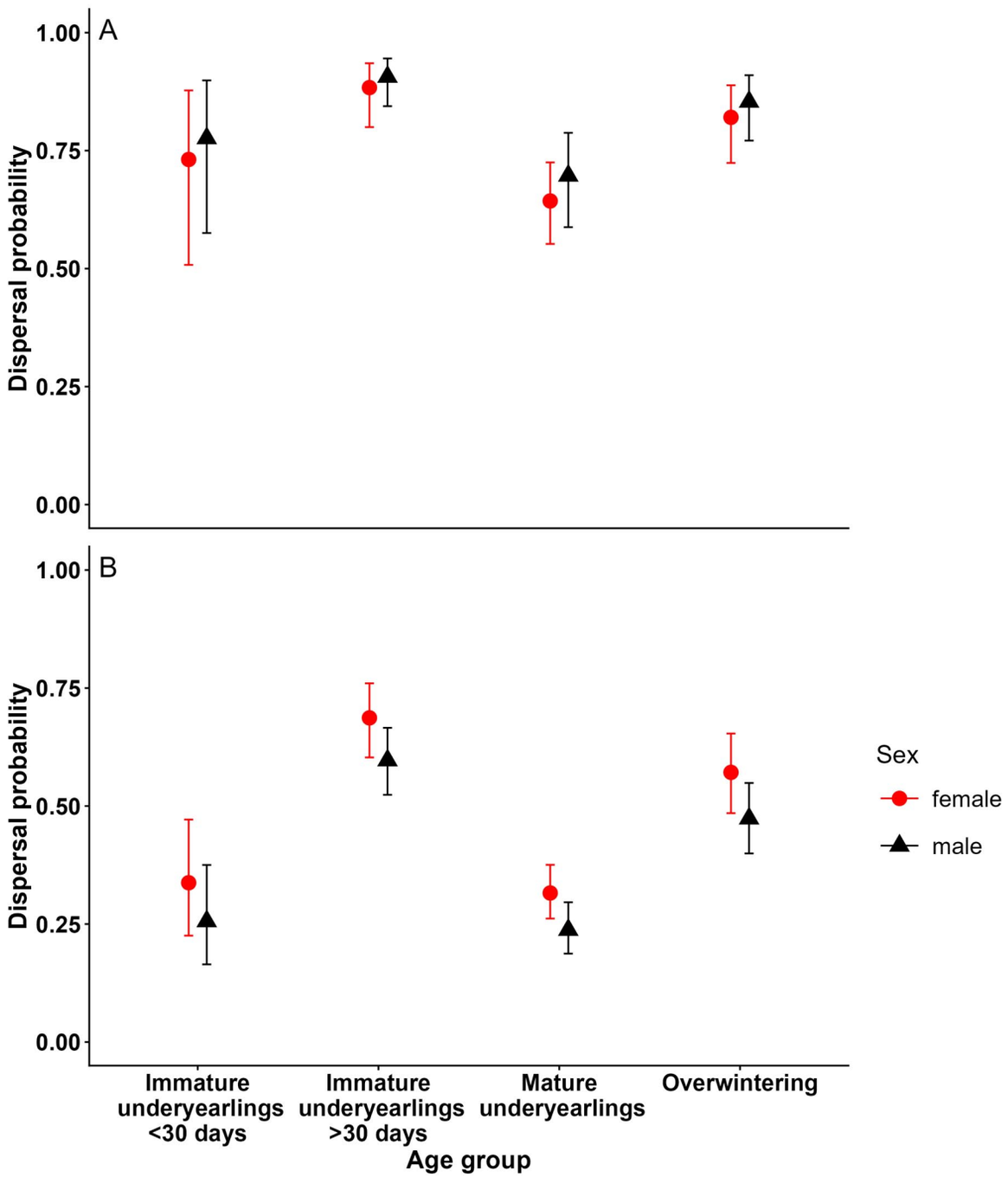


Fig. 7. Probability of dispersal for bank voles of four reproductive-age categories (whiskers — 95% CI). A — individuals of undetermined status were excluded from the analysis; B — individuals included in the analysis.

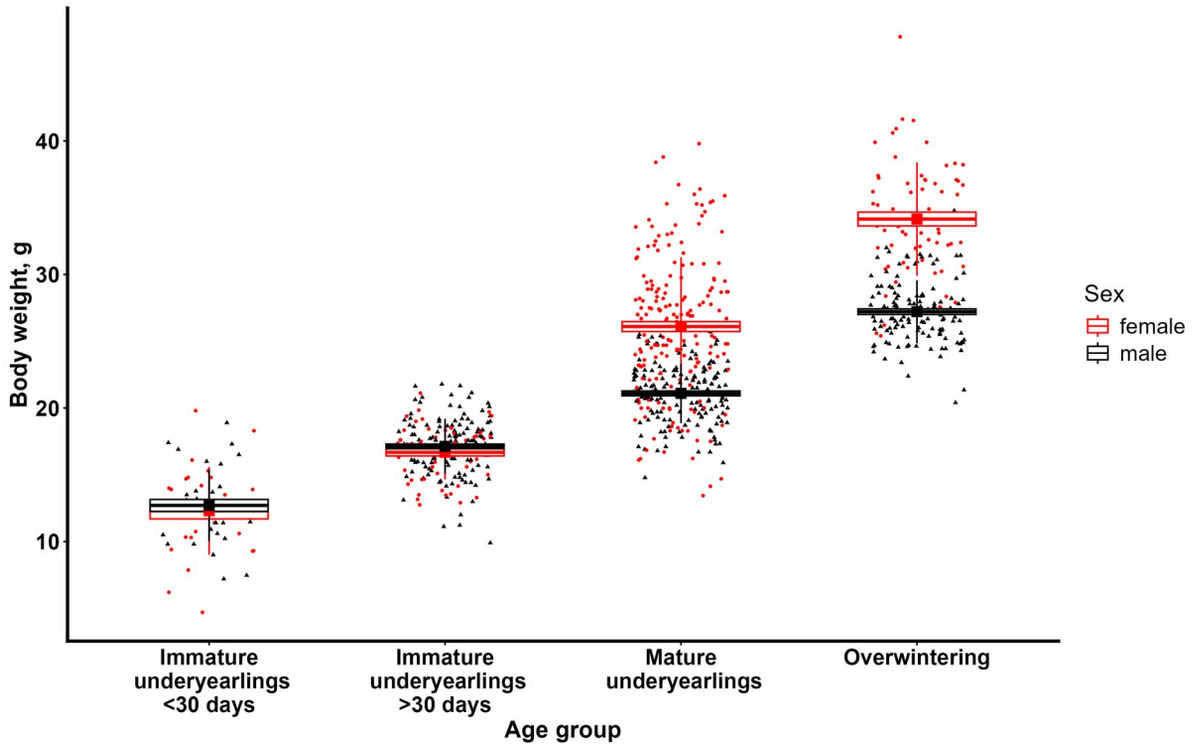


Fig. 8. Distribution of male and female bank voles by weight across four reproductive-age groups (mean, SE, SD).

proportion of mature underyearlings among dispersers are likely overestimated (Fig. 4). This is especially true for females, as they tend to start breeding at a younger age (1–1.5 months) compared to males. Among males aged 30–45 days (determined by teeth, *n*=96), only 10% were sexually mature, while among females of the same age (*n*=77), 26% were mature.

Overwintered voles of both sexes constituted the next largest group among dispersers (Table 2). Their dispersal probability was comparable to that of immature underyearlings (Fig. 3A). However, overwintered females may be more prone to dispersal than males (Fig. 3B). This aligns with the existing notion that female voles often leave their home range after weaning their offspring (Gliwicz, 1989; Cockburn, 1992; Rajska-Jurgiel, 2000). The lowest dispersal tendency was observed in mature underyearlings of both sexes — 0.2–0.6 by various estimates (Fig. 3). Apparently, a significant portion of maturing underyearlings begin breeding close to their birthplace.

Interestingly, among 32 mature female dispersers captured 22–28 days after marking began, five were lactating (three overwintered, two mature underyearlings), indicating they had conceived before dispersal. Similar cases have been previously reported in small mammals (Rajska-Jurgiel, 2000; Kozakiewicz *et al.*, 2007). These findings reflect both natal dispersal (immature individuals and partially mature underyearlings that matured after long-distance movements) and breeding dispersal (overwintered individuals and partially mature underyearlings that bred before long-distance movements) (sensu Greenwood, 1980).

This study demonstrates that the choice of age classification significantly impacts conclusions about bank vole dispersal. The objective was to determine the maximum number of biologically meaningful age categories that differ in their dispersal probability. Using only two categories (immature/mature) leads to the incorrect conclusion that mature individuals disperse less frequently than immature ones (Fig. 5). This occurred because the "overwintered" and "mature underyearlings" groups, which differ greatly in dispersal probability (Fig. 3), were combined. Analysis based on three reproductive-age categories yields more accurate results. Dividing into seven age groups seems excessive — these groups cluster into immature/mature underyearlings and overwintered individuals in terms of dispersal probability (Fig. 6). The only new insight from this finer division was the low dispersal probability in the youngest voles (Group 1: 25–30 days old, shortly after leaving the nest), which is important for demographic descriptions. However, excessive subdivision reduces statistical power and prevented testing factor interactions, which would have been valuable given prior knowledge. The four-age-group model appears optimal (immature underyearlings <30 days old, immature underyearlings >30 days, mature underyearlings, overwintered). It effectively distinguishes adja-

cent groups by their unique combination of ontogenetic stage and dispersal probability, while ensuring that each group is internally consistent, with no significant subdivisions in dispersal behaviour (Fig. 7).

Standard CMR protocols in small mammal research provide only elementary descriptors of individuals, namely sex, maturity, and body weight. However, precise categorisation of bank voles into the aforementioned four groups based solely on these traits is unfeasible (Fig. 8). Distinguishing these categories requires assessing tooth root formation stages.

Thus, it was found that in the studied bank vole population, most long-distance movements represent natal dispersal, with the highest propensity seen in immature underyearlings (35–55 days old) of both sexes. Breeding dispersal, primarily involving overwintered individuals of both sexes (with females possibly more active), was the second most common. The lowest dispersal probability was observed in mature underyearlings, many of which likely start breeding near their birthplace.

Different age-classification approaches demonstrated that four reproductive-age categories are optimal for analysing bank vole dispersal. Although small mammal dispersal has been studied for decades, a key question remains: Are dispersal movements spanning tens of metres and kilometres extreme values of the same process, or are they functionally distinct? Answering this requires further data on the demographic structure of dispersers.

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