Temporal scale influences demographic inference in a southern-range population of the bank vole *Clethrionomys glareolus*

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Abstract:
The bank vole *Clethrionomys glareolus* is a widespread rodent in European woodlands, but detailed demographic information from southern Europe is limited. We investigated its demography in a lowland woodland in the Po Plain (NW Italy) using CMR surveys conducted in 1994 and 2002. We estimated population abundance using closed-population models and analysed survival (Φ) and recapture probability (p) using Cormack–Jolly–Seber models at monthly and seasonal temporal scales.
Both study periods showed pronounced seasonal fluctuations in abundance, with peaks occurring during the reproductive season. Despite the 8 year between surveys, mean abundance remained similar (40.8±6.8 and 42.8±5.3), indicating medium-term demographic stability. Nevertheless, the two study periods differed markedly in demographic structure. A male biased sex ratio was observed in 1994 (0.47; $\chi^2 = 25.85$, $p < 0.001$) and 2002 (0.73; $\chi^2 = 4.17$, $p = 0.041$), whereas monthly variation was marginal or not significant in both periods.
Monthly survival analyses strongly supported temporal variation in apparent survival, with time-dependent models receiving strong support in both periods. However, seasonal aggregation of capture histories reduced support for temporal heterogeneity Seasonal survival was Φ = 0.318 (95% CI = 0.244–0.403) in 1994–1995, whereas in 2002–2003 it was Φ = 0.457 (95% CI = 0.352–0.566) for females and Φ = 0.327 (95% CI = 0.235–0.433) for males. Abundance and survival were not significantly related, suggesting that recruitment and/or dispersal probably contributed more than survival to population fluctuations.
The population trend we observed closely resemble those reported for non-cyclic bank vole populations in temperate European forests, indicating that our populations do not exhibit distinctive demographic patterns and retain the seasonal dynamics observed in Central Europe. The study highlights how the temporal resolution adopted in CMR analyses can substantially influence demographic inference, emphasizing the importance of evaluating survival processes at multiple temporal scales.

Keywords: apparent survival, capture–mark–recapture, temporal scale, Po Plain, population dynamic.

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ABSTRACT

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KEY WORDS: apparent survival; capture–mark–recapture; temporal scale, population dynamics; Po Plain.

INTRODUCTION

The bank vole *Clethrionomys glareolus* is one of the most widespread and abundant small mammals of European lowland woodlands and, together with mice of the genus *Apodemus*, it represents a dominant component of temperate forest rodent communities (Petrusewicz 1983; Pucek et al. 1993). The bank vole habitat ranges from boreal coniferous forests to mixed and deciduous broadleaf forests, showing a preference for structurally complex habitats characterized by dense ground vegetation, abundant litter and a well-developed shrub layer (Pucek et al 1993; Mazurkiewicz 1994). Owing to its abundance, broad distribution and relatively short generation time, the bank vole has been regarded as a model for studies of population ecology and demographic processes in small mammals (Petrusewicz 1983; Alibhai and Gipps 1985; Gorska et al 2025).

Bank vole populations are characterized by marked seasonal variation. Population growth is mainly driven by reproduction during spring and summer, whereas overwinter survival, dispersal and recruitment determine population persistence between years (Gliwicz 1988, 1993; Crespin et al. 2002). Consequently, demographic parameters such as abundance, survival and movement are strongly influenced by seasonal environmental conditions and resource availability (Flowerdew et al 2017). Because survival represents one of the key demographic processes affecting population dynamics, considerable effort has been devoted to its estimation through capture–mark–recapture studies. These investigations have shown that apparent survival may vary among seasons, sexes and habitats, reflecting the combined effects of mortality, dispersal and reproductive activity (Gliwicz 1993; Crespin et al. 2002).

The population ecology of the bank vole has been intensively investigated in northern and central Europe, where it has become one of the best-studied model species in small mammal population ecology (Gorska et al 2025). In boreal and subarctic regions, populations often exhibit pronounced multiannual cycles, with fluctuations recurring every three to five years and involving large changes in abundance (Henttonen et al. 1985; Hanski et al. 1993; Korpimäki et al. 2005). These cycles have been associated with complex interactions among food availability, predator pressure, climatic conditions and social processes (Hansson 1987; Marcström et al 1990; Hanski and Korpimäki 1995; Ivanter 2025). In contrast, populations inhabiting temperate deciduous forests generally show weaker multiannual fluctuations and are characterized by marked seasonal variation, with densities increasing during the reproductive season and declining during winter (Alibhai and Gipps 1985; Pucek et al. 1993). Mast seeding events, weather conditions, predation and dispersal have all been proposed as important drivers of these dynamics (Jensen 1982; Hansson 1998).

Despite the extensive literature available for northern and central Europe, information from southern populations remains comparatively scarce; to the best of our knowledge, for Italy there are only two

long-term studies available on this species, both relating to a mountainous area in the central Apennines (Amori et al 2000; Amori et al 2015). The bank vole is widespread throughout continental Italy and occurs in a variety of woodland habitats, including isolated populations inhabiting the residual forests of the Po Plain (Prigioni et al. 2001; Amori et al. 2010). However, most Italian studies have focused on distribution, habitat use and community composition, whereas detailed demographic investigations based on capture–mark–recapture methods are still relatively uncommon (Amori et al 2015). Consequently, the extent to which demographic patterns described in northern European populations also characterize populations living near the southern boundary of the species' range remains poorly understood. The lowland woodlands of the Po Plain provide an interesting system in which to address this issue. These forests are remnants of the extensive woodland cover that historically occupied large portions of northern Italy and now persist as highly fragmented habitat patches embedded in an agricultural landscape. Their location near the southern limit of the species' European range offers an opportunity to examine demographic processes under environmental conditions that differ from those typical of the better-studied forests of central and northern Europe.

The present study is based on two intensive capture–mark–recapture surveys conducted in a lowland woodland of the north-western Po Plain during 1994–1995 and 2002–2003. To our knowledge, this study provides a detailed year-long demographic assessment of *C. glareolus* in a lowland forest of northern Italy and allows direct comparison of population parameters between two sampling periods separated by almost a decade. Using capture–recapture models, we estimated abundance, sex ratio, apparent survival and recapture probability and examined demographic variation at both monthly and seasonal temporal scales.

Our objectives were threefold: (i) to provide a detailed demographic description of a bank vole population inhabiting a remnant lowland woodland of the Po Plain; (ii) to compare demographic patterns between two study periods separated by almost a decade; and (iii) to evaluate how temporal resolution (monthly versus seasonal encounter histories) influences demographic inference from capture–mark–recapture analyses.

STUDY AREA AND METHODS

Study area – The study area is located at the Site of Community Interest 'Riserva di Monticchie' (SCI IT 20900; 45°08'40.60'' 9°39'26.59''). The area covers 250 ha on the left bank of the River Po, of which 24.5 ha are hygrophilous forest and 225.5 ha are agricultural land. Residual forested areas

consist of alluvial woods with alder *Alnus glutinosa*, white willow *Salix alba* and common ash *Fraxinus excelsior* and deciduous riparian woods with oak *Quercus robur* and elms *Ulmus* spp. The Nature Reserve falls within the temperate-continental climatic regime of the central Po Plain, characterized by hot, humid summers and cold, fog-prone winters. Mean annual temperatures are around 14°C, with winter minima near 0°C and summer maxima frequently exceeding 30°C. Precipitation is moderate and distributed throughout the year, showing the typical autumn peak and summer minimum of the region, with monthly values generally ranging between 50 and 110 mm. Winds are usually weak (≈9 km/h) and predominantly from the eastern sector, contributing to frequent thermal inversions and high winter humidity. These climatic conditions shape the hydrological dynamics of the hygrophilous forest patches.

Field sampling – Bank vole population was monitored using capture–mark–recapture (CMR) methods during 1994–1995 and 2002–2003. Two trapping grids were established within the woodland and located in areas characterized by comparable vegetation structure, litter depth and soil conditions. The same trapping grids were sampled during both study periods. Each grid consisted of an 8 × 8 array of trapping stations spaced 12 m apart, following recommendations for woodland rodents (Gurnell and Flowerdew 1990). Sherman live traps baited with sunflower seeds were checked twice a day. When daily captures exceeded 50% of available traps, a second trap was added to each capture point to reduce the risk of trap saturation. Sampling sessions lasted seven consecutive days and were conducted simultaneously in both grids at monthly intervals; demographic closure during each session was considered a reasonable assumption because births, deaths and permanent movements were expected to be negligible over such a short interval (Otis et al. 1978). Captured individuals were permanently marked by toe-clipping (Twigg 1978). For each animal we recorded sex, body mass, age class and reproductive condition according to Gurnell and Flowerdew (1990). Adults were identified by reproductive conditions during the breeding season and by a body mass exceeding 17.5 g during winter.

Population abundance estimation - Population abundance was estimated separately for each monthly trapping session using closed-population capture–recapture models implemented in Program CAPTURE (Otis et al. 1978) through the RMark package (Laake 2013). Candidate models accounted for variation in capture probability due to time (Mt), behavioural response (Mb), individual heterogeneity (Mh) or their combinations. The most appropriate model was selected automatically by CAPTURE and the corresponding population estimate and standard error were retained for subsequent analyses. In addition to capture–recapture estimates, the Minimum Number Alive (MNA) was calculated for each trapping session and used as a descriptive index of population abundance to facilitate comparisons of temporal trends.

Survival analyses - Only adult individuals were included in survival analyses. Apparent survival (Φ) and recapture probability (p) were estimated using Cormack–Jolly–Seber (CJS) models implemented in RMark (Laake 2013). Preliminary model selection including trapping grid as an explanatory factor indicated only negligible improvements in model fit (ΔAICc < 2), whereas temporal variation represented the dominant source of heterogeneity. Capture histories from the two trapping grids were therefore pooled within each study period to increase sample size and improve parameter precision. Survival analyses were conducted at two temporal resolutions, using both monthly and seasonal encounter histories.

Monthly and seasonal analyses were carried out separately. Monthly encounter histories were constructed using successive trapping sessions as capture occasions. Candidate models included constant, sex-dependent and time-dependent structures for apparent survival, while recapture probability was modelled as either constant or time-dependent. Models were ranked according to Akaike's Information Criterion corrected for small sample size (AICc). Monthly analyses were primarily used to describe short-term demographic variation and to identify potential temporal heterogeneity in survival and recapture probabilities. To investigate broader demographic patterns and reduce short-term variability, monthly encounter histories were subsequently aggregated into seasonal capture histories; seasonal aggregation reduces stochastic short-term variation while retaining biologically meaningful phases of the annual cycle (winter, breeding season and post-reproductive period).

For the 1994–1995 study period, five seasonal occasions were defined (autumn 1994, winter 1995, spring 1995, summer 1995 and autumn 1995). For the 2002–2003 study period, four seasonal occasions were defined. Candidate CJS models included constant survival, sex-dependent survival and seasonal variation in survival. Model selection was based on AICc and Akaike weights. Seasonal analyses were performed to reduce short-term stochastic variation and evaluate broader demographic patterns associated with biologically meaningful periods of the annual cycle.

Statistical analyses - Relationships between abundance and apparent survival were evaluated using Spearman rank correlation. All analyses were conducted in R using the RMark package (Laake 2013).

RESULTS

Population abundance and seasonal dynamics - Estimated abundance of the bank vole varied throughout the study periods but despite differences in the shape of the annual trend, population size

showed the typical seasonal pattern of temperate woodland rodents. Population size increased during spring and summer, reached maximum values in summer/autumn and subsequently declined during winter (Figure 1). Despite the eight-year interval between surveys, mean estimated abundance of our populations was remarkably comparable, averaging 40.8±6.8 individuals in 1994 and 42.8±5.3 in 2002 (Table I). A comparable result was obtained using the minimum number alive (MNA), which averaged 25.8±4.7 and 25.9±3.2 individuals respectively (Table I). Both MNA direct counts and capture–recapture estimates therefore indicated very similar overall population sizes during the two study periods.

Although mean abundance was nearly identical between study periods, the temporal trajectories differed, with a wider observed range and a more pronounced bimodal pattern in 1994 than in 2002. The 95% confidence intervals around abundance estimates overlapped substantially, including those around the respective peak estimates (1994: 66.1–129.9; 2002: 54.1–99.9), indicating that these differences should be interpreted as differences in temporal pattern rather than as evidence of consistently higher abundance in one period. The highest abundance estimates recorded during the study were 98 and 77 individuals in autumn 1994 and summer 2002, respectively.

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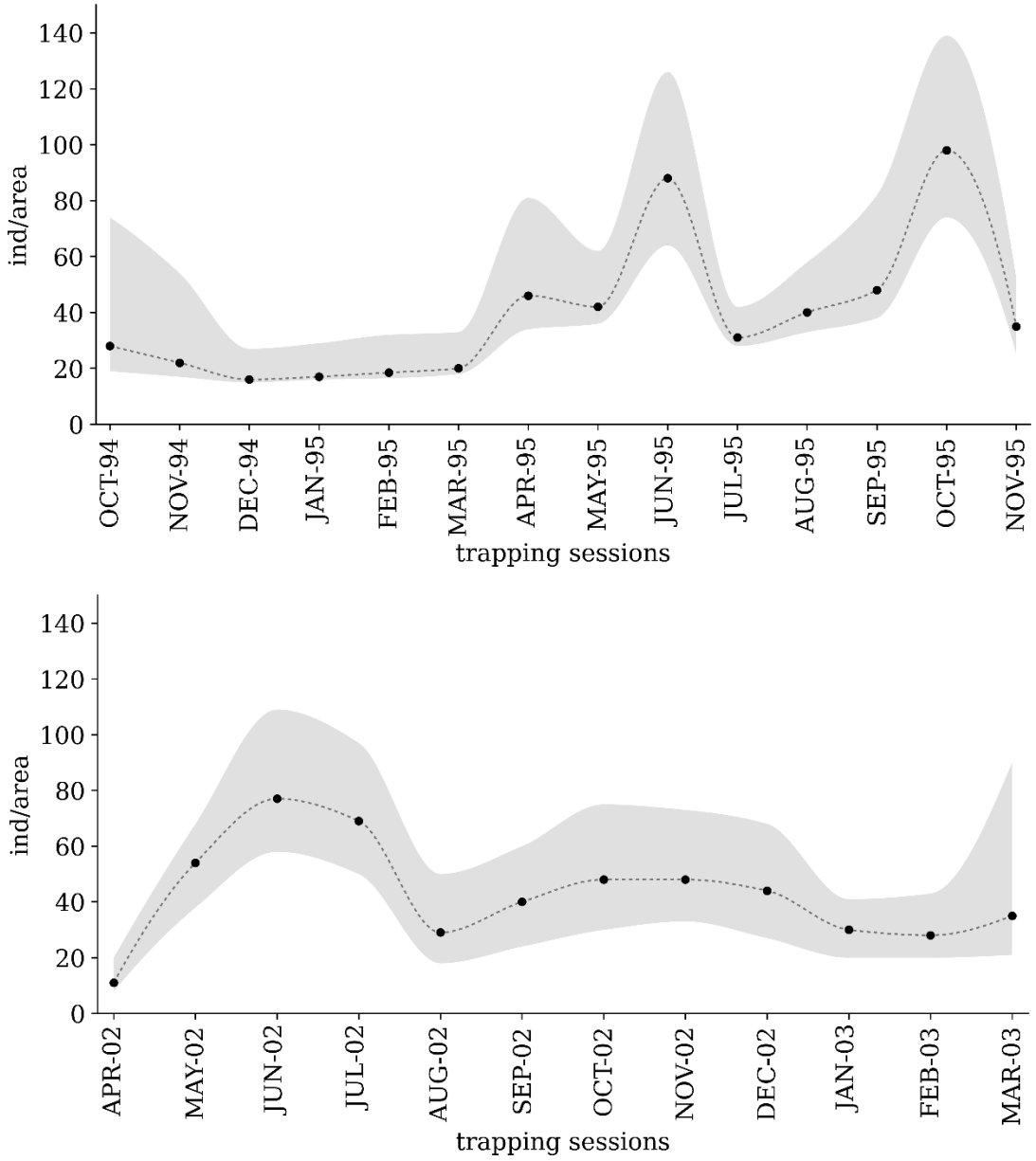

Figure 1. Abundance trend of the bank vole in 1994 and 2002. Dot represents abundance as estimated by Capture 2.0 on the best selected probabilistic model. Grey areas are 95% confidence intervals.

Table I. Seasonal average abundance (N±SE) of bank voles in the two trapping sessions. N is the abundance as estimated by Capture 2.0 on the basis of the best fitting probabilistic model. MNA is the Minimum Number Alive

	1994			2002		
season	**N**	**SE**	**MNA**	**N**	**SE**	**MNA**
Autumn	45.8	10.3	24.3	45.3	9.9	25.3
Spring	44.0	8.0	27.0	32.5	6.7	26.5
Summer	51.8	8.2	32.8	58.3	9.6	35.3
Winter	17.7	3.4	12.7	34.3	9.5	19.0

Seasonal mean abundance was remarkably comparable between years during spring, summer and autumn while winter abundance differed markedly (Table I). Mean winter abundance was 17.7 (±3.4) in 1994 but nearly doubled in 2002 with 34.3 (±9.5) thus indicating substantially greater overwinter population size during the latter period.

Within a context of broadly similar demographic characteristics, population trends in the two sampling periods showed qualitative differences. In 1994 the population trend showed a bimodal pattern, with two distinct peaks in June (N = 88±14.6) and a second higher peak in October (N = 98±16.3). Conversely population trend reached its maximum abundance in June 2002 (N = 77±11.7) and subsequently fluctuated around intermediate values without a pronounced autumn increase. Thus, while population size during the reproductive season was broadly consistent between years, overwinter abundance and seasonal population trends diverged.

To assess whether variation in population size was associated with changes in apparent survival, we examined the relationship between abundance and monthly survival estimates. No significant relationship resulted in either study period: in 1994, apparent survival tended to decrease with increasing abundance ($r_s = -0.37$, $p = 0.19$). Conversely, in 2002–2003 the relationship was positive but again not significant ($r_s = 0.61$, $p = 0.17$). No evidence of a monotonic relationship between abundance and apparent survival was detected in either study period, although the limited sample size reduced statistical power. It is interesting to observe that in 1994 the population was demographically open in December and October, meaning that birth/death rates and immigration/emigration had a significant effect on the abundance estimate during periods when the reproductive activity of the bank vole is low or absent. Conversely, in 2002 the closure test was significant, as expected, mainly in spring and summer, when the species' reproductive activity is at its peak.

Sex ratio - The sex composition of the population differed substantially between years. In 1994 the population was strongly male-biased, with a mean female to male ratio of 0.47 and a significant deviation from parity ($\chi^2 = 25.85$, $p < 0.001$). The mean sex ratio in 2002 was 0.73, indicating a population more close to parity; however also in this session we observed significant differences in female to male frequency ($\chi^2 = 4.17$, $p = 0.041$). Overall, sex composition differed significantly between the two study periods ($\chi^2 = 7.2$ $p = 0.007$), while we observed borderline evidence of sex variation among months ($\chi^2 = 22.4$, df=13, $p = 0.050$) and no significant monthly differences in 2002 ($\chi^2 = 10.7$, df=11, $p = 0.47$). Males predominance was a recurrent feature of the 1994 population while a weaker male bias in 2002 suggests a substantial change in demographic structure despite the similarity in overall abundance ((Figure 2).

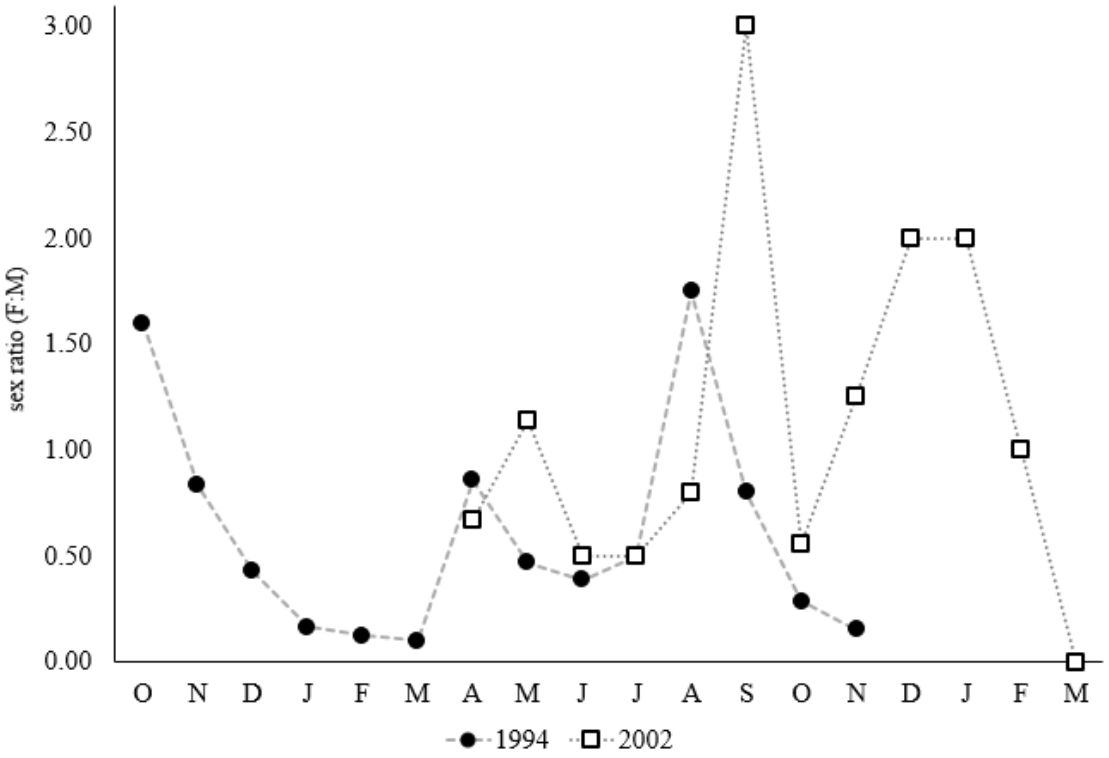

Figure 2. Variation of the sex-ratio (female:male) during the two trapping period

Monthly and seasonal variation in apparent survival –

Candidate models included constant survival and recapture [Φ(.)p(.)], sex-dependent survival [Φ(sex)p(.)], time-dependent survival [Φ(time)p(.)] and fully time-varying models [Φ(time)p(time)]. In 1994, model selection strongly supported temporal variation. The fully time-dependent model Φ(time)p(time) was best (AICc = 574.80, weight = 0.999), outperforming models with constant *p* (ΔAICc = 14.67), constant Φ (ΔAICc = 55.95), or sex effects (ΔAICc = 57.79). Because temporal variation was represented by multiple occasion-specific parameters, individual coefficient significance was not used to assess the overall temporal effect. Several coefficients approached parameter boundaries and show large SEs; therefore, temporal variation was evaluated through comparison of competing models using AICc and Akaike weights. Monthly survival varied widely, from 0.126 (May–June 1995; 95% CI = 0.056–0.261) to boundary estimates approaching 1.0, often with broad CIs. Another low estimate occurred in October–November 1995 (Φ = 0.187, 95% CI = 0.094–0.337). These results indicate strong temporal heterogeneity in both survival and recapture probability.

Table II. Model selection results for seasonal Cormack–Jolly–Seber analyses of apparent survival (Φ) and recapture probability (p) in bank voles. Models are ranked according to AICc. ΔAICc indicates the difference from the best-supported model within each study period. Abbreviations: Φ = apparent survival; p = recapture probability; npar = number of estimable parameters; AICc = Akaike Information Criterion corrected for small sample size.

Year	Model	npar	AICc	ΔAICc
1994	Φ(.) p(.)	2	266.33	0.00
	Φ(sex) p(.)	3	267.72	1.39
	Φ(time) p(.)	5	272.22	5.88
	Φ(sex + time) p(.)	6	273.44	7.11
2002	Φ(sex) p(.)	3	280.49	0.00
	Φ(time) p(.)	5	281.45	0.96
	Φ(.) p(.)	2	281.75	1.27

In 2002, temporal variation in survival was again supported. The best model was Φ(time)p(.) (AICc = 617.89, weight = 0.986), while constant survival and sex effect models performed worse (ΔAICc > 9.8). Allowing p to vary did not improve fit (Φ(time)p(time), ΔAICc = 12.56). Monthly survival was less variable than in 1994–1995, mostly between 0.44 and 0.85, with the highest value in November–December 2002 (Φ = 0.851, 95% CI = 0.497–0.971). Boundary estimates occurred only at the first and last intervals.

Both study periods showed strong temporal variation and little evidence for sex specific survival, but fluctuations were larger in 1994–1995, when both Φ and p varied substantially. In 2002–2003, survival was more stable and p was approximately constant.

To reduce short term fluctuations, capture histories were aggregated into seasonal encounter histories. For 1994–1995, five seasons were defined (autumn 1994, winter 1995, spring 1995, summer 1995, autumn 1995). For 2002–2003, four seasons were used (spring 2002, summer 2002, autumn 2002, winter 2003). CJS models included Φ(.), Φ(sex), Φ(time) and Φ(sex + time), with constant p.

Seasonal analyses contrasted sharply with monthly results. In 1994–1995, the constant survival model was best (AICc = 266.33; Table II). Models with sex (ΔAICc = 1.39), time (ΔAICc = 5.88), or sex + time (ΔAICc = 7.11) had less support. Estimated seasonal survival was Φ = 0.318 ± 0.041 SE (95% CI = 0.244–0.403), with high recapture probability (p = 0.847 ± 0.096 SE). In 2002–2003, model selection was less decisive: Φ(sex) had the lowest AICc (280.49), but Φ(time) (ΔAICc = 0.96) and Φ(.) (ΔAICc = 1.27) were also supported. Under Φ(sex), survival was Φ = 0.457 ± 0.055 SE (95%

CI = 0.352–0.566) for females and Φ = 0.327 ± 0.051 SE (95% CI = 0.235–0.433) for males. Recapture probability remained high (p = 0.862 ± 0.072 SE).

Table III. Seasonal apparent survival estimates (Φ) derived from the best-supported Cormack–Jolly–Seber models for bank vole populations monitored during 1994–1995 and 2002–2003. For 1994–1995, the best-supported model assumed constant survival across sexes and seasons, whereas for 2002–2003 the model with sex-specific survival received the strongest support. Estimates are reported with standard errors (SE) and 95% confidence intervals (CI)

Year	Sex	Φ	SE	95% CI
1994–95	pooled	0.318	0.041	0.244–0.403
2002–03	female	0.457	0.055	0.352–0.566
2002–03	male	0.327	0.051	0.235–0.433

Seasonal estimates converged across years: male survival in 2002–2003 (Φ = 0.327) closely matched the 1994–1995 estimate (Φ = 0.318) (Table III). Although females showed higher survival, model uncertainty suggests caution in interpretation.

Overall, seasonal analyses revealed much more stable apparent survival and greatly reduced support for temporal effects compared to monthly models.

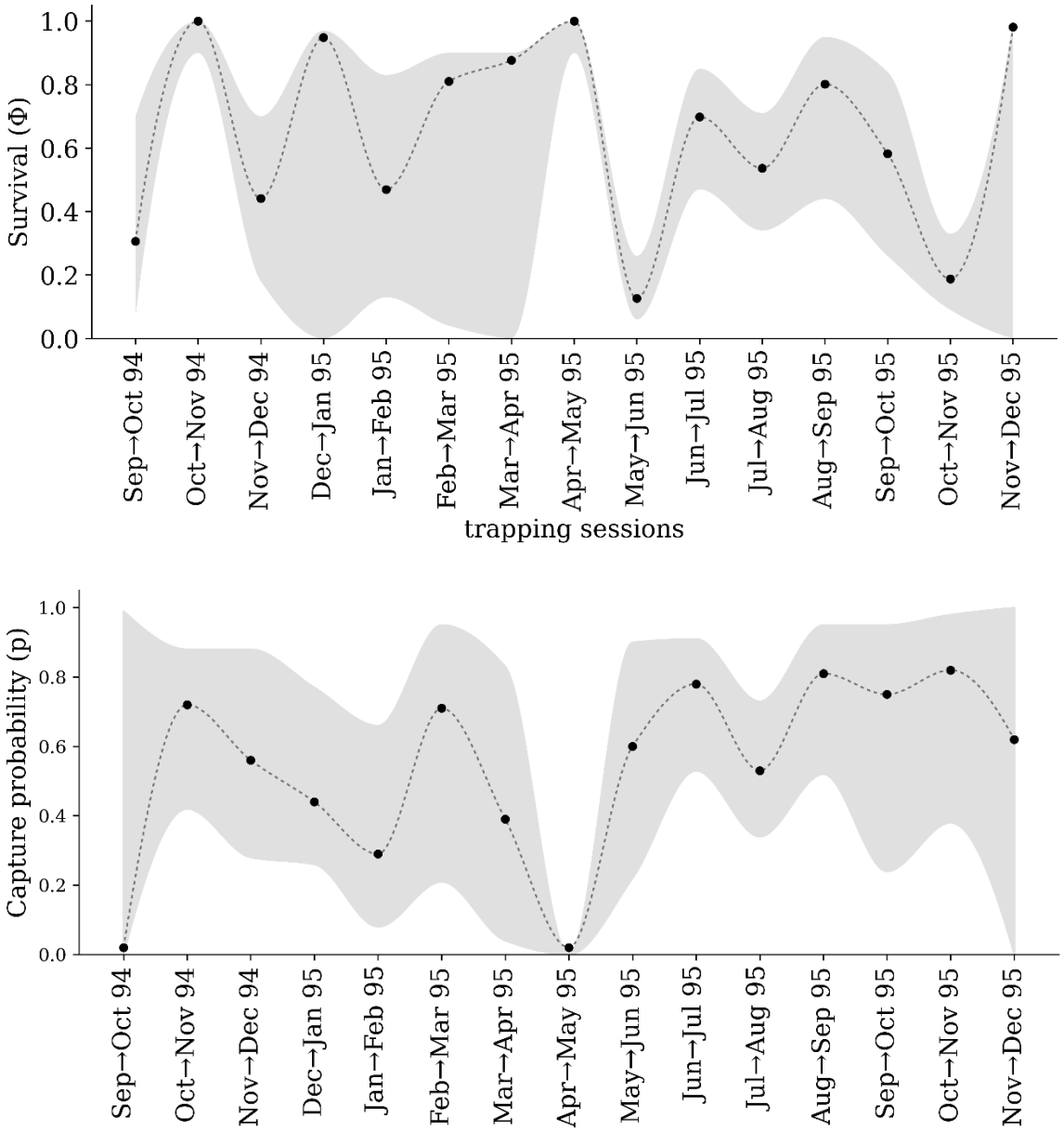

Figure 3 - Monthly estimates of apparent survival (Φ) and recapture probability (p) obtained from the best-supported Cormack–Jolly–Seber model for the 1994–1995 study period. Black circles represent point estimates and grey shaded areas indicate 95% confidence intervals.

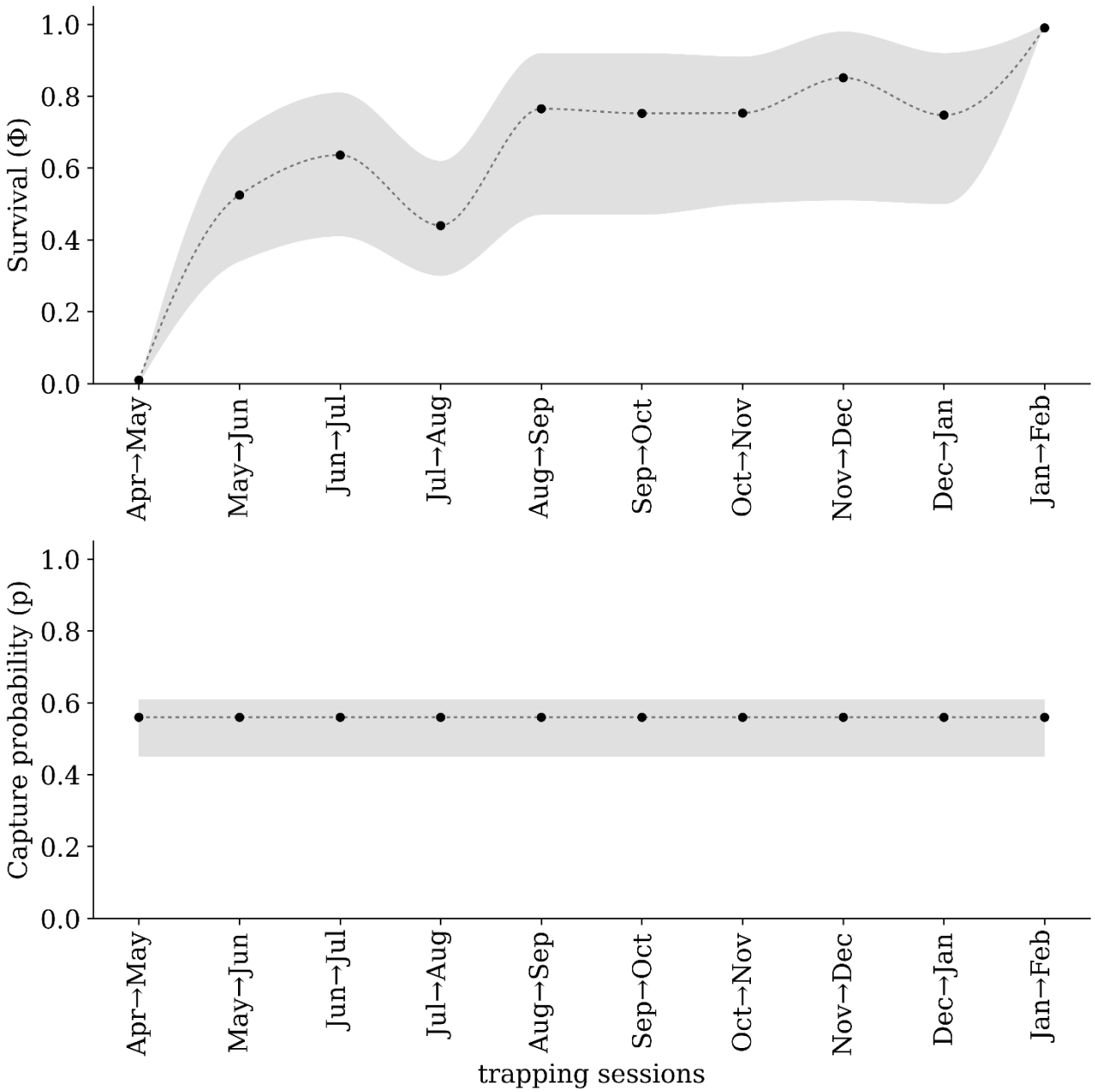

Figure 4 - Monthly estimates of apparent survival (Φ) and recapture probability (p) obtained from the best-supported Cormack–Jolly–Seber model for the 2002–2003 study period. Black circles represent point estimates and grey shaded areas indicate 95% confidence intervals. Apparent survival varied among monthly intervals whereas recapture probability remained constant through time.

DISCUSSION

Our bank vole population exhibited demographic patterns consistent with those reported for temperate European deciduous forests, while also providing insight into demographic variation within a lowland population located near the southern boundary of the species' European distribution.

The two study periods showed remarkably comparable overall abundance levels, whereas differences emerged in sex ratio, seasonal population trends and survival patterns. Furthermore, the comparison

between monthly and seasonal capture–recapture analyses demonstrated that the temporal scale adopted for demographic analyses strongly influences the interpretation of survival variability.

Population abundance and seasonal dynamics - Both study periods were characterized by pronounced seasonal fluctuations in abundance, a pattern typical of bank vole populations inhabiting temperate deciduous forests (Hansson et al 2000; Suchomel 2006). The average annual abundances, calculated on a monthly basis and based on probabilistic and MNA estimates, were very similar (Table I). These results suggest a remarkable long-term demographic stability of population size despite the eight-year interval separating the surveys. In 1994, the population showed two distinct peaks in abundance, in late spring and early autumn, whereas in 2002 abundance peaked in early summer and subsequently remained at intermediate levels. Previous CMR studies have investigated bank vole demography in central Italy (Amori et al. 2000, 2015; Casula et al. 2019), but these studies differed from the present work in elevation, habitat and temporal resolution. Population density and abundance patterns also differed from those observed in our study, suggesting that local environmental conditions may influence population dynamics. In the Majella population, the overall mean density was 8.59 ± 11.82 ind/ha, with values ranging from 0.08 in autumn to 49.26 ind/ha in spring. These values are generally lower than the abundance levels observed in our study. Notably, the pronounced autumn increase observed in our population was not evident in the Majella population where autumn density were lower than in spring; however, this comparison should be interpreted cautiously because trapping was restricted to spring–autumn periods and the seasonal sampling schedules differed between studies. Seasonal patterns have been reported throughout temperate Europe, where bank vole populations typically decline during winter and increase progressively during spring and summer as reproduction proceeds (Alibhai and Gipps 1985; Mazurkiewicz 1994). In the Białowieża Forest, for example, rodent abundance consistently reached annual maxima in autumn, with seasonal recruitment representing the principal driver of population growth (Pucek et al. 1993). Our results are fully consistent with this general demographic pattern.

Although average abundance was nearly identical, population trajectories differed between the two surveys. The 1994 population exhibited stronger fluctuations and reached a substantially higher peak abundance (98 ind/area) than the 2002 population, which showed a smoother seasonal trajectory and lower peak values.

Such differences are expected because bank vole populations respond rapidly to local environmental conditions, food availability, recruitment success and dispersal processes (Mazurkiewicz and Rajska-Jurgiel 1998; Crespin et al. 2002; Balčiauskas et al 2024). The similarity in average abundance despite

differences in seasonal trajectories suggests that comparable annual population sizes may result from different combinations of demographic processes.

In Northern Europe, bank vole populations commonly exhibit cyclic dynamics of 3-4 year periods and amplitudes exceeding one order of magnitude (Stenseth 1999; Sundell et al 2004; Korpimaki et al 2005). In contrast, populations from temperate Europe generally display annual fluctuations driven primarily by seasonal reproduction, overwinter survival and local resources availability (Alibhai and Gipps 1985; Gliwicz 1988, de la Huerta-Schliemann et al 2025).

Our data does not allow evaluation of long-term cyclicity because only two study periods were available. Nevertheless, the seasonal trajectories observed in both surveys, together with the remarkably consistent mean annual abundance values, are consistent with demographic patterns commonly reported for non-cyclic temperate populations.

The abundance levels observed in our population are also broadly comparable with those reported for several central European woodland populations. Alibhai and Gipps (1985), working in deciduous woodlands of southern England, described populations typically fluctuating between a few tens and approximately one hundred individuals, with annual peaks occurring in late summer or autumn. Similarly, studies from Poland reported strong seasonal changes but relatively stable average densities across years in favourable woodland habitats (Pucek et al. 1993; Mazurkiewicz 1994). The close correspondence between these studies and our results suggests that bank vole populations inhabiting suitable lowland forests of northern Italy may maintain demographic characteristics broadly comparable to those observed elsewhere in temperate Europe, despite their location near the southern boundary of the species' distribution (Torre and Arrizabalaga 2008; de la Huerta-Schliemann et al. 2025).

Similarities and differences between study periods - The two study periods were characterized by remarkably similar average abundance and some differences emerged in population structure and seasonal dynamics. The 1994 population exhibited stronger fluctuations, whereas the 2002 population fluctuated within a slightly narrower range and followed a smoother seasonal trajectory. Seasonal differences were particularly evident during winter, when abundance declined to approximately 17 individuals in 1994 but remained close to 35 individuals in 2002. These contrasting trajectories suggest that comparable annual population sizes can be achieved through different demographic pathways, especially during the autumnal peak and winter decline.

Overall sex ratio was significantly male biased in both study periods, with a stronger bias in 1994 than in 2002. Sex-biased demographic processes are common in woodland rodents (Lawson Handley

and Perrin 2007; Klemme et al. 2007). Rajska-Jurgiel (1992) reported sex-specific differences in mortality and dispersal in fragmented woodland habitats, while several studies have shown that males generally exhibit larger home ranges and lower site fidelity than females (Koskela et al. 1997; Bujalska and Saitoh 2000; Sipari et al. 2016). Our results are consistent with the possibility that movement and dispersal processes contributed to shaping local sex ratios and may also have contributed to the contrasting demographic trajectories observed during the two study periods; this is supported also by the lack of correlation between population abundance and survival.

The variation observed in our study is unlikely to be explained solely by sampling effects and may instead reflect differences in recruitment, dispersal behaviour or habitat use between years. The greater mobility of males, particularly before and during the reproductive season, may have contributed to the male-biased sex ratio observed in 1994. This interpretation is consistent with studies showing that dispersal processes can substantially alter local population structure without necessarily affecting overall abundance (Gliwicz 1988; Rajska-Jurgiel 1992). Furthermore, the absence of strong sex effects in monthly survival models and the limited support for sex-dependent survival in seasonal analyses suggest that differential mortality alone is unlikely to explain the marked male bias observed during that year.

Collectively, the comparison between the two study periods highlights an important feature of bank vole demography. Despite nearly identical average abundance, the two study periods differed substantially in sex ratio, winter abundance and seasonal population trajectories. Population size therefore appears to be a relatively stable property of the system, whereas the demographic processes underlying that abundance may vary considerably between years. Our population was consequently stable in overall abundance while remaining flexible in its internal demographic structure.

Survival patterns and temporal scale - An interesting result emerging from the capture–mark–recapture analyses concern the influence of temporal scale on the interpretation of apparent survival (Figure 3-4). Monthly analyses strongly support temporal variation in survival during both study periods. In 1994, the model Φ(time)p(time) received overwhelming support, outperforming the second-ranked model by more than 14 AICc units. Similarly, in 2002 the model Φ(time)p(.) was clearly favoured, whereas models assuming constant survival performed substantially worse. At face value, these results suggest marked temporal heterogeneity in apparent survival. This interpretation is reinforced by the wide range of monthly survival estimates (Table II). In 1994, apparent survival varied from 0.126 (May–June) to boundary estimates approaching 1.0 in several intervals, whereas in 2002 estimates ranged from approximately 0.44 to 0.85. At first sight, these results could be

interpreted as evidence of dramatic fluctuations in mortality risk. However, several monthly estimates were associated with wide confidence intervals and boundary values, indicating limited precision and suggesting that short-term estimates may be strongly influenced by stochastic demographic events.

A markedly different picture emerged when monthly encounter histories were aggregated into biologically meaningful seasonal periods (Table III). In 1994, the constant-survival model Φ(.)p(.) received the strongest support (AICc = 266.3; weight = 0.63), whereas the seasonal model Φ(time)p(.) was substantially less supported (ΔAICc = 5.88). Likewise, in 2002 the best-supported model Φ(sex)p(.) ranked first (AICc = 280.5) included a sex effect on survival, but competing models differed by less than two AICc units, providing only weak evidence for temporal variation. Thus, much of the apparent heterogeneity detected at the monthly scale disappeared when demographic processes were examined over longer intervals. This contrast highlights an intrinsic characteristic of apparent survival estimates. In capture–mark–recapture studies, apparent survival combines true survival and site fidelity; consequently, temporal variation in Φ may arise from mortality, dispersal, temporary emigration or changes in movement behaviour (Lebreton et al. 1992; Crespin et al. 2002). The strong temporal heterogeneity observed in monthly models therefore does not necessarily imply corresponding fluctuations in mortality. Rather, it may reflect short-term changes in space use and local residency associated with reproductive activity, juvenile recruitment and seasonal movements.

These results resemble those reported by Crespin et al. (2002), who found that seasonal variation in apparent survival of bank voles was strongly influenced by dispersal processes and that movement-related mechanisms often contributed as much as mortality to temporal changes in Φ. A similar interpretation may apply to our population. The absence of significant monotonic correlations between abundance and survival (1994: $r_s = –0.37$, $p = 0.19$; 2002: $r_s = 0.61$, $p = 0.17$) further suggests that fluctuations in local abundance were not driven primarily by survival. Instead, recruitment and/or movement probably played a major role in shaping short-term demographic variation.

From a methodological perspective, the comparison between monthly and seasonal analyses demonstrates that the temporal resolution adopted in capture–mark–recapture studies can substantially influence ecological inference. Monthly models were highly effective in detecting short-term demographic variability, whereas seasonal aggregation revealed a more stable underlying pattern. Overall, these results suggest that our population experienced considerable short-term turnover but relatively limited seasonal variation in survival, a conclusion that would not have emerged from either analytical approach considered in isolation

Comparison with European populations and ecological implications - Demographic parameters observed in this study fall within the range reported for non cyclic bank vole populations of temperate Europe (Zhigalski 1994). Seasonal fluctuations in abundance, including autumn peaks and winter declines, closely match patterns described for deciduous forests in Poland, Belgium, Great Britain and other regions (Pucek et al. 1993; Hansson et al. 2000; Stenseth et al 2002). Unlike northern European populations, our data provide no evidence of cyclic fluctuations typically associated with seed mast dynamics (Marcström et al. 1990; Oksanen et al. 2000; Gorska et al. 2025), suggesting that local ecological factors play a primary role in shaping demographic trends.

Recent work has shown that demographic responses of woodland rodents at latitudinal extremes are strongly influenced by local ecological conditions and resource availability. In a mountain environment, food supplementation increased wood mouse abundance and female survival, whereas bank voles showed reduced abundance and survival across sexes (Ferrari et al. 2025). Although our study was conducted in a lowland forest, the demographic patterns observed here support the broader conclusion that southern populations can resemble central European ones while remaining highly responsive to local ecological processes. Comparable findings have been reported at southern range margins, where habitat quality, climatic conditions and interspecific interactions often override broad geographical gradients (de la Huerta Schliemann et al. 2025; Ferrari et al. 2025).

This study provides one of the few detailed demographic assessments of *Clethrionomys glareolus* in Italy and provides one of the few quantitative demographic datasets from a population near the southern limit of the species' European distribution. The demographic characteristics observed in the Po Plain lowland woodland largely mirror those reported from temperate deciduous forests elsewhere in Europe (Alibhai and Gipps 1985; Pucek et al. 1993; de la Huerta Schliemann et al. 2025). At the same time, differences between 1994 and 2002 highlight the importance of local demographic processes in shaping population structure and dynamics. Beyond providing one of the few detailed demographic descriptions of an Italian bank vole population, this study illustrates how temporal resolution can substantially influence demographic inference from capture–mark–recapture data.

Continued long-term monitoring will be essential to determine whether the patterns documented here are representative of other lowland populations and to evaluate how habitat fragmentation, climatic variability and food availability influence demographic processes.

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Table II. Model selection results for seasonal Cormack–Jolly–Seber analyses of apparent survival (Φ) and recapture probability (p) in bank voles. Models are ranked according to AICc. ΔAICc indicates the difference from the best-supported model within each study period. Abbreviations: Φ = apparent survival; p = recapture probability; npar = number of estimable parameters; AICc = Akaike Information Criterion corrected for small sample size.

Year	Model	npar	AICc	ΔAICc
1994	Φ(.) p(.)	2	266.33	0.00
	Φ(sex) p(.)	3	267.72	1.39
	Φ(time) p(.)	5	272.22	5.88
	Φ(sex + time) p(.)	6	273.44	7.11
2002	Φ(sex) p(.)	3	280.49	0.00
	Φ(time) p(.)	5	281.45	0.96
	Φ(.) p(.)	2	281.75	1.27

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Table III. Seasonal apparent survival estimates (Φ) derived from the best-supported Cormack–Jolly–Seber models for bank vole populations monitored during 1994–1995 and 2002–2003. For 1994–1995, the best-supported model assumed constant survival across sexes and seasons, whereas for 2002–2003 the model with sex-specific survival received the strongest support. Estimates are reported with standard errors (SE) and 95% confidence intervals (CI)

Year	Sex	Φ	SE	95% CI
1994–95	pooled	0.318	0.041	0.244–0.403
2002–03	female	0.457	0.055	0.352–0.566
2002–03	male	0.327	0.051	0.235–0.433

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Table I. Seasonal average abundance (N±SE) of bank voles in the two study periods. N is the abundance as estimated by Capture 2.0 on the basis of the best fitting probabilistic model. MNA is the Minimum Number Alive

	1994			2002		
season	**N**	**SE**	**MNA**	**N**	**SE**	**MNA**
Autumn	45.8	10.3	24.3	45.3	9.9	25.3
Spring	44.0	8.0	27.0	32.5	6.7	26.5
Summer	51.8	8.2	32.8	58.3	9.6	35.3
Winter	17.7	3.4	12.7	34.3	9.5	19.0

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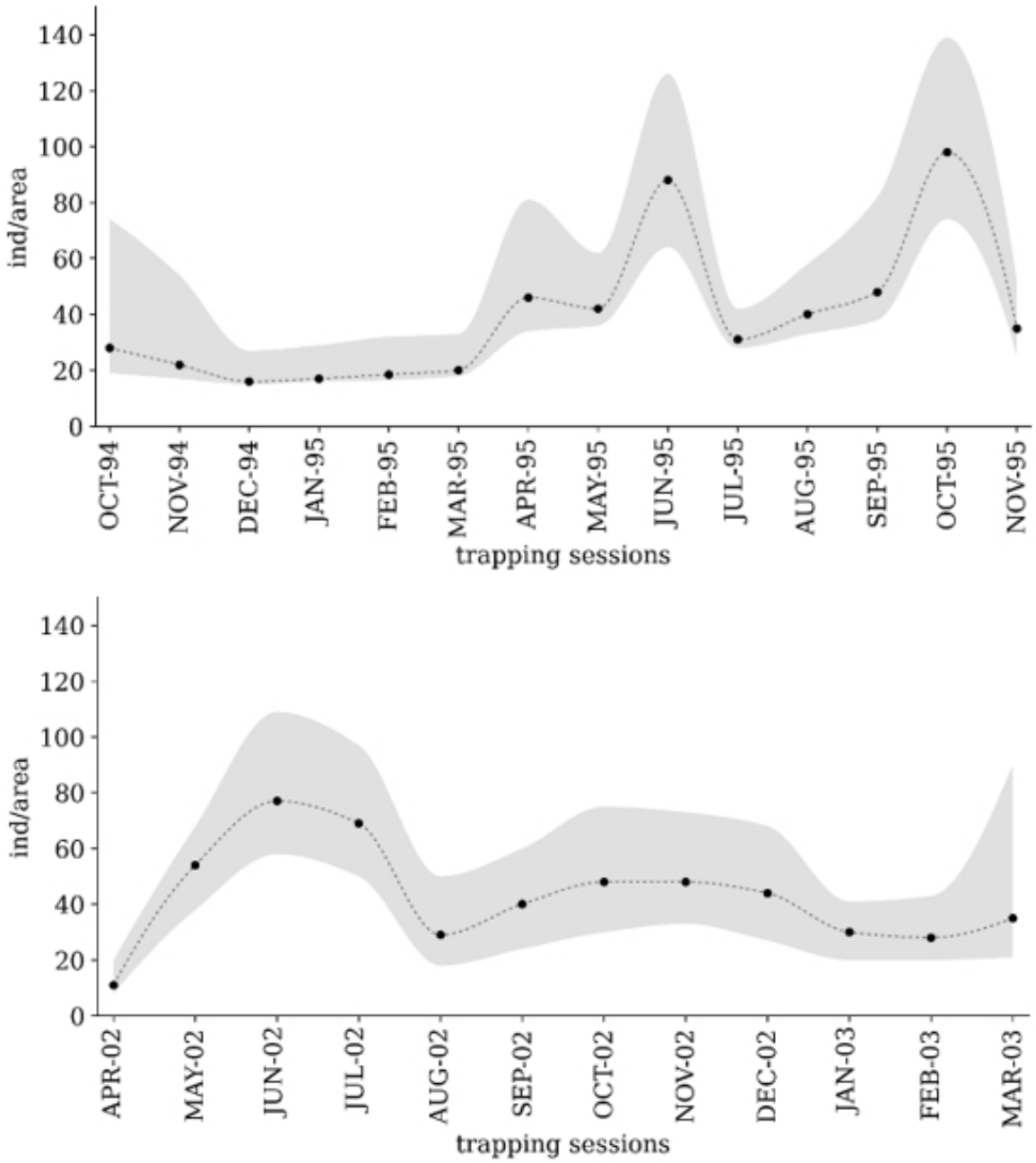

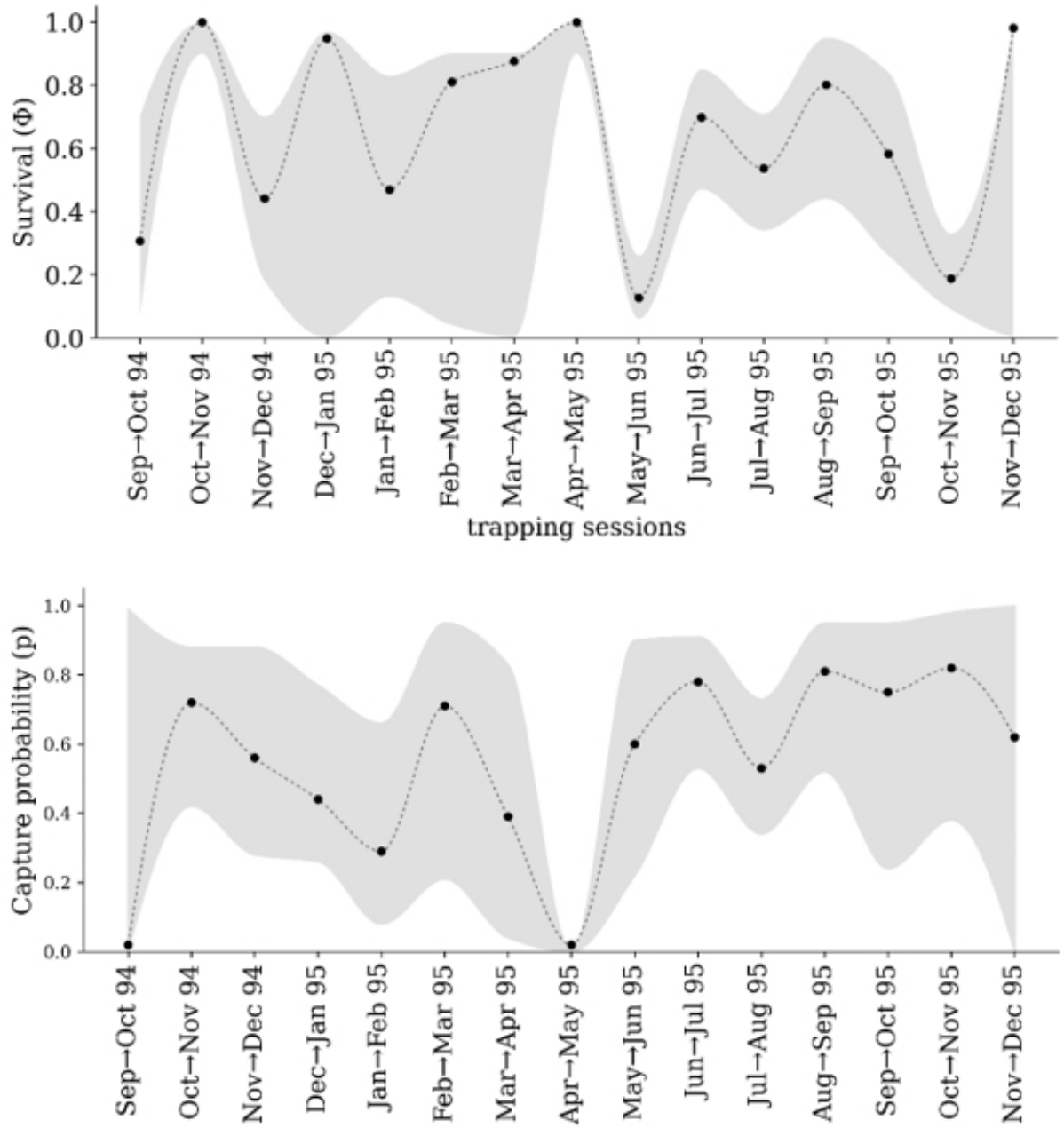
Survival (Φ)
1.0
0.8
0.6
0.4
0.2
0.0
Sep→Oct 94
Oct→Nov 94
Nov→Dec 94
Dec→Jan 95
Jan→Feb 95
Feb→Mar 95
Mar→Apr 95
Apr→May 95
May→Jun 95
Jun→Jul 95
Jul→Aug 95
Aug→Sep 95
Sep→Oct 95
Oct→Nov 95
Nov→Dec 95
trapping sessions
Capture probability (p)
1.0
0.8
0.6
0.4
0.2
0.0
Sep→Oct 94
Oct→Nov 94
Nov→Dec 94
Dec→Jan 95
Jan→Feb 95
Feb→Mar 95
Mar→Apr 95
Apr→May 95
May→Jun 95
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Aug→Sep 95
Sep→Oct 95
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Nov→Dec 95

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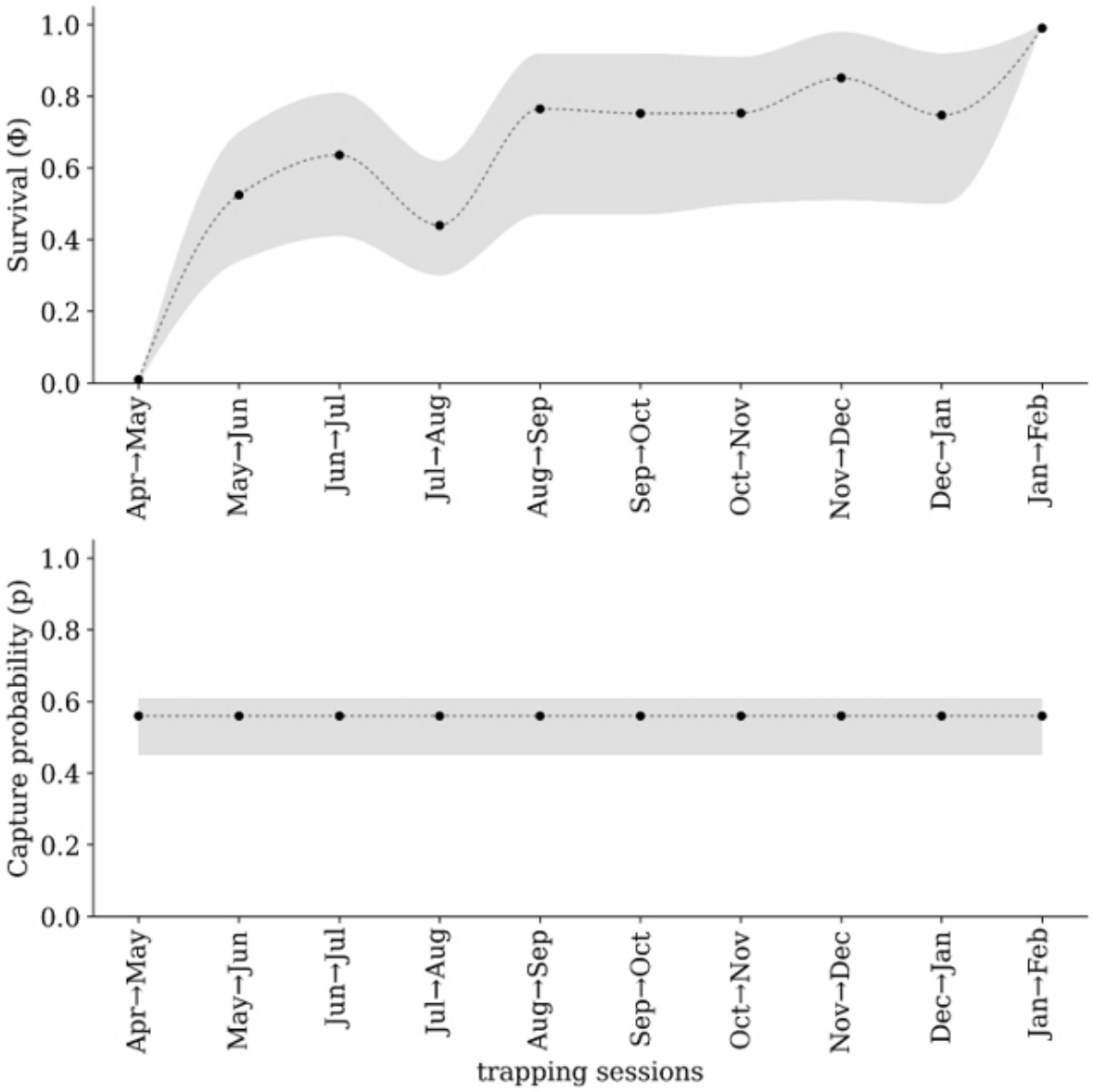

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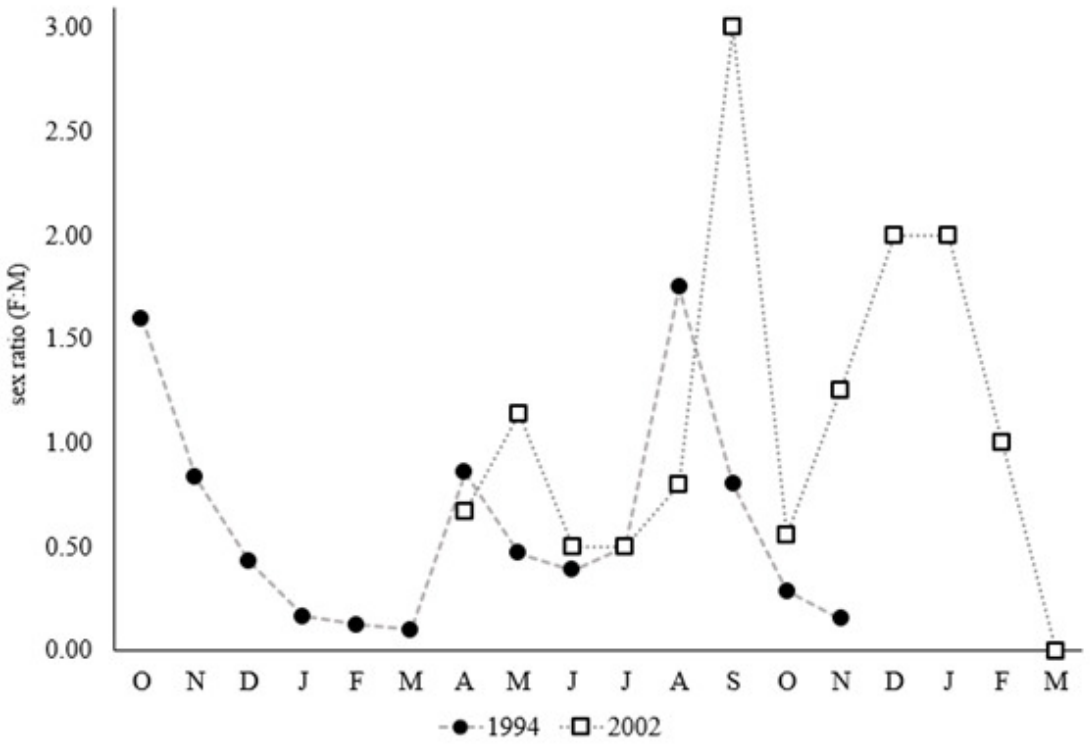

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