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RESEARCH

Comparative analysis of optional hunting behaviour in myomorph rodents: evolutionary and experience-dependent variations in attack patterns

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Abstract
This study presents a comparative analysis of original laboratory data on optional insect-hunting behaviour across 21 species of myomorph rodents, which revealed that, during the phase of prey attacks, the dropping out of elements from the "bite–seizing with paws" sequence followed distinct species-level patterns. The behavioural elements 'bite' and 'seizing with paws' differed in the degree to which their expression was evolutionarily constrained. Zero-inflated negative binomial phylogenetic generalized linear mixed model (ZINB PGLMM) analysis revealed a statistically significant negative association between the dropping out of these behavioral elements, indicating that most species tended to omit a single attack element rather than both. Cricetinae uniquely exhibited pronounced inter-individual variability, with individuals omitting either element. In Gerbillinae, the dropping out of 'bites' occurred not only during unsuccessful attacks but also during successful hunting sequences. Notably, this dropping out showed a strong phylogenetic signal, suggesting a close correspondence between variation in this trait and species relationships. Together, these results highlight the flexibility of sequential attack patterns in rodents, indicating that stereotyped action patterns can be reorganised in response to ecological and behavioural demands. The dropping out of 'bites' may represent a transitional step toward more derived attack strategies, such as initiating prey capture with the forepaws. Given the observed interspecific and individual-level variability, we propose that experience-dependent processes may contribute to the modification of hunting sequences. Stable individual differences in hunting behaviour may therefore provide a substrate for natural selection under changing ecological conditions, offering promising directions for future experimental and comparative research.

Keywords Rodents · Hunting behaviour · Fragmentation · Flexibility · Learning · Cognition

Introduction

Flexible animal behaviour arises from interactions between genetically encoded action patterns and individual experience, with species-specific cognitive capacities shaping how animals perceive, process, and respond to their environments (Guayasamin et al. 2017; Mearns et al. 2020; Zhao et al. 2023). In classical ethology (e.g., Lorenz 1950; Tinbergen 1951), many behaviours were described as innate fixed action patterns (FAPs): species-typical sequences of discrete acts reliably elicited by specific environmental stimuli. These sequences were viewed as largely stereotyped and relatively invariant, with motivational state and external cues determining whether and when they were expressed, rather than being flexibly reorganised under ongoing sensory control. Subsequent work, however, demonstrated that experience can play a significant role even in the development of apparently innate behaviours. Notably, Hailman's (1969) investigations of pecking behaviour in newly hatched gulls revealed that subtle forms of experience influence the emergence of species-typical motor patterns. This and related findings prompted a re-evaluation of the FAP concept, crystallised in the question "how fixed is a fixed action pattern?" (Schleidt 1974). It is now widely recognised that the relationship between innate and flexible components of behaviour is complex: in many species,

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highly sophisticated behavioural repertoires may be largely grounded in inherited patterns, whereas comparatively simple behaviours may depend on learning and even cognitive processes (Shettleworth 1998; Reznikova 2007). From a developmental perspective, Blumberg (2017) has argued that species-typical behaviours emerge through interactions between genetic predispositions and species-typical experiences occurring within reliable ecological contexts.

Until recently, there were no hypotheses of how the flexible segments within stereotyped behavioural patterns appeared during the evolutionary process. Optional predatory behaviour in primarily non-predatory myomorph rodents provides a particularly informative model for investigating the evolution and plasticity of stereotyped yet flexible behavioural sequences. Predation on mobile invertebrate prey in rodents engages motor routines that are sufficiently stereotyped to be recognisable across taxa, yet sufficiently flexible to permit learning-dependent modification (Galvin et al. 2021). Nevertheless, the evolutionary mechanisms underlying fragmentation or reorganisation of action patterns remain poorly understood.

The attack phase of insect hunting in myomorph rodents can be described as a compound action pattern comprising two core behavioural elements: 'bite' (prey capture using the incisors) and 'seizing with paws' (bilateral capture using the forelimbs). These elements are discrete, operationally definable, and consistently identified across ethological studies. Although the temporal order and relative timing of bite and seizing with paws vary among species, incisors and forelimbs typically operate in close coordination, and both elements have traditionally been considered necessary for successful prey capture (Langley 1987, 1994, 2021; Timberlake and Washburne 1989; Whishaw and Coles 1996; Reznikova et al. 2017, 2019; Levenets et al. 2024). Notably, initiating an attack by seizing prey with the forepaws has been proposed as an indicator of predatory specialisation and, in this sense, an evolutionary elaboration of hunting behaviour (Eisenberg and Leyhausen 1972; Langley 1994, 2021). Broad comparative analyses further suggest that, in rodents, forepaws involvement during prey attack is associated with more specialised predatory strategies, whereas some species retain a more "core" or putatively ancestral hunting sequence – approach, bite, followed by seizing and handling (Reznikova et al. 2022).

Recent observations, however, challenge the assumption that all constituent elements of the attack action pattern are obligatorily expressed in every successful predatory event. In two Gerbillinae species, *Meriones unguiculatus* and *Pachyuromys duprasi*, a non-trivial proportion of successful hunts (8.6% and 31.6%, respectively) were completed using bilateral paw seizing alone, without execution of the bite element – an instance of element drop-out. These findings prompted the hypothesis that evolutionary divergence and specialisation of rodent predatory behaviour may proceed via fragmentation or reconfiguration of ancestral action patterns, including the loss or recombination of some behavioural elements (Reznikova et al. 2022).

The proximate mechanisms underlying element drop-out from behavioural sequences remain unclear. Nevertheless, studies of object manipulation and skilled reaching in rodents demonstrate that species-typical forelimb grasping elements can be modified, reorganised, or supplanted by alternative motor solutions through experience-dependent plasticity (Whishaw et al. 2018a, b; Parmiani et al. 2021). More generally, motor learning is known to restructure the relative contribution and coupling of elements within action sequences, giving rise to stable alternative behavioural organisations without abolishing the overarching action pattern (Graybiel 2008). By analogy, repeated engagement with prey during optional hunting may promote cognitive–motor reorganisation of flexible elements within the rodent predatory attack pattern. Neurophysiological evidence further suggests that biting and forelimb-based grasping rely on partially distinct sensorimotor control pathways, supporting their treatment as separable components at the level of motor organisation (Han et al. 2017; Yu et al. 2021).

In the present study, we examined the occurrence of attack element drop-out during insect hunting across multiple species of primarily non-predatory myomorph rodents, including representatives of Murinae, Deomyinae, Arvicolinae, Cricetinae, and Gerbillinae. We define 'element drop out' as the omission of a commonly described behavioural element from an otherwise intact attack action pattern. Importantly, element drop out refers to a specific behavioural phenomenon, namely the disappearance of a component from an otherwise species-typical hunting pattern during its execution (Reznikova et al. 2022). We tested the prediction that the dropping out of 'bite' and/or 'seizing with paws' is not randomly distributed across species or individuals, but instead reflects structured variation in the organisation of the attack action pattern. To address this, we assessed the phylogenetic signal in the distribution the dropping out of elements and applied phylogenetic generalised least squares (PGLS; Blomberg et al. 2003; Garland and Ives 2000) and phylogenetic generalized linear mixed models (PGLMM; Ives and Helmus 2011), which allow modelling of trait–trait relationships across species while incorporating the expected covariance structure imposed by shared evolutionary history. Specifically, we use PGLS/PGLMM to evaluate whether bite and forepaws seizing function as evolutionarily independent elements of the attack pattern once shared ancestry is taken into account. Finally, because these attack elements exhibit measurable behavioural variability, we propose that experience-dependent learning may contribute to modifications of an otherwise stereotyped predatory action pattern.

Materials and methods

We analysed original laboratory data on predatory behaviour toward mobile insect prey in 21 species of Myomorphi at the individual level (Table 1). These data were collected between 2012 and 2025. For each individual, we quantified the number of hunting sequences in which specific behavioural elements were entirely absent (hereafter termed 'dropped out'). Behavioural elements were identified from coded behavioural sequences following established ethological protocols (for details see Supplementary and Table 2), and the main stages of the experimental procedure were standardised across species (Reznikova et al. 2017, 2022; Levenets et al. 2024).

All animals were housed in plastic cages with cotton nesting material under a 16:8 h light/dark cycle at 23–25 °C; *T. paedulcus* was maintained at 27 °C. Animals were fed once daily and had *ad libitum* access to water. Herbivorous species received hay or fresh grass, vegetables, and fruits, whereas species with a mixed diet were provided with mixed seeds, dried shrimp, mealworms, and cottage cheese. To standardise nutritional state prior to testing, all animals were offered all food types before being transferred to the experimental arenas. All studied species of the genus *Alticola*, as well as the narrow-headed vole (*Lasiopodomys gregalis*) and the steppe lemming (*Lagurus lagurus*), are predominantly herbivorous. The remaining species are characterized by different forms of mixed feeding that differ in the relative contribution of plant and animal food, ranging from the predominantly granivorous striped field mouse (*Apodemus agrarius*) to the highly omnivorous Norway rat (*Rattus norvegicus*) and Cairo spiny mouse (*Acomys cahirinus*).

The number of testing sessions varied among species and was determined primarily by sample size and species-specific patterns of hunting behaviour. In most species, hunting occurred irregularly, with substantial variation both among individuals and across sessions. For example, the same individual could hunt during the first test session, show no hunting behaviour in several subsequent sessions, and then resume hunting in a later session.

To minimize the influence of prior experience on the expression of hunting behaviour, laboratory-born animals were not exposed to live insect prey before testing. This applied to both omnivorous and predominantly herbivorous species, as the aim of the study was to assess spontaneous responses to live prey rather than learned hunting performance. Exceptions included wild-caught individuals

Table 1 Volume of collected data

Studied species	Number of animals	Number of test sessions	Potential number of prey in the test
Murinae			
Norway rat (*Rattus norvegicus*)	133	1	3
Acacia rat (*Thallomys paedulcus*)	7	6	3
Striped field mice (*Apodemus agrarius*)	26	2	3
Deomyinae			
Cairo spiny mouse (*Acomys cahirinus*)	13	3	3
Arvicolinae			
Narrow-headed vole (*Lasiopodomys gregalis*)	46	3	3
East European vole (*Microtus levis*)	22	3	3
Northern red-backed vole (*Clethrionomys rutilus*)	33	10	1
Tuva silver vole (*Alticola tuvinicus*)	Total 52: 16 36	3 10	3 1
Flat-headed vole (*A. strelzowi*)	Total 52: 20 32	3 10	3 1
Olkhon mountain vole (*A. olchonensis*)	104	10	1
Mongolian silver vole (*A. semicanus*)	16	10	1
Steppe lemming (*Lagurus lagurus*)	39	10	1
Cricetinae			
Desert hamster (*Phodopus roborovskii*)	14	3	3
Campbell's dwarf hamster (*P. campbelli*)	19	7	3
Djungarian hamster (*P. sungorus*)	Total 54: 30 24	3 30	3 3
Eversmann's hamster (*Allocricetulus eversmanni*)	8	3	3
Mongolian hamster (*Al. curtatus*)	13	3	3
Gerbillinae			
Mongolian gerbil (*Meriones unguiculatus*)	61	10	1
Fat-tailed gerbil (*Pachyuromys duprasi*)	21	10	1
Pale gerbil (*Gerbillus perpallidus*)	Total 30: 18 12	10 60	3 3
North African gerbil (*Dipodillus campestris*)	10	10	3

of *Ap. agrarius* (17 of 26 individuals) and *L. gregalis* (38 of 46 individuals), for which prior experience with insect prey was unknown. The remaining individuals of these species (*Ap. agrarius*, 6 of 9; *L. gregalis*, 3 of 8) were born and raised in the vivarium and expressed hunting behaviour while naïve to live insect prey.

Most animals included in the study were sexually mature adults older than three months. Juvenile individuals were included for only two species: *R. norvegicus* (52 individuals tested from 30 days of age) and *P. sungorus* (18 individuals tested from 21 days of age), because only these species were represented by both juvenile and adult individuals in the available dataset. To assess whether the inclusion of juveniles could bias the results for these species, we tested for age-related differences in the frequency of dropping out of the analysed behavioural elements within each species. These analyses served as within-species controls and were not intended to infer the absence of age effects across all studied species. No statistically significant differences were detected between juvenile and adult individuals in either species. In *R. norvegicus*, the dropping out of 'bite' did not differ between age groups (Fisher's exact test, $p=0.81$), while that of 'seizing with paws' was not observed; similarly, no significant age-related differences were detected in P. *sungorus* for the dropping out of either 'bites' ($p=0.13$) or 'seizing with paws' ($p=0.66$). Accordingly, data from juvenile and adult individuals were pooled for subsequent analyses.

Animals were tested individually in transparent plastic arenas. Arena size was adjusted to body size: 45 × 45 × 60 cm for species with a body length exceeding 16 cm, 40 × 30 × 60 cm for species with a body length of 14–16 cm, and 30 × 30 × 35 cm for species with a body length below 14 cm. After a 5-min habituation period, video recording began, and a mobile prey item was gently released onto the arena floor. Prey consisted of imago and late-instar larvae of the cockroach *Nauphoeta cinerea* (body length 26.00 ± 1.33 mm). Cockroaches were selected because they are harmless, palatable to rodents, and do not elicit defensive reactions in small mammals.

Testing schedules and the number of prey items per session varied among and, in some cases, within species; for some species, more than one value is reported in Table 1 because different testing schedules were used. For most species, test sessions were separated by 1 day; an exception was a group of 18 juvenile *P. sungorus*, which were tested daily for 30 consecutive days. As noted above, juvenile and adult individuals were pooled because no age-related differences were detected in the frequency of omission of the analysed behavioural elements. In some sessions, individuals were allowed to hunt sequentially on three prey items, with each subsequent prey presented only after successful capture of the previous one. This regime was typically applied to species that hunted frequently and consumed prey regularly. In other tests, a single prey item was offered, which was more common for species that hunted less frequently or did not fully consume the prey (Reznikova et al. 2017, 2019, 2022; Panteleeva et al. 2020; Levenets et al. 2019, 2024). At the species level, the mean number of tests was not significantly correlated with the mean frequency of dropping out of either 'bite' or 'seizing with paws' (Spearman's rank correlation: $\rho=0.29$, $p=0.20$ and $\rho=-0.13$, $p=0.59$, respectively). Thus, there was no evidence that the interspecific pattern of dropping out frequencies was explained simply by variation in the number of tests.

All hunting attempts were analysed for each individual, including both successful and unsuccessful events. A hunting attempt was classified as successful if the animal captured the prey and consumed it, or, in rare cases, inflicted critical damage preventing active escape (e.g., removal of all locomotory appendages). An attempt was considered unsuccessful if the prey escaped and the animal ceased pursuit, defined as either immobility lasting longer than 3 s or movement away from the prey. Individuals could exhibit an unlimited number of unsuccessful attempts before a successful one. Individuals that eventually captured, consumed, or critically damaged prey were classified as successful hunters; those that never succeeded were classified as unsuccessful hunters.

Video data were processed following established protocols (Reznikova et al. 2017, 2019, 2022) using Observer XT 12.5 software (Noldus Information Technology) at 5× and 25× slow motion. Each behavioural element was assigned a unique letter code, and hunting sequences were represented as strings of these letters (see supplementary Table 2). For example, the sequence SDWEWWWGER corresponds to: approach by walking (S), sniffing (D), bite (W), seizing with paws (E), repeated bites (W), carrying prey in teeth (G), seizing with paws again (E), and handling prey (R). Sequences were saved as space-separated text files per species. This study focused on the complete omission of attack-related elements – bite (W) and seizing with paws (E) – within individual hunting sequences.

The frequency of dropping out of attack-related elements (hereafter, mean frequency of dropping out) was calculated in two steps. First, for each individual, the proportion of hunting sequences (including both successful and unsuccessful attempts) in which a given element was omitted was computed. Second, species-level values were obtained by averaging individual proportions across all individuals of that species. This approach accounts for variation in the number of test sessions and hunting events among individuals and species. Consequently, the frequencies of dropping out were expressed as proportions rather than absolute counts. Mean values ± standard error (M ± SE) were reported at the subfamily level. To assess the relative occurrence of the dropping out of 'bites' versus 'seizing with paws', ratios were calculated for each individual, ranging from 0 to 1: values closer to 1 indicate more frequent dropping out of

'bites' relative to 'seizing with paws', whereas values closer to 0 indicate the opposite.

In line with the STRANGE framework, data on hunting behaviour (Fig. 1) and behavioural element omission (Figs. 2, 3 and 4) are presented descriptively without formal statistical comparisons.

Phylogenetic analyses were performed at the species level using the mean frequencies of dropping out for 'bite' and 'seizing with paws'. Phylogenetic relationships among species were obtained from the Open Tree of Life database (Hinchliff et al. 2015), with branch lengths assigned using Grafen's method. Hierarchical clustering was conducted

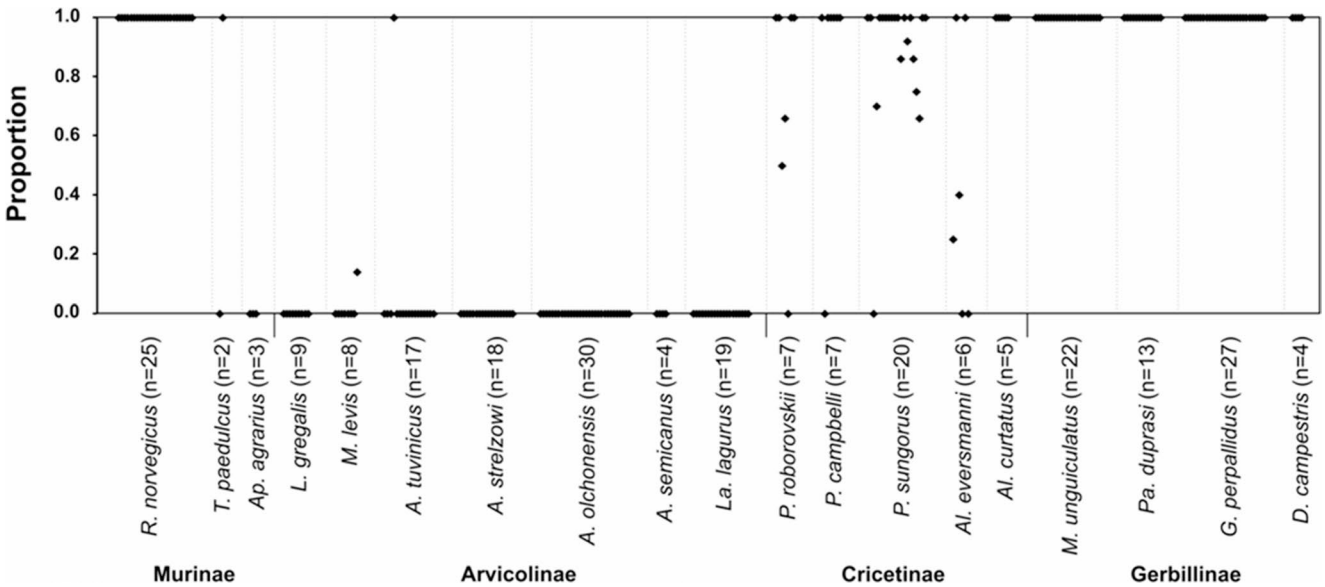

Fig. 1 Occurrence of hunting behaviour in the studied species. Numbers indicate the number of tested individuals per species

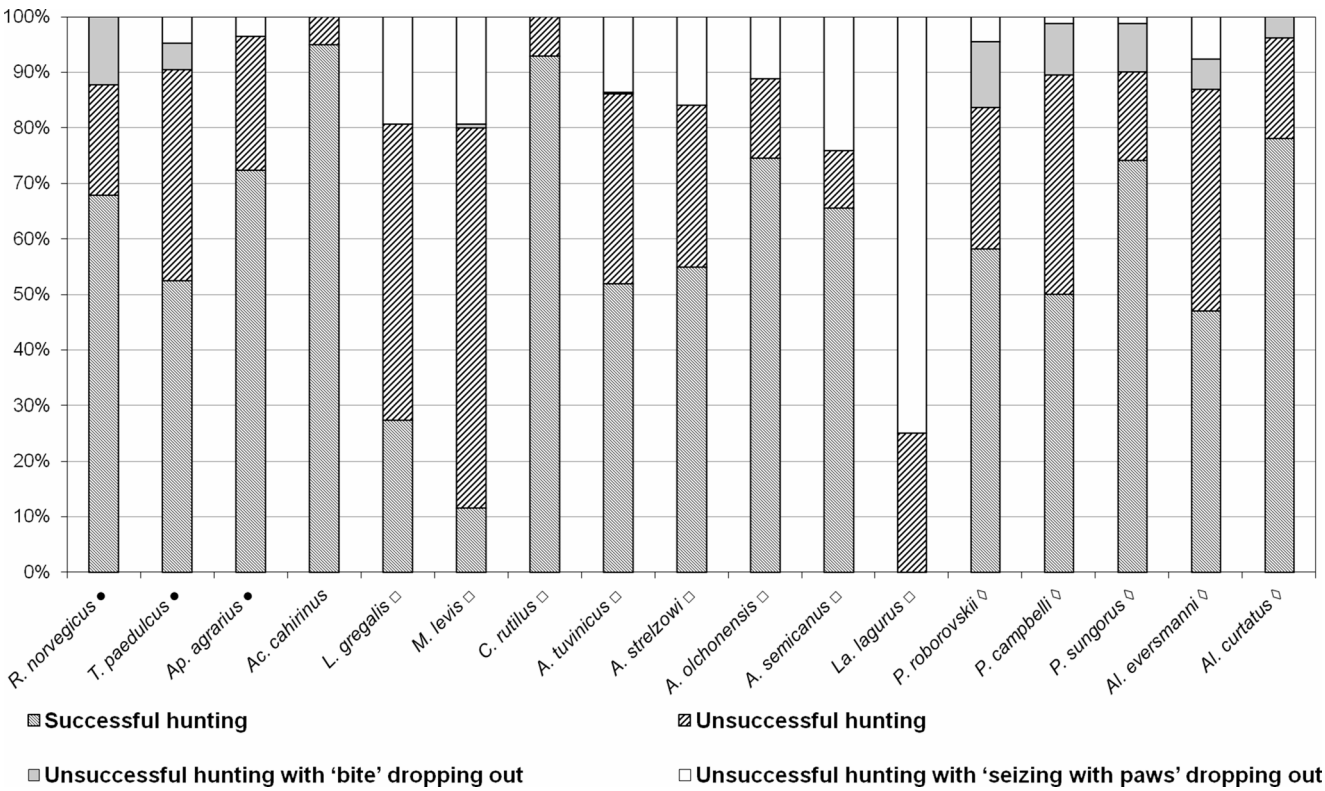

Fig. 2 Mean frequency of the dropping out of behavioural elements in hunting sequences of Gerbillinae individuals

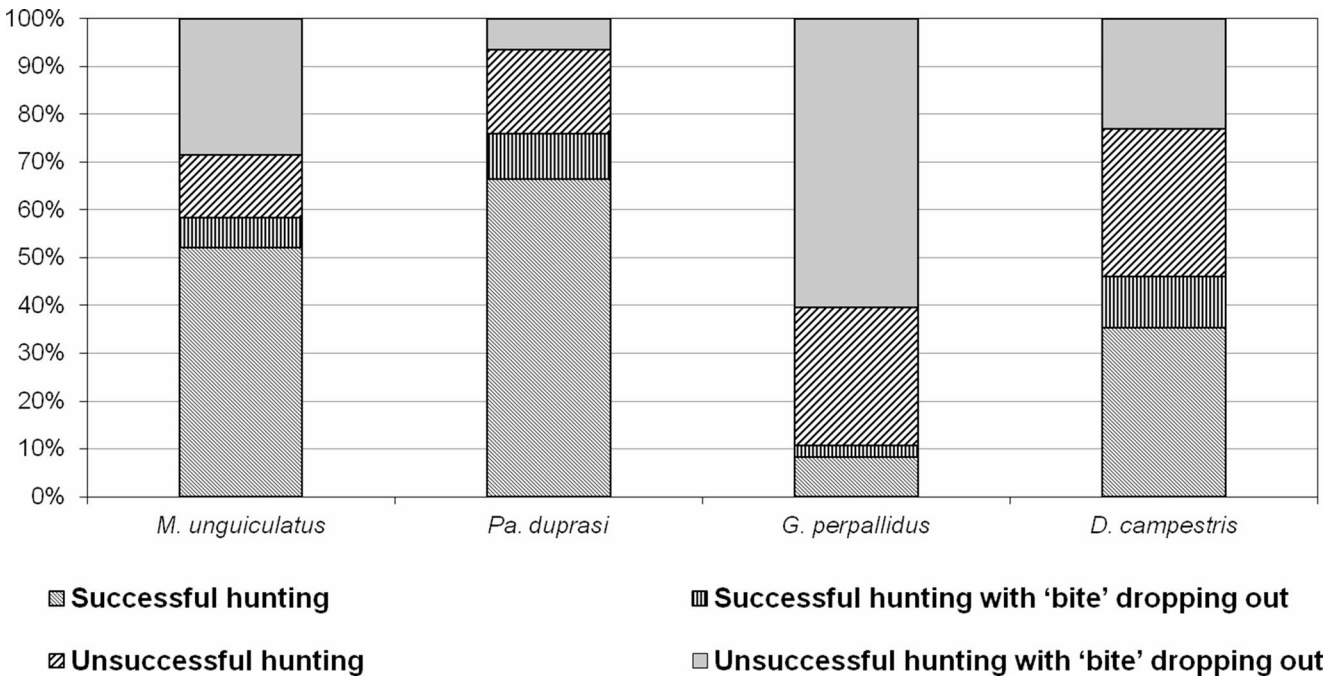

Fig. 3 Mean frequency of the dropping out of behavioural elements in hunting sequences of Murinae (●), Deomyinae (no symbol), Arvicolinae (□), and Cricetinae (◊)

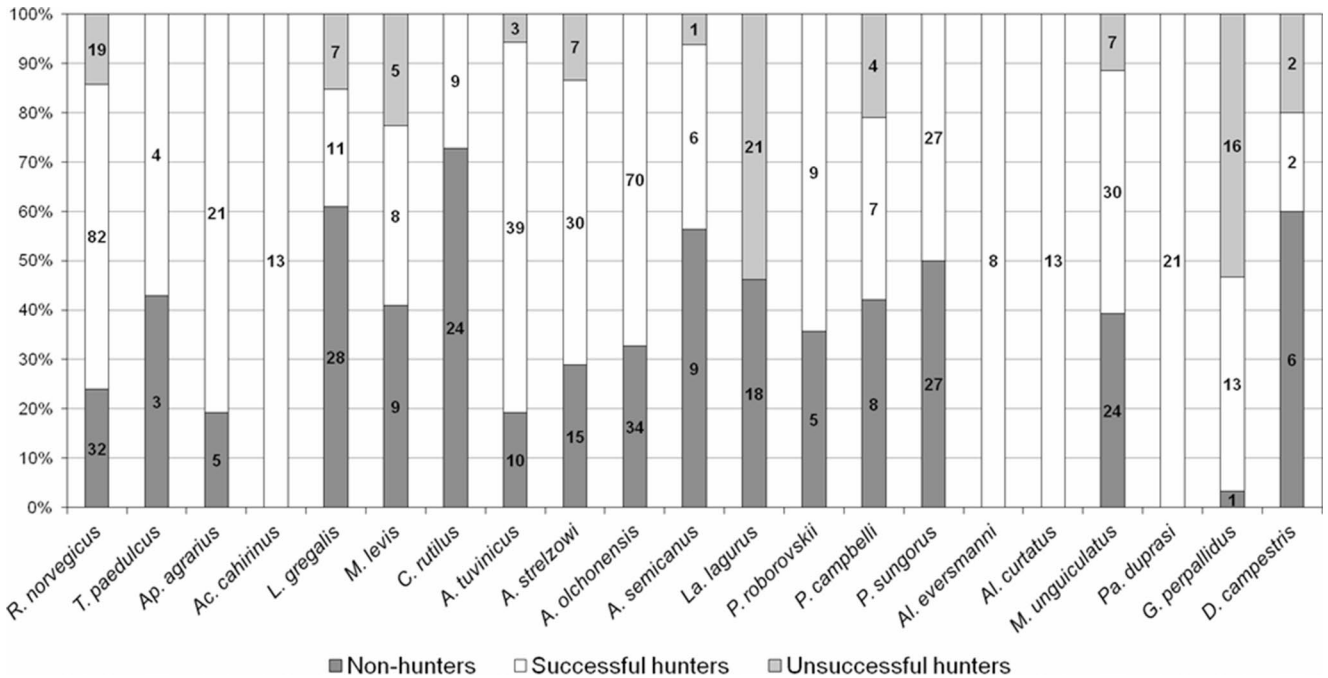

Fig. 4 Ratio of the frequencies of dropping out of the behavioural element 'bite' in hunting sequences of individual animals (each point represents one individual). Values closer to 1 indicate more frequent dropping out of 'bites' relative to 'seizing with paws', whereas values closer to 0 indicate more frequent dropping out of 'seizing with paws'

using Ward's method. Phylogenetic signal in the frequencies of dropping out of 'bite' and 'seizing with paws' was estimated using Pagel's λ (Pagel 1999). To test for an association between the frequencies of dropping out of the two behavioral components while accounting for phylogenetic non-independence, we applied phylogenetic generalized least squares (PGLS) analyses using species mean frequencies of dropping out as continuous traits.

Because the original observations were count data and included many zero values, we additionally fitted

count-based phylogenetic generalized linear mixed models (PGLMM). For these analyses, individual-level observations were aggregated at the species level as total counts of dropping out events. The total number of dropping out of 'seizing with paws' per species was used as the response variable, whereas the frequency of dropping out of 'bite' was used as the predictor.

The log-transformed number of individuals sampled per species was included as an offset term. Preliminary Poisson models showed substantial overdispersion. Therefore, the final count-based model was fitted as a zero-inflated negative binomial phylogenetic generalized linear mixed model using the 'glmmTMB' package in R. Phylogenetic covariance among species was incorporated as a random effect using a phylogenetic variance–covariance matrix derived from the species tree. Zero inflation was modelled using an intercept-only component. Model diagnostics based on simulated residuals generated with DHARMa (Hartig 2024) indicated no substantial deviations from the expected residual distribution, overdispersion, or excess zero inflation.

All analyses were performed in R (version 4.6.0; R Core Team) using the packages: ape (Paradis and Schliep 2019), dplyr (Wickham et al. 2026), stringr (Wickham 2025), phytools (Revell 2024), rotl (Michonneau et al. 2016), caper (Orme et al. 2025), phylolm (Ho and Ané 2014), MCMCglmm (Hadfield 2010), phyr (Li et al. 2020), and glmmTMB (Williams et al. 2025).

Results

The occurrence of hunting behaviour across the studied species is shown in Fig. 1. All tested individuals of *Ac. cahirinus*, *Al. eversmanni*, *Al. curtatus*, and *Pa. duprasi* exhibited hunting behaviour at least once during testing. Among the remaining species, the proportion of optional hunting individuals (including both successful and unsuccessful hunters) ranged from 27% in *C. rutilus* to 97% in *G. perpallidus*. Notably, *La. lagurus* was the only species in which optional hunting behaviour was observed exclusively as unsuccessful attempts.

The mean frequency of dropping out of the behavioural elements 'bite' and 'seizing with paws' in hunting sequences of Gerbillinae is shown in Fig. 2, whereas the corresponding frequencies for Murinae, Deomyinae, Arvicolinae, and Cricetinae are shown in Fig. 3. Gerbillinae were presented separately because this subfamily exhibited a qualitatively distinct pattern: successful prey capture could be achieved exclusively via 'seizing with paws', with dropping out of the 'bite' element. In contrast, in all other studied taxa, dropping out of either 'bite' or 'seizing with paws' occurred only during unsuccessful hunting attempts. Based on the mean values calculated per hunting individual, the frequency of dropping out of elements ranged from 75% in *La. lagurus* to 4% in *Ap. agrarius*, *Pa. duprasi*, and *Al. curtatus*. For Murinae, Arvicolinae, and Cricetinae, the mean proportion of dropping out was 15% ± 9% (M ± SE), whereas for Gerbillinae it was 31% ± 36%.

The ratio of the frequencies of dropping out for the behavioural elements 'bite' and 'seizing with paws' is shown in Fig. 4. In hunting individuals of *Ac. cahirinus* (Deomyinae) and *C. rutilus* (Arvicolinae), neither element was found to drop out; consequently, these species are not shown in Fig. 4. Within Murinae, patterns of dropping out differed among species: in *R. norvegicus* only the 'bite' element was dropped out, in *Ap. agrarius* only 'seizing with paws', whereas in *T. paedulcus* rare cases of dropping out of both elements were observed. Among Arvicolinae, the dropped element was predominantly 'seizing with paws', with the dropping out of 'bite' recorded only in isolated individuals of *M. levis* and *A. tuvinicus*. In Cricetinae, the dropping out of the 'bite' element was observed exclusively in *Al. curtatus*, whereas in *P. campbelli*, *P. roborovskii*, *P. sungorus*, and *Al. eversmanni* the dropping out of either element could occur. In all examined Gerbillinae species, dropping out was restricted strictly to the 'bite' element.

Both behavioural components exhibited significant phylogenetic signal (see Supplementary, Fig. 5). The frequency of the dropping out of 'bites' showed a strong signal (Pagel's $\lambda = 0.99$, LR = 4.8, $p = 0.026$), consistent with a Brownian motion model of evolution, whereas that of 'seizing with paws' was significant but weaker ($\lambda = 0.71$, LR = 5.6, $p = 0.018$).

Species with a higher mean frequency of dropping out of 'bite' (Pagel's $\lambda = 0.99$, LR = 4.8, $p = 0.026$) therefore tended to show lower mean frequency of that of 'seizing with paws' ($\lambda = 0.71$, LR = 5.6, $p = 0.018$) (see supplementary: Fig. 6). Phylogenetic generalized least squares (PGLS) analysis revealed a significant negative association between the dropping out of the two behavioral components ($\beta = -0.31 \pm 0.13$ SE, $t = -2.42$, $p = 0.026$). The estimated Pagel's λ for the PGLS model was 0.69, indicating moderate phylogenetic dependence.

Because the original observations were count data and included many zero values, additional count-based analyses were performed. Preliminary Poisson models showed substantial overdispersion, indicating that a simple Poisson error structure was inappropriate for the data. We therefore fitted a zero-inflated negative binomial phylogenetic generalized linear mixed model (ZINB PGLMM) incorporating phylogenetic covariance as a random effect (Fig. 5). The ZINB PGLMM supported a significant negative association between the dropping out of the two behavioral components ($\beta = -0.82 \pm 0.32$ SE, $z = -2.54$, $p = 0.011$). Thus,

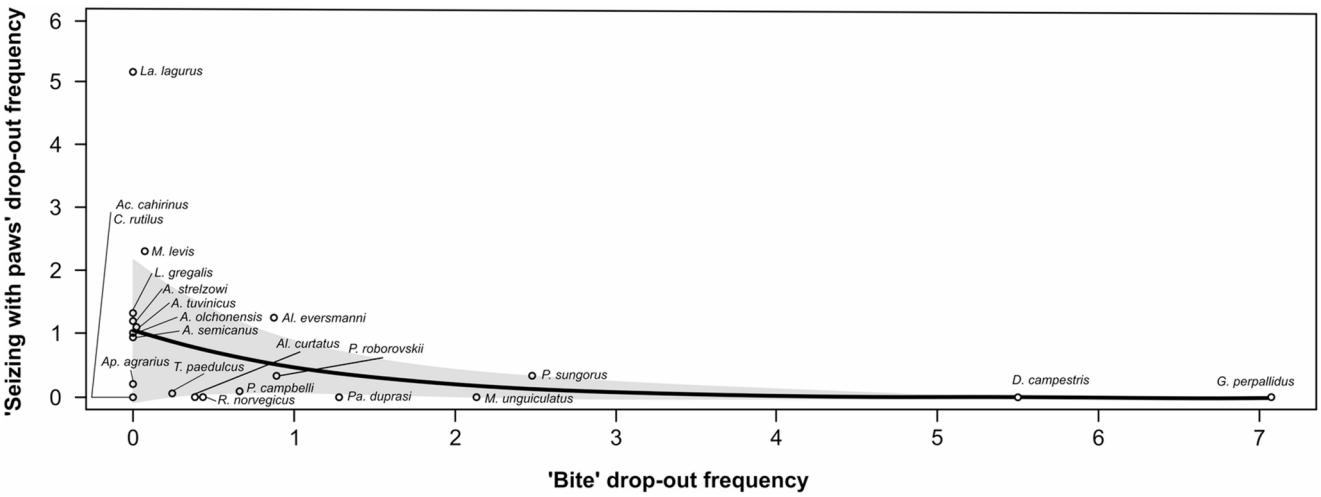

Fig. 5 Predicted relationship between the frequencies of dropping out of 'bite' and 'seizing with paws' elements across the studied rodent species. Points represent observed species-level values. The solid line shows predictions from the zero-inflated negative binomial phylogenetic generalized linear mixed model (ZINB PGLMM), and shaded areas indicate 95% confidence intervals

direction of the relationship was consistent between the initial PGLS analysis and the subsequent count-based ZINB PGLMM. The ZINB PGLMM model diagnostics based on simulated DHARMa residuals did not indicate overdispersion ($p = 0.92$), excess zero inflation ($p = 1.00$), or outliers ($p = 1.00$), supporting the adequacy of the zero-inflated negative binomial PGLMM.

Discussion

Comparative analysis of optional insect-hunting behaviour in 21 species of myomorph rodents revealed that, during phase of prey attacks, the dropping out of either the bite or seizing with paws typically accompanied exploratory or otherwise inefficient motor configurations, rather than reflecting a stable alternative attack strategy. Comparable variability in the expression of attack components has been reported in other mammalian predators and is attributed to the flexible organisation of complex action patterns (Leyhausen and Tonkin 1979; Han et al. 2017; Yu et al. 2021). Gerbillinae, however, constituted a notable exception in our study. In this group, the dropping out of bite was observed not only during unsuccessful attacks but also during successful hunting sequences, indicating that forepaw-based capture alone can repeatedly result in successful prey capture at the individual level. This contrast highlights pronounced interspecific differences in the organisation and flexibility of attack patterns and suggests that, in some taxa, constituent attack elements may be functionally decoupled to a greater extent than previously assumed.

The predominance of the dropping out of behavioral elements during unsuccessful hunts in most species suggests that these events should not be interpreted simply as behavioural noise. Rather, they can be viewed as transient deviations within a flexible attack pattern that arise when individuals attempt to solve challenging sensorimotor tasks. From this perspective, the dropping out of bite or seizing with paws may reflect exploration of alternative motor configurations when canonical action sequences fail to achieve successful prey capture. Such transient deviations are consistent with the view that motor exploration constitutes an integral component of learning and behavioural adaptation (Bateson 1991, 2004; Krakauer et al. 2017). In Gerbillinae, however, the repeated occurrence of successful attacks relying exclusively on seizing with paws indicates that the dropping out of bite can be consistently expressed without preventing prey capture. This contrast suggests that, in some taxa, specific components of the attack pattern may be differentially emphasised or suppressed, potentially reflecting species-specific motor capacities and ecological contexts.

A plausible proximate mechanism underlying element omission involves experience-dependent modification of motor routines. The evolution of advanced manipulative abilities of the forelimbs in rodents has been linked to selective pressures associated with dietary diversity and ecological versatility (Iwaniuk et al. 2000a, b; Whishaw et al. 2020). Experimental studies further demonstrate that species-typical grasping patterns can be reshaped through learning: in skilled reaching tasks, rodents can replace incisor-initiated object acquisition with forelimb-dominated strategies when task constraints favour such solutions (Whishaw et al. 2018a, b; Parmiani et al. 2021). Although these experiments rely on artificial setups, analogous constraints may arise in natural contexts. During insect hunting, prey may occupy narrow crevices, rock fissures, or other spatially constrained

microhabitats that limit access by the head while remaining reachable by the forelimbs. Repeated encounters with such situations could reinforce forepaw-based capture strategies and, in some cases, reduce reliance on biting within the attack pattern. At a more general level, motor learning has been shown to reorganise the contribution of individual elements within complex action sequences, yielding stable alternative motor solutions (Graybiel 2008). By analogy, repeated engagement with mobile prey during optional hunting may facilitate cognitive–motor reorganisation of flexible components within the rodent attack pattern.

Additional support for rapid reorganisation of attack sequences under natural conditions comes from recent observations of Norway rats (*R. norvegicus*) preying on Daubenton's bats (*Myotis daubentonii*). Although this study did not explicitly focus on the mechanics of prey capture, qualitative inspection of the supplementary video material reveals instances in which attacks on flying prey appear to be initiated using the forepaws rather than the bite (Gloza-Rausch et al. 2025). This contrasts with the typically bite-initiated attack sequence documented for rat predation on insects and other terrestrial prey (Gregoire and Smith 1975; Ivanco et al. 1996; Reznikova et al. 2017). Notably, this alternative attack organisation appears to have emerged over a relatively short timespan, making explanations based solely on long-term evolutionary change unlikely and instead suggesting a role for learning or behavioural reorganisation within the lifetime of individuals. Together with our results, this example supports the view that the sequential organisation of attack elements in rodents is flexible and can be reorganised in response to novel ecological challenges.

Across the studied taxa, element omission exhibited clear species-level structure. Most species predominantly omitted one specific attack element rather than both, whereas Cricetinae uniquely displayed the dropping out of either 'bite' or 'seizing with paws' in different individuals. This pattern aligns with previous reports of increased flexibility in the ordering and expression of attack elements in this group (Levenets et al. 2019, 2024). Phylogenetic analyses further revealed contrasting evolutionary patterns for the two elements. The dropping out of bite showed a very strong phylogenetic signal, indicating close correspondence between variation in this trait and species relationships. In contrast, the dropping out of 'seizing with paws' exhibited a weaker phylogenetic signal, suggesting a greater contribution of factors not strictly aligned with phylogeny. Together, these results indicate that 'bite' and 'seizing with paws' differ in the degree to which their expression is evolutionarily constrained.

Comparative ethological data across terrestrial vertebrates suggest that prey capture initiated by the jaws represents a putatively ancestral condition, whereas active involvement of the forelimbs is a derived feature associated with increased manipulative capacity (Eisenberg and Leyhausen 1972; Langley 1994, 2021). Within Myomorphi, the frequent use of both incisors and forelimbs points to a mixed condition, in which ancestral and derived components coexist within a single attack pattern. In this context, the dropping out of bite can be interpreted as expanding the role of forelimbs in prey capture, allowing attack sequences to be initiated or executed primarily via seizing with paws. The ability of Cricetinae to initiate attacks either with bite or seizing with paws may represent an intermediate condition along such a continuum, whereas the forepaw-dominated attacks observed in some Gerbillinae could reflect a further shift in this direction. Importantly, our data support a model of gradual reorganisation of attack patterns rather than abrupt replacement of one functional system by another. Such gradual change aligns with evolutionary frameworks in which behavioural plasticity generates alternative functional configurations that can subsequently be shaped and stabilised by selection under changing ecological conditions (West-Eberhard 2003; Pigliucci 2005).

The zero-inflated negative binomial phylogenetic generalized linear mixed model (ZINB PGLMM) showed a significant negative association between the dropping out of 'bite' and that of 'seizing with paws'. Species in which 'bite' were dropped out more often tended to show lower frequency of dropping out of 'seizing with paws', even after accounting for phylogenetic relatedness, unequal sample sizes, overdispersion, and the large number of zero observations. This does not imply that the two elements are strict alternatives. Rather, the relationship was gradual: an increase in the dropping out of one element was associated with a decrease in that of the other, while both elements could still vary across species. This pattern suggests that bite and forepaw use can change partly independently within the hunting sequence. Such partial independence may allow species to shift the relative contribution of these elements without replacing the entire behavioural pattern.

Taken together, our findings suggest that optional predatory behaviour in rodents is supported by a fragmented and flexible attack pattern, within which individual elements can be omitted, recombined, or differentially weighted, potentially reflecting cognitive modulation. Across species, patterns of dropping out are consistent with differences in the flexibility of attack organisation: taxa in which the dropping out of 'bites' occur may allow a broader range of motor solutions, whereas taxa characterised by the dropping out of 'seizing with paws' may exhibit comparatively more constrained attack patterns. At the population level, a small but stable proportion of individuals displaying increased fragmentation of the attack sequence may contribute disproportionately to

overall behavioural variation. Stable individual differences in behaviour are known to influence evolutionary dynamics under changing selection regimes (Dall et al. 2012; Réale et al. 2010). Such individuals may therefore represent a source of behavioural variation upon which selection could act under shifting ecological conditions. This hypothesis provides a clear direction for future experimental and comparative studies.

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Data availability Phylogenetic relationships were obtained from the Open Tree of Life (Hinchliff et al. 2015; https://doi.org/10.1073/pnas.1423041112), and branch lengths assigned using Grafen's method, hierarchical clustering was carried out using Ward's method. All analyses were conducted in R (version 4.5.2; R Core Team).

Declarations

Ethics approval All the experiments with rodents were performed in accordance with the rules adopted by the European Convention for the Protection of Vertebrate Animals used for Experimental and other Scientific Purposes. The experimental protocol was approved by the Bioethics Committee of the Institute of Systematics and Ecology of Animals, Siberian Branch Russian Academy of Sciences (protocol No. 1 dated April 14, 2014).

Competing interests The authors declare no competing interests.

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