



## The function of ultrasonic vocalizations during territorial defence by pair-bonded male and female California mice

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Acoustic communication is vital to complex social behaviours such as territorial defence. The use of ultrasonic vocalizations, particularly in territorial defence by monogamous species and females, remains understudied. We studied ultrasonic vocalization production and associated aggression in the monogamous, biparental and territorial California mouse, *Peromyscus californicus*, in which both males and females were found to display similar levels of physical aggression against same-sex intruders. We identified specific ultrasonic vocalization calls that are modulated based on social context: (1) sustained vocalizations, which are long, low-bandwidth calls ranging from 22 to 25 kHz, and (2) barks, which are short, high-intensity calls beginning and ending in the audible range. Despite similarities in physical aggression, sex differences emerged in vocal communication. Only resident males, and not females, produced sustained vocalizations prior to the onset of physical aggression, and were found to shorten the duration of individual sustained vocalization calls over both the course of the pre-encounter phase and from the pre-encounter to encounter phase. In addition, the degree of sustained vocalization shortening in males predicted offensive aggression of the resident. Males exhibited shorter sustained vocalization calls during encounters than females. Barks occurred more frequently during female–female physical aggression than in male–male encounters, and correlated highly with defensive aggression by intruders. Finally, a newly identified highly complex call, sweep phrases, was recorded in a subset of both sexes in the pre- and post-encounter phases. The overall results indicate that ultrasonic vocalizations may play an important role in territorial defence during both territorial advertisement and aggression in a monogamous rodent. Overall, this monogamous species showed sex similarities in physical aggression but sex differences in vocal communication and a more sophisticated function for sustained vocalizations than previously recognized.

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Vocalizations play a distinct role in the expression and escalation of aggressive behaviours in many species (van Staaden, Searcy & Hanlon, 2011). These signals can provide information to conspecifics about the resource-holding potential (RHP) and/or fighting ability of the signaller, thus determining whether contests will escalate (Maynard Smith, Price, Smith, & Parker, 1973). Vocal signals during aggression can differ or be modulated in several ways including their amplitude, frequency, complexity and duration (Seyfarth & Cheney, 2010; van Staaden et al., 2011). High-amplitude calls are indicators of aggression in many species (Brumm, 2004; Brumm & Ritschard, 2011; but see ; Maddison, Anderson, Prior, Taves, & Soma, 2012), and low-frequency calls

often signal larger body size and greater fighting ability (Reby et al., 2005; Reichert & Gerhardt, 2014). Complexity of calls, such as bird trills, indicate fighting quality, and playback studies reveal that producing more trills by an “intruder” reduces the aggressive response of territory holders (Cramer & Jordan Price, 2007; Illes, Hall, & Vehrencamp, 2006). Alterations in call duration can signal aggression in some species; for example, black redstarts, *Phoenicurus ochruros*, shorten call duration to produce more calls in the same time frame (Apfelbeck, Kiefer, Mortega, Goymann, & Kipper, 2012), while others such as European starlings, *Sturnus vulgaris*, increase song length during territorial defence (Alger, Larget, & Ritters, 2016). Taken together, this information on non-rodent species indicates that modulation of call types and spectral properties is of particular importance to aggression.

In rodents, the role of vocalizations in both aggressive behaviour and territorial defence remains understudied with limited overlap

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with the species just described. Generally, rodents produce ultrasonic vocalizations at frequencies >22 kHz as a means of vocal communication during social behaviour (Arriaga et al., 2012; Holy & Guo, 2005; Sales, 2010). Rats, for instance, produce ultrasonic vocalization calls in two major frequency bands, 22 kHz and 50 kHz (Burgdorf et al., 2008; Kroes, Burgdorf, Otto, Panksepp, & Moskal, 2007; Sales, 1972; Sirotin, Costa, & Laplagne, 2014), whereas house mice, *Mus musculus*, produce a variety of ultrasonic vocalization calls at a frequency of >45 kHz (Hoffman, Musolf, & Penn, 2012; Portfors, 2007; von Merten et al., 2014). However, lower-frequency calls do not uniformly indicate increased aggression or body size across rodent species (Hoffman et al., 2012). Furthermore, increased call amplitude, a signal of aggression or territoriality in many nonrodent species, has instead been linked to submissive behaviour in rodents (Constantini & D'amato, 2006; Portfors, 2007). Other call attributes, therefore, may be more important to rodent aggression. Calls are altered during aggression in species such as the Turkish spiny mouse, *Acomys cilicicus*, in which males increase the number of ultrasonic vocalizations produced and alter the proportion of call types in response to agonistic encounters (Griffiths, Dow, & Burman, 2010). In contrast, house mice and Syrian hamsters, *Mesocricetus auratus*, decrease ultrasonic vocalization calling and increase lower-frequency broadband calls (<20 kHz) during aggression (Arriaga et al., 2012; Fernández-Vargas & Johnston, 2015; Keesom, Rendon, Demas, & Hurley, 2015). Call duration and complexity have been tied to aggressive output in rodents. For example, castrated Alston's singing mice, *Scotinomys teguina*, produce fewer trills with shorter durations while expressing less aggression compared to testosterone-implanted controls (Alger et al., 2016; Pasch, George, Hamlin, Guillette, & Phelps, 2011). Further exploration of the role of ultrasonic vocalizations in aggression in rodents is warranted, particularly in females and monogamous species, which to this point remain understudied.

The vast majority of studies of vocal communication within aggressive contexts have focused on males (Cain & Langmore, 2015; Cain, Cockburn, & Langmore, 2015). In many rodent and nonrodent species, males are both more aggressive and more vocal than females (Reby et al., 2005; Reichert & Gerhardt, 2013). However, across taxa, in species where females are territorial and in monogamous species, aggressive behaviour is more similar between sexes, with both males and females displaying aggression towards novel intruders (Langmore, 1998). In monogamous species, pairs that share territorial defence responsibilities often do so in a sex-specific manner, defending territories against same-sex intruders as a form of mate guarding, with both males and females using similar vocal repertoires during aggression (Cross, Zedrosser, Nevin, & Rosell, 2014; Fedy & Stutchbury, 2005; Koloff & Mennill, 2011; Levin, 1996; Levin & Wingfield, 1992; but see Yang, Zhang, Cai, Stokke, & Liang, 2011). While there is evidence in both duetting birds (Colombelli-Négrel, 2016; Quinard & Cézilly, 2012) and California mice, *Peromyscus californicus* (Rieger & Marler, n.d.) for coordinated territorial defence that is not sex specific, same-sex intruders were used to induce reliable aggression. Here we expand our understanding of the role of vocal communication, particularly ultrasonic vocalizations, across different phases of an aggressive encounter by studying male–male and female–female aggression and the associated vocalizations of the monogamous California mouse.

We worked with the California mouse, a strictly monogamous biparental species that forms lifelong pair bonds (Gubernick, 1988; Ribble, 1991). Both male and female California mice exhibit reliable aggression against intruders, especially in the context of territorial defence (Ribble & Salvioni, 1990). California mice have a rich and distinct set of ultrasonic vocalization call

types that have been categorized both in the field and laboratory (Kalcounis-Rueppell, Metheny, & Vonhof, 2006; Kalcounis-Rueppell et al., 2010), that vary based on social context (Pultorak, Fuxjager, Kalcounis-Rueppell, & Marler, 2015; Pultorak, Matusinec, Miller, & Marler, 2017) and do not appear to differ spectrally between sexes (Briggs & Kalcounis-Rueppell, 2011). In this study, we focused on three major call types: sustained vocalizations, barks and 'complex sweep phrases' (which are described here for the first time; see Methods). Briefly, sustained vocalizations have been hypothesized to act as long-distance communication between individuals and can be modulated both in duration and total number of calls produced (previously referred to as syllables) as well as the number of calls produced within a bout (previously referred to as a phrase) (Kalcounis-Rueppell, Pultorak, & Marler, in press). Barks are hypothesized to be aggressive in nature. The function of sweep phrases is to this point unknown. Individual sweeps that make up these phrases, however, are simple frequency-modulated calls whose production can be altered in response to changing social context (Kalcounis-Rueppell et al., in press).

To understand the role of ultrasonic vocalizations in intra-sexual territorial defence of monogamous pairs we used a resident–intruder paradigm encompassing three main objectives. The first was to directly compare the aggressive behaviours and territorial defence of male and female California mice using same-sex encounters. We hypothesized that, as a monogamous species in which both sexes display aggression (Davis & Marler, 2004, 2003; Fuxjager, Oyegbile, & Marler, 2011; Oyegbile & Marler, 2005; Trainor et al., 2011), males and females would exhibit few sex differences in aggression when compared directly. Second, we sought to characterize the ultrasonic vocalization call types produced by male and female residents at different stages of a territorial intrusion: baseline (prior to the introduction of an intruder), pre-encounter (before any physical aggression but after initial visual, olfactory and auditory contact), encounter and post-encounter (after contest resolution). We were able to isolate the vocalizations of individuals both prior to and after physical aggression but not during physical encounters. We predicted that sustained vocalizations would be the predominant vocalization for males and females prior to physical aggression as previous field research suggested that these calls function in long-distance communication (i.e. communication with the mate; Kalcounis-Rueppell et al., 2006). We further explored both the duration of single sustained vocalization calls and the number of sustained vocalization calls in a bout across social contexts to determine whether sustained vocalization characteristics were modulated based on physical aggression. We also predicted that barks would be the predominant call during aggression due to their role in male–female interactions, where after a period of separation, reunited mates produced barks only when aggression also occurred (Pultorak et al., 2017). Finally, we tested whether these vocalizations were predictive of aggressive behaviour. Overall, we sought to bring a greater understanding of the role of ultrasonic vocalizations in the dynamic aggressive interactions of rodents.

## METHODS

### Animals

Twenty-four male (12 bonded and 12 sexually naïve, age 4–6 months) and 24 female California mice (12 bonded and 12 sexually naïve, age 4–6 months) were obtained from a laboratory colony at the University of Wisconsin-Madison. Mice were housed either in opposite-sex pairs or with one or two same-sex conspecifics in

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