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ORIGINAL PAPER

Flexibility and rigidity in hunting behaviour in rodents: is there room for cognition?

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Abstract

Predatory hunting is a complex species-typical behaviour involving different skills, some of which may include learning. This research aims to distinguish between rigid and flexible parts in live-insect hunting behaviour in nine herbivorous and granivorous rodent species, and to find out whether there is room for cognition in this activity. In laboratory experiments, all species studied manifest skilful attacks towards insects in a manner that is typical for specialised predators chasing a fleeing prey. Voles demonstrate a "core" and somewhat primitive scheme of a hunting pattern: approaching a potential victim, biting it, and then seizing and handling. Hamsters display the tendency to start their attacks by actions with paws, but they can achieve success only using teeth as well. Gerbils can successfully use both paws and teeth to start the attack, which brings their hunting behaviour closer to that of specialised rodent predators. We revealed variability in the display of hunting in different species, methods of seizing the prey, and the number of attempts to attack an insect before catching it. We found specific flexible fragments within the "bite–grasp–handle" bouts that can be precursors for adaptive phenotypic variations and include some cognitive attributes. We hypothesise that the divergence and specialisation of predatory behaviour in rodents can be based on the natural fragmentation of the original hunting patterns, that is, on the loss or recombination of particular behavioural elements. We consider a possible link between the fragmentation of hunting behaviour and social learning in different classes of animals and conjecture an intriguing correlation between predatory activity, cognitive skills and personal traits in rodents.

Keywords Rodents · Behavioural patterns · Hunting tuplets · Flexibility · Learning · Cognition

Introduction

Members of many species, from ants to whales, demonstrate a sophisticated combination of behaviours: some are based on innate patterns, whereas others are flexible and cognitively demanding. An individual's behavioural phenotype is a combination of its unique behavioural propensities and its responsiveness to environmental variation, also known as behavioural plasticity (Guayasamin et al. 2017). Recently, many studies have explored the problem of the concept of behavioural plasticity encompasses all learning to adapt to the particular conditions of an individual's environment. Some of these publications (though not all of them) are relevant to comparative cognition (review in: Lea et al. 2020). Cognition, broadly defined, includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it (Shettleworth 2001). In contrast to this broad definition, soft around the edges, some authors consider "higher" behaviours as cognitive, from associative learning to concept and social learning (Reznikova 2007, 2021; Zentall et al. 2008; Pepperberg 2020). A recent review of intelligence in cephalopods considers the cognitive attributes that are thought to be precursors for more complex cognitive abilities (Schnell et al. 2021). Recent studies have demonstrated the role of behavioural variability and learning in adaptive phenotypic variations of such a complex instinctive behaviour as hunting in different classes of animals. Zoratto et al. (2018) found some variability in stereotyped prey capture sequences in cuttlefish, which could relate to personality traits in different contexts. The

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authors see a perspective to explore the potential interplay between personality and cognition in cephalopods. Investigating skilled movements of the hands and mouth in cricket capture and consumption in laboratory mice, Galvin et al. (2021) showed that practice is necessary for these behaviours to be linked together to result in an efficient outcome. The authors claim that, although the behavioural acts may be instinctive and species-typical, their effective use requires learning. Since Hailman (1969) demonstrated the influence of subtle forms of experience through his investigations of pecking in newly hatched sea gulls, we know that learning is involved in the emergence of many behaviours that are typical of a species. The notion of "fixed action pattern" was challenged by posing the question of "how fixed is a fixed action pattern" (Schleidt 1974). Basing on current research in this area, Blumberg (2017) concludes that species-typical behaviours develop under the guidance of species-typical experiences occurring within reliable ecological contexts.

One of the most intriguing problems in studying animal cognition is how learning abilities relate to species-specific behaviours and how hereditary components influence highly developed cognitive skills. For example, the multifaceted panorama of numerical reasoning in humans and non-human animals includes the core systems of processing numerical information (Beran 2008; Reznikova et al. 2019a), which seem rooted in our biological heritage (Nieder 2017). Not only primates (Beran and Beran 2004; Livingstone et al. 2014) but also ants (Reznikova and Ryabko 1994, 2011), honeybees (Howard et al. 2019), and newly hatched domestic chicks (Rugani et al. 2009) display impressive proto-arithmetic capacities. These examples of the close intertwining of innate behaviour and sophisticated cognitive abilities in different classes of animals enable us to investigate the precursors for the manifestation of intelligence in species-specific behaviour within ecological contexts. Predatory hunting is a good example of a complex species-typical behaviour involving different skills, some of which may include learning. There are many examples of consistent individual differences in the behaviour parameters even within a particular foraging method in different species. Behavioural ecology has revealed many cases where the behaviour of a given species varies depending on the environmental conditions, either between individuals living in different environments, or within the lifetime of an individual (review in Lea 2020). However, as far as we know, the current study presents the first attempt to distinguish between rigid and flexible parts in optional hunting behaviour in rodents and to find a potential interplay between predatory activity and cognitive skills in these animals.

Rodents are a diverse and thriving group of species, which occupy extremely diverse habitats requiring both very distinct motor specializations (Han et al. 2017; Whishaw et al. 2017) and flexible cognitively demanding skills (Rabi et al. 2017; Ferkin 2018; Reznikova et al. 2019a). Displays of hunting behaviour in rodents vary from highly specialised predation in carnivorous grasshopper mice to skilful but optional insect hunting in species with different types of diet (Timberlake and Washburne 1989; Langley 2021). We assume that optional predators such as some rodent species could serve as an even better model to study the variability of hunting behaviour than specialised predators, such as birds of prey, cats, dragonflies, cuttlefishes, and many others. We consider optional hunting when not all individuals in the population hunt, and those who hunt do not always do so. Note that all rodents can be considered omnivorous to some degree (Landry 1970). Insect-hunting studies have noted the high hedonistic value of insects to rodents (Comoli et al. 2005), which is possibly associated with the accumulation of certain microelements (Panteleeva et al. 2013). Hunting behaviour in wild non-predatory rodents towards live insects (such as crickets) has been studied in several rodent species, from highly carnivorous *Onychomys leucogaster*, through omnivorous (*Peromyscus californicus, P. maniculatus, P. leucopus*), to more herbivorous *Meriones unguiculatus, Acomys cahirinus, Sigmodon hispidus* (Timberlake and Washburne 1989), and *Myodes glareolus* (Konczal et al. 2016). The details of the hunting behaviour have been investigated mainly in the carnivorous grasshopper mice *O. leucogaster* and *O. torridus* (Langley 1994, 2021) that possess morphological and physiological adaptations as obligate predators (Rowe and Rowe 2008; Sarko et al. 2011; Rowe et al. 2013). Behaviourally, the predatory attack of carnivorous rodents differs from that of the omnivorous ones in their ability to overcome the flight initiation distance of potential prey, biting capabilities, use of their sensory modalities, seizure of prey, early and rapid development of a proficiency in its attack, vigour and resistance to inhibition of the attack (Langley 2021). Our recent studies revealed an optional hunting behaviour towards live insects (cockroaches) in nine herbivorous and granivorous rodent species (13 species in total, including those of the current study), which surprisingly appeared to be succinct and effective as much as in a specialised insectivorous predator common shrew (Reznikova et al. 2017, 2019b; Levenets et al. 2019a, b; Panteleeva et al. 2020a).

Here we present a thorough comparative analysis of spontaneous reactions to live insects (cockroaches) in nine rodent species under standard experimental conditions. We concentrate, in particular, on bite/grasp/handling bouts within their hunting sequences. In recent years, the ability of rodents to use their hands and fingers has attracted more and more attention to the evolutionary origins of the visiomotor mechanisms of reaching and grasping within the rodents-primate lineage (Karl and Whishaw 2013). Until recently, comparative studies of manipulatory activity in diverse rodent species included the movements used for handling motionless objects: mainly seeds and pasta (Whishaw et al. 2017). Manipulation of food objects including digit patterns (Whishaw and Coles 1996) and even tool use (Nagano and Aoyama 2017) has been studied in detail in rats, and these animals were shown to be able to catch moving crickets with a single paw (Ivanco et al. 1996).

There were no previous hypotheses of how the flexible segments within stereotyped behavioural patterns appeared during the evolutionary process. The current research demonstrates experimentally that the natural fragmentation, as a form of variability of optional insect hunting, manifests itself to different degrees in rodent species and may be the basis for the divergent evolution of hunting behavioural sequences in rodents. We revealed that there is variability in the display of hunting in different species, methods of seizing the prey, and the number of attempts to attack an insect before catching it in nine rodent species with different types of diet. We found flexible fragments of rodents' hunting patterns which can be precursors to cognitive abilities such as associative and social learning.

Methods

Terms and notions

To describe and compare hunting behaviours in rodents, we distinguish between *behavioural sequence*, as an arbitrary sequence of behavioural acts, and a relatively stable and recurrent chain of behavioural elements (a "tuplet"). In contrast to stereotyped actions displayed by cuttlefish (Zoratto et al. 2018) and zebrafish larvae (Mearns et al. 2020) catching their prey, in rodents, we consider complex sequences which include detection of a potential victim, chasing and biting it, and then seizing and handling. Applying a classical ethological approach, we consider behavioural elements (Lorenz 1950) as minimal units of behavioural sequences not mapping sub-second structure in rodents' "body language" (Wiltschko et al. 2015). In the previous studies (Reznikova et al. 2012, 2017), we used the term *behavioural stereotype,* referring to relatively stable and recurrent sequences of behavioural elements. However, this term can be confused with the unrelated term *stereotypies* (abnormal behaviour described, for example, in animals confined to zoos or farms, when animals lack control over important aspects of their environment (Broom 2019). The term *fixed-action pattern* historically has described behaviours in which a single ''releasing'' stimulus is sufficient to drive an entire sequence of movements (Tinbergen 1951). Recently, neurobiologists and ethologists have applied the term *stereotyped motor patterns* (Mearns et al. 2020) or strong stereotypic sequence pattern (Zoratto et al. 2018) to describe targeted sequences of stereotyped actions. Alternatively, ethologists use the term behavioural pattern in a general sense to denote identifiable types of behaviour (Levenets et al. 2019a, b a), including those patterns that have a socially learnt origin (Gruber et al. 2019). In the current study, we use the term behavioural pattern in its general sense to describe identifiable hunting behaviour. To denote a relatively stable and recurrent chain of behavioural elements, we suggest the term tuplet of elements of hunting behaviour ("*hunting* tuplet" or "behavioural tuplet" for brevity). This term, as far as we know, has not been used in behavioural literature and so should be not cause any confusion.

We call fragmentation a rearrangement or a complete loss of any part of a behavioural tuplet. Although Schleidt (1974) noted the possible absence or presence of a particular element out of which the pattern is composed, we did not find in the literature any other mentions of natural fragmentation of behavioural sequences. Fragmented behaviour is usually described in animals under stress, emotional and physical disorders as well as in hybrids (see details in "Discussion").

Study species and housing

The experiments were conducted in the laboratory in 2014–2019 on nine species of rodents with various types of diet and modes of social life. We used 61 Mongolian gerbils *Meriones unguiculatus* (31 females and 30 males), 21 fat-tailed gerbils *Pachyuromys duprasi* (12 females and 9 males), 22 East European voles *Microtus levis* (14 females and 8 males), 46 narrow-headed voles *Lasiopodomys gregalis* (23 females and 23 males), 28 Djungarian hamsters *Phodopus sungorus* (14 females and 14 males), 19 Campbell's dwarf hamsters *Ph. campbelli* (8 females and 11 males), and three species of high-mountain voles of the genus *Alticola*: 52 Tuva silver voles *A. tuvinicus* (26 females and 26 males), 104 Olkhon mountain voles *A. olchonensis* (42 females and 62 males), and 52 flat-headed voles *A. strelzowi* (25 females and 27 males). In nature, Mongolian gerbils live in groups and use a mixed type of diet, mainly consisting of seeds and plants; fat-tailed gerbils display various modes of social life, from solitary to colonial, and they are mostly insectivorous (Felt et al. 2008; Hoath 2009), but they also eat a variety of plants and seeds; high-mountain voles are mainly herbivorous and live in groups (Litvinov et al. 2013; Panteleeva et al. 2020a); Campbell's dwarf hamsters and Djungarian hamsters are solitary-living species that feed on grass and herb seeds, green plants, and insects (Levenets et al. 2019b); East European voles, similarly to common voles *Microtus arvalis*, is a predominantly herbivorous species with a family-group lifestyle (Levenets et al. 2019b); narrow-headed voles live in family groups and sometimes in colonies, which comprise several reproducing individuals and their offspring (Potapov et al. 2014; Modorov 2016), strictly herbivorous (Shuai et al. 2019).

Out of 61 Mongolian gerbils, 48 were born in the laboratory as the progeny of outbred animals purchased from breeders, while 13 were descendants of animals captured in Tuva in 2001 and bred at the Moscow Zoo. Fat-tailed gerbils were descendants of animals captured in Egypt in 2007 and bred at the same Zoo. Tuva silver voles and flat-headed voles are the descendants of the first and second generations of animals captured in the mountains of Altai and Khakassia in 2014–2015. From 104 Olkhon mountain voles, 11 individuals were caught shortly before experiments. Others were the descendants of the first generation of animals captured on the islands of Olkhon and Khubyn and the mainland coast of Baikal Lake in 2016–2018. All narrow-headed voles were caught shortly before the experiments in the Karasuk Field Station of ISEA (the south of Novosibirsk region). East European voles and Campbell's dwarf hamsters were descendants of animals bred in the Centre for collective usage "Gene pool of laboratory animals" of the Institute of Cytology and Genetics (ICG), and Djungarian hamsters were bred in the Vivarium of Institute of Systematics and Ecology of Animals (ISEA). All animals that were born in laboratory have not previously encountered live insects.

All animals were housed in plastic cages containing cotton nesting material under a 16:8 light/dark cycle at 23–26 °C. They were fed each day once and had ad libitum access to water. Members of herbivorous species were given hay or fresh grass, vegetables and fruits. Rodents with a mixed diet were given mixed seeds, dried shrimps, meal worms, and cottage cheese. All animals were provided with all types of food before being taken into experimental arenas. We chose cockroaches (of the average sizes of 26 mm) as suitable prey, since they are innocuous, easily overcome, palatable for rodents and do not induce defensive reactions in small mammals.

Experimental procedures

We placed each rodent in a separate plastic arena ($30 \times 30 \times 35$ cm) covered with a transparent lid to prevent animals from getting out. The experiments were conducted in lighted arenas. Experiments with laboratory mice have demonstrated that vision is necessary for them to perform accurate orienting and approach behaviours leading to prey capture (Hoy et al. 2016). Animals were tested individually, once a day, with the intervals of 1–2 days between the test sessions. All laboratory-reared animals were naïve with respect to the potential victim. The number of test sessions varied from 3 to 10 in different species and depended on the degree of manifestation of hunting behaviour (protocol details in: Levenets et al. 2019a; Reznikova et al. 2019b; Panteleeva et al. 2020a). In each trial, the insect was placed into the arena manually, 5 min after the rodent. In cases of unsuccessful hunting, we waited for 10 min since the last contact between the animal and the prey, and then finished the observation. Each animal received between one and three insects in turn during each test session. Video recordings were made using a Sony Handycam DCR-SR68 camera (frame rate, 25 frames per second) and a Sony HDR-AS200V (60 frames per second). After each test, the arena was cleaned using 70% alcohol. In total, we obtained 3374 video records with the total duration of 381 h.

Video processing was carried out at 5–25 times slowdown in the Observer XT 12.5 software (Noldus Information Technology). The unit of time used to measure the length of a video is 0.01 s. Similarly to the previous studies (Reznikova et al. 2017, 2019b), we used an alphabet of 19 letters devised for the analysis of hunting behaviours. For example, the "bite" includes a piercing contact of the hunter's teeth with prey, damaging or scratching the insect's integument. "Seizing the insect with paws" includes grabbing the prey with both forepaws and lifting it in front of the muzzle. A letter is assigned to each of the elements of behaviour, in the order of their appearance, without taking into account their duration. For example, if a rodent pursued the insect by walking for a few seconds and then captured it with paws, the sequence would be SE ("S" for walking and "E" for seizing with paws, irrespective of the duration of the walk). If the animal repeated a behavioural act several times, then the corresponding letter was repeated. For example, seizing with paws 4 times is recorded as EEEE, seizing with paws and then handling ("R") twice is recorded as ERR. Thus, we obtained sequences of letters encoding the hunting tuplets observed, such as: QWEWER, SEWEHSWEHSEWWEHR, etc. For example, QWEWER means the following sequence of elements (see details in "Results"): running (Q), biting (W), seizing the insect with paws (E), biting again (W), seizing with paws again (E), handling the prey (R).

We call "successful" all cases of hunting that ended with catching the prey (even after several false attacks), and the rest of the situations we call "unsuccessful." We consider capturing, not eating the prey, as a criterion of success because we investigate the hunting and not the foraging behaviour. All animals received enough protein food outside the experiments, and they did not always eat the insects they captured. Note that an animal could manifest its attempts to hunt during subsequent tests, and not from the very first test. We evaluated the number of successful and unsuccessful cases of hunting as well as the number of different behavioural elements per hunting tuplet. Based on the results of the first three tests, we compared the number of animals who did not show interest in prey ("non-hunters") with those who actively interacted with the victim, pursued and attacked it, regardless of the success ("hunters").

We investigated the intraspecific variability of the hunting behaviour of rodents according to the following characteristics: (1) manifestation and the degree of success of hunting behaviour; (2) method of starting the attack: by seizing the prey using teeth or paws; (3) the number of unsuccessful attempts to attack the prey before catching it. Statistical analysis was performed using Fisher's exact test in free statistical software "R" (v.3.6.0); the alpha level is 0.05, with Bonferroni amendment it is 0.0014.

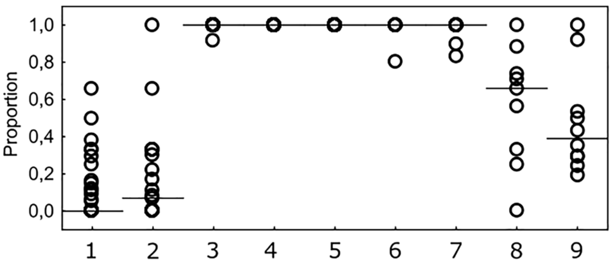

Fig. 1 The proportion of attacks that began with biting in the complete stereotypes of successful hunters. Numbers indicate species: (1) Mongolian gerbil ($n=30$), (2) Fat-tailed gerbil ($n=21$), (3) Tuva silver vole ($n=39$), (4) Flat-headed vole ($n=30$), (5) Olkhon mountain vole ($n=71$), (6) East European vole ($n=7$), (7) Narrow-headed vole ($n=11$), (8) Campbell's dwarf hamster ($n=8$), (9) Djungarian hamster ($n=11$). The species and corresponding numbers of animals are the same as in Fig. 2. The line indicates the medians

Results

Hunting activity

According to the results of the first three tests, we compared the proportion of "hunters" and "non-hunters" in different species. We also evaluated the ratio of successful hunts cumulatively, according to the results of all tests (Table 1). The largest (relative) number of hunters was observed in the fat-tailed gerbils, and the smallest in the narrow-headed voles and Djungarian hamsters. In the fat-tailed gerbil, the proportion of hunters was higher than in all other species, except the Tuva silver vole and the East European vole. In the latter species, the data were insufficient to detect significant differences from any of the other species. We did not reveal significant differences in the ratio of hunters between the sexes in any of the species (Fisher's exact test): in Mongolian gerbils (15 females out of 29, 16 males out of 32), Tuva silver voles (17 females out of 26, 18 males out of 26), East European voles (8 females out of 14, 5 males out of 8), flat-headed voles (16 females out of 29, 13 males out of 23), and narrow-headed voles (8 females out of 23, 9 males out of 23) $p=1$; in fat-tailed gerbils (11 females out of 11, 9 males out of 10) $p=0.48$, in Olkhon mountain voles (26 females out of 49, 31 males out of 55) $p=0.85$, in Campbell's dwarf hamsters (4 females out of 8, 7 males out of 11) $p=0.66$, and in Djungarian hamsters (4 females out of 14, 7 males out of 14) $p=0.44$. In some individuals, the first display of hunting behaviour ended with capturing the prey; these individuals immediately demonstrated the hunting tuplet in full (Table 1). It is worth noting that among the voles, some individuals hunted but never caught the prey in any of the tests: 6% (3 out of 52) in Tuva silver vole, 6% (3 out of 52) in flat-headed vole, 22% (5 of 22) in East European vole and 13% (6 of 46) in narrow-headed vole.

The structure of hunting tuplets in different rodent species

In all voles, all attacks on prey began with seizing it with the teeth (bite). If an animal managed to grab the insect with its teeth, it handled it with both forepaws. Note that rodents bring the prey to their mouth to eat, in contrast to shrews, which pin an insect down to the ground with one paw (see Reznikova et al. 2017). In each of the vole species, we observed isolated cases when the attack began with seizing the insect with paws, but all these attacks were unsuccessful (Fig. 1). Gerbils and hamsters were able to start attacking the insect both with their teeth and forepaws.

Table 1 Hunting success in different species

Species	Proportion of hunters (first three tests)	Proportion of animals hunted successfully from the first time (first three tests)	Proportion of successful hunts (all tests)
Mongolian gerbil	51% (31 out 61)^{a,d}	74% (23 out 31)^{a,c}	60% (133 out 221)
Fat-tailed gerbil	95% (20 out 21)^{b,c}	55% (11 out 20)^{a,b}	68% (75 out 110)
Tuva silver vole	67% (35 out 52)^{a,c}	51% (18 out 35)^{a,b}	52% (175 out 335)
Flat-headed vole	56% (29 out 52)^{a,d}	55% (16 out 29)^{a,b}	59% (151 out 257)
Olkhon mountain vole	55% (57 out 104)^{a}	84% (48 out 57)^{a}	75% (435 out 577)
East European vole	59% (13 out 22)^{a,c,d}	8% (1 out 13)^{b}	11% (18 out 160)
Narrow-headed vole	35% (16 out 46)^{d}	25% (4 out 16)^{b,c}	27% (34 out 126)
Campbell's dwarf hamster	53% (10 out 19)^{a,d}	11% (2 out 19)^{b}	51% (43 out 85)
Djungarian hamster	25% (7 out 28)^{d}	57% (4 out 7)^{a,b}	74% (74 out 110)

Different letters in each column indicate significant differences between species ($p<0.0014$) according to Fisher's exact test with Bonferroni amendment. See the values of the criterion in Table 1A

Since the elements “bite” and “seizing with paws” are critical for the successful capture of prey, we consider them to be “key elements” of the hunting tuplet. However, gerbils can start their attacks successfully without the help of the jaws, only with the use of the paws. Therefore, gerbils have one key element (seizing with paws). Elements that are not directly related to prey capture but play a particular role in hunting behaviour are called “auxiliary” (for example, “running”, “handling”, “carrying the prey in the teeth”, etc.). The third group consisted of the “noise” elements which do not influence the performance of the hunting tuplet at all: free-standing rearing, self-grooming, jump, and some others (details in Reznikova et al. 2017). The time intervals between the behavioural elements “biting” and “seizing with paws”, regardless of their order within sequences, are given in Table 2 according to the results of all tests.

Table 2 The time interval (in seconds) between the behavioural elements “bite” and “seizing the prey with paws” and the number of attacks preceding the successful capture of prey

Species	Interval (in seconds) Median (Min–Max)	Number of attacks Median (Min–Max)
Mongolian gerbil	0.24 (0.02–0.96)	0 (0–9)
Fat-tailed gerbil	0.24 (0.04–0.88)	1 (0–5)
Tuva silver vole	0.20 (0.02–0.88)	1 (1–5)
Flat-headed vole	0.20 (0.04–0.60)	1 (1–4)
Olkhon mountain vole	0.20 (0.04–0.92)	1 (1–7)
East European vole	0.07 (0.03–1.08)	1 (1–7)
Narrow-headed vole	0.13 (0.02–0.64)	1 (1–51)
Campbell’s dwarf hamster	0.04 (0.02–0.64)	3 (1–14)
Djungarian hamster	0.13 (0.02–0.67)	2 (1–8)

In the case of a successful attack, rodents could handle the prey with their paws, turn, move to another place in the arena, and then proceed to eat (Fig. 2a). Sometimes, having bitten the insect, a rodent with a cockroach in its teeth moved to another place in the arena and then grabbed it with its paws (Fig. 2b). If the first attack was unsuccessful, that is, the rodent failed to grab the prey, or if the captured cockroach slipped out, then one or more attacks could follow (Fig. 2c, d). The hunting tuplets, which include both key elements in voles and hamsters, are called complete; such tuplets could be both successful and unsuccessful. In some cases, the grip with the teeth did not follow seizing with the paws (Fig. 2e, f, g), and such attacks were not successful. In such cases, we refer to these behavioural elements as “dropped out” of the hunting tuplet. If seizing with paws dropped out after each bite (Fig. 2g), we call this tuplet incomplete. Obviously, incomplete tuplets could not be successful. Gerbils could make several seizures with their paws in a row and catch prey, after which auxiliary elements that precede eating followed. Note that only gerbils can successfully catch insects among the species studied without the help of their jaws (Fig. 2h). In hamsters, after successful capture of the insect with their paws, a bite preceding eating necessarily followed (Fig. 2i, j).

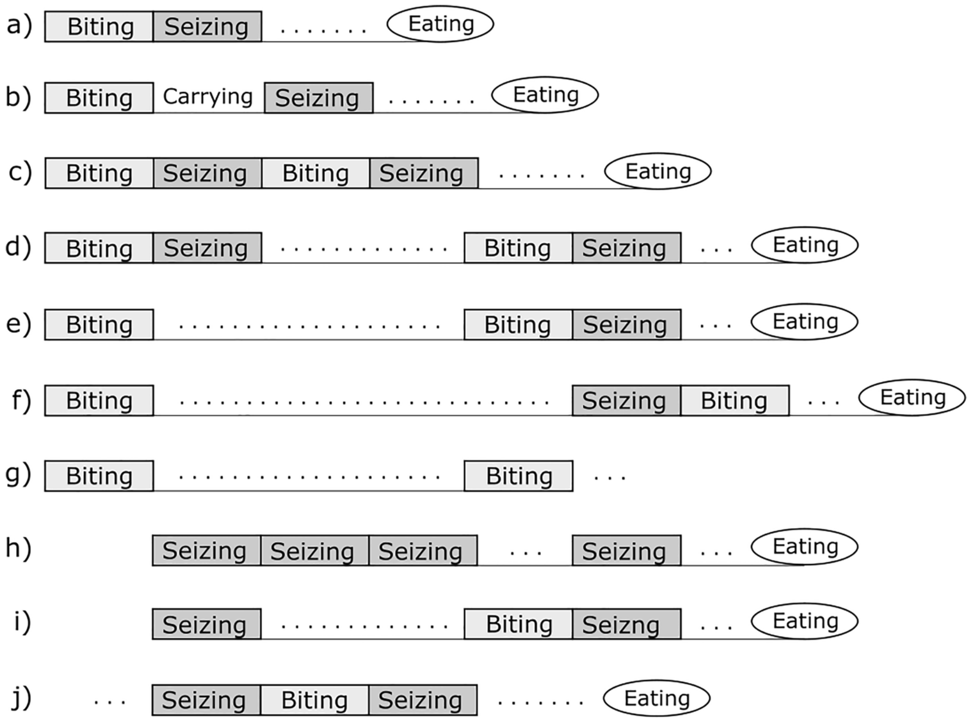

Fig. 2 Variants of the arrangement of behavioural elements in the hunting stereotypes of rodents. “Seizing with paws” and “biting” are the key ones. Dots show “auxiliary” and “noise” elements. The element “eating” indicates that the stereotype may end in catching the prey

The number of unsuccessful attacks preceding the successful capture of prey varied (Fig. 3). Only gerbils could successfully catch their prey at the first attack; the maximum number of attacks was 9 for the Mongolian gerbil and 5 for the fat-tailed gerbil. In all other species, successful capture was preceded by at least one unsuccessful attack; the maximum number of attacks was recorded in the narrow-headed vole (Table 2). The most significant variability in the ways the attacks began (starting with seizing with paws or with biting) was found in gerbils and hamsters (Fig. 1).

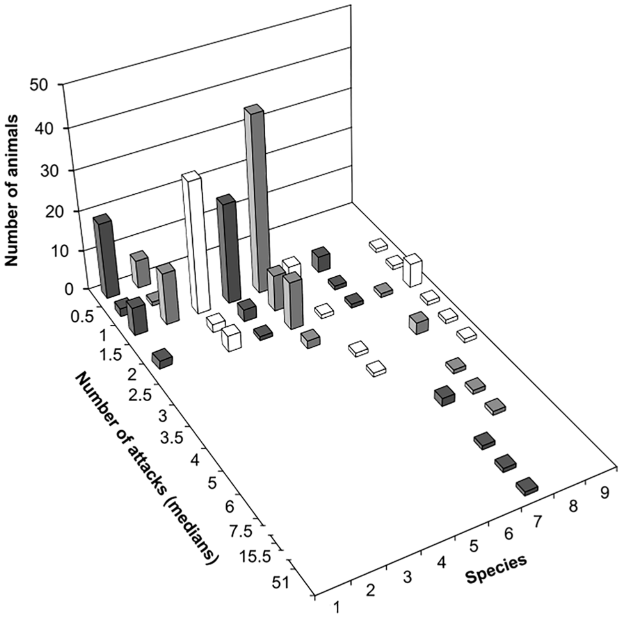

Fig. 3 Median values of unsuccessful attacks preceding the successful capture of the prey (cumulative data on all hunting animals). Numbers indicate species. The species and corresponding numbers of animals are the same as in Fig. 1

We compare the composition of behavioural elements in hunting tuplets in different species (Table 3). To eliminate the possible effect of pseudo-replication, we applied a randomization procedure: we randomly selected approximately 50% of the entire pool of tuplets obtained for each species. When considering non-successful tuplets, one can see some elements dropping out in some situations (Table 3). The element "seizing with paws" dropped out from the unsuccessful tuplets most often in the Olkhon mountain vole and the flat-headed vole, less often in the Tuva silver vole and the narrow-headed vole, even less often in the Campbell's dwarf hamster and the Djungarian hamster and never in either of the gerbils species. The element "biting" turned out to be a necessary one for all successful tuplets in hamsters and voles, but not in gerbils (see Supplementary Videos 1, 2). As one can see in Table 3, the proportion of successful tuplets in which the element "biting" was absent was 8.6% (5 out of 58) in Mongolian gerbils and 31.6% (12 out of 38) in fat-tailed gerbils. This means, as mentioned before, that when

Table 3 The proportion of hunting tuplets with various combinations of the elements "seizing the prey with paws" and "biting"

Species	The proportion of tuplets in which the element "seizing the prey with paws" dropped out		The proportion of tuplets in which the element "biting" dropped out		The proportion of attacks starting with the element "biting"	
	Successful	Unsuccessful	Successful	Unsuccessful	"Complete"	"Incomplete"
Mongolian gerbil	0.0%^{a} (0 out of 58)	0.0%^{a} (0 out of 51)	8.6%^{a} (5 out of 58)	68.6%^{a} (35 out of 51)	11.4%^{a} (21 out of 184)	NA
Fat-tailed gerbil	0.0%^{a} (0 out of 38)	0.0%^{a,b} (0 out of 15)	31.6%^{b} (12 out of 38)	13.3%^{b,c} (2 out of 15)	13.4%^{a} (9 out of 67)	NA
Tuva silver vole	0.0%^{a} (0 out of 90)	20.8%^{b} (15 out of 72)	0.0%^{a,c} (0 out of 90)	1.4%^{c} (1 out of 72)	99.4%^{b} (176 out of 177)	94.1%^{a} (16 out of 17)
Flat-headed vole	0.0%^{a} (0 out of 66)	35.8%^{b} (19 out of 53)	0.0%^{a,c} (0 out of 66)	0.0%^{c} (out of 53)	100.0%^{b} (127 out of 127)	100.0%^{a} (20 out of 20)
Olkhon mountain vole	0.0%^{a} (0 out of 196)	34.7%^{b} (25 out of 72)	0.0%^{c} (0 out of 196)	0.0%^{c} (0 out of 72)	100.0%^{b} (348 out of 348)	100.0%^{a} (34 out of 34)
East European vole	0.0%^{a} (0 out of 8)	15.6%^{b} (13 out of 83)	0.0%^{a,c} (0 out of 8)	2.4%^{c} (2 out of 83)	96.1%^{b} (149 out of 155)	90.0%^{a} (20 out of 22)
Narrow-headed vole	0.0%^{a} (0 out of 15)	28.9%^{b} (13 out of 45)	0.0%^{a,c} (0 out of 15)	0.0%^{c} (0 out of 45)	98.0%^{b} (99 out of 101)	100.0%^{a} (14 out of 14)
Campbell's dwarf hamster	0.0%^{a} (0 out of 26)	5.3%^{a,b} (1 out of 19)	0.0%^{a,c} (0 out of 26)	21.1%^{b,c} (4 out of 19)	68.4%^{c} (91 out of 133)	20.0%^{b} (1 out of 5)
Djungarian hamster	0.0%^{a} (0 out of 48)	12.5%^{a,b} (3 out of 24)	0.0%^{a,c} (0 out of 48)	29.2%^{b} (7 out of 24)	32.1%^{d} (50 out of 156)	25.0%^{b} (3 out of 12)

Different letters (a, b, c, d) inside each column indicate the significant differences according to Fisher's exact test with Bonferroni amendment ($p < 0.0014$), See the values of the criterion and their significance in Table 2A; "NA" (not available): incomplete tuplets do not exist in these species of gerbils attacking the insect, gerbils do not need to use their jaws, they only need to capture the victim with paws for success. It is worthy of noting that Mongolian gerbils displayed more unsuccessful tuplets that lacked biting (65.9%, 58 out of 88) than successful ones (12%, 16 out of 133) (Fisher's exact test, $p < 0.01$). Although the bite is not necessary for the Mongolian gerbil to capture the insect, it likely contributes to success. The element "biting" dropped out from the unsuccessful tuplets more often in Mongolian gerbils (68.6% of cases) than in the following three species ($p < 0.01$): fat-tailed gerbils (13.3%), Campbell's dwarf hamsters (21.1%), and Djungarian hamsters (29.2%).

Analysing those cases of insect hunting when some elements drop out of the tuplet, we found the flexible fragments within the key "bite-grasp-handle" bouts. In successful hunting tuplets of all species, seizing with paws is always present before eating the prey (Table 3). Zeros in the column 1 (Table 3) indicate that the element "seizing with paws" never drops out of successful tuplets. During unsuccessful hunting, in five vole species, this element drops out in nearly a quarter of cases (see Supplementary Video 3), whereas this rarely happens in hamsters, and never in gerbils. Gerbils in most cases start their attacks from seizing the insect with their paws (88.6% of complete tuplets in Mongolian gerbils and 86.6% in fat-tailed gerbils) (see Table 3). In contrast, voles, in nearly in all of the cases, and hamsters, in some of the cases, start their attacks by capturing the insect with their teeth. The element "biting" turned out to be a strongly necessary element for successful hunting in all voles and hamsters. Taking into account the fact that the element "seizing the prey with paws" never drops out of either successful or unsuccessful tuplets in gerbils, one can suggest that "seizing with paws" is a crucial element of hunting tuplets in these animals, whereas the "biting" is not. In contrast to voles and similar to gerbils, hamsters often start their attacks from capturing insects with their paws: 67.9 and 31.6% of complete tuplets and 75 and 80% of incomplete tuplets in Djungarian and Campbell's dwarf hamsters correspondingly. However, in contrast to gerbils, in hamsters, the attacks that start with seizing the insect with paws and do not include biting always fail.

Discussion

Summing up our data with those in previous studies (Reznikova et al. 2017, 2019b; Levenets et al. 2019a, b; Panteleeva et al. 2020a, b), we now have 13 rodent species with different types of diet that manifest skilful attacks towards highly mobile insects in a manner that is typical for specialised predators chasing a fleeing prey. Herbivorous and granivorous species keep in their repertoire and display in all details the same hunting tuplet with that of insectivorous predators. In contrast to the grasshopper mice, which possess morphological and physiological adaptations as obligate predators (Langley 1994, 2021; Rowe and Rowe 2008; Rowe et al. 2013), these species lack any specific predatory traits; instead, they display the hunting pattern as a behavioural adaptation that helps them to include live insects in their diet. The question arises whether adaptive phenotypic variations of foraging behaviour include some cognitive attributes.

Reznikova et al. (2019b) considered variability of the order of committing behavioural elements in hunting tuplets in eight rodent species, applying the data-compression method to compare ethograms as ethological "texts". This approach (Ryabko et al. 2013) allows one to search for regularities within sequences of symbols using data compressors. The authors found the most variable and complex behaviour in the Norway rat, a generalist predator. Out of the species investigated in the current study, variabilities in composition of hunting tuplets were found in narrow-headed vole, Tuva silver vole, Campbell's dwarf hamster, and Djungarian hamster (Reznikova et al. 2019b). In the current study, variabilities in the display of hunting, methods of attacking the prey, and the number of unsuccessful attempts to attack the insect before catching it were revealed in all of the species studied.

The display of hunting behaviour within laboratory groups of animals varied in different species: from 33.3% "hunters" in Djungarian hamsters to 67.3% in Tuva silver voles and 95.2% in fat-tailed gerbils (Table 1). We do not assume that these ratios of behaviour phenotypes are the same in natural populations, since they may vary as a flexible response to novel environmental conditions (sensu: Foster 2013). Experiments on the bank vole showed that the percentage of hunting individuals could be selectively increased within the space of several generations (Konczal et al. 2016). These experiments support our hypothesis about switching to insect hunting as a possible evolutionary stable strategy in rodents (Panteleeva et al. 2020b). In some individuals, the first hunt ended with capturing the prey, that is, they immediately demonstrated the hunting tuplet in full: from 8% in East European vole and 11% in Campbell's dwarf hamster to 80% in Olkhon mountain voles (Table 1). Thus, the success of hunting is rather variable in different species. However, in all our species, the interval between seizing the mobile prey with paws and biting was short, indicating a highly stereotypical and purposeful hunting behaviour (Table 2). Note that all laboratory-reared animals were naïve with respect to the potential victim. We suppose that similarly with the recent mice hunting study (Galvin et al. 2021), some of our rodents have had to encounter live prey several times to activate their innate neural circuits and to establish a link to species-typical hunting behaviour. Han et al. (2017)

delineated a neural network that integrates distinct predatory patterns in laboratory mice.

The methods of pursuing the prey also varied in the species studied. We found two ways the animals start an attack: biting with the teeth and seizing with the paws. Voles behaved most conservatively, starting their attacks with their teeth, and only rarely did they attempt (unsuccessfully) to seize the insect with forepaws. We found the most significant variabilities in the ways the attacks began in gerbils and hamsters (Fig. 1). Gerbils and hamsters started attacking insects with both teeth and paws, and displayed most significant variabilities in these behaviours. Most of the hamsters displayed both methods (Fig. 1), while in gerbils, the attack often started from seizing the prey with paws. We revealed an essential variability of the number of unsuccessful attacks preceding the capture of prey (Table 2, Fig. 3). In 63% (19 out of 30) individuals in Mongolian gerbils and 33% (7 out of 21) in fat-tailed gerbils, the first attack was already successful; they needed a maximum of 9 and 5 encounters, respectively. Gerbils could attack the prey and immediately grab it; the rest of the species need at least one unsuccessful attack before successfully capturing the insect. This feature is explained by the fact that gerbils can catch prey only with their paws without the assistance of their jaws, while voles and hamsters strongly need to perform the two actions—to grab the insect with their teeth and paws. The probability of failure, in this case, is higher than when only one action is used. In voles, the order of elements during an attack is rigid: a bite and then a seizure with paws. As noted before, in contrast to shrews that eat live prey without picking it up but pressing it to the ground (Reznikova et al. 2017), rodents lift an insect to the mouth with their hands and then manipulate it in a manner described by Whishaw et al. (2017) for laboratory mice eating pasta. Without bringing the prey to their mouths with their paws, rodents cannot start eating it. If seizing with paws drops out at this stage, or the animal fails to keep the prey, it must attack again. Unlike voles, hamsters can start an attack with either a bite or a seizure with paws. However, to complete an attack successfully, they also need the sequential performance of the two elements.

The presence of flexible fragments of hunting tuplets indicates a link to cognition. From the evolutionary point of view, it is interesting to consider the variability of a hunting pattern that plays a different role in the adaptations of different species: necessary to some, and spurious or atavistic in others. The fact that there is a variety of herbivorous and granivorous species that have preserved an optional hunting pattern in their repertoire makes this type of behaviour a good candidate for studying the interplay between rigid and flexible traits. We consider the natural fragmentation of hunting patterns in rodents as a possible evolutionary source of novel behaviours and suggest that, in some situations, learning may be the mechanism facilitating the establishment of novel traits.

The idea of the evolution of behavioural patterns based on particular species-specific fragments goes back to Heinroth (1911), who proposed using parts of behavioural sequences in birds to determine differences between species. Parts of the ancestral behavioural patterns can appear in the behaviour of modern species rather unexpectedly if this gives an evolutionary advantage. For example, opening molluscs' shells in a way characteristic only of oystercatchers was observed in dabbling ducks endemic to New Zealand (Moore and Battley 2003). This behaviour was possibly inherited from common ancestors and became a stable part of the foraging pattern. Recently, on the example of ancestral (oceanic) and benthic (freshwater) populations of the three-spine stickleback fish, Foster et al. (2019) demonstrated that unexpressed phenotypes can persist for thousands or more generations in a condition that permits re-expression when an appropriate stimulus appears in the environment. In the current study, we consider the possible role of natural fragmentation of hunting patterns in the evolution of predatory behaviour in rodents, trying to find out a window of opportunity for cognitive decisions.

Fragmented behaviour is usually described in animals under stress, emotional and physical disorders (Molet et al. 2016). For example, in stressful situations, laboratory rats skip distinct stages of grooming, change their sequence, or fail to complete it (Kalueff et al. 2007). Some vivid examples of fragmentation of behavioural patterns come from hybrids. A classic example is that of hybrids of a yellow-collared lovebird and a rosy-faced lovebird, which show alternating fragments of patterns of transporting nesting materials of the parent species (Dilger 1962). The patterns of inheritance of the coyote defensive threat gestures in coyote-beagle hybrids provide an impressive example of the complexities involved in the inherited patterns of communication (Moon-Fanelli 2011). Coyotes display a mouth-gape threat with attendant arched back defensive posture; this threat display is absent from the repertoire of the domestic dog and the grey wolf. Hybrids displayed the changeover from the dog snarl-threat to the coyote gape-threat. In natural situations, as far as we know, fragmented behaviour has been studied in playing animals only (Bekoff and Byers 1998; Dinets 2015).

Focusing on which fragments the hunting pattern in rodents can consist of, we found the flexible segments within the key "bite–grasp–handle" bouts (Table 3). In gerbils and hamsters, the "bite–grasp" bout turned out to be the most flexible segment of their hunting tuplets. Whereas dropping a single element can sometimes result in unsuccessful hunting, we hypothesize that the natural fragmentation of the original hunting pattern may lead to the divergence and specialization of predatory behaviour in rodents. The natural fragmentation of the original complex pattern enables the loss or recombination of particular behavioural elements by means of microevolutionary processes. Several studies on neurophysiological mechanisms of insect hunting in mice and rats (Comoli et al. 2005; Dos Santos et al. 2012; Han et al. 2017) enable us to suggest that different genes might regulate the flexible and the stable parts of the hunting tuplet.

Basing on the example of the carnivorous grasshopper mice, Langley (1994, 2021) suggests that starting the attack by seizing the prey with paws is an indicator of predatory specialisation and, accordingly, an evolutionary advancement of hunting behaviour. In our experiments, all rodents use their paws when interacting with mobile prey. However, the start of the attack differs in different species in accordance with the Langley's (1994) statement, that is, the use of the paws when attacking indicates more specific predatory behaviour. Summing up our data obtained on optional predatory behaviour in 13 rodent species, we conclude that voles demonstrate a "core" and somewhat primitive scheme of a hunting pattern: approaching a potential victim, biting it, and then seizing and handling. Hamsters display the tendency to start their attacks by actions with paws, but they can achieve success only using teeth as well. Gerbils can successfully use both paws and teeth to start an attack, which brings their hunting behaviour closer to that of specialised rodent predators (Fig. 1).

We assume that the fragmentation might serve as a source of new behaviours. There is only one case described in the literature regarding the natural fragmentation of species-specific behaviours in *Myrmica* ants (Reznikova and Panteleeva 2008). The behaviours studied were those the ants use for hunting jumping springtails, which are difficult to catch and are not *Myrmica*'s typical prey. That is, the specific complex hunting pattern revealed is optional. Within ants populations, there were carriers of an "at once and entirely" available hunting pattern and specimens with only fragments of it. The authors suggest that "distributed social learning" plays an important role in spreading new traditions in animal communities: initial performances by a few carriers of the complete hunting pattern propagate this type of behaviour among specimens which have only dormant fragments of it. Spread of these behaviours in populations is based on relatively simple forms of social learning, such as social facilitation. Social learning may underlay species-specific predisposition to learn certain sequences of behavioural acts. To be triggered, carriers of dormant fragments of a relevant hunting pattern should encounter performances of this behaviour with sufficient frequency. The study of the ritual courtship behaviour in *Drosophila* (Pan and Baker 2014) can support the hypothesis of distributed social learning (Reznikova and Panteleeva 2008). In *Drosophila* study, males with a missing gene responsible for essential details of mating behaviour, can learn the missing elements of this behaviour when kept in a group, which leads to successful mating. We conjecture that in both insect studies, social learning serves as the driving mechanism of filling the missing fragments of behaviour. Our preliminary results obtained on Mongolian gerbils enable us to suggest that some individuals can learn the missing fragments of the hunting behaviour when observing the carriers of the complete pattern, similar to how it has been shown in insects (Reznikova and Panteleeva 2008; Pan and Baker 2014). We are planning experiments to examine the possibility of completion of predatory pattern in "spectators" when observing successful hunting in "actors."

We also assume an intriguing link between predatory activity, cognitive skills, and personal traits in rodents. It is possible that optional predatory behaviour can create precursors for the manifestation of exploration and cognitive abilities. In experiments on the multi-purpose artificial selection of bank voles, members of the predatory line with high intensity of predatory behaviour tended to be bold, and they moved faster and on straighter trajectories in the open field, whereas members of the "herbivorous line" moved slower and were less explorative (Maiti et al. 2019). The striped field mouse, which is one of the best "hunters" among our species studied (Reznikova et al. 2017, 2019b), appeared to display a high accuracy in distinguishing between large numbers of geometric items at a level comparable with monkeys (Reznikova et al. 2019b). The authors found striking individual variation in cognitive performance among striped field mice and considered this variability in the context of cognitive specialisation within rodents' populations (sensu: Reznikova 2007). These variable cognitive skills are likely to be based on the ability of wild hunters to capture subtle changes in their environment. It is possible that at the level of intraspecific variability, there is a correlation between predatory activity and characteristics of attention and learning in optional predatory rodent species. It is also possible that predatory behaviour traits correlate with personality measures in other contexts, as was recently suggested in cuttlefishes (Zoratto et al. 2018). Until recently, hunting behaviour has been overlooked in the context of studying individual variability. Our preliminary results enable us to hypothesize a correlation between hunting activity and the level of exploration in Mongolian gerbils. We are planning experiments to examine whether agile hunters are also fast learners in rodents.

Finally, we conjecture that the divergence and specialisation of predatory behaviour in rodents can be based on the fragmentation of the original hunting pattern, that is, the loss or recombination of some behavioural elements. Further investigation of this phenomenon may give insight into the evolutionary and cognitive mechanisms of predatory behaviour.

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Author contributions Study concept and design: ZR, SP, JL, and AN methodology: ZR, SP, JL, and AN. Software: JL and AN. Acquisition of data: SP, AN, JL, YL, and NL. Analysis and interpretation of data: all authors. Writing original draft: ZR, SP, JL, and AN. Writing, review and editing: all authors. Funding acquisition: ZR. Resources: YL, NL, AN, and JL. Supervision and project administration: ZR and SP.

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Declarations

Conflict of interest The authors have no conflicts of interest or competing interests.

Ethical approval All 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 Institute of Systematics and Ecology of Animals Siberian Branch Russian Academy of Sciences (protocol No. 1 from 14.04.2014).

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