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# Advances in ethological approaches to explore rodent vocal communication

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Vocal communication is widespread across animals, from mammals to amphibians. In recent years, rodents have become an increasingly valuable group in which to study vocal communication. Rodents offer rich opportunities to examine vocalizations from proximate and ultimate ethological perspectives. Here, we identify recent advances in ethological research on rodent vocal communication by synthesizing contemporary studies from the past decade. We carried out a scoping review of research published between 2014 and 2024. This review involved a broad search for peer-reviewed primary research studies in APA PsycINFO, Embase, MEDLINE, PubMed, Scopus, and Web of Science databases. The search yielded 403 eligible studies on rodent vocalizations. We extracted information about the ethological perspectives, species, research environment, and animal sex and age groups. We also identified studies that focused on method development. We found that rodent vocal communication studies varied across ethological perspectives, with more studies carried out on vocal mechanisms and adaptive functions than on development and evolution. These studies covered a broad range of 88 rodent species, with high species diversity in function and evolution studies and low species diversity in mechanism studies. Artificial environments were used more often than naturalistic environments, especially in mechanism and development studies. Naturalistic environments were common in function and evolution studies. Adult males were used more often than any other sex and age groups. The use of age groups, but not sexes, varied across ethological perspectives. Together, these findings highlight several advantages of contemporary rodent research, including opportunities to carry out in-depth studies of vocal mechanisms and to compare diverse species. Based on these findings, we also identify potential areas for future research. These research areas include non-mechanistic

questions, as well as expanding species diversity, research environments, and animal sex and age groups. Rodent research from multiple ethological perspectives will be crucial for building a comprehensive understanding of animal acoustic communication.

#### KEYWORDS

**Rodentia, vocalization, acoustic signaling, evolution, function, development, mechanism, methods**

## 1 Introduction

Vocalization is a fundamental behavior for communication in animals. As an ancestral form of acoustic signaling, vocalizations have a long phylogenetic history spanning tetrapod vertebrates from amphibians to mammals (Kelley, 2022). Individuals use vocalizations to convey information about their physical status and internal states, as well as information about the outside world like predators and food resources. Several decades of ethological research have been carried out on animal vocalizations from both proximate (mechanism and development) and ultimate (function and evolution) perspectives. This combination of ethological perspectives was initially described by Niko Tinbergen (e.g., Tinbergen's four questions) (Tinbergen, 1963), and it has become a valuable integrative framework to study animal behavior (Krakauer et al., 2017). Most ethological research on animal communication, however, has been biased towards a handful of taxonomic groups, such as primates, birds, bats, and anurans (Nieder and Mooney, 2019; Mooney, 2020; Janik and Knörnschild, 2021; Kelley, 2022). To build a comprehensive understanding of the proximate and ultimate origins of acoustic communication, investigations are needed across a broader species range.

Rodents are another promising taxonomic group for exploring acoustic communication. With over 2,000 species, the order Rodentia makes up about 40% of known mammal species (Solari and Baker, 2007). Although traditionally, rodents were used as a model for olfactory communication (Eisenberg and Kleiman, 1972; Johnston, 2003), a complementary body of research also explored rodent communication in acoustic channels. Some of the first studies on rodent vocal communication were done in the mid-20<sup>th</sup> century, when researchers discovered that rats and mice can hear and vocalize in the ultrasonic frequency range (> 20 kHz), similar to bats (Gould and Morgan, 1941; Dice and Barto, 1952; Anderson, 1954; Rosenzweig et al., 1955; Zippelius and Schleidt, 1956; Ralls, 1967). Indeed, 'bat detectors' were some of the first types of equipment used in rodent studies (Brudzynski, 2009). Building on these initial discoveries, research shifted towards characterizing rodent vocalizations and their potential functions. One line of work showed that infant vocalizations may facilitate maternal care (Sewell, 1970; Noirot, 1972; Colvin, 1973). Another

line of work showed that adult vocalizations may facilitate social interactions like mating and aggression (Barfield and Geyer, 1972; Sales, 1972a, 1972b; McIntosh et al., 1978; Nyby and Whitney, 1978; Pomerantz et al., 1983). Together, these initial studies revealed that rodent species vocalize at a wide range of frequencies, from ultrasonic vocalizations to lower frequency calls (< 20 kHz) that are audible to humans (Roberts, 1975).

The turn of the century brought with it the widespread use of microphones and speakers integrated with computer software for acoustic recording, playback, and analysis (Stoddard, 1990; McGregor and Ranft, 1994). These technologies advanced the ethological study of rodent vocal communication from multiple perspectives (Branchi et al., 2001; Portfors, 2007; Scattoni et al., 2009; Wöhr and Schwarting, 2013; Brudzynski, 2014; Mooney, 2020; Kelley, 2022; Grijseels et al., 2024). Early studies revolved around characterizing communication at key life stages, primarily in laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*). Infant rats and mice readily vocalize when isolated from their mother and nest (Hofer, 1996; Wöhr and Schwarting, 2008), and these vocalizations evoke maternal care behaviors (Ehret, 1987; D'Amato et al., 2005; Okabe et al., 2010, 2013). An extensive line of early work examined the developmental trajectories, biomechanics, and neurobiological mechanisms that regulate infant vocalizations and maternal responses (Hofer, 1996). Ontogenetic processes like vocal tract maturation and control, or perhaps even learning, were thought to drive the acoustic changes from infantile to adult-like vocalizations (Grimsley et al., 2011). Studies showed that isolation-induced vocalizations involve biomechanical mechanisms related to cold exposure (Blumberg and Alberts, 1990), and vocalizations potentiated by maternal stimuli involve the parasympathetic nervous system (Shair et al., 2012). Infant vocalizations are regulated by opioid, oxytocin, and other neuromodulator systems (Hofer, 1996; Winslow et al., 2000; Moles et al., 2004). It is thought that isolation-induced vocalizations are behavioral markers of anxiety and negative affect (Wöhr and Schwarting, 2008; Wöhr et al., 2008a).

Juvenile communication during affiliative interaction is another research theme that has received much attention (Knutson et al., 1998; Panksepp et al., 2007). Young rats produce high-frequency 50-kHz vocalizations during, and in anticipation of, rough-and-tumble play with conspecifics (Knutson et al., 1998; Burgdorf et al.,

2008). These high frequency vocalizations also occur alongside heterospecific play (Panksepp and Burgdorf, 2000; Schwarting et al., 2007), and the propensity to vocalize has a heritable component (Burgdorf et al., 2005). It is thought that high-frequency vocalizations are a behavioral marker of positive affect in juvenile and young adult rats (Panksepp and Burgdorf, 2000; Burgdorf et al., 2008). These vocalizations attract conspecifics (Wöhr and Schwarting, 2007) and involve dopaminergic and opioid neural systems that facilitate reward processing (Gordon et al., 2002; Wöhr and Schwarting, 2009).

In addition to infant and juvenile vocalizations, early studies characterized adult rodent vocalizations across many contexts. Adult rodents vocalize during, and anticipation of, aversive contexts like predator alarm (Blanchard et al., 1991), social defeat (Kroes et al., 2007), and fear conditioning (Wöhr et al., 2005; Borta et al., 2006; Kim et al., 2010). Adult rodents also produce a diverse vocal repertoire during, or in anticipation of, appetitive contexts like courtship (Holy and Guo, 2005; Yang et al., 2013) and interaction with familiar conspecifics (Wright et al., 2010). In rats, it is thought that low-frequency 22-kHz vocalizations communicate negative affect during aversive contexts, while higher-frequency 50-kHz vocalizations communicate positive affect during appetitive contexts (Schwarting et al., 2007; Wöhr et al., 2008b; Brudzynski, 2009). Supporting this idea, rats avoid playbacks of 22-kHz vocalizations but are attracted to 50-kHz vocalizations (Wöhr and Schwarting, 2007, 2012; Burgdorf et al., 2008). Adult rat and mouse vocalizations produced during appetitive and aversive contexts are associated with distinct hormonal and neural mechanisms (Depaulis et al., 1992; Goldstein et al., 1996). In mice, estrogen and androgen systems affect communication during appetitive contexts like mating (Ogawa et al., 2000). In rats, aversive 22-kHz vocalizations involve the mesolimbic cholinergic system, and brain areas like the amygdala, periaqueductal grey, and perirhinal cortex (Koo et al., 2004; Furtak et al., 2007; Kroes et al., 2007; Kholodar-Smith et al., 2008; Sadananda et al., 2008). Appetitive 50-kHz vocalizations involve the opioid and mesolimbic dopamine systems, and brain areas like the frontal cortex, nucleus accumbens, and paraventricular nuclei (Burgdorf et al., 2000; 2007; Thompson et al., 2006; Ciucci et al., 2007; Sadananda et al., 2008; Ahrens et al., 2009; Brudzynski, 2009; Wöhr and Schwarting, 2009; Wright et al., 2010).

Although laboratory rats (*R. norvegicus*) and mice (*M. musculus*) were the focus of early studies, several other rodents were also shown to communicate with acoustic signals. Other rodents include black rats (*Rattus rattus*) (Kaltwasser, 1990), deer mice (*Peromyscus* spp.) (Dice and Barto, 1952; Ralls, 1967; Wright and Brown, 2004; Kalcounis-Rueppell et al., 2006), degus (*Octodon degus*) (Nakano et al., 2013), gerbils (*Meriones unguiculatus*) (Hashimoto et al., 2004; Nishiyama et al., 2011), guinea pigs (*Cavia porcellus*) (Hennessy et al., 2006), hamsters (*Allocricetulus* spp., *Cricetulus* spp., *Mesocricetus* spp.) (Hashimoto et al., 2004; Kapusta et al., 2006; Simeonovska-Nikolova and Dekov, 2013), wild house mice (*Mus musculus musculus*) (Musolf et al., 2010; Hoffmann et al., 2012), naked-mole rats (*Heterocephalus glaber*) (Yosida et al., 2007; Yosida and Okanoya, 2009), voles (*Myodes* spp.,

*Microtus* spp.) (Colvin, 1973; Lepri et al., 1988; Kapusta et al., 2007; Szentgyorgyi et al., 2008), and wood mice (Sewell, 1970). In naturalistic settings, a common research theme was on the evolution of alarm calling and communicative complexity in rodents like yellow-bellied marmots (*Marmota flaviventris*) (Blumstein and Armitage, 1997; Blumstein and Munos, 2005; Shelley and Blumstein, 2005; Pollard and Blumstein, 2012), Richardson's ground squirrels (*Spermophilus richardsonii*) (Sloan and Hare, 2008; Swan and Hare, 2008; Thompson and Hare, 2010), and other ground squirrel species (Eiler and Banack, 2004; Matrosova et al., 2007; Volodina et al., 2010; Schneiderova and Policht, 2012). These alarm calls have unique acoustic properties that communicate information about arousal and individual identity (Blumstein et al., 2004; Sloan and Hare, 2004, 2008; Blumstein and Recapet, 2009; Matrosova et al., 2009, 2010). Most naturalistic studies focused on vocalizations audible to humans, which are easier to record in the wild than more inconspicuous ultrasonic vocalizations. However, even ultrasonic vocalizations have been studied in some wild-living rodents, like deer mice (*Peromyscus* spp.) (Kalcounis-Rueppell et al., 2006, 2010; Briggs and Kalcounis-Rueppell, 2011; Petric and Kalcounis-Rueppell, 2013).

The widespread use of rodent models in ethological studies of vocal communication is relatively nascent compared to other tetrapod groups like birds, primates, bats, and anurans. And yet, several decades of work show that rodent vocalizations can be studied from different ethological perspectives across species, research environments, and demographic groups. During the past decade, in particular, a rapid evolution of technologies to detect and analyze rodent vocalizations is supporting a shift towards more rodent research (Neunuebel et al., 2015; Binder et al., 2021; Sterling et al., 2023). Here, we review contemporary research trends and advances in rodent vocal communication. Using a scoping review approach, we compile a list of ethological studies on rodent vocalizations from the past decade. We investigate how these studies fit into mechanism, development, function, and evolution perspectives. Then, we compare the rodent species used to examine vocal communication from these perspectives. Next, we examine research environments and demographic sex and age groups, across perspectives and species. We also identify potential research areas for future study. Finally, we summarize new technologies to record, detect, and analyze rodent vocalizations. Together, recent advancements in the integrative study of rodent vocalizations hold exciting opportunities for understanding how and why animals communicate.

## 2 Methods

### 2.1 Framework

Scoping reviews are conducted to provide the synthesis from existing literature on a broad topic, identify key concepts, evidence types, research gaps, and clarify definitions and terminology. This review followed the Arksey and O'Malley framework (Arksey and O'Malley, 2005), which consists of six steps: 1) identification of

research questions; 2) identification of relevant studies in existing literature; 3) screening studies for eligibility; 4) data extraction; 5) data analysis; and 6) an optional stakeholder consultation. A stakeholder consultation was not performed as this review synthesizes existing knowledge from the field rather than exploring practical applications where stakeholder perspectives are relevant (Arksey and O'Malley, 2005).

## 2.2 Search strategy and study selection

A comprehensive search strategy was developed under two definitions: 1) Rodent species, such as “Mice”, “Rodent”, “Chinchilla”, and “Guinea pig”, and 2) Vocalization, such as “vocal repertoire”, “animal communication”, and “calling patterns”. The keywords were tailored to the interfaces of six databases: APA PsycINFO, Embase, MEDLINE, PubMed, Scopus, and Web of Science (Supplementary Data 1). The database search was conducted for primary research papers published between January 1, 2014 and December 31, 2024. A supplementary database search was conducted for primary research papers published between January 1, 2004 and December 31, 2013. Covidence (Veritas Health Innovation, Melbourne, Australia; available at [www.covidence.org](http://www.covidence.org)) was utilized for title and abstract screening, full-text screening, and extraction of publication metadata.

A duo-reviewer system was used to independently evaluate the records. Any conflicts between the two reviewers were resolved through consensus, with a third reviewer consulted when necessary to provide another perspective and facilitate the final decision. We included peer-reviewed primary research papers published in English. Studies were used regardless of geographic location and study setting. Non-research articles (e.g., errata, commentaries, book chapters, letters to the editor, protocols, editorials, perspectives and opinion pieces), thesis dissertations, conference proceedings, and reviews were excluded. Grey literature – research and information produced outside of traditional commercial publishing channels, including reports, theses, conference proceedings, and government documents, which may not undergo formal peer review – was not considered for inclusion in this study. Studies were excluded when they did not assess vocalization or when they used non-rodent species. Finally, we focused our search strategy on ethology-oriented research by excluding biomedical studies that used rodents as translational models for human disease (e.g., transgenic strains for a human disorder).

A streamlined version of this search strategy was carried out for research published between January 1, 2004 and December 31, 2013. Following the removal of duplicates, irrelevant studies were excluded at the title and abstract screening stage.

## 2.3 Data extraction

Data were extracted for eligible studies published between January 1, 2014 and December 31, 2024. The extraction form for each study was independently completed by two reviewers, detailing

the methodological and study subject characteristics, as well as the principal findings. A third reviewer consolidated the extracted data through consensus. A fourth reviewer provided a final check of the extracted data for accuracy and formatted the data for statistical analyses. The Covidence metadata extraction template was adapted to include the following: first author's last name, print publication year, title of study, study design, country where study was conducted, study objectives, and types of behaviors that were studied. Information collected for analysis purposes included the primary Tinbergen perspective(s) (i.e., mechanism, development, function, evolution) for vocalization-based study objectives, species, research environment (i.e., artificial, naturalistic, or both), animal sex (i.e., female, male, or both) and age groups (i.e., infant, juvenile, or adult).

The ‘mechanism’ Tinbergen perspective included studies on the physiological substrates that drive vocal production and perception. The mechanism perspective also was assigned to studies that characterized the spectral-temporal properties of vocalizations. The ‘development’ perspective included studies on how vocal behavior changes across time and in response to ontogenetic processes. The ‘function’ perspective included studies that focused on the meaning of vocalizations (e.g., information encoding), their effect on conspecifics, and their adaptive value for reproduction and survival. The ‘evolution’ perspective included phylogenetic studies that focused on describing inter-specific and inter-population variation in vocal behavior, as well as evolutionary processes like natural or artificial selection. Multiple perspectives were assigned if studies contained experiments from different perspectives. Studies were assigned to a ‘method’ perspective if their primary purpose was to design better hardware or software tools.

When assigning study species, multiple strains of laboratory-derived mice or rats were labeled as house mice (*Mus musculus*) or brown rats (*Rattus norvegicus*), respectively. When assigning the research environment, an ‘artificial’ category was used for studies that took place in experimental laboratory settings (e.g., home cage, testing arena). These were settings that were not designed to simulate an animal's natural environment. The ‘naturalistic’ category was used for studies that took place in the wild or in semi-natural enclosures. The naturalistic category also was used when laboratory testing arenas were made to simulate aspects of an animal's natural environment. Animal sex was assigned based on the reported sexes of the study subjects and stimuli. Studies that involved several animals that were not checked for sex, but came from a random population (e.g., infants, wild animals), were assigned as both sexes. When assigning age groups, ‘adult’ was used when authors noted that the animals were adults, young adults or subadults, or when an age group was not explicitly stated. Animals were assigned to the ‘juvenile’ group when authors identified them as adolescents or juveniles. The ‘infant’ group was used when animals were identified as infants, pups, and neonates.

## 2.4 Data analysis

Data were analyzed in R (v.3.5.3). Chi-square goodness of fit tests were used to examine whether the frequencies of studies



assigned to distinct categories differed from expected proportions. These categories were not considered mutually exclusive, and so expected probabilities for chi-square tests were rescaled to a sum of 1. Spearman rank correlations were used to test whether study characteristics changed across publication years. Simpson Diversity Index (Keylock, 2005) was used to quantify species diversity across studies. This index (D) is a quantitative measure of biodiversity that takes species richness and evenness into account, with higher values indicating increased biodiversity. Phylogenetic trees of Rodentia species come from a published mammalian supertree (Fritz et al., 2009), and trees were plotted with R “ape” package (Paradis and Schliep, 2019).

### 3 Results

A total of 17,165 references were identified for screening between January 1, 2014 and December 31, 2024, (Figure 1), of which 9,439 duplicates were removed (133 manually and 9,306 via Covidence). 7,726 studies were used for title and abstract screening, and 6,073 of these studies were excluded as irrelevant. Then, 1,653 studies underwent full-text assessment. During this stage, 1,250

studies were excluded for various reasons: 760 were disease model studies, 248 had the wrong study design (e.g., review paper), 59 did not include a rodent species, and 183 did not assess vocalization. Metadata for disease model studies that were excluded at the full-text screening stage ( $n = 760$ ) are provided in the [Supplementary Materials \(Supplementary Data 2\)](#). In total, 403 studies met the eligibility criteria and were used for data extraction and analyses ([Supplementary Data 3](#)). The publication dates of these studies included all years between 2014 to 2024. One of the included studies was published online in 2024 but was printed in a 2025 issue of the journal (Dymyskaya et al., 2025). On average, there were  $37 \pm 5$  (mean  $\pm$  sd) studies published per year, ranging from 27 (in 2014) to 44 (in 2022).

A supplementary search for eligible studies was carried out for research published between January 1, 2004 and December 31, 2013. A total of 10,374 references were identified for screening ([Supplementary Figure 1](#)), of which 5,780 duplicates were removed (9 manually and 5,771 via Covidence). 4,594 studies were used for title and abstract screening. Of these, 4,356 studies were excluded, which left 238 potentially eligible studies. These studies are listed in the supplement ([Supplementary Data 4](#)), and they were not used for data extraction and analyses.

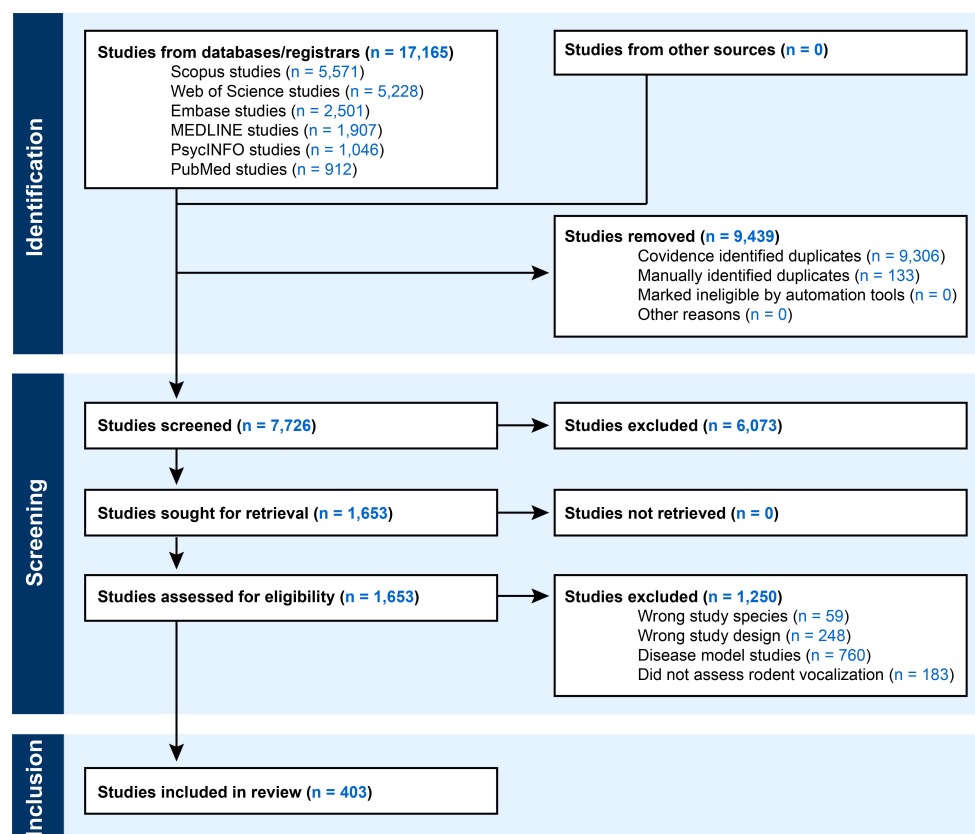


FIGURE 1

Study search and exclusion process. Studies were selected through a three stage process that involved study identification, screening, and inclusion. Identification involved the use of six databases to find potential studies published between January 1, 2014 and December 31, 2024. Duplicates and ineligible citations were removed. During the screening stage, studies that did not meet inclusion criteria were removed. During the inclusion stage, eligible studies were reviewed to extract information on research objectives, species, research environment, demographic group, and methods.

### 3.1 Ethological perspectives

All ethological perspectives were represented in the 403 extracted studies (Figure 2). Of these extracted studies, 42% were assigned as mechanism ( $n = 171$  studies), 17% as development ( $n = 70$ ), 32% as function ( $n = 129$ ), and 9% as evolution ( $n = 38$ ). Most studies were focused on one of the four perspectives ( $n = 330$ ), and a minority involved multiple perspectives ( $n = 38$ ). The frequencies of studies categorized under the four perspectives deviated from the expected proportion of 0.25 (Chi-squared goodness of fit test:  $\chi = 104.02$ ,  $df = 3$ ,  $p < 0.0001$ ; Figure 2A). These frequencies were relatively stable across publication year. We found no support that yearly frequencies increased or decreased for mechanism (Spearman rank correlation:  $\rho = 0.491$ ,  $df = 9$ ,  $p = 0.1292$ ), development ( $\rho = -0.155$ ,  $df = 9$ ,  $p = 0.6540$ ), function ( $\rho = -0.351$ ,  $df = 9$ ,  $p = 0.2902$ ), or evolution ( $\rho = -0.036$ ,  $df = 9$ ,  $p = 0.9244$ ) studies (Figure 2B).

### 3.2 Study species and species diversity

The extracted studies included 88 distinct rodent species across 43 Genus groups. Of these 88 species, 28% ( $n = 25$  species) were used in mechanism studies, 18% ( $n = 16$ ) in development studies, 45% ( $n = 40$ ) in function studies, and 68% ( $n = 60$ ) in evolution studies. The four most common species were brown rats (*Rattus norvegicus*,  $n = 170$  studies), house mice (*Mus musculus*,  $n = 116$  studies), California mice (*Peromyscus californicus*,  $n = 12$ ), and Mongolian gerbils (*Meriones unguiculatus*,  $n = 10$  studies). All other species were represented in seven or fewer studies. Most studies focused on single rodent species ( $n = 375$  studies), and a minority included multiple species ( $n = 28$  studies, 2–7 species per study). A variety of species were represented across all ethological perspectives (Figure 3). Rats (*Rattus* spp.) and mice (*Mus* spp.)

were represented across all perspectives (Figure 3A). The only other Genus groups that were represented across all perspectives were deer mice (*Peromyscus* spp.), gerbils (*Meriones* spp.), grasshopper mice (*Onychomys* spp.), singing mice (*Scotinomys* spp.), and voles (*Microtus* spp.) (Figure 3A). Six distinct species were represented across all perspectives: Alston's singing mice (*S. teguina*), brown rats (*R. norvegicus*), house mice (*M. musculus*), California mice (*P. californicus*), Mongolian gerbils (*M. unguiculatus*), and northern grasshopper mice (*O. leucogaster*).

Ethological perspectives varied in their representation of three species groups – laboratory rats (*R. norvegicus*), laboratory mice (*M. musculus*), and non-traditional rodents (i.e., all other species combined) (Figures 3B, C). Frequencies of species groups deviated from expected for mechanism (Chi-squared goodness of fit test:  $\chi = 22.92$ ,  $df = 2$ ,  $p < 0.0001$ ), function ( $\chi = 7.68$ ,  $df = 2$ ,  $p = 0.0215$ ), and evolution ( $\chi = 45.16$ ,  $df = 2$ ,  $p < 0.0001$ ) studies, but not for development studies ( $\chi = 1.77$ ,  $df = 2$ ,  $p = 0.4123$ ). Expected proportions for each species group were based on the entire dataset. Overall, rats were used more than non-traditional rodents in mechanistic studies. Conversely, non-traditional rodents were used more than rats in functional studies, and non-traditional rodents were used more than rats and mice in evolution studies.

Species diversity also varied across ethological perspective (Figure 3C). The Simpson Diversity Index for the entire dataset was 0.79, which was consistently higher than mechanism studies (0.63) and lower than evolution studies (0.99) across publication year. Simpson Diversity Indices for development (0.78) and function (0.83) studies tended to be similar to the entire dataset. There was no evidence that Simpson Diversity Indices changed across publication year, either for the entire dataset (Spearman rank correlation:  $\rho = 0.445$ ,  $df = 9$ ,  $p = 0.1728$ ), or for mechanism ( $\rho = 0.464$ ,  $df = 9$ ,  $p = 0.1543$ ), development ( $\rho = 0.118$ ,  $df = 9$ ,  $p = 0.7343$ ), function ( $\rho = -0.164$ ,  $df = 9$ ,  $p = 0.6339$ ), and evolution ( $\rho = 0.500$ ,  $df = 9$ ,  $p = 0.1173$ ) studies.

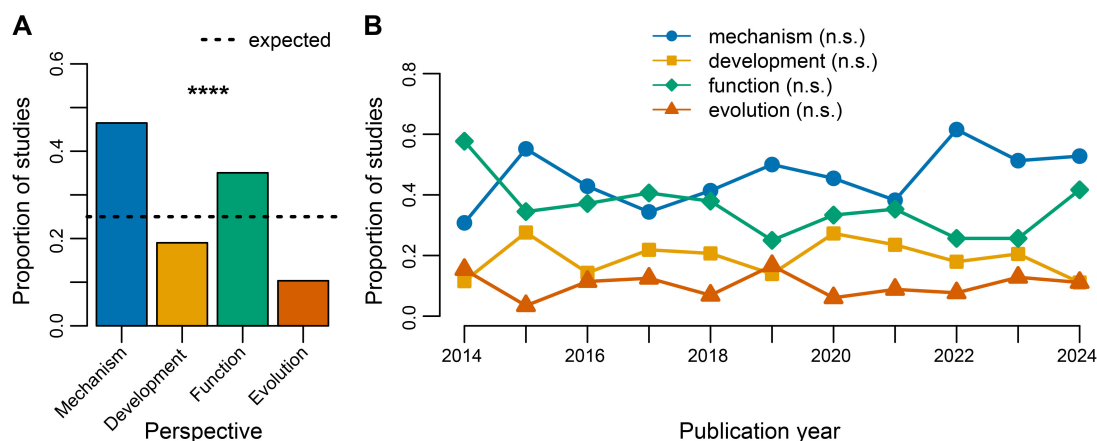


FIGURE 2

Proximate and ultimate approaches to rodent vocal communication studies. (A) Comparison of studies ( $n = 368$ ) used to address research objectives related to mechanistic, developmental, functional, and evolutionary ethological perspectives. Frequencies of studies assigned to each of the perspectives (colored bars) are compared to the expected proportions (i.e., all perspectives have equal likelihood, shown with dotted line). (B) Associations between publication year and the frequencies of studies that focus on different ethological perspectives. Statistical significance is represented by n.s.  $p > 0.05$ , \*\*\*\* $p < 0.0001$ .

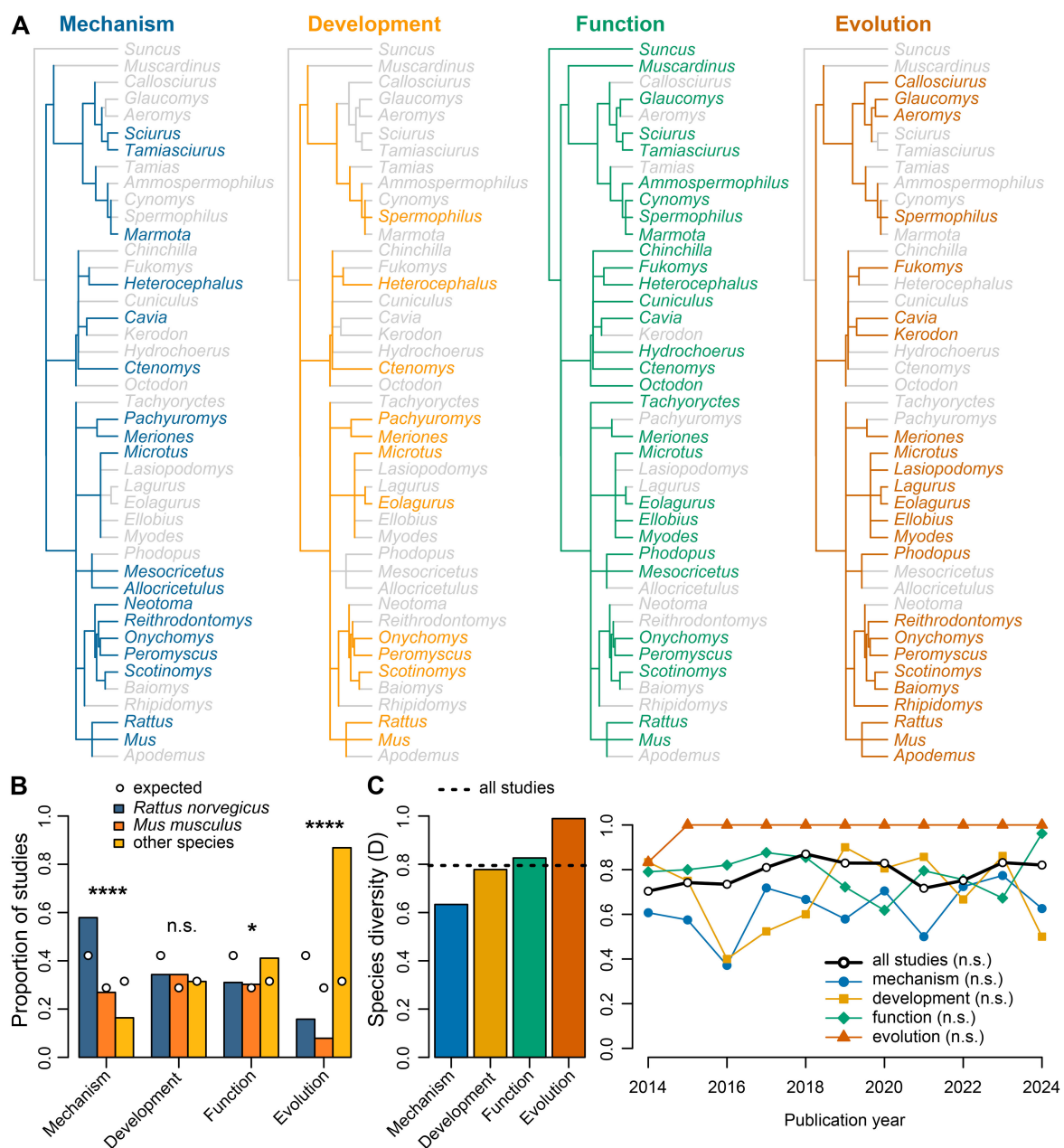


FIGURE 3

Rodentia species in vocal communication studies. (A) Phylogenetic trees for rodent species used to address research objectives related to mechanistic, developmental, functional, and evolutionary perspectives on vocal communication. Trees are mapped at the Genus level, with darker colored lines and text for groups represented in studies. Non-represented Genus groups are shown in light gray. (B) Comparison of rodent species groups used in studies for each ethological perspective. Species groups include brown rats (*Rattus norvegicus*,  $n = 170$ ), house mice (*Mus musculus*,  $n = 116$ ) and all other species combined ( $n = 127$ ). Expected proportions (circle symbols) of each species group are calculated from the entire dataset ( $n = 403$  studies). (C) Comparison of species diversity across studies that take different ethological perspectives (171 mechanism studies, 70 development, 129 function, and 38 evolution). Comparisons are shown for ethological perspectives (left) and across publication years (right). Species diversity is represented with the Simpson Diversity Index, with higher values representing increased diversity. Statistical significance is represented by n.s.  $p > 0.05$ , \* $p < 0.05$ , \*\*\*\* $p < 0.0001$ .

### 3.3 Research environment

Of the 403 included studies, 91% ( $n = 367$ ) were carried out in artificial environments, while 11% ( $n = 44$ ) were carried out in naturalistic environments (artificial only = 359 studies, naturalistic only = 36, both artificial and naturalistic = 8). This bias towards

artificial environments was consistent across years. The proportion of studies set in different environments did not correlate to publication year (Spearman rank correlations: artificial:  $\rho = 0.227$ ,  $df = 9$ ,  $p = 0.5031$ ; naturalistic:  $\rho = -0.278$ ,  $df = 9$ ,  $p = 0.4080$ ; Figure 4A).

Ethological perspectives varied in their representation of research environments (Figure 4B). Of the 367 artificial studies, 45% ( $n = 166$

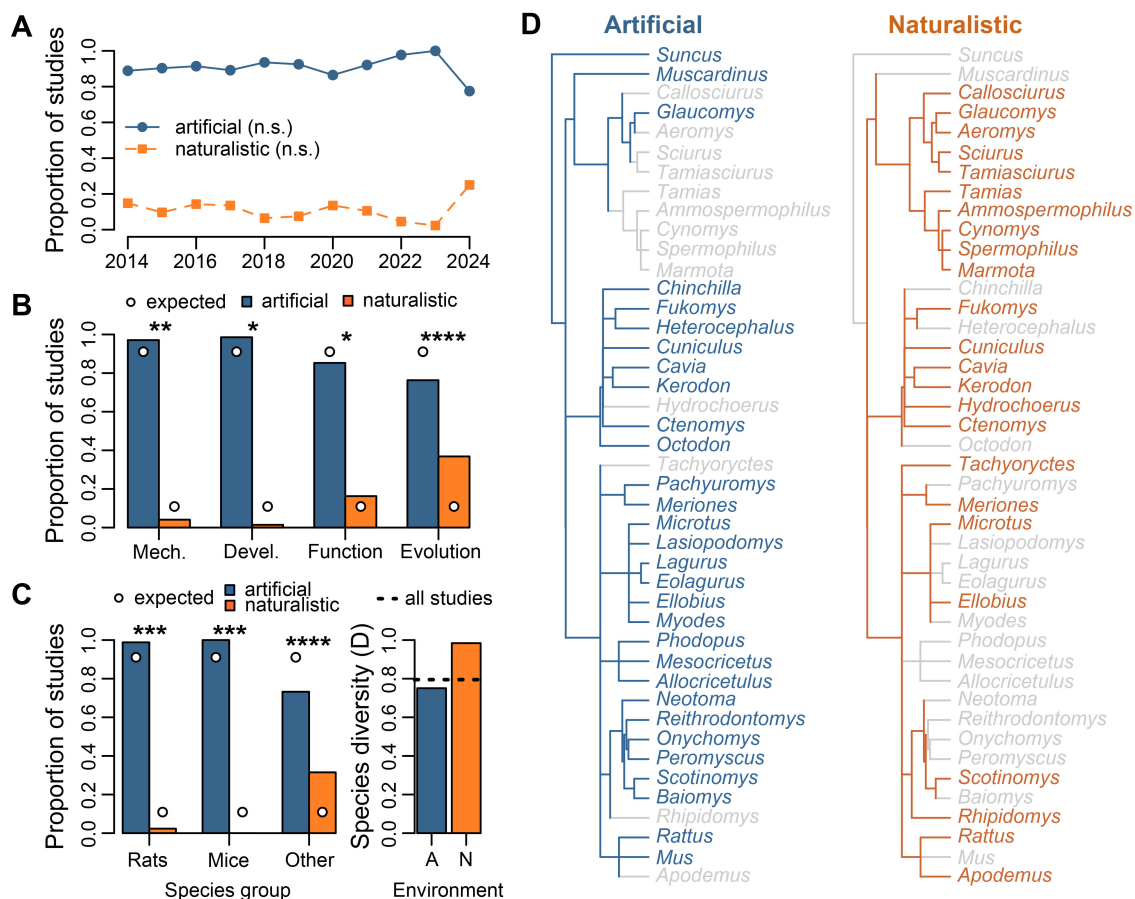


FIGURE 4

Research environments in rodent vocal communication studies. (A) Associations between publication year and the frequencies of studies carried out in artificial ( $n = 367$  studies) and naturalistic ( $n = 44$ ) environments. (B) Comparison of environments used in studies for each ethological perspective. Expected frequencies (circle symbols) of artificial and naturalistic environments are calculated from the entire dataset. (C) Comparison of environments used in studies for each rodent species group (left) and comparison of species diversity across artificial (A) and naturalistic (N) environments (right). Species groups include brown rats (*Rattus norvegicus*), house mice (*Mus musculus*) and all other species combined. Expected frequencies (circle symbols) of environments are calculated from the entire dataset. Species diversity is represented with the Simpson Diversity Index, with higher values representing increased diversity. (D) Phylogenetic trees for rodent species used in artificial and naturalistic environments. Trees are mapped at the Genus level, with darker colored lines and text for taxonomic groups represented in artificial and naturalistic studies. Non-represented Genus groups are shown in light gray. Statistical significance is represented by n.s.  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , \*\*\*\* $p < 0.0001$ .

studies) were assigned to the mechanism perspective, 19% ( $n = 69$ ) to development, 30% ( $n = 110$ ) to function, and 8% ( $n = 29$ ) to evolution. Of the 44 naturalistic studies, 16% ( $n = 7$  studies) were assigned to the mechanism perspective, 3% ( $n = 1$ ) to development, 48% ( $n = 21$ ) to function, and 32% ( $n = 14$ ) to evolution. Frequencies of each study environment deviated from expected for mechanism (Chi-squared goodness of fit test:  $\chi = 8.03$ ,  $df = 1$ ,  $p = 0.0046$ ), development ( $\chi = 6.30$ ,  $df = 1$ ,  $p = 0.0121$ ), function ( $\chi = 3.89$ ,  $df = 1$ ,  $p = 0.0487$ ), and evolution ( $\chi = 21.48$ ,  $df = 1$ ,  $p < 0.0001$ ) studies. Expected proportions for research environment were based on the entire dataset. Overall, artificial environments were represented more than expected in mechanism and development studies. Conversely, naturalistic environments were represented more than expected in function and evolution studies.

Species diversity also varied across research environments (Figures 4C, D). Artificial environments were used across the three main species groups (*Rattus norvegicus*:  $n = 168$  studies;

*Mus musculus*:  $n = 116$ ; all others:  $n = 93$ ). Naturalistic environments were only used for rats and non-traditional species (*R. norvegicus*:  $n = 4$ ; *M. musculus*:  $n = 0$ ; all others:  $n = 40$ ). Frequencies of each environment deviated from expected for studies on laboratory rats (Chi-squared goodness of fit test:  $\chi = 12.64$ ,  $df = 1$ ,  $p = 0.0004$ ), laboratory mice ( $\chi = 13.91$ ,  $df = 1$ ,  $p = 0.0002$ ), and non-traditional species ( $\chi = 52.20$ ,  $df = 1$ ,  $p < 0.0001$ ). Expected proportions for each environment were based on the entire dataset. Overall, artificial environments were represented more than expected in laboratory rat and mice studies. Conversely, naturalistic environments were represented more than expected in non-traditional rodent studies. In total, artificial studies involved 62 rodent species across 30 Genus groups, while naturalistic studies involved 37 rodent species across 24 Genus groups (Figure 4D). Naturalistic studies had a higher Simpson Diversity index ( $D = 0.984$ ; Figure 4D) than artificial studies ( $D = 0.751$ ) and the entire dataset ( $D = 0.795$ ).



### 3.4 Animal sex and age groups

Of the 403 extracted studies, 67% ( $n = 272$ ) involved females, while 87% ( $n = 351$ ) involved males (females only = 33 studies, males only = 112, both sexes = 239, unknown sex = 19). A bias towards male studies was consistent across years, and the proportions of studies involving either sex did not correlate with publication year (Spearman rank correlation: females:  $\rho = 0.464$ ,  $df = 9$ ,  $p = 0.1543$ ; males:  $\rho = 0.347$ ,  $df = 9$ ,  $p = 0.2957$ ; [Figure 5A](#)). In terms of age group, 81% of studies ( $n = 326$ ) involved adults, while 16% ( $n = 65$ ) involved juveniles and 19% ( $n = 78$ ) involved infants. A bias towards adult studies was consistent across years, while juveniles and infants were used in a similar proportion of studies. The proportion of studies for age group did not correlate with publication year (Spearman rank correlation: adults:  $\rho = -0.296$ ,  $df = 9$ ,  $p = 0.3766$ ; juveniles:  $\rho = -0.345$ ,  $df = 9$ ,  $p = 0.2994$ ; infants:  $\rho = 0.382$ ,  $df = 9$ ,  $p = 0.2484$ ; [Figure 5A](#)).

Ethological perspectives were similar in their representation of animal sexes ([Figure 5B](#)). Of the 272 female studies, 36% ( $n = 98$  studies) were assigned to the mechanism perspective, 22% ( $n = 59$ ) to development, 36% ( $n = 97$ ) to function, and 12% ( $n = 32$ ) to evolution. Of the 351 male studies, 42% ( $n = 148$  studies) were assigned to the mechanism perspective, 16% ( $n = 55$ ) to development, 33% ( $n = 117$ ) to function, and 9% ( $n = 33$ ) to evolution. Frequencies of each animal sex did not deviate from expected for mechanism (Chi-squared goodness of fit test:  $\chi = 1.46$ ,  $df = 1$ ,  $p = 0.2268$ ), function ( $\chi = 0.24$ ,  $df = 1$ ,  $p = 0.6229$ ), and evolution ( $\chi = 0.83$ ,  $df = 1$ ,  $p = 0.3651$ ) studies. However, there was a tendency for the observed frequencies of animal sex to deviate from expected for development studies ( $\chi = 3.04$ ,  $df = 1$ ,  $p = 0.0814$ ), with females used more than expected and males used less. This was a marginal effect ( $p < 0.1$ ) that did not pass the significance threshold ( $p < 0.05$ ). Expected proportions for each sex were based on the entire dataset.

Ethological perspectives varied in their representation of animal ages ([Figure 5B](#)). Of the 326 adult studies, 43% ( $n = 140$  studies) were assigned to the mechanism perspective, 13% ( $n = 42$ ) to development, 35% ( $n = 113$ ) to function, and 11% ( $n = 35$ ) to evolution. Of the 65 juvenile studies, 40% ( $n = 26$  studies) were assigned to the mechanism perspective, 26% ( $n = 17$ ) to development, 35% ( $n = 23$ ) to function, and 8% ( $n = 5$ ) to evolution. Of the 78 infant studies, 29% ( $n = 23$  studies) were assigned to the mechanism perspective, 49% ( $n = 38$ ) to development, 12% ( $n = 9$ ) to function, and 9% ( $n = 7$ ) to evolution. Frequencies of the three age groups deviated from expected for development (Chi-squared goodness of fit test:  $\chi = 40.17$ ,  $df = 2$ ,  $p < 0.0001$ ) and function ( $\chi = 11.37$ ,  $df = 2$ ,  $p = 0.0034$ ) studies, but not for mechanism ( $\chi = 2.83$ ,  $df = 2$ ,  $p = 0.2429$ ) and evolution ( $\chi = 0.60$ ,  $df = 2$ ,  $p = 0.7396$ ) studies. Expected proportions for each age group were based on the entire dataset. Overall, adults were underrepresented, and infants overrepresented, in development studies. The opposite pattern was found in function studies.

Species diversity varied across animal sexes ([Figure 5C](#)). Females were used across the three main species groups (*Rattus*

*norvegicus*:  $n = 74$  studies; *Mus musculus*:  $n = 98$ ; all others:  $n = 108$ ), as were males (*R. norvegicus*:  $n = 146$ ; *M. musculus*:  $n = 101$ ; all others:  $n = 112$ ). Frequencies of animal sexes deviated from expected for studies on laboratory rats (Chi-squared goodness of fit test:  $\chi = 8.99$ ,  $df = 1$ ,  $p = 0.0027$ ), but not for laboratory mice ( $\chi = 2.53$ ,  $df = 1$ ,  $p = 0.1121$ ) and non-traditional rodents ( $\chi = 2.64$ ,  $df = 1$ ,  $p = 0.1043$ ). Expected proportions for each sex were based on the entire dataset. Overall, females were represented less than expected in studies on laboratory rats. In total, studies that used female rodents involved 77 species across 40 Genus groups, while male studies involved 81 rodent species across 40 Genus groups ([Supplementary Figure 2](#)). Female studies showed a slightly higher Simpson Diversity Index ( $D = 0.842$ ) than the entire dataset ( $D = 0.795$ ; [Figure 5C](#)). Male studies had a similar diversity index ( $D = 0.799$ ) to the entire dataset.

Species diversity also varied across animal age groups ([Figure 5C](#)). All age groups were used throughout the three main species groups (*Rattus norvegicus*: adults = 127 studies, juveniles = 37, infants = 24; *Mus musculus*: adults = 94, juveniles = 6, infants = 30; all others: adults = 114, juveniles = 22, infants = 26). Frequencies of animal age groups deviated from expected for studies on laboratory rats (chi-squared goodness of fit test:  $\chi = 6.39$ ,  $df = 2$ ,  $p = 0.0410$ ) and laboratory mice ( $\chi = 11.41$ ,  $df = 2$ ,  $p = 0.0033$ ), but not for non-traditional rodents ( $\chi = 0.59$ ,  $df = 2$ ,  $p = 0.9708$ ). Expected proportions for each age group were based on the entire dataset. Overall, adults and juveniles were overrepresented, and infants underrepresented, in rat studies. In mouse studies, juveniles were underrepresented and infants overrepresented. In total, studies that used adults rodents involved 85 species across 42 Genus groups, juvenile studies involved 22 rodent species across 18 Genus groups, and infant studies involved 29 rodent species across 15 Genus groups ([Supplementary Figure 3](#)). Studies carried out with adults showed a similar Simpson Diversity Index ( $D = 0.820$ ) to the entire dataset ( $D = 0.795$ ; [Figure 5C](#)). Juvenile studies had a lower diversity index ( $D = 0.690$ ) than the entire dataset. Infant studies had a similar diversity index ( $D = 0.827$ ) to the entire dataset.

### 3.5 Characteristics of method studies

Of the 403 extracted studies, (9%,  $n = 36$ ) were identified as methods-focused studies. We found that the proportion of methods-focused studies tended to increase across publication year (Spearman rank correlations:  $\rho = 0.584$ ,  $df = 9$ ,  $p = 0.0590$ ). This correlation showed a marginal trend ( $p < 0.1$ ) but did not pass the significance threshold ( $p < 0.05$ ).

Method studies varied in the representation of different species groups – laboratory rats (*Rattus norvegicus*), laboratory mice (*Mus musculus*), and all other species combined. Frequencies of studies across these three species groups deviated from expected proportions based on the entire dataset (Chi-squared goodness of fit test:  $\chi = 19.60$ ,  $df = 2$ ,  $p < 0.0001$ ). Method studies only included 7% ( $n = 6$  species) of the 88 rodent species: house mice (*M. musculus*, 23 studies), brown rats (*R. norvegicus*, 12 studies),

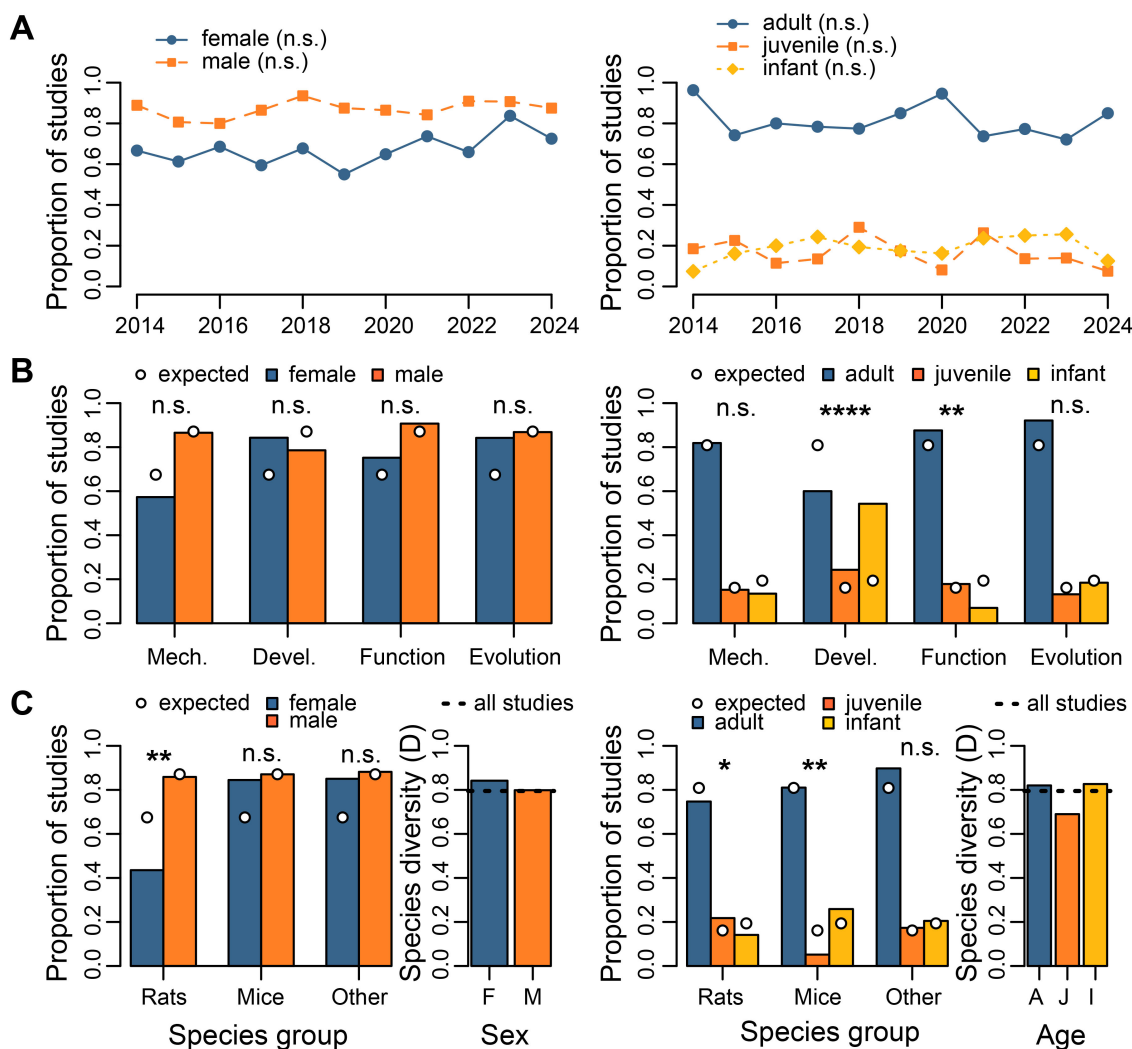


FIGURE 5

Sex and age of animals used in rodent vocal communication studies. **(A)** Associations between publication year and the frequencies of studies carried out with different sexes (left; 272 female studies, 351 male) and age groups (right; 326 adult studies, 65 juvenile, 78 infant). **(B)** Comparison of animal sex (left) and age groups (right) in studies for each ethological perspective. Expected frequencies (circle symbols) of sex and age groups are calculated from the entire dataset. **(C)** Comparison of animal sex (left) and age groups (right) in studies for each rodent species group and for species diversity. Species groups include brown rats (*Rattus norvegicus*), house mice (*Mus musculus*) and all other species combined. Sexes are females ('F') and males ('M'), and age groups are adults ('A'), juveniles ('J'), and infants ('I'). Expected frequencies (circle symbols) of sex and age groups are calculated from the entire dataset. Species diversity is assessed with the Simpson Diversity Index, with higher values representing increased diversity. Statistical significance is represented by n.s.  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\*\* $p < 0.0001$ .

northern and southern flying squirrels (*Glaucomys sabrinus* and *G. volans*, 2 studies), Mongolian gerbils (*Meriones unguiculatus*, 1 study), and Eastern chipmunks (*Tamias striatus*, 1 study). The Simpson Diversity Index across all method studies was 0.609, and there was no evidence that diversity indices were correlated with publication year (Spearman rank correlation:  $\rho = -0.196$ ,  $df = 9$ ,  $p = 0.6137$ ).

Method studies typically occurred in artificial settings with male study animals, but these observed patterns did not differ from expected patterns based on the entire dataset. Of the 36 method studies, 92% ( $n = 33$ ) of them involved an artificial environment, and 8% ( $n = 3$ ) involved naturalistic environments. However, the frequencies of these two study environments did not deviate

from expected (Chi-squared goodness of fit test:  $\chi = 0.21$ ,  $df = 1$ ,  $p = 0.6453$ ). Methods studies tended to be male-biased, with 64% ( $n = 23$ ) of them involving females and 81% ( $n = 29$ ) involving males. However, frequencies of studies across the two sexes did not deviate from expected (Chi-squared goodness of fit test:  $\chi = 0.01$ ,  $df = 1$ ,  $p = 0.9338$ ).

Finally, method studies were biased towards adults and infants, with 78% ( $n = 28$ ) of studies on adults, 3% ( $n = 1$ ) on juveniles, and 31% ( $n = 11$ ) on infants. The frequencies of the three age groups deviated from expected proportions based on the entire dataset (Chi-squared goodness of fit test:  $\chi = 6.57$ ,  $df = 2$ ,  $p = 0.0375$ ). Overall, infants were used more than expected, and juveniles were used less than expected.

## 4 Discussion

We present here an overview of contemporary trends and advancements in the ethological study of rodent vocal communication. We found that mechanism and function perspectives were more common than development and evolution perspectives. Also, studies from different perspectives varied in their use of species, research environments, and animal age groups. Overall, contemporary studies had higher species diversity when using an evolutionary perspective and lower species diversity when using a mechanistic perspective. Artificial environments were more common in mechanistic and developmental studies, while naturalistic environments were more common in functional and evolutionary studies. In addition, contemporary studies tended to use male adults more than other sex and age groups, but these demographics depended on the ethological perspective and taxonomic group. Species diversity also varied across research environments and demographic groups. Finally, methods-focused studies became more common over the past decade, and these studies introduced many new tools to better record, detect, and analyze vocalizations.

### 4.1 Ethological perspectives on rodent communication

Integration across ethological perspectives is important for developing a holistic understanding of behavior (Tinbergen, 1963; Krakauer et al., 2017). We found a strong bias towards mechanism studies on rodent vocalization, with relatively few studies focused on evolution and development. Function studies were relatively common, but not as common as mechanism studies. Such findings suggest that a current strength of rodent research is in characterizing the biological causes of vocal production and perception. This trend is expected, given that rodents are common in neuroscience research and method development (Bernstein and Boyden, 2011; Ellenbroek and Youn, 2016; Roth, 2016).

Contemporary mechanistic studies identified in this review make use of variety of neuroscience tools, such as pharmacological manipulations (Berz et al., 2021), optogenetics (Tschida et al., 2019), and brain-wide mapping of immediate early genes (Mai et al., 2023). This body of work shows that neural circuits for rodent vocalization span the entire brain, from regions of the hindbrain and midbrain, like retroambiguus and periaqueductal gray (Tschida et al., 2019), to regions of the forebrain, like nucleus accumbens and the motor cortex (Muller and Shair, 2016; Okobi et al., 2019). Several regions are also integral to vocal perception (e.g., auditory cortex and inferior colliculus) (Garcia-Lazaro et al., 2015; Agarwalla et al., 2023). Neural pathways that regulate vocal communication involve a variety of neuromodulator systems (e.g., dopamine, serotonin, androgens) (Furlanetti et al., 2016; Kikusui et al., 2021; Hood and Hurley, 2024). Outside of the brain, many morphological studies explore the biomechanics of rodent vocalization (Alves et al., 2016; Riede et al.,

2020; Hakansson et al., 2022). This morphological work shows that rodent vocalizations involve the complex coordination of respiration and laryngeal structures. Indeed, some species emit vocalizations that are temporally strung together into song-like sequences with 'syntax' (Hertz et al., 2020), and others participate in speech-like dynamics of vocal 'turn-taking' (Okobi et al., 2019). Taken together, contemporary mechanism studies show that rodents are valuable animal models for investigations of vocal production and perception (Mooney, 2020; Kelley, 2022; Grijseels et al., 2024).

Complementary research from a function perspective provides insights into why rodents vocalize. Studies identified by this review show that vocalizations can facilitate advertisement displays (Burkhard et al., 2023a, 2023b; Siracusa et al., 2017), agonistic interactions (Keesom et al., 2015), juvenile play (Burke et al., 2018; Himmler et al., 2014), mating interactions (Finton et al., 2017; Neunuebel et al., 2015), pair bonding (Pultorak et al., 2018; Rieger et al., 2021), parental care behaviors (Harmon-Jones and Richardson 2021; Yu et al., 2020), and predator alarms (Loughry et al., 2019; McRae and Green, 2017; Wilson-Henjum et al., 2019). Although most of the functional studies identified in this review used observational methods (e.g., recording vocalizations in different contexts), it is important to recognize that playback experiments are equally important. Playback experiments allow researchers to determine the types of information encoded in vocalizations, as well as to categorize vocalizations into calls or songs. Playback studies identified in this review show that rodent vocalizations can encode identity, affective state, and referential information (Pultorak et al., 2017; Barker et al., 2021; Hammond et al., 2024). Playback studies further reinforce hypotheses that rodent vocalizations can facilitate advertisement displays, social interactions, and predator alarms (Seffer et al., 2014; Pultorak et al., 2017; Fendt et al., 2018; Okobi et al., 2019; Hood et al., 2023). These findings suggest that rodent vocalizations have adaptive value for parental care, social cohesion, courtship, territory defense, and predator avoidance (Grijseels et al., 2024).

Of the four perspectives, development and evolution were relatively uncommon in contemporary ethology studies on vocal communication. The development perspective offers insight into how rodent vocalizations change across the lifespan, and studies identified in this review show that rodent vocalizations gradually transition from infancy to adulthood (Campbell et al., 2014; Zaytseva et al., 2020; Warren et al., 2022). Moreover, rodent vocalizations are impacted by early-life experiences (Keesom et al., 2017), and they can be innate (Jefferson et al., 2023) or involve learning (Barker et al., 2021; Janik and Knörnschild, 2021; Volodin et al., 2023). Supporting earlier research, these contemporary studies show that several ontogenetic processes shape how communication behaviors emerge and change during development. This review also identified a small number of evolutionary studies that test phylogenetic hypotheses. For example, divergent evolution of vocal communication is thought to occur through allopatric or sympatric speciation (Von Merten et al., 2014). Acoustic variation in mating calls may support sympatric speciation by providing a means for reproductive

isolation and species recognition (Campbell et al., 2019; Chen et al., 2017; Tamura et al., 2018; Wang et al., 2023). Vocal divergence may come about through inter-specific variation in temperament (Kalcounis-Rueppell et al., 2018). Inter and intra-specific comparisons provide insights into how morphological and neural structures evolved in ways that support or constrain vocalization (Fernández-Vargas et al., 2022; Kelley, 2022). Because of their expansive phylogeny, rodents are a great taxonomic group for testing hypotheses about how vocal communication changes across time. A valuable area for future rodent communication research would be to build upon the evolution perspective with more comparative studies.

## 4.2 Rodent communication across study taxa

Of the over 2,000 living species that make up Rodentia, 88 were identified in contemporary vocalization studies. On the one hand, these 88 species seem small when compared to the sheer number of potential rodent species. Many rodent taxa have yet to be used in communication studies. On the other hand, these study species cover a broad spectrum of 43 Genus groups. A strength of this phylogeny is that it covers species with diverse social systems, life history traits, habitats, and geographic distributions (Gliwicz and Taylor, 2002; Solari and Baker, 2007; Lukas and Clutton-Brock, 2013). This means that there are rich opportunities to explore variation in vocal behavior within and across species. Some studies identified by this review take advantage of novel model species to address unique study questions (Brito et al., 2017; Amaya and Areta, 2018). Other studies use comparative methods to examine variable and conserved traits amongst sister taxa (Kalcounis-Rueppell et al., 2018; Tamura et al., 2018; Jourjine et al., 2023). As a large taxonomic group, Rodentia is excellent for testing hypotheses about how vocal communication evolved in rodents and other mammals.

This review identified a couple potential limitations in how rodent species are used in contemporary studies. One potential limitation is that there are few species used in mechanistic research. Despite being the most common perspective, mechanistic studies had the least species diversity. The majority of mechanism studies used lab-derived strains of rats (*R. norvegicus*) and mice (*M. musculus*). This homogeneity means that there are missed opportunities to study behavioral phenomena that are not applicable to traditional laboratory rodents. For example, research on androgen hormones in California mice (*P. californicus*) (Timonin et al., 2018) and heart rate in prairie voles (*M. ochrogaster*) (Stewart et al., 2015) has led to new insights into vocal mechanisms in socially monogamous species. Another potential limitation is that few species are studied from all four perspectives. Aside from laboratory rats and mice, we only found four species studied from all perspectives: Mongolian gerbils (*M. unguiculatus*) (Paraouty et al., 2021; Furuyama et al., 2022; Hardy et al., 2023; Volodin et al., 2024), California mice (*P. californicus*) (Johnson et al., 2017; Pultorak et al., 2017; Kalcounis-Rueppell et al.,

2018; Malone et al., 2023), Northern grasshopper mice (*O. leucogaster*) (Pasch et al., 2016, 2017; Campbell et al., 2019; Kobrina et al., 2021), and singing mice (*S. teguina*) (Campbell et al., 2014; Giglio and Phelps, 2020; Burkhard et al., 2023a, 2023b). A potential direction for future work would be to integrate across perspectives in more species and Genus groups.

## 4.3 Rodent communication in artificial and naturalistic environments

Another advantage of rodent vocal communication research is the regular use of both artificial and naturalistic study environments. Within this spectrum, rodent studies identified in this review were carried out primarily in artificial environments. Common artificial environments included laboratory testing arenas like open field (Rojas-Carvajal et al., 2022) and the Y-maze (Asaba et al., 2014; Chabout et al., 2015). Artificial environments were often used in mechanism and development studies. This finding is consistent with the idea that controlled conditions are conducive to study designs that involve physiological manipulations (Furlanetti et al., 2016; Muller and Shair, 2016; Taylor et al., 2017) and sampling at precise ages (Schwartz, 2018; Kamitakahara et al., 2021). We also found that artificial environments were common in function studies. This finding is consistent with the idea that artificial environments are valuable for tracking communication in controlled contexts, such as food reward (Brenes and Schwartz, 2015; Wardak et al., 2024), aversive stimuli (Ayers et al., 2016; Burnett and Koprowski, 2020), social interaction (Warren et al., 2021; Chen et al., 2023), and social isolation (Schwartz and Wöhr, 2018; Broadfoot et al., 2023; Piastolov et al., 2023). In contrast to proximate-level and function studies, artificial environments were underrepresented in evolution studies. Although rare, evolutionary studies in artificial environments provide unique insights into the phylogenetic history of rodent vocalizations. For example, research on pup isolation calls across *Peromyscus* species shows that vocalization types can be controlled by distinct genetic loci and evolve quickly among sister taxa (Jourjine et al., 2023).

One potential limitation of studies in artificial environments is low species diversity. We found that artificial studies largely focused on lab-derived strains of rats and mice. An area for future work would be to bring wild animal species into captivity for controlled studies. Of course, doing so involves unique ethical and logistical considerations. Animals may be stressed by being captured, brought into a new environment, and then handled by humans. Wild-caught animals are likely to carry pathogens, which may require quarantine, testing, and treatment. Also, wild-caught species may have unique housing requirements for space, temperature, food, enrichment, and social needs. Despite these challenges, this review identified several successful examples of wild-derived species studied in the lab. These species include California mice (*P. californicus*) (Pultorak et al., 2018), pinyon mice (*Peromyscus truei*) (Brzozowski et al., 2023), singing mice (*S. teguina*) (Campbell et al., 2014; Tripp and Phelps, 2024), and voles (*Microtus* spp.) (Stewart et al., 2015; Robison et al., 2016; Warren et al., 2022; Madrid et al., 2024). Singing mice, for



instance, are insectivores from Central American cloud forests and grasslands. They thrive in captivity with extra humidity in their housing room and a carnivorous diet (Banerjee et al., 2019; Tripp and Phelps, 2024). North American voles vary in their social structure across species and seasons. Prairie voles (*M. ochrogaster*) are socially monogamous and thrive with stable female-male breeding pairs and social housing for weaned animals, while meadow voles (*M. pennsylvanicus*) show shifting levels of social affiliation with day length (Kenkel et al., 2021). Thus, although there are unique challenges, using wild-derived rodents in artificial environments is feasible.

We found a small collection of contemporary studies on rodent vocalizations in naturalistic environments. Naturalistic studies involved observations in wild habitats (e.g. (Wilson et al., 2015; Brito et al., 2017; Loughry et al., 2019; Hrouzkova et al., 2020)), as well as in urban areas (McRae and Green, 2014, 2017) and semi-naturalistic enclosures in zoos (Schneiderova et al., 2017) or on farms (Lima et al., 2018, 2022). Naturalistic environments have even been set up in laboratories, where enclosures simulate burrow systems (Riede, 2014; Dvořáková et al., 2016; Heinla et al., 2021). We found that naturalistic studies tend to focus on ultimate rather than proximate perspectives. However, there is much to be gained by addressing proximate questions in naturalistic settings. Doing this will require researchers to consider unique ethical and logistical issues. Experimental manipulations in the wild could cause unnecessary stress or influence behavior in a way that affects reproductive success or survival. Also, strategies are needed to track individual animals as they move across their territories. Rodents are small and inconspicuous, and many of them produce ultrasonic vocalizations that are above the frequency range of human hearing (Wöhr and Schwarting, 2013; Brudzynski, 2014).

Despite ethical and logistical challenges, this review identified a handful of species where naturalistic studies were carried out from proximate perspectives. Model species include North American red squirrels (*Tamiasciurus hudsonicus*) and European ground squirrels (*Spermophilus citellus*). Long-term research on a wild population of North American red squirrels involves the continuous tracking of ear-tagged squirrels and routine trapping to collect biological samples (Sehrsweney et al., 2019; Hare et al., 2024). Combined with behavioral observations and acoustic recordings, this long-term field research has supported studies on stress and reproductive condition. An alternative to studying rodents in the wild is to study them in semi-free ranging settings. The use of semi-natural outdoor enclosures has supported developmental research in European ground squirrels (Schneiderov et al., 2015). Taken together, valuable areas for future research would be to address proximate-level questions in naturalistic environments and to increase species diversity in artificial environments.

We also found that species diversity was higher in naturalistic over artificial studies, and these two environments tended to focus on different taxonomic groups. Some taxonomic groups have been studied in both environments (e.g., gerbils (*Meriones*), lemmings (*Lagurus*), mole voles (*Ellobius*), New World flying squirrels (*Glaucomys*), and rats (*Rattus*)). However, only a few species have been studied in both environments, such as the brown rat (*R.*

*norvegicus*) (Takacs et al., 2016), guinea pig (*Cavia intermedia*) (Verzola-Olivio and Monticelli, 2017), and rock cavy (*Kerodon rupestris*) (Monticelli and Alencar-Jr, 2021). Artificial and naturalistic environments come with their own advantages and disadvantages. As such, future research that spans these environments in diverse species would be an important step for building a comprehensive understanding of rodent communication.

## 4.4 Rodent communication in females and males across the lifespan

Contemporary ethological research on rodent vocalization studies involved both sexes. A strength of these inclusive studies is that they occurred across both proximate and ultimate perspectives. On the other hand, we found some evidence for sex differences. Despite the use of females in over half of the studies, consistently more studies used males as subjects or stimuli. We found that this pattern is likely due to an underrepresentation of females in studies on laboratory rats. A potential area for future work would be to focus more on the female perspective. Indeed, female-oriented studies have led to findings that challenge existing assumptions about sex differences. Recent studies identified by this review show that female mice and rats vocalize with males during mating interactions (Neunuebel et al., 2015; Borner et al., 2016; Finton et al., 2017; Ronald et al., 2020). These findings challenge prior research that set the precedent that mating vocalizations were primarily from males (e.g. (Sales, 1972b; Holy and Guo, 2005)).

Multiple age groups – from infancy to adulthood – were used in contemporary rodent vocalization studies. We found that both proximate and ultimate-level studies involved younger animals, which is crucial for a comprehensive understanding of vocal behavior across the lifespan. Despite the use of multiple age groups, however, infants were overrepresented in development studies. Infant studies that take a mechanistic, functional, or evolutionary perspective are an important complement to developmental work. For example, mechanistic studies describe unique neural circuits for infant vocalizations (Zimmer et al., 2019), and function studies describe unique roles for infant vocalizations in maternal and paternal care (Robison et al., 2016). We also found that contemporary studies on juvenile rodents showed low species diversity. This was likely due to an overrepresentation of juveniles in studies on laboratory rats (*R. rattus*) as opposed to mice (*M. musculus*) and other species. Rats have been an excellent model for juvenile studies because they engage in play behaviors that co-occur with vocalization (Himmler et al., 2014; Burke et al., 2017). However, studies in other species would be useful to characterize juvenile-specific behaviors and vocalizations across species.

## 4.5 Methodological innovations in rodent communication research

Methods-focused studies introduce new hardware and software tools that innovate the common versions. Types of common

hardware used in contemporary rodent research include high-quality recording equipment like condenser microphones for ultrasonic vocalizations (e.g. (Asaba et al., 2014; Sirotin et al., 2014; Binder et al., 2018; Cox et al., 2024)), directional shotgun microphones for audible vocalizations (e.g. (McRae and Green, 2017; Lima et al., 2024)), and their respective data acquisition systems. Other common hardware include high-quality electrostatic and dynamic speakers for acoustic playback experiments (Seffer et al., 2014; Schonfeld et al., 2020; Hood et al., 2023). Common software used in contemporary rodent studies allows researchers to record or play audio with recording and playback equipment. Common software also transforms audio recordings into spectrograms, detects vocalizations with user-defined thresholds or labels, and extracts an extensive array of spectro-temporal parameters. Example software packages include Avisoft SASLab Pro (Binder et al., 2018, 2020), Raven (Monticelli and Alencar-Jr, 2021; Fernández-Vargas et al., 2022; Eddington et al., 2024), and Metris Sonotrack (Riede, 2014; Jeon et al., 2019; Pupikina and Sitnikova, 2023).

This review identified a handful of methods-focused studies that innovated hardware tools. These innovations included novel equipment for passive wildlife recordings and sound localization. In the wild, ultrasonic microphones have been used to survey an area for various squirrel species (Diggins et al., 2020a, 2020b). Wearable microphones have been used to continuously record chipmunk vocalizations (Couchoux et al., 2015). In the lab, multiple condenser microphones around a testing arena (i.e., a microphone array) is an approach used to triangulate the locations of ultrasonic vocalizations (Neunuebel et al., 2015; Heckman et al., 2017; Warren et al., 2018; Oliveira-Stahl et al., 2023). Another novel method for sound localization is with an acoustic camera, which is a multi-microphone device that maps noise and vibration intensity (Matsumoto et al., 2022; Sterling et al., 2023). Combined with high-speed video to track animals, both of these non-invasive approaches enable researchers to assign caller identities in animal groups.

This review also identified several methods-focused studies that innovated software tools. A key innovation is new software for high-throughput processing of audio files. Example software packages include XBAT (Barker et al., 2014), MUPET (Van Segbroeck et al., 2017), Ultravox (Binder et al., 2018), DeepSqueak (Coffey et al., 2019), Mouse Song Analyzer (Binder et al., 2020), BootSnap (Abbasi et al., 2022), HybridMouse (Goussha et al., 2022), AMVOC (Stoumpou et al., 2023), and MoUSE (Kania et al., 2024). These software packages help to automate the detection, feature analysis, and classification of rodent vocalizations. Many of these software packages take advantage of computer vision and machine learning, including deep learning-based approaches like convolutional neural networks (CNNs). Other software innovations focus on computational pipelines and algorithms to improve downstream analyses of vocalization data. These innovations often improve the accuracy of caller identity assignments (Heckman et al., 2017; Oliveira-Stahl et al., 2023), linking vocalizations to other behaviors (Vendrig et al., 2019; John et al.,

2023; Chen et al., 2024), and analysis of complex acoustic features (Barker and Johnson, 2017; Ivanenko et al., 2020).

Finally, we found that methods-focused studies tended to use a homogenous group of species, environments, and animal demographics. Method studies focused on rats and mice. They also were biased towards adult male study subjects in artificial environments, although these observed biases did not differ from expected patterns based on the entire dataset. Interestingly, method studies were more likely to include infants, and less likely to include juveniles. A potential area for future work would be to develop and validate tools for more species, environmental conditions, and demographic groups.

## 4.6 Limitations and future directions

A few limitations to this scoping review require consideration. First, it is unlikely that the search strategy could detect every relevant study. The search strategy included several databases for biological research, which should find most recent studies on rodent vocalization. However, these databases can still miss relevant studies from low-impact or obscure journals. In some cases, relevant studies may be missed due to vocalization terminology that was not included in the comprehensive list of search terms. In other cases, studies would be missed if vocalization terminology was not included in the abstract or title. For example, data has been published on vocal production during prairie vole (*M. ochrogaster*) pair bonding (Gustison et al., 2024), but this aspect of the research is not described in the title or abstract. Second, our search strategy focused on recent studies from the past decade, and therefore, older studies were not included in analyses. These older studies may focus on different perspectives, species, research environments, and demographic groups. Although outside the scope of this review, our database search strategy can be applied to alternative time periods (Supplementary Data 4).

Finally, our search strategy was focused on ethological studies and removed those that used rodents as ‘disease models’ to make translational inferences about human disease and disorders. Research from a translational perspective can provide valuable insights into rodent communication. Biomedical studies represent a major component of laboratory rodent research, and they often characterize mechanisms and developmental processes (Scattoni et al., 2009). Data from wildtype or untreated animals in biomedical studies can be comparable to data from animals in ethological studies. Moreover, experimental animals can be used to identify genetic and neural mechanisms. Although outside the scope of this review, our database search strategy can be used to synthesize rodent communication research from a translational perspective (Supplementary Data 2).

## 4.7 Conclusions

The proximate and ultimate origins of vocal communication are traditionally studied in anurans, birds, bats, and primates. This review

synthesizes contemporary studies on vocal communication in Rodentia. These studies showcase rodents as a valuable taxonomic group for investigations across ethological perspectives, from mechanism and development to function and evolution. With several species, research environments, demographic groups, and novel technologies, rodents offer a plethora of opportunities for research at both proximate and ultimate levels. Integration across these ethological perspectives will help to build a comprehensive understanding of acoustic communication in rodents, mammals and vertebrates.

## Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

## Author contributions

AA: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, Data curation, Project administration. YW: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, Data curation, Project administration. RH: Formal analysis, Investigation, Writing – review & editing, Data curation. ET: Formal analysis, Investigation, Writing – review & editing, Data curation. CW: Formal analysis, Investigation, Writing – review & editing, Data curation. SA: Data curation, Formal analysis, Investigation, Writing – review & editing. AR: Formal analysis, Investigation, Writing – review & editing, Data curation. MA: Formal analysis, Investigation, Writing – review & editing, Data curation. AA: Formal analysis, Investigation, Writing – review & editing, Data curation. HK: Formal analysis, Investigation, Writing – review & editing, Data curation. RKS: Formal analysis, Investigation, Writing – review & editing, Data curation. TS: Formal analysis, Investigation, Writing – review & editing, Data curation. AJ: Formal analysis, Investigation, Writing – review & editing, Data curation. SJ: Formal analysis, Investigation, Writing – review & editing, Data curation. MLG: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fetho.2025.1563374/full#supplementary-material>

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