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Similar acoustic structure and behavioural context of vocalizations produced by male and female California mice in the wild

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Ultrasonic vocalizations (USV) are an important part of multimodal communication in mice; however, nothing is known about the behavioural context of USV production by individual mice in the wild. Using remote-sensing methods we recorded USVs from individual adult free-living *Peromyscus californicus*. Because adult male and female *P. californicus* share duties in rearing offspring and defending territories, we predicted that male and female *P. californicus* would produce USVs in similar behavioural contexts and with similar spectral and temporal characteristics. We found that adult male and female *P. californicus* produced USVs, with the most common motifs being one-, two- and three-syllable vocalizations. USVs of males and females did not differ significantly in type or number, or in spectral or temporal characteristics. *Peromyscus californicus* produced USVs when alone and when they were with another mouse, and the three-syllable vocalization (3SV) motif, which has a relatively long first syllable, was more likely to be produced in the presence of another mouse than when a mouse was alone. The likelihood of vocalizing and the spectral and temporal characteristics of vocalizations did not differ when an individual was producing a USV in the presence of a mate or nonmate. Males and females produced USVs in the same behavioural contexts. Thus, as with other behaviours associated with parenting and territorial defence in *P. californicus*, USVs of males and females are produced in similar behavioural contexts and have similar spectral and temporal characteristics.
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Rodents are the most speciose and behaviourally diverse group of mammals (Kay & Hoekstra 2008) and have a great potential as a comparative model for studying acoustic communication, in addition to birds and anurans. In particular, they provide study systems of acoustic communication as a secondary modality to olfaction. Ultrasonic vocalizations (USVs) are an important component of multimodal communication in rodents (Sales 1999; Costantini & D'Amato 2006; Brudzynski 2007; Portfors 2007; Scattoni et al. 2009; Takahashi et al. 2010). However, what we know about the context and function of adult rodent USVs is limited and based on evidence mainly from laboratory mice (*Mus musculus*-derived strains) and rats (*Rattus norvegicus*-derived strains) in the context of mating (but see Pasch et al. 2011). Evidence suggests that USVs indicate an individual's affective state, rank or status and/or facilitate social interactions, including reproduction. Laboratory rats produce USVs to establish dominant–subordinate relationships (Inagaki et al. 2005), convey an individual's affective state and coordinate reproductive behaviour (Brudzynski 2007; Portfors 2007). Laboratory mice produce USVs to coordinate reproductive behaviour and reduce aggression (Sales 1972; Costantini & D'Amato 2006), attract mates (Hammerschmidt et al. 2009; Musolf et al. 2010), retain conspecifics in close proximity (Pomerantz et al. 1983; Hammerschmidt et al. 2009), convey social status (Nyby et al. 1976) and facilitate social recognition (D'Amato 1997; D'Amato & Moles 2001; Moles et al. 2007; Musolf et al. 2010). Work with laboratory mice suggests that there is individual variation in USVs (Holy & Guo 2005; Musolf et al. 2010) that may reflect individual quality. Despite what we have learned about rodent USVs from laboratory studies, we have no information about whether rodents use USVs as part of their behavioural repertoire in the wild.

In addition to laboratory mice and rats, other muroid rodents in the genus *Peromyscus* also produce USVs as adults (Pomerantz & Clemens 1981; Nunez et al. 1985; Kalcounis-Rueppell et al. 2006, 2010). A particularly well-studied species of *Peromyscus* is the California mouse, *Peromyscus californicus*, because it is a model for monogamy and parental care in mammals (e.g. Dudley 1974a, b; Gubernick 1990; Gubernick & Laskin 1994; Gubernick et al. 1994;

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Vieira & Brown 2002, 2003; Wright & Brown 2004; Bester-Meredith et al. 2005; Lee & Brown 2007; Trainor et al. 2008a, b) where monogamy is rare (Mock & Fujioka 1990). The California mouse is an obligate behaviourally and genetically monogamous mouse (Ribble 1991) that displays high levels of parental care (Dudley 1974a, b; Gubernick & Alberts 1987; Gubernick & Nordby 1993; Ribble & Salvioni 1990; Ribble 1991; Bester-Meredith et al. 1999) and territoriality (Ribble 1992a; Gubernick & Nordby 1993; Bester-Meredith & Marler 2001, 2003, 2007; Davis & Marler 2003). Individuals establish a pair bond with another individual and mate for life unless their mate dies or disappears (Ribble 1992b). All of a female's offspring are sired by her mate (Ribble 1991). Mated pairs nest together during breeding and nonbreeding seasons and maintain an exclusive territory (Ribble & Salvioni 1990). Ribble & Salvioni (1990) and Ribble (1991) demonstrated that genetically monogamous pairs are consistent in their home range use. The territory is protected year round by both the male and female, which both display aggression towards any intruder. Males participate in all aspects of parental care except for nursing (Dudley 1974a; Gubernick & Alberts 1987; Gubernick & Teferi 2000). Male care is needed for offspring survival in the wild (Dudley 1974b; Gubernick & Alberts 1987; Gubernick & Teferi 2000) and is mediated by chemosignals in the female's urine and by copulation (Gubernick 1990; Gubernick et al. 1994). Dispersal of subadults occurs 60 days postpartum and is female biased; males either disperse a distance equivalent to one home range (1161 m^2), or inherit their parent's home range, whereas females disperse at least two home ranges from their natal home range (Ribble & Salvioni 1990; Ribble 1992a).

As with other muroid rodents, USVs in *P. californicus* are an integral component of their behaviour (Scattoni et al. 2009). In *P. californicus*, USVs are produced by both neonates and adults (Vieira & Brown 2002; Wright & Brown 2004; Kalcounis-Rueppell et al. 2006, 2010). Previously reported ultrasonic vocalizations from *P. californicus* in the wild (Kalcounis-Rueppell et al. 2006, 2010) were not attributed to individuals because these studies sought to eavesdrop on, and examine USVs from, groups of mice. Therefore, it is not clear which individuals (i.e. male or female) produce USVs, whether USVs vary in spectral and temporal characters (i.e. between males and females), or whether USVs are produced in multiple behavioural contexts (i.e. when alone or not alone).

In *P. californicus*, USVs may not function in the same way as in laboratory rats and mice because of their monogamous mating system. Neither *R. norvegicus* nor *M. musculus* are monogamous, nor do they form strong pair bonds with their mates as is seen in *P. californicus* (Ribble & Salvioni 1990). Rather than mediating relationships among unrelated individuals and potential mates, as is the pattern with *R. norvegicus* and *M. musculus*, USVs in *P. californicus* probably function to facilitate maintenance of an established pair. For example, USVs could facilitate pair bond maintenance as in other vocalizing animals with strong bonds between individuals (Ford 1989; Sugiura 1998; Kazial et al. 2001; Hall & Peters 2008). Alternatively, or in addition, USVs may be important for the coordination of territorial defence, as is seen in pair-bonded birds (e.g. Payne 1971; Harcus 1977).

Here, for the first time, we determine the context of USV production by free-living adult *P. californicus* individuals in the wild. Using remote-sensing methods we recorded USVs in the wild and assigned them to the individuals that produced them. We describe (1) the individuals that produced USVs, (2) the spectral and temporal characteristics of USVs from individual mice and (3) the behavioural contexts in which USVs were produced. Our remote-sensing methods focused on individuals moving about their home ranges during nightly activities, rather than on individuals at the nest. Because adult male and female *P. californicus* share similar duties in rearing offspring and defending territories, we predicted that they would produce USVs in similar behavioural contexts and with similar spectral and temporal characteristics.

METHODS

Fieldwork took place at The Hastings Natural History Reservation (HNHR) in upper Carmel Valley, California, U.S.A. (Monterey Co: 36°22′N, 121°33′W). Details of the study site and live-trapping grids can be found in Kalcounis-Rüppell & Millar (2002). Our study occurred on the Lower Robertson Creek grid (Grid LRC), which consists of a 4×34 configuration of trap stations encompassing 2.2 ha. Our study took place during December 2007–June 2008 and January 2009, with focal areas (see below) covered during February–June 2008 and January 2009. All animal capture, handling and recording methods were approved by the Institutional Animal Care and Use Committees of the University of North Carolina at Greensboro (UNCG IACUC Protocol No. 07-05) and the University of California Berkeley (approval of UNCG IACUC Protocol No. 07-05) and were authorized by the California Department of Fish and Game through Scientific Collecting Permits (SC-001358, SC-9663, SC-9661, SC-9806).

Establishment of Focal Areas

Eleven 10 m^2 sections of the grid were designated as focal areas for the purpose of recording USVs from individual mice. Focal areas were chosen sequentially because it was only possible to collect data from a single focal area at a time. Focal areas were placed along the grid based on two main considerations. First, there needed to be relatively high densities of resident *P. californicus* and *Peromyscus boylii* (for a companion study) to maximize the probability of recording USVs. Second, the forest canopy had to accommodate our pulley system (see below). Details on placement of focal areas relative to mouse densities and home ranges are described in Supplementary Information A. At each focal area, we set up a microphone array, a radiotelemetry system and a thermal-imaging camera to record USVs from individual mice. Briefly, the 12 microphones recorded broadband sound (including mouse USVs) from within the focal area and were set out in a 4×3 configuration approximately 1–2 m apart. The telemetry system surveyed all resident mice in the focal area so that we could localize individuals that were producing USVs. The thermal camera system surveyed the focal area from the canopy of the forest and recorded all mammal activity in the focal area. The thermal images were used, where possible, to ensure that only known, resident mice were present when a particular USV was recorded. A schematic diagram of our remote-sensing equipment on a focal area, with two focal areas shown as examples, can be found in Supplementary Information B.

Live Trapping

We used live trapping to determine where to establish focal areas based on density of resident *P. californicus*. Sections of the entire trapping grid were consecutively trapped for three nights throughout the entire field season using standard live-trapping techniques. Mice were captured using Sherman and Longworth traps provisioned with oats and bedding. Two Sherman traps and one Longworth trap were set at each station at sunset and checked approximately 4 h prior to sunrise. Upon capture of a new individual, a single eartag (Monel Numeric, National Band and Tag Co., Newport, KY, U.S.A.) with a unique number was attached. Standard measures including mass, sex, age and reproductive status were recorded for every individual upon every capture. Mice were released at the site of capture. An individual that was captured at least three times between two trapping sessions was classified as

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