Behaviors associated with vocal communication of squirrels

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Abstract. Vocal communication is an important method squirrels (Sciuridae) use to transfer information from one individual to others. While behaviors associated with vocal communication have been explored in individual species or single call-types in specific groups of squirrels, no comprehensive review of these behaviors exists for Sciuridae. Herein, I review the current literature to describe behaviors associated with vocal communication in three groups of squirrels: ground squirrels, tree squirrels, and flying squirrels. I discuss the behavioral functions of squirrel vocalizations. A wide variety of behaviors are associated with particular call-types produced by squirrels, including alarm, agonistic, discomfort, affiliative, mating, and neonatal calls. There are large knowledge gaps in cataloging the vocal repertoires and associated behaviors of many species of squirrels, including commonly studied species such as marmots and ground squirrels, as alarm calls are typically focused on and other call-types are understudied or ignored. Since vocal communication is important to the development, reproduction, and survival of squirrels, further understanding the biological and ecological drivers behind vocal repertoires is critical to evaluating the ethology of this family as a whole.

Key words: calls; flying squirrel; ground squirrel; Rodentia; Sciuridae; tree squirrel; vocalizations.

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INTRODUCTION

For many mammals, the ability to communicate effectively with conspecifics is critical to survival. Vocal communication arose early in the evolution of vertebrates (Brudzynski 2014) and is typically associated with social species (Blumstein and Armitage 1997, Fichtel and Manser 2010, Okanoya and Screven 2018). Vocal communication facilitates many biologically important functions that increase survival and reproductive success, including predator defense, mate solicitation, territory establishment and maintenance, individual recognition, and group cohesion (Owings and Hennessy 1984, Gurnell 1987, Blumstein 2005, Arch and Narins 2008, Dent 2018). Compared to visual communication, vocal communication is advantageous in certain situations because signals can be conveyed over a greater distance, are not dependent on good viewing conditions (e.g., daylight), can mask the caller’s location (e.g., choirs), and may only be detectable by conspecifics (Dent 2018). Due to these factors, vocalizations can efficiently provide conspecifics with information that could be more difficult to obtain from other stimuli (Brudzynski 2014).

Sciuridae (squirrels) is a diverse family of rodents consisting of 296 species in 58 genera found on all continents except Antarctica (Wilson and Reeder 2005, Thorington et al. 2012). They occur in terrestrial habitats throughout the
world, including forests, grasslands, and deserts in lowland and mountainous environments. Squirrels can generally be divided into three groups: ground squirrels, tree squirrels, and flying squirrels. The body size of squirrel species ranges from 13.5 g to ~9 kg. They exhibit varying degrees of sociality which may be relatively consistent within a genus (e.g., chipmunks Tamias spp. tend to be solitary and territorial, whereas North American flying squirrels Glaucomys spp. are highly social, have overlapping home ranges, and are communal nesters throughout the year). However, sociality can drastically vary within a genus (e.g., marmots Marmota spp.; Blumstein 2003).

Ground squirrels are diurnal and tend to live in open habitats, such as deserts, alpine meadows, and grasslands. Although chipmunks can occur in forested habitats and occasionally forage in trees (Gurnell 1987, Thorington et al. 2012), they are mainly terrestrial and are categorized as ground squirrels in this review. Ground squirrels range from solitary (e.g., chipmunks, woodchucks Marmota monax) to colonial with highly complex social structures (e.g., prairie dogs Cynomys, marmots). Tree squirrels are diurnal and occur in forested habitats. They are arboreal in nature, spending the majority of their time in trees. Most tree squirrels are solitary or live in small groups (Gurnell 1987, Thorington et al. 2012). Certain species, such as Tamiasciurus spp., are highly territorial and defend territories year-round (Gurnell 1987). Other species, such as Sciurus spp. and beautiful squirrels (Callosciurus spp.), are not territorial, have overlapping home ranges, exhibit dominance hierarchies, and may communally den with conspecifics (e.g., Farentinos 1972a, Benson 1980, Tamura et al. 1988, Koprowski 1994). Flying squirrels are arboreal and nocturnal, occurring in temperate, boreal, and tropical forests. They are distinguishable from tree squirrels because flying squirrels have a patagium and use gliding as a form of locomotion. This group ranges from highly social species with overlapping home ranges and communal nesting to solitary species that only occur in small groups during the mating season (Thorington et al. 2012).

While vocal communication in squirrels is generally well studied, a disproportionate number of published studies focus on alarm-calling behaviors in ground squirrels. To date, there is no comprehensive review of behaviors associated with vocal communication among all three groups of squirrels, including non-alarm-calling behaviors associated with vocal communication. In this review, my objective is to discuss the behaviors associated with squirrel vocal communication. I also discuss vocal repertoires of squirrels, indicating which behaviors have been researched in order to highlight data gaps and future research directions.

**Methods**

I conducted a systematic literature review on all families, genera, and species of Sciuridae in January to April 2020. I searched articles on Web of Science and Google Scholar using the key words “alarm call,” “behavior,” “call,” “noise,” “sound,” “vocal repertoire,” “vocalize,” “vocalization” with combinations of “Sciuridae,” “squirrel,” and each genus and species name. In addition, I reviewed several field guides from around the world, all available Mammalian Species accounts, and Squirrels of the World (Thorington et al. 2012), as these sources may state if species produce vocalizations, especially for species without quantitatively described vocal repertoires. Since my literature search via search engines was largely restricted to works published in English, I searched references related to vocalizations mentioned in field guides, Mammalian Species accounts, and Squirrels of the World in an attempt to accumulate the most complete and up-to-date knowledge I could on squirrel vocal repertoires, including multiple non-English references. While I aimed to compile all known information on the vocal repertoire of each species, many species of squirrels were not well studied and information on the vocal repertoires of certain species may be in gray literature in other languages or unpublished and therefore missed in my review. In total, I evaluated over 550 pieces of literature for this review (Appendix S1). Specific references for each species with a vocal repertoire can be found in Appendix S2, although I only included pertinent references that quantitatively or qualitatively described calls.
**Terminology**

In bioacoustics, terminology can be ambiguous and the exact meaning of certain terms is dependent on the author. In this review, I define a vocalization as any sound that is produced orally by a squirrel. Since the exact physical mechanisms related to the production of vocalizations in different squirrel species are typically unknown and some species produce sounds by rattling their teeth (e.g., tooth-chattering), I include these sounds as vocalizations. A call is a single unit of sound produced by a squirrel and is unbroken by silence. A call-type is a unique call that is characterized by a specific range of frequencies, durations, and modulations. A call bout is when one or multiple call-types are produced in succession and may vary in order, number, and reoccurrence during the bout. Within a call bout, call-types can be repeated in a structured or seemingly random order.

For most descriptions of vocalizations, researchers tend to name the calls according to how they look on a spectrogram or how they sound (i.e., onomatopoeias). When I discuss certain call-types, I refer to the name most typically used, as different authors may call the same call-type from the same species by different names. For species with described call-types, I attempt to standardize similar names of a call-type from different sources under one name. However, I do not attempt to do this across species regardless of taxonomic relation. It is important to note that two call-types from different species with the same name may not be equivalent in their behavioral function and may or may not have the same structure (i.e., call properties such as call shape or frequency ranges). Additionally, two call-types from two different species with different names can have a behaviorally similar function and may or may not be similar in structure.

**VOCAL REPETOIRES OF SCIURIDAE**

**Ground squirrels**

Vocal communication of ground squirrels is well studied compared to tree or flying squirrels because calling is typically conspicuous and behavior associated with vocalizations is easily observable in the open habitats ground squirrels usually occupy. However, the majority of research pertains to alarm calls, wherein other functional call-types are understudied in this group. Ground squirrels include 115 species in 21 genera found in North America, Europe, Asia, and Africa (Thorington et al. 2012). Vocal communication is known in 17 genera and ~85% of species are described in the literature to produce vocalizations (Appendix S2). The best-studied species in this group includes Old World ground squirrels (*Spermophilus* spp.), New World ground squirrels (*Urocitellus* spp.), chipmunks, marmots, antelope squirrels (*Ammospermophilus* spp.), and prairie dogs, and quantitative descriptions of the call repertoire exist for most of the species belonging to these genera. Ground squirrels produce alarm, agonistic, discomfort, mating, affiliative, and neonatal calls, although alarm, aggression/annoyance, and discomfort calls are the most observed (Appendix S2). Of the species of ground squirrel known to vocalize, ~97% of species produce alarm calls. Approximately 37% of species only have one call-type described, wherein 94% of those calls are described as alarm calls and 6% have unknown behavioral functions. Most species have a described call repertoire of 1–10 distinct call-types, with the largest known call repertoire of 10 calls occurring in yellow-pine chipmunk (*Tamias amoenus*), Columbian ground squirrels (*Urocitellus columbianus*), and arctic ground squirrels (*U. parryii*; Appendix S2). Although all ground squirrels produce sonic calls, some species also produce calls with ultrasonic harmonics (e.g., Matocha 1975, Blumstein et al. 2008, Furrer and Manser 2009). Only Richardson’s (*U. richardsonii*) and speckled ground squirrels (*S. citellus*) are known to produce a call-type where the fundamental frequency is in the ultrasonic range (Wilson and Hare 2004, Matrosova et al. 2011).

**Tree squirrels**

Tree squirrels include 128 species in 22 genera that occur on all continents except Antarctica (Wilson and Reeder 2005, Palmer et al. 2007, Thorington et al. 2012). Tree squirrels are not native to Australia, but were introduced by European settlers. For tree squirrels, ~54% of species and 20 genera are known to produce vocalizations. Most of the vocal repertoires of temperate tree squirrels in North America and Europe are quantitatively described, whereas the majority of species from Africa, South America, and Asia are
either not described at all or only qualitatively described (but see work by Viljoen 1977, 1983, Emmons 1978, Tamura 1993, 1995, Tamura and Yong 1993, Tamura et al. 2018). Tree squirrels produce alarm, agonistic, discomfort, mating, affiliative, and neonatal calls, although ~33% of species do not have any known behaviors associated with their calls (Appendix S2). Species with described call repertoires have 1–13 distinct call-types with the largest known call repertoires occurring in North American red squirrels (Tamiasciurus hudsonicus; 13 calls), eastern gray squirrels (Sciurus carolinensis, 11 calls), eastern fox squirrels (S. niger, nine calls), and red-legged squirrels (Heliosciurus rufobrachium; nine calls, Appendix S2). Tree squirrels are only known to produce sonic vocalizations, but can emit calls with ultrasonic harmonics (e.g., Zelley 1971, Lishak 1982a, b).

**Flying squirrels**

There are 53 species of flying squirrels in 15 genera (Wilson and Reeder 2005, Yu et al. 2006, Thorton et al. 2012, Arbogast et al. 2017, Li et al. 2019). The highest diversity of flying squirrels is found in tropical regions of Indochina (Thorton et al. 2012, Datta and Nandini 2015, Krishna et al. 2016). Flying squirrels are the least studied group of Sciuridae due to their secretive and nocturnal nature, wherein most species are considered data deficient (Koprowski and Nandini 2008). Approximately 36% of flying squirrel species are reported to produce vocalizations in the literature and only five species (Glaucomys spp., Petaurista spp.) have quantitatively described vocal repertoires (Appendix S2). However, eight genera are noted to vocalize: *Euglaucomys*, *Eupetaurus*, *Glaucomys*, *Hylopetes*, *Iomys*, *Petaurista*, *Petinomys*, and *Pteromys*. Flying squirrels produce alarm, agonistic, discomfort, mating, affiliative, and neonatal calls. Of all the flying squirrel species known to call, 52% are only known to produce one call type and 42% have no described behaviors associated with their calls. Of the quantitatively described vocal repertoires forSciuridae, southern flying squirrels (*G. volans*) have the largest call repertoire with 27 unique call-types (Gilley et al. 2019, Appendix S2). The majority of flying squirrel species known to vocalize produce audible calls. The only species in this group currently known to emit calls where the fundamental frequency is ultrasonic are within two genera: *Glaucomys* spp. and *Pteromys* spp. (e.g., Gilley 2013, Eisinger et al. 2016, Diggins 2018, Gilley et al. 2019), whereas the former genus emits multiple call-types where the fundamental frequency is in the ultrasonic range.

**Vocalizations and Associated Behaviors**

A vocalization conveys a message from one individual squirrel to others. A vocal repertoire is the total number of individually unique call-types an animal makes. Each call-type within a vocal repertoire has distinctive parameters (i.e., call length and frequency range) allowing it to be differentiated from other call-types. Some species of squirrels are known to have diverse call repertoires (e.g., Zelley 1971, Viljoen 1977, Emmons 1978), including species-specific call-types (e.g., Brand 1976, Nikolski 1979, Eiler and Banack 2004, Matrosova et al. 2012, Tamura et al. 2018, Gilley et al. 2019). A specific call-type may communicate the behavior of the calling squirrel and may influence the behavior of the receiving squirrels. I placed vocalization-associated behaviors into six categories: alarm, agonistic, discomfort, affiliative, mating, and neonatal calls. For each section, I describe general behaviors associated with each category and highlight examples of those behaviors from ground squirrels, tree squirrels, and flying squirrels.

**Alarm calls**

Alarm calls are the most frequently heard vocalization emitted by squirrels (Emmons 1978, Blumstein 2003). These calls typically serve as a warning call and are associated with the detection of predators, although squirrels may alarm call at a falling tree, harmless animals, or other disturbances (Emmons 1978, Hoogland 1981, Matrosa et al. 2011). For example, Sulawesi squirrels (*Prosciurillus* spp., *Hyosciurus* spp.) produce a cacophony of alarm calls prior to the first drops of rain from an impending rainstorm (Musser et al. 2010). Alarm calls are typically described as loud and can carry long distances (Emmons 1978, Lenti Boero 1992, Blumstein 2005, Eason 2010, Matrosova et al. 2011). As a result of their prevalence and detectability, alarm calls are extensively studied compared to other...
Sciurid vocalizations. Of the 185 species with described vocal repertoires, ~75% are known to produce alarm calls with 45 of those species only having one call-type described (Appendix S2). In this review, I attempt only to generally highlight behaviors associated with these calls, but will not go into extensive detail as reviews on alarm calls pertaining to Rodentia (Shelly and Blumstein 2004, Blumstein 2005), Sciuridae (McRae 2020), or specific squirrel genera (i.e., marmots, Blumstein 2007) are available.

Species in all three groups of squirrels produce alarm calls: ground squirrels (e.g., Waring 1966, Turner 1973, Smith 1978a, Sherman 1985, Blumstein 1999), tree squirrels (e.g., Farentinos 1974, Emmons 1978, Smith 1978b, Lishak 1984, Datta 1998), and flying squirrels (e.g., Sollberger 1940, Ando and Kuramochi 2008, Shen 2013). Most diurnal species of squirrels with known call repertoires produce alarm calls (Sherman 1977, Gurnell 1987, Blumstein 2005). Diurnality is evolutionarily linked to alarm calling. This may be because predators are typically detected visually prior to individuals emitting alarm calls (Shelly and Blumstein 2004, Blumstein 2005). A few species of nocturnal flying squirrels are known to produce alarm calls, but alarm calling in most species is unknown as this group is understudied and call-associated behaviors are difficult to observe in the wild. Since observing the behavior associated with a vocalization is needed to determine if that call-type is indeed an alarm call (Blumstein 2005), it remains to be seen if alarm calls are universal in all genera of squirrels. While most squirrel species known to vocalize have at least one alarm call-type, certain species have multiple alarm call-types (e.g., Waring 1966, Blumstein 2003, Sloan et al. 2005, Komarova et al. 2014). Call-types used as alarm calls may have other behavioral uses and may be context-dependent (see Multi-use calls section below).

In the literature, the two main theories on the behavioral function of alarm calls are squirrels produce these calls to (1) warn kin, dependent young, or neighboring group members of a predator (Sherman 1977, 1980, Thompson and Hare 2010) or (2) directly communicate with the predator (Blumstein 2003, Shelly and Blumstein 2004). The first theory typically invokes an evolutionary benefit to warn close relatives, especially offspring, on the approach of a predator. In some species of ground squirrels, lactating females with newly emerged young produce alarm calls at higher rates than non-reproductive females or males (Sherman 1980, Davis 1984, Hoogland 1996, Swaisgood et al. 1999). Southern Amazon red squirrels (*Sciurus spadiceus*) are usually solitary, but may forage in small groups. When in groups they produce alarm calls, but are typically silent when alone, indicating that this species may use alarm calls to communicate with group members instead of the predator (Eason 2010).

The second theory proposes that alarm calls directly warn the predator. Diurnality may be more important to the evolution of alarm calling in squirrels than sociality, indicating that the main function of alarm calls is to communicate with predators (Shelly and Blumstein 2004). Foxes (*Vulpes* spp.) detected by alpine marmots (*Marmota marmota*) are less likely to pursue a marmot after an alarm call is given (Lenti Boero 1992). Upon sighting a long-tailed weasel (*Mustela frenata*), Richardson’s ground squirrels usually give alarm calls and in some instances chase the weasel away (Davis and Murie 1985). Observations on Indian giant squirrels (*Ratufa indica*), a solitary and territorial species, show they alarm call and mob crested-hawk eagles (*Nisaetus cirrhatus*). The squirrel’s behavior is seemingly suicidal, as the squirrel does not flee, but approaches within 1–2 m of a perched eagle and calls repeatedly (Datta 1998). This behavior is hypothesized to not warn conspecifics, but functions as a direct warning signal to the eagle (Datta 1998, but see Ramachandran 1988). When in a burrow with a snake, California ground squirrels (*Otospermophilus beecheyi*) vocalize toward the snake, but use a call typically given in agonistic interactions with conspecifics (Coss and Owings 1978). Since passages in an underground tunnel system absorb sound (Nikol’skii and Vinogradov 2000, Nikol’skii 2018), it is unlikely this calling behavior is directed toward other conspecifics in the burrow. The vocalization is more likely directed as a signal of aggression toward the snake, especially since visual cues of aggression are absent in the darkness of a burrow. Most squirrels normally run to a safe place prior to vocalizing (e.g., burrow entrance or cover; Barash 1975, Betts 1976, Frost 1978,
can be differentiated by ear in the badgers compared to other terrestrial predators and aerial predators, and alarm calls given to ground squirrels have distinct calls for terrestrial predators (e.g., Frederiksen and Slobodchikoff 2006). Prairie dogs emit alarm calls that vocally distinguish predators and convey descriptive information about the predator in their alarm calls, such as size, shape, or color of individual predators (e.g., Frederiksen and Slobodchikoff 2006, Kiriazis and Slobodchikoff 2006, Slobodchikoff et al. 1991, 2009, 2012; but see recent research to definitively determine context-dependent information in alarm calls even in well-studied species, meriting further investigation.

An alarm call may change in length or temporal arrangement to signify how much of a threat a predator is. Many species produce shorter alarm calls to aerial predators and longer calls to terrestrial predators (e.g., Heard 1973, Dunford 1977, Davis 1984, Sherman 1985, Lenti Boero 1992, Greene and Meagher 1998, Blumstein 1999), but this is not always true as some species emit continuous calls for aerial predators (Burke da Silva et al. 1994). The production of short alarm calls for aerial predators is evolutionarily appropriate as it represents a fast-approaching threat inciting faster responses (i.e., attack by a raptor), whereas longer calls indicate terrestrial predators seen at a greater distance away requiring less urgency (i.e., attack by a coyote). Squirrels may increase or decrease the rate of calling depending on distance of the predator, wherein some species decrease (Blumstein 1995) and others increase alarm call repetition as the predator approaches (Burke da Silva et al. 1994, Nikoł’ski and
An alarm call should presumably incite the same response behavior or range of behaviors from all individuals to the stimuli. However, the probability of calling or responding to alarm calls may be influenced by individual characteristics (e.g., age, sex, reproductive condition, level of arousal, personality; Sherman 1977, Owings and Virginia 1978, Smith 1978a, Loughry and McDonough 1989, Sloan and Hare 2008, Lea and Blumstein 2011, Petelle et al. 2013, Couchoux et al. 2018) or other factors that might mitigate an individual's actions (e.g., proximity to cover, distance from the predator, familiarity with caller, isolation from the group; Sherman 1985, Fuong et al. 2015, Blumstein et al. 2017). While some species have different calls and responses to specific predators (e.g., Turner 1973, Kiriazis and Slobodchikoff 2006), others do not have predator-specific calls (e.g., Blumstein 1999, Loughry et al. 2019) or responses (e.g., Dunford 1970, Farentinos 1974, Furrer and Manser 2009), indicating certain squirrel species may have evolved with particular behaviors depending on predator type and the predator’s hunting strategy, as well as risk perception and avoidance techniques used by the squirrels. Standardized methods to determine how predator type, predator distance, and factors of individual squirrels (e.g., sex, individual call variation, isolation, and proximity to cover) influence alarm calls may illuminate variation in vocal behavior and responses to alarm calls in different groups of squirrels.

In certain species, when one individual produces an alarm call, others may also begin calling forming a chorus. Choruses serve two purposes: (1) to alert others to the predator’s presence or movements and (2) to mob the predator. Choruses occurring during mobbing behaviors may involve other species, including birds, monkeys, and heterospecific squirrels (Emmons 1978, 1980, Musser et al. 2010). In African squirrels, mobbing behaviors associated with alarm calling is contagious and draws other squirrels (conspecifics and heterospecifics) to the mobbing group (Emmons 1978). Mobbing behavior of snakes is relatively well studied and certain species of squirrels have specific alarm call-types for snakes (e.g., Owings and Loughry 1985, Tamura 1989). When chipmunks emit chip alarm calls, others also began chipping, forming choruses of several individuals that vocalize until the predator leaves (Dunford 1970, Brand 1976, Burke da Silva et al. 1994). Prairie dogs have a contagious alarm call that once initiated will be repeated by multiple neighbors and can be used to probe vigilance of their neighbors (Waring 1970, Hoogland 1981, Hare et al. 2014). Increased vigilance in Richardson’s ground squirrels corresponds to chorus alarm calls sequentially approaching the receiver, indicating predator movements may be conferred through the spatial pattern of caller recruitment relative to receivers (Thompson and Hare 2010). Community vigilance reduces the hunting success of a predator while reducing the amount of time an individual squirrel spends toward vigilance, potentially increasing the survival of squirrels who evolved to vocalize in choruses.

Squirrels may respond to the alarm calls of sympatric heterospecics. Eastern chipmunks (Tamias striatus) and groundhogs (Marmota monax) respond to each other’s alarm calls (Aschemeyer and Maher 2011), as do yellow-bellied marmots (M. flaviventris) and golden-mantled ground squirrels (Callospermophilus lateralis; Shriver 1998). In tropical forests, squirrels forage and move with mixed flocks of birds. Both squirrels and birds produce and respond to each other’s alarm calls, potentially reducing predation risk in dense forested habitat due to enhanced group vigilance (Limparungpatthanakij et al. 2017). Alarm calling in mixed flocks also leads to multi-species predator mobbing, where different species of squirrels and birds mob a predator. Foraging with mixed flocks is seen in southern Amazon red squirrels, palm squirrels (Funambulus spp.), Western striped squirrels (Tamiops mcclellandii), Indochinese ground squirrels (Menetes berdmorei), and beautiful squirrels (Kotagama and Goodale 2004, Goodale and Kotagama 2005, Della-Flora et al. 2012, Limparungpatthanakij et al. 2017). Eavesdropping on the alarm calls of or foraging with other species may especially be beneficial to solitary species, territorial species, or species that live in dense habitat, such as tropical rain forests, where group vigilance from conspecifics is limited. However, Cape ground squirrels, who live in groups in arid grasslands, also respond to bird alarm calls (Waterman and Mai 2020), indicating
behavioral responses to vocal signals from heterospecifics may be important for predator vigilance in multiple species of squirrels across different habitat types, even if they live colonially.

An interesting evolutionary development in squirrel vocalizations that has not received much attention is vocal similarity to avifauna. The montane long-nosed squirrel (Hyosciris heinrichi) has a bird-like alarm call that is difficult to differentiate from actual bird calls (Musser et al. 2010). Franklin’s ground squirrel (Poliocitellus franklinii) and several species of African squirrels also have bird-like alarm calls (Sowls 1948, Emmons 1978, Viljoen 1983). The mechanisms of how and why certain species of squirrels evolved alarm calls than are acoustically similar to bird calls are unknown, but bird-like alarm calls could reduce predator attention or have ventriloquist properties making the caller difficult to locate. Whether these types of calls are a form of mimicry or evolutionary emulation is unknown. Regardless, this adaptation may be beneficial in solitary squirrel species or species living in densely vegetated environments and should be investigated.

Agonistic calls

Agonistic calls are aggressive vocalizations given toward conspecifics or heterospecifics (Kondo and Watanabe 2009). I categorize two types of agonistic calls that occur in Sciuridae: aggression/annoyance calls and territorial calls. Both juvenile and adult squirrels emit aggression and annoyance calls, although juveniles typically disperse and establish a territory prior to using territorial calls.

Aggression/annoyance calls.—Aggression and annoyance calls are directed at conspecifics and heterospecifics, typically functioning to inhibit unwanted contact from an approaching individual. These calls are usually used in close-quarter situations (Matocha 1975, O’Shea 1976, Emmons 1978). Vocalizations interpreted as aggression or annoyance calls may be interchangeable and dependent on the context of the situation. This includes the intent of the approaching squirrel, which is typically displayed by the approacher’s body positioning and vocalizations toward the individual being approached. Aggression and annoyance call-types are seen in ground squirrels (e.g., Mayer 1953, Waring 1966, 1970, Betts 1976, O’Shea 1976, Smith et al. 1977, Taulman 1977, Balph and Balph 1996), tree squirrels (e.g., Farrentinos 1972b, Viljoen 1977, Emmons 1978, Lishak 1982b), and flying squirrels (Linzey and Linzey 1979, Wells-Gosling 1985, Shen 2013). Annoyance calls occur during unwanted, but non-threatening, behavior from a conspecific, such as a juvenile. Aggression calls usually occur during the breeding season, prior to the emergence of young, during territory disputes (for discussion on territorial calls, see the Territorial call section), in close-range interactions with a heterospecific, and other social situations with conspecifics (e.g., fights over food). Aggression calls may be followed by fighting or other agonistic visual displays between individuals. The frequency and intensity of aggressive interactions may depend on the sociality or territoriality of the species in question, the time of year, whether young are present, or during interactions over a resource (e.g., food).

Most aggression or annoyance calls are described as scolding or harsh sounding. While many colloquial names are used to categorize aggression or annoyance calls, several categorizations appear frequently in species with well-described vocal repertoires: growls, hisses, rasps, snarls, and tooth-chatters. However, these calls are not necessarily equivocal and may have different call parameters among species. Additionally, other call-types not mentioned above may be used to communicate aggression or annoyance. Most squirrel species with known vocal repertoires produce tooth-chattering (e.g., Waring 1966, Carl 1971, Zelley 1971, Lishak 1982b), which seems to be a universal warning to inhibit contact by an approaching individual. Typically, species that produce tooth-chattering also have one or more other aggression or annoyance calls. For example, growls and tooth-chatters are given by thirteen-lined ground squirrels (Ictidomys tridecemlineatus; Ryshke 1972, Matocha 1975), hoary marmots (Marmota caligata; Taulman 1977), and prairie dogs (Waring 1970). While being approached, some species change which aggression or annoyance calls they give depending on the distance of the approaching individual (Carl 1971, Balph and Balph 1996). Vocalizing squirrels may also take defensive postures indicating an intention to attack (Waring 1970, Emmons 1978),
but in most cases the vocalization is enough to inhibit the approach of conspecific and physical alterations are avoided.

Annoyance calls occur when squirrels are irritated by the close presence or crowding of another non-aggressive individual, such as a juvenile squirrel (Waring 1970, Smith et al. 1977). Young squirrels may annoy adults and vocalizations are used to reject these juveniles instead of physical contact. For example, when juvenile black-tailed prairie dogs (Cynomys ludovicianus) attempt to initiate play, allogrooming, or rubbing with an unreceptive adult, the adult chitters and the juveniles cease their attempt at contact (Smith et al. 1977). The rejection of boisterous juveniles is seen in other squirrels. In North American red squirrels, when juveniles attempt to play with or allogroom an unwilling adult squirrel, they are vocally rebuffed (Lair 1990). In eastern gray squirrels, siblings annoy each other and agonistic vocalizations, such as tooth-chattering, toward nestmates will increase as the nestlings age (Lishak 1982). Squirrels may also reject amicable interactions with adults. Black-tailed prairie dogs bark to reject coterie members attempting to initiate amicable contact (e.g., anal-sniffing, kissgreeting, or allogrooming), usually because the caller is foraging or engaging in another activity that would be interrupted if they allow contact (Smith et al. 1977).

During the breeding season, agonistic interactions between males tend to increase. As males become scrotal, they become more aggressive and will fight to compete for estrous females (Gurnell 1987). In tree squirrels and North American flying squirrels, multiple males show up to compete for an opportunity to mate with an estrous female and as they jostle for a position close to the female, they will fight with one another (Thompson 1977, Wells-Gosling 1985, Gurnell 1987). Vocalizations made by males during mating chases include aggression calls typically heard during physical altercations. While aggressive interactions can occur during territory disputes and fighting over a potential mate, hostility by females toward males during the mating season is common for many species (for information on mating-specific calls, see Mating calls section below). Black-tailed prairie dog females in estrous give chatter bark calls when being approached by an unwanted male (Waring 1970). In tree squirrels and chipmunks, scrotal males follow and chase an estrous female. Prior to females becoming receptive, they vocalize and aggressively chase males away (e.g., Farentinos 1972, 1974, Betts 1976, Brand 1976, Smith et al. 1977). When male North American red squirrels attempt to approach within 1 m of an unreceptive estrous female, she repels them by lunging and growling (Embry 1970, Frost 1978, Smith 1978b, Lair 1990). Attacks toward suitors typically decline as a female becomes ready to copulate (Farentinos 1972b).

Aggressive calls toward heterospecifics also function to inhibit the approach of an individual (e.g., a potential predator) toward the caller. Most heterospecific confrontations are observed in trapped squirrels, wherein a human approaching a trap elicits aggression calls and defensive posturing by the trapped squirrel. A Vancouver Island marmot (Marmota vancouverensis) hisses and lunges when its trap is approached, attempting to bite the human (Heard 1973). When Smith’s bush squirrels (Paraxerus cepapi) are approached in a trap or their nest site is disturbed, they usually grunt or growl (Viljoen 1977, 1983). While North American red squirrels are trapped, they vocalize and aggressively ram the gate of the trap (C. Diggins, pers. obs.). This behavior is seen in countless other live-trapped squirrels (e.g., Carl 1971, Betts 1976, Fagerstone 1987), but is not a universal behavior in all species.

Territorial calls.—Territory defense is seen in many squirrel species, whether it is to defend year-round territories of solitary individuals (e.g., Tamiasciurus spp.; Smith 1968, Gurnell 1987) or groups (e.g., prairie dogs; Hoogland 1995, Slobodchikoff et al. 2009), or a female’s nest site when rearing young (McLean 1984, Gurnell 1987). Although territorial advertisement calls are typically distinct, vocalizations heard during territory defense can be heard in other aggression/annoyance situations within the same species. Territorial advertisement calls allow an individual squirrel to broadcast its territory boundaries to surrounding neighbors. With the exception of colonial species (e.g., prairie dogs, marmots), these calls are typically used when other squirrels are not in sight. North American red squirrels have non-overlapping territories, each defended year-round by an individual
squirrel using a rattle call (Smith 1968, 1978b, Gurnell 1987). Red squirrels regularly advertise the boundaries of their territory throughout the day (Frost 1978) and these calls act as temporary deterrents to intruders (Siracusa et al. 2017). The solitary Indian giant flying squirrel (Petaurista philippensis) calls prior to entering its nest cavity and emits the same vocalization frequently in the area around its nest tree, suggesting a territorial advertisement call (Koli and Bhatnagar 2014). Bobak marmot (Marmota bobak) alarm calls may also serve as a territorial call, since the calls are frequently heard by neighbors and confirm the continued occupation of a territory by the calling animal (Nikol’skii and Suchanova 1994).

Intentional or accidental wandering into another squirrel’s territory can lead to close-range agonistic chases. Squirrels vocalize as they chase the intruder or immigrant squirrel from their territory (Zelley 1971, Smith 1978b, Gurnell 1987), using similar vocalizations heard in other agonistic social interactions (see Aggression/annoyance calls section above). Eastern gray squirrels, which display a dominance hierarchy with overlapping home ranges, become more aggressive during the dispersal of juveniles, causing increased aggressive interactions. Dominant eastern gray squirrels chase the immigrants from their home range, occasionally fighting with immigrants in noisy tussles (Thompson 1978). North American red squirrels commonly use aggression calls when another squirrel enters their territory and they can be heard vocalizing as they chase the intruder away (Smith 1968, 1978b). In prairie dog coterie, all members defend the coterie’s territory from intruders. Prairie dogs use barks to repel intruders and recruit coterie members to assist in the defense of their territory (Smith et al. 1977, Michener and Murie 1983, Raynor 1998). Individual prairie dogs may occasionally rush the intruder or the coterie boundary and initiate fights. Black-tailed prairie dogs use the jump-yip display to defend coterie territories, wherein the squirrel calls and throws its body forward to a nearly vertical position (King 1955, Smith et al. 1976). The jump-yip call tends to be contagious and is usually immediately repeated by other coterie members (Waring 1970, Slobodchikoff et al. 2009, Hare et al. 2014). Prairie dogs also use tooth-chattering during disputes over territory boundaries (Smith et al. 1977, Slobodchikoff et al. 2009).

Whereas territory in certain species can occur year-round, some species exhibit seasonal territoriality in females. Once female squirrels are pregnant or lactating, individuals of many species establish territories around their burrow or nest and do not permit other squirrels to den with them (McLean 1984, Wells-Gosling 1985, Gurnell 1987). During this time, the female becomes intolerant toward other squirrels and aggressively defends the area around her burrow or den from intruders until her young are weaned (Dunford 1977, McLean 1984, Wells-Gosling 1985, Balph and Balph 1996). Infanticide occurs in some species of squirrels (e.g., Michener 1982, Jenkins and Eshelman 1984, Vestal 1991, Coulon et al. 1995), which may promote aggressive behaviors by the mother to protect her young. However, factors such as social structure and density dependence might determine the amount of defensive behavior (Wolff 1993). Vocalizations noted during burrow and nest defense are most likely similar to those heard in other aggressive interactions (see Aggression/annoyance calls section above), although work on intraspecific behaviors associated with natal den defense in squirrels is generally lacking.

Discomfort calls

Discomfort calls communicate uneasiness, fear, pain, or injury. They may occur in a variety of contexts and are emitted by both juveniles and adult squirrels. Discomfort calls are heard in the majority of squirrel species with relatively well-known call repertoires. Squirrels that emit discomfort calls include ground squirrels (Waring 1966, Carl 1971, Barash 1975, Brand 1976, Smith et al. 1977, Fagerstone 1987, Blumstein et al. 2008, Manno 2012), tree squirrels (Zelley 1971, Parentinos 1974, Emmons 1978, Frost 1978), and flying squirrels (Linzy and Linzy 1979, Wells-Gosling 1985). Most discomfort calls are described as screams, squeaks, or squeals, and these calls may be more specific to pain and injury or the fear of pain and injury.

A squirrel experiencing pain may emit discomfort calls. Waring (1970) observed an injured black-tailed prairie dog limping with an injured leg. The squirrel then shrieked, darted a meter away, and began grooming its hind legs before
limping off again. The call was a high-pitched version of a black-tailed prairie dog scream call. Waring also heard a Gunnison's prairie dog scream as it was toe-clipped for identification. Fights between conspecifics can cause injury and discomfort calls may be given during physical altercations. In ground squirrels (*Urocitellus* spp.), juveniles squeal when attacked by adult squirrels (Fagerstone 1987). In North American red squirrels, screams are heard during fights with another squirrel (Frost 1978), whereas North American chipmunks emit a high-pitched sound when attacked by another chipmunk (Brand 1976). Captive ribboned rope squirrels (*Funisciurus lemniscatus*) squeal during fights (Emmons 1978). Emmons notes this call-type is used when a squirrel is in distress, but more typically when the squirrel is restrained or injured. Squirrels may emit squeals and screams when they are being chased by dominant individuals (Waring 1966, Farentinos 1974, Betts 1976), possibly as a fear response to potential injury or pain that might occur if a physical altercation happens.

Attacks by predators can also cause an individual to produce discomfort calls. Both Arctic ground squirrels and yellow-bellied marmots are known to scream when attacked by a fox (Carl 1971, Blumstein et al. 2008). This response behavior is also seen in Uinta ground squirrels when a young squirrel is being attacked by an adult conspecific (Balph and Balph 1996). During the initial week post-emergence, Columbian ground squirrel pups are susceptible to infanticide and emit screams when attacked by adults, prompting a response from the juvenile’s mother (Manno 2012). When a juvenile thirteen-line ground squirrel is seized by a roadrunner (*Geococcyx* spp.), the juvenile gives a discomfort call and the mother attacks the road runner, who may subsequently release the juvenile, allowing the juvenile to escape (McCarley 1966). Adults are typically responsive to screams of juveniles and these calls might incite adults to come to the juvenile’s aid (Balph and Balph 1996, Blumstein et al. 2008). Although the production of screams during an attack may be an involuntary response to pain, these behaviors may have also evolved to recruit conspecifics to aid the attacked squirrel and need to be further studied.

Many species also emit screams and squeals when they are being handled by humans (e.g., Waring 1970, Zelley 1971, Betts 1976, Frost 1978, Fagerstone 1987, Blumstein 2007, Matrosova et al. 2011). These calls are readily given by juveniles and can be easily observed in captive colonies (Farentinos 1974, Sherman 1977, Linzey and Linzey 1979, Lishak 1982b). Other calls may also convey discomfort or fear. Eastern chipmunks give a trill when escaping from a predator (Burke da Silva et al. 1994, 2002). The exact communication function of the chipmunk trill is unknown, but it may convey a sense of fear since the chipmunk is fleeing a predator. Other discomfort calls are known for neonates, but these are discussed in the Neonatal calls section below.

**Affiliative calls**

Affiliative calls function to maintain social connections between conspecifics, including reuniting visually separated individuals and maintaining group cohesion (Kondo and Watanabe 2009). While some mating calls could fall under the umbrella of affiliative calls, some calls associated with mating bouts are agonistic (e.g., some mate guarding vocalizations). Because of this, I addressed mating calls in the Mating calls section below. Additionally, calls produced by neonates may also function to maintain social cohesion. However, production of certain call-types cease after the neonate matures (see Neonatal calls section below). Therefore, I only discuss contact calls in this section.

**Contact calls**.—Contact calls have a variety of different social contexts, including communicating group membership. They are emitted by both adult and juveniles at a distance or in close contact in a variety of circumstances. Contact calls are produced in non-aggressive interactions, such as during the greeting of familiar conspecifics, play, grooming, an individual’s peaceable approach toward an unknown conspecific, sleeping, or situations when the animal is relaxed (Waring 1970, Pizzimenti and McLenaghan 1974, Smith et al. 1977, Emmons 1978).

When approaching another squirrel, contact calls are often associated with submissive posturing to communicate non-aggressive intentions toward the receiving individual (Emmons 1978). In the solitary unstriped ground squirrel (*Xerus rutilus*), subordinate squirrels produce a chirring...
sound when approaching a dominant squirrel, taking a prostrate posture and rolling onto their sides (O’Shea 1976). European red squirrels, North American red squirrels, and thirteen-lined ground squirrels give specific call-types accompanied by submissive posturing when approaching another squirrel, especially a dominant male (Eibl-Eibesfeldt 1951, Embry 1970, Ryshke 1972). The communication of non-aggressive intent toward another squirrel is critical to reduce physical confrontation, which may lead to injury or death.

To attract conspecifics to the area where the caller is located or during physical contact, contact calls are also used. Western striped squirrels are highly social, emitting a high-pitched staccato vocalization to attract members of its group and when squirrels are greeting each other (Viljoen 1978). The buzz calls of North American red squirrels are associated with a range of non-aggressive behaviors including the establishment of non-aggressive contact, as a juvenile play call, and as a call given by mothers approaching their young (Embry 1970, Smith 1978b, Lair 1990). Juvenile Cape ground squirrels (Xerus inauris) produce a distinctive call when playing with other juveniles (Herzig-Straschil 1978). Contact calls occur between a green bush squirrel mother greeting her juveniles outside the nest and are typically followed by allogrooming (Emmons 1978). Gunnison’s prairie dogs make a purring sound when being allogroomed by conspecifics or when a captive prairie dog is being scratched by a human (Waring 1970). This species also gives a raspy chatter when outside its burrow during times of calm for no apparent reason (Waring 1970). Sociality and territoriality may influence the diversity and context of contact calls within a species’ vocal repertoire. These call types are generally overlooked in squirrel communication research and should be studied further to determine their behavioral and evolutionary development in Sciuridae.

Mating calls

Ground squirrels, tree squirrels, and flying squirrels are all known to produce mating calls (e.g., Eibl-Eibesfeldt 1951, Thompson 1977, Lishak 1982a, Yanagawa et al. 1991, Blake 1992, Tamura 1995, Hoogland 1998, Airapetyants and Fokin 2003, Manno et al. 2008, Madhavi et al. 2012). Call-types associated with mating behaviors may vary in frequency depending on the time of year. During the breeding season, hormonal changes occur in both males and female adult squirrels. An increase in certain vocalizations during this time period is potentially linked to reproductive condition, especially for specific call-types that only occur during the mating season (Nikol’skii 1999). Male red bush squirrels (Paraxerus palliatus) and Smith’s bush squirrels give a mating call that is associated with scrotal size: The call-type is given frequently when the scrotum is descended, but disappears from the male’s vocal repertoire as scrotal size decreases and the male is not in reproductive condition (Viljoen 1983). Indian giant flying squirrels and Taiwan red-and-white flying squirrels (Petaurista alborufus lena) have the highest calling rates during the breeding season, which may help these solitary species make contact with potential mates (Shen 2013, Koli and Bhatnagar 2014). Thirteen-lined ground squirrels produce trills during the mating season, but this call is typically absent during other times of year (Schwagmeyer 1980). There are currently no studies linking changes in vocalizations in Sciurids to hormonal fluctuations, so how hormonal changes alter vocal communication to increase reproductive success is unknown.

Types of mating calls and behaviors associated with them vary from species to species, but I attempt to give examples of the main stages typically seen during a mating bout. Some species have distinctive calls only given during the mating season, while other species modify or emit calls typically used in other contexts (e.g., alarm calls; see Multi-use call-types section below). Additionally, some calls are only made by males, while others are specific to females (e.g., estrus calls). I consider mating calls those produced prior to, during, or directly after copulation. One or both of the sexes may emit calls prior to and during copulation, specifically to attract mates or potentially induce receptivity of the estrous female. Only males give post-copulation calls, which are associated with mate guarding. Vocalizations that occur prior to and during mating can be categorized into three groups: advertising, approach, and copulation calls.

When females produce advertising calls (i.e., estrous calls), they are communicating their
reproductive condition to potential mates. A female Siberian chipmunk (*Tamias sibiricus*) in estrus produces advertisement calls and continues to vocalize while in close contact with a male prior to copulation (Blake and Gillett 1984, Blake 1992). Female eastern gray squirrels emit a high-pitched vocalization allowing males to locate her (Koprowski 1992). Female Gunnison’s prairie dogs emit estrus calls the day before and the day they are in estrus (Hoogland 1998). Female North American chipmunks sit on exposed perches and loudly emit a modified alarm call for up to 30 min a few days prior to estrous (Callahan 1981), a method that may be beneficial during years with low population densities for these solitary species. A modified alarm call is also used by female bush squirrels to attract mates (Viljoen 1983). Males may also advertise their readiness to mate using specific pre-copulatory calls, which enable females to locate them and may serve to arouse the female. A male Malabar giant squirrel (*Rattus indicus maxima*) produces a mating call that attracts females from up to 50 m away (Ramachandran 1988). Advertising calls may be especially beneficial to solitary species with large home ranges or species that live in habitats with low visibility, allowing them to locate potential mates more efficiently (Blankenship and Brand 1987).

Approach calls occur when a male is soliciting a female and attempting to make physical contact with her. In tree squirrels, North American flying squirrels, and chipmunks, males call while approaching and chasing the female. Aply known as the chase stage, the estrus female is typically pursued by multiple males who noisily follow her, producing chase calls and vocalizing aggressively to fend off rival males (Smith 1978b, Lair 1990). In most species, the female may vocalize while she is being trailed by the males and seems to reject close contact by aggressively and loudly rebuffing suitors when she is not receptive (see Aggression/annoyance calls section).

Vocalizing while pursing the female during the chase phase is seen in multiple species of squirrels. The tassel-eared squirrel (*Sciurus aberti*) males emit alarm calls, typically near the estrus female, although the call is directed at her other suitors to ward them off (Farentinos 1972b, 1974). Eastern gray squirrel males make a distinctive sneezing sound during mating chases and only produce this call during the mating season (Thompson 1977). Male northern flying squirrels (*Glaucomys sabrinus*) produce vocalizations while chasing a potential mate (Muul 1969), although it is unknown if this vocalization is specific to mating. North American chipmunks have a distinctive chatter call similar to their alarm call during mating bouts (Brand 1976). However, the mating chatter and alarm chatter of chipmunks varying in two ways: The harmonic structure and elements of the mating chatter are different and only males produce this call during the mating season when following the female during the approach phase (Brand 1976). The chase phase is generally absent in some colonial species of squirrels, but males will still fight and vie for a chance to mate with an estrus female.

Once a female allows a male to approach her, he usually does so in a submissive fashion. Many males take a submissive posture and emit calls typically heard in juveniles and subordinate squirrels. European red squirrel (*Sciurus vulgaris*) males emit a muk-muk vocalization when approaching females, which is also used by juveniles (Eibl-Eibesfeldt 1951). In several species of African tree squirrels, Emmons (1978) notes males emit contact calls during the mating chase or approach phase that are similar to those given by juveniles or subordinate squirrels. Male North American red squirrels give juvenile appeasement calls when initiating contact with an estrus female (Frost 1978, Smith 1978b, Lair 1990). The use of juvenile calls when approaching a female may reduce her aggressiveness and could function to attract her (Farentinos 1974). However, it is not known if using juvenile vocalization to appease the female occurs in most squirrel species. Male northern flying squirrels emit vocalizations during the chase and approach phase (Muul 1969), although it is unknown if juveniles emit a similar vocalization or if the male is attempting to mimic a juvenile to appease the female. Smith’s bush squirrels give a distinct soft nasally murmur continually while following the female (Viljoen 1983). While both adult and juvenile Smith’s bush squirrels give this call, the male murmur is different from female and juvenile murmurs. Since murmurs seem to serve as a general contact call for this species, males may emit a modified version that specifically pertains to mating, but is not similar to juvenile calls.
However, not all species use juvenile calls during the approach phase. Gunnison’s prairie dog males emit a mating call similar to an alarm call prior to entering an underground burrow with the female to copulate (Hoogland 1998).

Once the female has accepted the male, she may vocalize to communicate her decision. In alpine marmots, the female may give a low-pitched call when a male attempts to mate with her (King and Allainé 1998). Indian palm squirrels (*Funambulus palmarum*) produce specific mating calls and both sexes vocalize while allogrooming prior to mating (Madhavi et al. 2012). In some species, females and males occasionally give vocalizations during copulation (Muul 1969, Viljoen 1983). While mating behavior in diurnal species is typically easy to observe, mating behavior in flying squirrels is more difficult due to their nocturnal behavior. Certain aspects of mating behavior in ground squirrels can also be difficult to observe because they typically copulate in their burrows (Hoogland 1995, 1998, King and Allainé 1998).

Most species of squirrels are not monogamous and they can mate with several partners during a mating season. Females tend to come into estrous for a short time period (a few hours to a few days) and are typically polyandrous during this time, which can be an evolutionary disadvantage to breeding males. After a male successfully mates with a female, if she subsequently mates with different males, this may lead the female’s offspring to have mixed paternity, potentially decreasing the number of offspring that belongs to one male. Post-copulatory vocalizations by male squirrels are a form of mate guarding that prevents or delays other males from mating with an estrus female the caller just successfully mated with. In forest-dwelling squirrels, these vocalizations often elicit freeze responses from conspecifics, similar to behavior that occurs in the presence of a predator. Several genera of squirrels are known to vocalize while mate guarding, including beautiful squirrels, prairie dogs, ground squirrels (*Spermophilus* spp., *Urocitellus* spp.), and territorial North American tree squirrels (*Tamiasciurus* spp.; e.g., Farentinos 1972b, Sherman 1989, Tamura 1995, Lacey et al. 1997, Hoogland 1998, Manno et al. 2007, Raveh et al. 2011). However, this may not be a universal strategy in all squirrel species.

Examples of mate guarding calls vary: Some are variations of alarm calls, while others are specific vocalizations only heard during the mating season. After successfully mating with a female, male beautiful squirrels (gray-bellied squirrel, *Calliosciurus caniceps*; Pallas’s squirrel, *C. erythraeus*, and plantain squirrel, *C. notatus*) produce post-copulatory calls that last up to 35 min (Tamura 1993, 1995). During this time, all the squirrels in the vicinity, including the estrous female, freeze as the post-copulatory calls sound similar to the staccato barks used when a terrestrial predator is near (Tamura 1993, Tamura and Yong 1993). Using this call-type, the calling male manipulates the behavior of the estrous female as well as the surrounding males, allowing him to decrease the chances that another male will mate with the female during the post-copulatory calling bout. Similar to chase calls, post-copulatory calls that do not incite this freeze behavior may attract other males toward the estrous female (Manno et al. 2007), which require other strategies of mate guarding. A male black-tailed prairie dog produces a mating call, occasionally giving the call after copulation, and then subsequently herds the female as he defends her from other males (Grady and Hoogland 1986). In Idaho ground squirrels (*Urocitellus brunneus*), males guard their mates (Sherman 1989). If a male temporarily loses contact with his mate, he utters a staccato chirping call until she is located. This call is specific to males during mate guarding and is not heard in any other context (Sherman 1989). Strategies of mate guarding in squirrels vary from species to species and may depend on sociality or other environmental factors, highlighting the need for more research on these behaviors.

**Neonatal calls**

In Sciuridae, neonates are altricial and require care from their mother until maturity. Communication between the mother and her young functions to increase their survival. I distinguish neonates from juveniles in that neonates spend the majority of their time in the nest, whereas juveniles have emerged from their nest and are increasingly independent of their mothers, but have not dispersed. Neonatal calls include discomfort calls, separation calls, food calls, follow calls, elation calls, and sleep calls (Pizzimenti...
and McClenaghan 1974, Emmons 1978, Lishak 1982, Wells-Gosling 1985). Most pups begin vocalizing within the first few days of life (see Age and ontogeny section below). As they develop, neonates may stop producing certain call types by the time they mature and leave the nest (see Age and ontogeny section below; Lishak 1982, Sherman 1977). Neonates produce vocalizations in ground squirrels (McCarley 1966, Pizzimenti and McClenaghan 1974, Loughry 1992, Blumstein et al. 2008), tree squirrels (Emmons 1978, Lishak 1982b, Viljoen 1983, Madhavi et al. 2012), and flying squirrels (Shook 1976, Yanagawa et al. 1996, Airapetyants and Fokin 2003, Gilley et al. 2019).

Discomfort calls are produced when a neonate is restrained or cornered and may be related to calls an adult produces when injured or scared (for example, see Discomfort call section; Waring 1970, Hall 1981). These calls are also heard when the pup is generally uncomfortable, such as when the pup is cold (Shook 1976) or they are forcibly groomed by their mother (Herzig-Straschil 1978). Separation calls of neonates elicit the mother to immediately search for and retrieve the neonate back to the nest (McCarley 1966, Farentinos 1974, Emmons 1978, Viljoen 1983). Japanese flying squirrel (Pteromys momonga) and Hokkaido flying squirrel (P. volans orii) juveniles emit continuous low-frequency calls when removed from their nest, inducing the mother to retrieve the calling pup (Yanagawa et al. 1996). When separated from their nest, Funisciurus spp. and Paraxerus spp. became immobile and call until their mother retrieves them (Emmons 1978, Viljoen 1983). The isolation calls of some species may sound similar to bird alarm calls and might allow the isolated pup to call for the mother without attracting predators. Neonates may produce food calls when they are hungry (Viljoen 1983, Madhavi et al. 2012), which the mother responds to by allowing them to nurse. Follow calls are produced by the mother to encourage neonates to follow her, especially when they are too large to carry. For example, a North American red squirrel mother produces a buzz call to entice her young to follow her to a new nest (Smith 1978b, Lair 1990). Elation calls are given when the pups are excited and playful. Upon returning to their mother after separation, Mexican ground squirrel neonates nuzzle and kiss their mother while producing elation calls (Pizzimenti and McClenaghan 1974). Elation calls and associated kissing behaviors decrease as the neonates mature. Sleep calls are associated with a drowsy or tired pup. Indian palm squirrels infants make a distinct series of chirps during the same time every evening approximately 1 h before sleep (Madhavi et al. 2012). Mexican prairie dog pups also give a unique weep call when they are sleepy and this call can be heard when pups are sleeping (Pizzimenti and McClenaghan 1974). The variety of call-types given by neonates may be associated with complexity of maternal care. However, since most neonate vocal repertoires are not cataloged, it is unknown how the diversity of neonate vocal repertoires is associated with species sociality and length of maternal care, requiring further investigation.

**Age and ontogeny.**—For squirrels, vocal communication is important right from beginning of life. As stated earlier, communication between the mother and her pups helps facilitate their growth and development, potentially leading to increased survival to adulthood. Certain aspects of vocal communication seem to be innate. For example, hybrids tend to have intermediate calls similar to both parent species (Smith 1968, 1978b, Koeppl et al. 1978, Nikol’skii et al. 1983, Nikol’skii and Starikov 1997). However, there are aspects of vocal communication that appear to be learned, although which aspects of vocal communication are innate and which are learned is relatively unknown as mechanisms of squirrel vocal development are understudied in general.

Within the first few days of life, squirrels start producing vocalizations. Southern flying squirrels begin vocalizing cries on their second day of life, which is the same time their pinnae start to seal (Ritter and Vallowe 1978, Linzey and Linzey 1979), although Sollberger (1940) noted neonates produce whimpering cries a few minutes after birth. A 1-d-old Smith’s bush squirrel is able to produce a recognizable alarm call, although it has several call parameters that differ from an adult alarm call (Viljoen 1983). Squeaks are heard in Richardson’s ground squirrel at 2 d old (Clark 1970), whereas golden-mantled ground squirrels begin emitting squeaks at 3 d old (Clark and Skryja 1969). Some species, such as Cape ground squirrels and Townsend’s ground squirrels,
produce calls at approximately one week of age (Svihla 1939, Herzig-Straschil 1978). Newborn squirrels also produce audible squeaks as early as the first day of life (Tamias spp., Broadbrooks 1958, Forbes 1966, Hirshfeld and Bradley 1977; Belding’s ground squirrel, Morton and Tung 1971; thirteen-lined ground squirrel, Bridgewater 1966). Variation in when pups of a particular species start producing calls may vary due to differences in ontogenesis or other evolutionary reasons, but are not currently understood.

The development of certain vocalizations may coincide with specific points of ontogenesis. Aggression/annoyance calls occur in Eastern gray squirrels when their eyes open around 30 d old (Lishak 1982b). This is also seen in bush squirrels, whose rattle coincides with the opening of their eyes at 7 d (Vilojen 1977). Golden-mantled ground squirrel pups begin tooth-chattering when their incisors erupt at one month old (Clark and Skryja 1969), whereas Eastern gray squirrels produce tooth-chattering when their incisors emerge at 8 weeks old (Lishak 1982b). Thirteen-lined ground squirrels begin emitting trill calls similar to adults when they are able to stand on their feet around 18–20 d old (Bridgewater 1966). Alarm calls are typically well developed by the time juveniles leave the nest or emerge from their burrows (e.g., Nikol’skii 1999, Blumstein 2007). Because ontogenesis varies between species (Ferron 1981), the age at which certain vocalizations develop may vary among species even within the same genera (e.g., Matocha 1975).

Some juvenile call-types mature and begin to develop similar characteristics to adult vocalizations, whereas other call-types are specific to neonates and disappear as a squirrel ages. At approximately 3–4 weeks after juvenile Belding’s ground squirrel and thirteen-lined ground squirrels emerge above ground they cease producing squeaks, a call-type that would attract the attention of their mother (McCarley 1966, Sherman 1977). Southern flying squirrels’ isolation calls disappear with age (Shook 1976), as the need for the mother to retrieve her young decreases as they became more mobile and independent. Screams heard in yellow-bellied marmot pups are not heard in adults (Blumstein et al. 2008), suggesting this call is lost from the vocal repertoire as the marmot matures. Elation calls given by Mexican prairie dogs decrease in frequency as the pups age and the mother does not emit this call-type (Pizzimenti and McClanahan 1974), suggesting elation calls are only given by neonates before emergence. The disappearance of certain call-types may be related to their reduced use as juveniles develop and are less reliant on their mothers.

As the pups age, their call-types begin developing and changing in call parameters. These differences are probably related to the development of lungs and abdominal muscles, as well as morphological changes to the vocal tract (Brandler et al. 2019). Changes in hormones that occur with development may influence sound production and structure of calls (Nikol’skii 1992, 2014). Typically vocalizations decrease in frequency (kHz) as juvenile squirrels become adults (Pizzimenti and McClanahan 1974, Blumstein 2007, Nikol’skii 2007). For example, juvenile southern flying squirrels produce trill calls heard in adults (Giley et al. 2019), but these calls develop as they age, becoming more modulated and lower in frequency (Shook 1976). In some species, the frequency of a certain call-type might lower, rise, or stay the same. For russet ground squirrels, as juveniles became adults the fundamental frequency of male alarm calls drop by ~150 Hz, while rising ~300 Hz in females (Brandler et al. 2019). This is also seen in contact calls of green bush squirrels (Paraxerus poensis), where the fundamental frequency drops ~500 Hz in males and increases ~250 Hz in females (Emmons 1978). Frequencies of juvenile California ground squirrels alarm calls are lower than adults (Hanson and Coss 2001). In Speckled ground squirrels and Richardson’s ground squirrels, juveniles and adults exhibit no difference in frequency of whistle alarm calls, even though juveniles are smaller-bodied and have smaller larynxes (Matrosova et al. 2007, 2011, Swan and Hare 2008, Volodina et al. 2010). The reasons why call frequency changes with age in some squirrel species and not others is presently unknown. However, these changes may aid in the distinction between juvenile and adult conspecifics, potentially influencing interactions or behavior between individuals.

The complexity and arrangement of calls also change as a juvenile ages. Frequency modulation in juvenile bobak marmots is absent or less pronounced than adults (Nikol’skii 2014). Young
thirteen-lined ground squirrels initially emit alarm calls consisting of three notes with longer pauses between calls. As the squirrels mature, the number of notes in a call increase and duration between calls decrease, becoming more similar to adult alarm calls (Ryshke 1972, Matocha 1975). In North American red squirrels, juveniles frequently used single note chee calls, whereas adults used double, triple, and quad note chee calls (Embry 1970). Call-type duration is significantly shorter in juvenile yellow and speckled ground squirrels compared to adults (Volodina et al. 2010). In European ground squirrels, juveniles produce an alarm call with one tonal element prior to their first hibernation. After hibernation, the juvenile ground squirrels add an additional element to their call: a frequency-modulated note directly after the tonal note (Schneiderová et al. 2015). In some species, calls of older juveniles are not very different from adult calls (Matrosova et al. 2011), highlighting that juvenile calls become more similar to adults as they age. Whether changes in call complexity are a result of learning, development of physical structures in the body (i.e., lungs and larynx), or a combination of both is unknown.

Age may influence how juveniles perceive and react to vocalizations (but see Swan and Hare 2008). This is best studied in alarm calling and predation risk. Rearing history can influence the behavioral responses to alarm calls in juveniles, indicating that responses may not be innate and develop with experience (Mateo and Holmes 1999, Shriner 1999). Inexperienced juveniles tend to have heightened or suppressed reactions to alarm calls and the presence of adults may teach juveniles how to evaluate an alarm call (McCarley 1966, Nikol'skii and Nesterova 1990, Mateo 1996b, Hanson and Coss 1997, Mateo and Holmes 1997). For example, if older marmots are present when an alarm call is heard, juveniles have reduced reactions and do not hide in burrows as often as when adults are absent (Nikol'skii and Nesterova 1990). Additionally, behavioral responses to different call-types may develop at varying rates. For example, Belding's ground squirrels develop responses to alarm calls associated with an aerial predator faster than alarm calls associated with terrestrial predators (Mateo 1996b). However, juveniles squirrels appear be able to differentiate call-types prior to emergence, but apparently do not have the innate ability to associate certain response behaviors with the different call-types (Mateo 1996a). Understanding differences in the innate and learned ability of juvenile squirrels to differentiate calls and associate calls with particular behaviors is important to determine underlying behavioral and evolutionary mechanisms of squirrel vocalizations.

**Multi-use call-types**

While some call-types are specific to particular situations and not used in other contexts (e.g., pre-copulatory calls of Arctic ground squirrels and elation calls of juvenile Mexican prairie dogs; Pizzimenti and McClanaghan 1974, Lacey et al. 1997), certain call-types of a species are used in multiple contexts. For example, male Columbian ground squirrels emit a mating call similar in acoustic structure to an alarm call, but each call elicits a different response in nearby conspecifics: The alarm call induces vigilance in neighboring squirrels, whereas conspecifics ignore the mating call and continue to forage (Manno et al. 2007).

The yip-jump display of black-tailed prairie dogs is used as a territorial call, to indicate the presence of a snake, or to assess vigilance in other coterie members (Owings and Loughry 1985, Hoogland 1995, Hare et al. 2014). This call is also used by juvenile black-tailed prairie dogs to garner attentions from adults. As the adults become habituated and increasingly ignore the juveniles’ constant yip-jumps, juveniles decrease the use of this call-type (Loughry 1992). Similarly, bark calls of black-tailed prairie dogs are used in the presence of a predator or as an annoyance call to members of the coterie (Smith et al. 1977). Post-copulatory calls of male beautiful squirrels resemble terrestrial predator alarm calls and a successful male produces these calls to delay other males from mating with a female he recently copulated with (Tamura et al. 1988, Tamura and Yong 1993, Tamura 1995). Understanding possible differences between call-types uttered in different contexts using spectral analysis may reveal if there are subtle differences in the call-types that enable squirrels to differentiate what the caller is communicating. Additionally, since vocalizations are usually accompanied by visual signals (e.g., tail flagging), body posturing may indicate how the call is interpreted by...
receiving squirrels, especially in close interactions where the caller is visible. The ability to adapt similar call-types to different situations may be beneficial to species with limited vocal repertoires.

**DISCUSSION**

Vocal communication is important throughout the life of a squirrel and is essential to their development, survival, and reproductive success. Biological functions associated with squirrel vocalizations range from predator defense to territory defense to mate solicitation to social cohesion. Each call-type within a vocal repertoire has distinctive structural parameters (i.e., call length and frequency range) allowing it to be differentiated from other call-types. A call-type might have one behavioral function or several. Behaviors associated with specific call-types in a vocal repertoire are variable and some call-types can be used for multiple behavioral functions indicating other factors, such as visual displays, may provide context for certain call-types. Production of vocalizations occurs soon after birth and call-types develop or are lost as a squirrel matures. A squirrel’s sex may influence call parameters and certain call-types may be sex specific. Seasonality can influence the type and rate of calls emitted, including calls produced during the mating season and after the emergence of young. There is interspecific variation in the number of and behaviors associated with call-types found in vocal repertoires between species, although most species of squirrels lack a well-described vocal repertoire.

Alarm-calling behavior of diurnal squirrels is extensively studied because these vocalizations and behaviors are easily observed. However, alarm calls and their associated behaviors represent a small proportion of the possible behaviors and vocalizations most species may produce, leading other aspects of squirrel behavior associated with vocalizations to be understudied or ignored completely. For example, alarm-calling behaviors of ground squirrels are well-documented, as are potential evolutionary drivers for variation between alarm calls behaviors in different species according to a species’ sociality and their associated predators. However, some ground squirrels species do not have non-alarm call-types described in the literature (Appendix S2). This is surprising considering several species are highly social and young may remain with their mothers for extended periods, especially in hibernating species occurring in regions with short growing seasons and harsh winters (e.g., marmots; Barash 1973, Barash 1974). Since ground squirrel species range in their level of sociality, a complete vocal repertoire may promote a more comprehensive understanding of the connection between vocal communication and social complexity within this group, especially in regard to call-types associated with affiliative behaviors rather than alarm-calling behaviors. Additionally, the lack of certain behavioral call-types in one species vs. another may also help elucidate the evolutionary mechanisms underlying the development of vocal communication associated with certain behaviors, although most species have understudied vocal repertoires so this currently may be difficult to ascertain across species and genera.

Wherein the behavioral function of vocalizations in certain squirrel genera is extensively explored, other groups of squirrels are understudied due to their habits or geographic location. In general, I found there is a paucity of information on the vocal repertoire of most squirrel species, especially nocturnal species and species not located in Europe, North American, and Russia. This is especially true for flying squirrels, as the highest species diversity occurs in Southeast Asia but data on the basic ecology of the majority of these species are non-existent (Koprowski and Nandini 2008). For the majority of nocturnal squirrel species (e.g., flying squirrels), there are no records of vocalizations in the literature. For those with described vocalizations, most species do not have behaviors described for those calls. For example, the vocal repertoires of North American flying squirrels are very diverse with southern flying squirrels having 27 described call-types (Gilley et al. 2019). However, it is unclear how most call-types and call bouts convey different meanings in various social contexts for this species (Gilley et al. 2019) as behaviors associated with vocalizations of nocturnal squirrels can be difficult to observe compared to diurnal species (Blumstein 2005). The size of the vocal repertoire for a particular species is
influenced by various environmental and evolutionary selective pressures (Blumstein 2005). For the Sciurid family as a whole, the large data gaps in vocal repertoires and their associated behaviors hinder the understanding of how and why squirrels developed variation in different call-types to communicate their behavior or influence the behavior of conspecifics, especially in non-alarm call-types. Due to the variability of evolutionarily drivers in the development of vocal repertoires, understanding distinctions in call-types among species may illuminate differences or similarities in behavior to equivalent environmental stimuli. Additionally, filling data gaps about the behavioral function of these call-types may aid in surveying and the conservation of these species. Bioacoustics monitoring of squirrels may be important to determine distribution and habitat occupancy (Lishak 1977, Tamura et al. 2013, Diggins et al. 2016, 2020a, b). Quantifying vocal repertoires and understanding behaviors associated with call-types could lead to bioacoustic surveys with the ability to also monitor the behavior of species (e.g., detection of mating calls, juvenile vocalizations), as well as demographic and distribution data.

While many species of squirrels are lacking a quantitatively described vocal repertoire, there are problems that arise in described vocalizations of the same species in the literature (Waring 1970, Emmons 1978, Gurnell 1987, Matrosova et al. 2012). The same call type can be given a different name in two different studies, whereas two different call types might be given the same name. For example, Robinson (1981) and Turner (1973) call the same vocalization of Belding’s ground squirrel a trill and churr, respectively. Additionally, variation in recording devices could hinder comparisons between different studies on the same species. Gilley et al. (2019) attempted to compare southern flying squirrel vocalizations they recorded on full-spectrum detectors to calls Eisinger et al. (2016) recorded using zero-crossing detectors. Because of the sound transformation via zero-crossing recordings for ultrasonic calls, Gilley et al. (2019) stated it was difficult to compare the majority of call-types. Since call information can be lost (e.g., harmonics) or accentuated (intraspecific variation) when using recording methods that transform sound (e.g., zero-crossing) vs. direct recording of sound (e.g., full spectrum, time expansion; Fenton et al. 2001), zero-crossing should not be used to determine vocal repertoires or vocalization-associated behaviors of squirrels, especially if they produce ultrasonic calls. Additionally, a call-type produced in one species may serve a different behavioral function than a similar call-type in another species. These factors may hinder cross-study or cross-species comparisons, especially when trying to determine the behavioral evolution of a call-type or vocalization-associated behavior within a genus or group (e.g., ground squirrels). Therefore, more standardized naming methods for call-types are needed, as well a standardized classification of the behavioral function of a call. Behavioral categories outlined in this review would be helpful to determining a standardized behavioral classification system for squirrels, as well as other rodents.

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