

# What makes a cry a cry? A review of infant distress vocalizations

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**Abstract** In contrast to the cries of human infants, sounds made by non-human infants in different stressful behavioral contexts (hunger or physical discomfort, isolation, capture by humans or predators) are usually treated as distinct types of vocalizations. However, if distress vocalizations produced by different species and in different contexts share a common motivational state and associated neurochemical pathways, we can expect them to share a common acoustic structure and adaptive function, showing only limited variation that corresponds to the infant's level of arousal. Based on this premise, we review the acoustic structure and adaptive function of two types of distress calls, those given when infants were isolated from their mothers (*isolation calls*) or captured by humans (*capture calls*). We conducted a within-context comparison examining the two call types across a diverse selection of mammalian species and other vertebrate groups, followed by a comparison of how acoustic structure and function differs between these contexts. In addition, we assessed acoustic traits that are critical to the response of caregivers. Across vertebrate species, distress vocalizations produced in these two behavioral contexts tend to be tonal with a simple chevron, flat or descending pattern of frequency modulation. Reports that both isolation and capture calls of vertebrate infants serve to attract caregivers are universal, and the fundamental frequency of infant vocalizations is often critical to this response. The results of our review are consistent with the hypothesis that differences in the acoustic structure of isolation and capture distress vocalizations reflect differences in arousal, and not discrete functions. The similarity in acoustic structure and caregiver response observed across vertebrates adds support to the hypothesis that the production and processing of distress vocalizations are part of a highly-conserved system of social vocal behaviour in vertebrates. Bioacoustic research may move forward by recognizing the commonality among different forms of infant solicitations that attract caregivers, and the commonality of these solicitations with vocalizations that attract conspecifics in still other behavioral contexts [*Current Zoology* 58 (5): 698–726, 2012].

**Keywords** Crying, Mother-infant communication, Isolation calls, Distress calls, Motivational-structural rules, Parental care, Phylogeny

## 1 Phylogenetic Continuity in Infant Distress Vocalizations

Human *Homo sapiens* infants cry when hungry, in pain, alone, and sometimes for no identifiable reason (reviewed by Newman, 2004; Newman, 2007; Zeifman, 2001). People do not hesitate to label vocalizations of human infants as “cries” despite considerable variation in the context in which these sounds are produced. Indeed, although acoustic indications of urgency can be identified (Gustafson et al., 2000), even mothers are unable to reliably distinguish the specific context in

which particular cries are made (Gustafson and Harris, 1990; Zeifman, 2001).

Infants from other species also vocalize when hungry, in pain or alone (Newman, 2004; Puppe et al., 2005; Weary et al., 1997), when attacked by predators (Curio, 1976; Driver and Humphries, 1969; Högstedt, 1983) or when handled by humans (Chaiken, 1992; Smith, 1987). Similar to the cries of human infants, these vocalizations have a powerful effect on mothers and other caregivers who quickly approach to accompany, retrieve, hold or feed the infant (Newman, 2004; Newman, 2007; Zeifman, 2001) or to defend it against predators (Bene-

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Received Aug. 19, 2012; accepted Oct. 3, 2012.

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dict, 2007; Chaiken, 1992; Lingle et al., 2005). In contrast to the literature on human infants (Newman, 2004; Newman, 2007; Panksepp, 1998; Panksepp, 2005), much of the work generated within the fields of animal behaviour and communication treats vocalizations emitted in these different contexts as categorically discrete. “Distress calls” made when an animal is captured by humans or predators, are typically distinguished from “isolation calls”, made when an animal is isolated from its mother, which are further distinguished from “begging calls” made when an animal is hungry, and from “contact or group cohesion calls” made when an animal is in its normal social group. If these are simply graded vocalizations that differ in urgency but share a common acoustic structure and adaptive function within and across species (Fichtel and Hammersmidt, 2002; Mendl et al., 2010), considerable insight into mechanisms underlying their production and perception will be gained by recognizing these similarities.

A large body of work from the field of neuroscience highlights the similarity in infant isolation calls produced by different species, even proposing that these vocalizations are homologous with the cries of human infants (Christensson et al., 1995; Newman, 2004; Newman, 2007; Panksepp, 1998; Panksepp, 2005; Panksepp and Biven, 2012; Zeifman, 2001). Other researchers have been hesitant to compare distress vocalizations of non-humans with the cries of human infants (Blumberg and Alberts, 1990). While it is true that human infants, in contrast with other species, are well known for crying in contexts that defy current explanation (Hofer, 2002) – the label “colic” was created for this apparent anomaly – the neurochemical mechanisms supporting the basic capacity to cry are rooted in the brainstem and do not require a cerebral cortex (reviewed by Newman, 2004; Newman, 2007). Even though structures within the forebrain are recruited in the production of distress vocalizations in higher mammals (Newman, 2007), anencephalic human and domestic cat *Felis catus* infants, and rodents with the brain stem severed from the forebrain, are capable of crying (Barnet et al., 1966; Kyuhou and Gemba, 1998; Middlemis-Brown et al., 2005; Nielsen and Sedgwick, 1949). Another reason for hesitancy in labeling the sounds of non-human infants as cries is the perceived association of crying in humans and tears – an emotional expression unique to humans. However, tears are not essential for crying: newborn humans are described as crying but do not produce tears until they are two to three months in age (van Haeringen, 2001).

The discovery that unconscious rat *Rattus norvegicus*

pups emit ultrasonic vocalizations when hypothermic was initially used to reject the claim that calls made by non-human infants serve a communicative function as expected if they are homologous with the cries of humans (Hofer and Shair, 1992). The movement of the larynx occurring during the ultrasonic vocalizations of rat pups helps to regulate tracheal pressure to prevent pulmonary edema, which can occur as the animal recovers from hypothermia (Hofer and Shair, 1993). This information led some to suggest that the isolation calls of rodent infants are as reflexive as a sneeze and do not serve a role in social communication (Blumberg and Alberts, 1990). However, these same vocalizations are effective in eliciting a search by the mother and retrieval of the comatose infant to the nest (Brunelli et al., 1994), illustrating that the same behaviour can have communicative as well as physiological functions.

Indeed, across and within species of mammals and birds, the rate at which infants emit isolation calls varies in an adaptive way with the system of parental care and associated antipredator strategies (cache vs. carry, Benson et al., 1992; Blake, 2002; Zeifman, 2001; solitary vs. colonial, Schmidt-French et al., 2006). Neonates from species that are carried with the parents, and neonates that have fledged the nest, face a higher probability of becoming unintentionally separated from the parent, and they vocalize at a greater rate than infants that are cached in a nest (Benedict, 2007; Blake, 2002; Mandelli and Sales, 2004; Schmidt-French et al., 2006; Zeifman, 2001). Forms of physical stress that tend to be coupled with isolation, including hunger and cold, also lead to an increase in the rate at which calls are produced and the probability that the mother retrieves the infant (Blake, 2002; Weary et al., 1997).

Within the field of animal communication, Morton (1977) and others (August and Anderson, 1987; Briefer, 2012; Ehret, 2006; Scherer, 1986) suggest that vocalizations that share a common underlying motivation will assume a similar acoustic structure that influences receivers in a similar way (Owings and Morton, 1998; Owren and Rendall, 2001). The classic distinction is that calls that attract or appease conspecifics will be tonal and high in frequency, whereas calls that serve an aggressive or repellent function should be low in frequency and harsh (Morton, 1977). Some researchers working in the fields of animal behaviour and animal communication have suggested that these vocal and functional similarities are the result of convergence (Morton, 1977). However, the presence of a common motivational state implies the presence of a common

cognitive structure (i.e., common neurochemical pathways) that is associated with the motivational state. If this common cognitive substrate gives rise to acoustically similar vocalizations that result in similar neurochemical and behavioral responses by caregivers from different species, it is more parsimonious to suggest that both the pathway and its products (infant vocalizations and caregiver responses) have been highly conserved (Newman, 2004; Newman, 2007) than to suggest the neural pathways and its behavioral products have arisen independently through convergence.

This neurobiological perspective is supported by recent discoveries that neural pathways underlying social vocal behaviour have been highly conserved across vertebrates (Bass et al., 2008; Bass and McKibben, 2003). Similarities in neural mechanisms involved in the production and processing of infant isolation calls of different species are consistent with the view that mechanisms underlying the production and processing of these calls have been conserved across species (Newman, 2004; Newman, 2007). Panksepp (1998, 2005) and Panksepp and Biven (2012) propose the existence of a social-affect neural pathway that mediates physiological and vocal expressions of separation-distress. When a mammalian infant is separated from its mother or companions, increased separation-distress is manifested in reduced levels of oxytocin and opioids and the onset of distress vocalizations. Once the animal is reunited with its mother or companions, levels of oxytocin and opioids increase and distress vocalizations wane (reviewed by Panksepp, 1998; Panksepp and Biven, 2012).

Our premise in this review is that distress vocalizations made by different species and in different behavioral contexts are grounded in the same neural substrate that has been conserved across vertebrates (Newman, 2004; Newman, 2007). Our overall objective is to review infant distress vocalizations of diverse mammalian orders, with additional records from other vertebrate groups, to assess the similarity in acoustic structure and caregiver response across species and different contexts of distress. Our first goal is to investigate the similarity in acoustic structure and adaptive function of infant distress vocalizations across taxonomic groups when the infants are a) isolated from their mothers (*isolation calls*), and b) captured by humans (*capture calls*, analogous to capture by a predator). We predict that the acoustic structure of vocalizations made by infants within these specific distress contexts will be similar across vertebrates having parental care. Indeed, previous studies and reviews of infant isolation calls concur that the

most common form of vocalization is a long, tonal call that is highly effective in recruiting help from mothers or other caregivers (Newman, 2004; Newman, 2007; Zeifman, 2001). We extend these reviews, which have emphasized the neural mechanisms involved in the production and perception of isolation calls and the behavioral responses of primates including humans (Newman, 2004; Newman, 2007; Zeifman, 2001) by comparing acoustically-explicit data from two different distress contexts for a wide range of vertebrates.

Our second goal is to examine the acoustic similarity and adaptive function of infant distress vocalizations between the contexts of isolation and capture. If infants share a common motivation (distress associated with separation from their mothers) when producing vocalizations in these two contexts, we can predict that the basic acoustic structure of vocalizations will be similar across the two contexts, and would serve a similar function in recruiting help. We therefore predict that the basic acoustic structure of infant distress vocalizations in these two contexts will be similar (e.g., tonal) yet will also display consistent, graded changes that reflect increasing states of urgency (i.e., from semi-distressful short-term isolation to highly-distressful capture) (Fichtel and Hammerschmidt, 2002; Mendl et al., 2010). An alternative hypothesis, which will also be evaluated, is that distress vocalizations given in the contexts of isolation or capture have a different underlying motivation, and therefore would differ considerably in acoustic structure and function. Specifically, although vocalizations emitted in conditions of isolation might be expected to be tonal and function to attract caregivers, vocalizations made when captured might consist of harsh noisy broadband screams that startle predators (Högstedt, 1983; Møller and Nielsen, 2010) or social adversaries (Rendall et al., 2009). Although our focus is on infant distress vocalizations, we include a limited description of distress vocalizations of adults when it lends insight into structural features or functions that may or may not apply strictly to infants.

Our third goal is to use the results of this review of acoustic structure in different vertebrates to consider the specific acoustic traits that make infant distress vocalizations highly evocative to caregivers. We will close by discussing the evolution of infant distress vocalization, highlighting their structural similarities and a possible evolutionary relationship to other vocalizations that serve to attract conspecifics, such as male courtship calls that attract females, which may be grounded in the same cognitive substrate.

## 2 Acoustic Structure of Infant Distress Vocalizations

The predictions we examine in this section are: (1) that the acoustic structure of vocalizations made by infants of different species will be similar within specific distress contexts (e.g., isolation or capture), and (2) that the acoustic structure of vocalizations produced in these two contexts will be similar but show graded changes that correspond to the difference in urgency between a context of isolation and one of capture. Our primary emphasis was on identifying the structure of the call (tonal, broadband, or a combination) and the pattern of frequency modulation (shape of the fundamental frequency or harmonic contour) to test the predictions that a similar tonal structure would be found across species

and behavioral contexts and would serve the function of attracting caregivers. Data were also collected on call duration, timing of call elements, fundamental frequency (F0), dominant frequencies, and nonlinear phenomena to enable us to identify acoustic traits that may be associated with the response of caregivers to infant distress vocalizations, including graded acoustic transitions that occur with increased distress. This detailed information (Table A1) was used to prepare a summary table (Table 1) highlighting the basic structure (tonal, mixed or broadband) of distress vocalizations within different contexts and taxonomic groups to assess the above predictions. In evaluating the structure of calls produced in different contexts, it was particularly useful when calls were available for the same species in both contexts. For practical reasons of availability, we gener-

**Table 1** A summary of the basic acoustic structure for vocalizations produced in the contexts of isolation and capture by neonates, juveniles or their mothers (adult females), or by other adults (see explanatory note below table for definitions)

Age or Age/Sex category <sup>a</sup>	Isolation				Capture			
	Tonal	Mixed	Low amp BB	High amp BB	Tonal	Mixed	Low amp BB	High amp BB
<b>Class Mammalia</b>								
<b>ARTIODACTYLA: Cervidae, Bovidae, Antilocapridae (14 species)</b>								
Neonate (I:2,5; C:3,10)	2(5 <sup>1</sup> )	1(1 <sup>1</sup> )	0	0	3(10)	0	0	0
Juvenile (I:2,3)	2(3 <sup>1</sup> )	2(2 <sup>1</sup> )	0	0	-	-	-	-
Adult, female (I:2,4)	2(4 <sup>2</sup> )	1(2 <sup>2</sup> )	0	1(1 <sup>1</sup> )	-	-	-	-
<b>CETACEA: Delphinidae (two species)</b>								
Juvenile (C:1,2)	-	-	-	-	1(2 <sup>1</sup> )	1(1 <sup>1</sup> )	0	0
<b>PERISSODACTYLA: Equidae (one species)</b>								
Juvenile (I:1,1)	1(1)	0	0	0	-	-	-	-
<b>CARNIVORA (terrestrial): Felidae, Canidae, Herpestidae (three species)</b>								
Neonate (I:2,2; C:1,1)	2(2)	0	0	0	1(1)	0	0	0
<b>CARNIVORA (aquatic): Otariidae, Phocidae, Odobenidae (six species)</b>								
Neonate (I:3,6)	3(6 <sup>2</sup> )	2(2 <sup>2</sup> )	0	1(1 <sup>1</sup> )	-	-	-	-
Adult, female (I:3,5)	3(5 <sup>3</sup> )	2(3 <sup>3</sup> )	0	1(1 <sup>1</sup> )	-	-	-	-
<b>PROBOSCIDEA: Elephantidae (one species)</b>								
Neonate to Juvenile (I:1,1)	1(1 <sup>1</sup> )	1(1 <sup>1</sup> )	0	1(1 <sup>1</sup> )	-	-	-	-
<b>SIRENIA: Trichechidae (one species)</b>								
Juvenile (I:1,1)	1(1) <sup>b</sup>	0	<sup>b</sup>	0	-	-	-	-
Adult, male/female (I:1,1)	1(1) <sup>b</sup>	0	<sup>b</sup>	0	-	-	-	-
<b>RODENTIA: Muridae, Cricetidae, Sciuridae, Caviidae (six species)</b>								
Neonate (I:3,3; C:1,2)	3(3 <sup>1</sup> )	0	1(1 <sup>1</sup> )	0	1(2 <sup>2</sup> )	1(2 <sup>2</sup> )	0	0
Juvenile (I:1,1; C:1,1)	1(1)	0	0	0	1(1)	0	0	0
Adult (C:1,1)	-	-	-	-	1(1)	0	0	0
<b>PRIMATES: Cheirogaleidae, Galagidae, Cebidae, Cercopithecidae (four species)</b>								
<b>Strepsirhini: Cheirogaleidae, Galagidae</b>								
Neonate (I:2,2)	1(1)	0	1(1)	0	-	-	-	-

Continued Table 1

Age or Age/Sex category <sup>a</sup>	Isolation				Capture			
	Tonal	Mixed	Low amp BB	High amp BB	Tonal	Mixed	Low amp BB	High amp BB
<b>Haplorhini: Cebidae, Cercopithecidae</b>								
Neonate (I:2,2)	2(2 <sup>2</sup> )	2(2 <sup>2</sup> )	0	2(2 <sup>2</sup> )	-	-	-	-
<b>CHIROPTERA: Phyllostomidae, Vespertilionidae, Molossidae, Rhinolophidae, Pteropodidae (22 species)</b>								
Neonate (I:5,11; C:1,1)	5(11 <sup>1</sup> )	1(1 <sup>1</sup> )	0	1(1 <sup>1</sup> )	1(1 <sup>1</sup> )	0	1(1 <sup>1</sup> )	0
Adult, male/female (I:2,4; C:3,9)	2(4)	0	0	0	3(6)	0	0	1(3)
<b>DIPROTODONTIA: Macropodidae (two species)</b>								
Neonate (I:1,2)	0	0	0	1(2)	-	-	-	-
<b>Class Aves<sup>c</sup></b>								
<b>PASSERIFORMES: Sturnidae, Emberizidae, Fringillidae, Furnariidae, Thamnophilidae, Thraupidae, Troglodytidae, Turdidae, Tyrannidae, Vireonidae (15 species)</b>								
Neonate (I:1,1)	1(1 <sup>1</sup> )	1(1 <sup>1</sup> )	0	0	-	-	-	-
Adult, male/female (C:12,14)	-	-	-	-	5(7)	4(4)	0	3(3)
<b>GALLIFORMES: Phasianidae (one species)</b>								
Neonate (I:1,1)	1(1)	0	0	0	-	-	-	-
<b>GRUIFORMES: Odontophoridae (one species)</b>								
Neonate (I:1,1)	1(1)	0	0	0	-	-	-	-
<b>Adopodiformes: Trochilidae (two species)</b>								
Adult, male/female (C:1,2)	-	-	-	-	1(2)	0	0	0
<b>Class Reptilia</b>								
<b>CROCODYLIA: Crocodylidae, Alligatoridae (two species)</b>								
Neonate (I:2,2)	2(2)	0	0	0	2(2 <sup>1</sup> )	0	0	1(1 <sup>1</sup> )
<b>Class Amphibia<sup>c</sup></b>								
<b>ANURA: Ceratophryidae, Hylidae, Leptodactylidae, Bufonidae (11 species)</b>								
Larval, tadpole (C:1,1)	-	-	-	-	1(1)	0	0	0
Adult, male/female (C:3,10)	-	-	-	-	3(7)	-	-	2(3)
<b>Summary totals<sup>a</sup></b>								
Neonates: (I:11,26,39; C:6,9,17)	10,24,36	6,8,8	2,2,2	5,6,7	6,9,17	1,1,2	1,1,1	1,1,1
Juveniles (I:4,5,6; C:2,2,2)	4,5,6	1,2,2	0,0,0 <sup>b</sup>	0,0,0	2,2,2	1,1,1	0	0
Adult, male/female (I:4,8,14; C:5,20,36)	4,8,14	2,3,5	0,0,0 <sup>b</sup>	2,2,2	5,13,23	1,4,4	0,0,0	3,6,9

**Explanatory note.** Acoustic structure categories include tonal, mixed, low amplitude broadband ("low amp BB") or high amplitude broadband ("high amp BB"). Numerical values indicate the number of taxonomic families with the combined number of species for those families in parentheses. Superscripts show the number of species emitting calls that vary in structure (e.g., tonal or mixed). The maximum number of families and species available for each order is shown adjacent to the age category. Data are summarized from studies examined within this review (i.e. zero values apply only to this sample of studies). "--" indicates that no data were obtained. See Table A1 for more detailed information on vocalizations produced by these groups and their references.

**Contexts.** *Isolation*: a neonatal or juvenile animal is separated from its mother, a mother from her offspring, or an adult, male or female from its social group. This includes cases of natural separation and experimental isolation. Contact calls (i.e., calls made by neonates and their mothers when together) made by neonates and their mothers were included with isolation calls for three species of pinniped (walrus, northern fur seal and northern elephant seal) and the two crocodylians. Calls emitted by elephant juveniles were made in different contexts of distress including isolation but not capture. *Capture*: cases in which an individual is captured and held by a human or restraining device such as a mist net. As a special note, the tadpole in the study above was prodded, not captured.

**Acoustic structure.** *Tonal*: clear harmonic structure without broadband noise; *Mixed*: harmonic structure clear for all or part of the call but broadband noise also present in specific sections or throughout the call; *Low amp BB*: a low amplitude broadband sound (e.g., soft short clicks); *High amp BB*: a high amplitude broadband sound, such as a loud scream, growl or hiss, that is readily distinguished from background noise.

**Age categories.** Animals less than one month in age were considered neonates. The term "juvenile" was applied to animals beyond one month in age that were sexually immature, still in a group with their mother and probably reliant on maternal care. The upper age range of "juvenile" extended much further for groups such as primates and dolphins that mature slowly.

<sup>a</sup>I (isolation calls): number of families for which isolation calls were available, number of combined species for those families; C (capture calls): number of families for which capture calls were available, number of combined species for those families. For the summary totals, the first number represents the number of orders.

<sup>b</sup>Manatees were reported to emit low amplitude broadband clicks, in addition to their more frequent tonal calls, but the age of the animals that produced clicks was not specified.

<sup>c</sup>Data for adult capture calls for 16 species of birds (Martin et al., 2011) and ten species of amphibians (Hödl and Gollman, 1986) were included in this table, although they are not presented in Table A1.

ally had to rely on comparisons of calls emitted by different species in the two contexts. We begin by providing a brief overview of the taxonomic distribution of neonatal distress vocalizations.

## 2.1 Overview of taxonomic distribution

Data were obtained for neonate or juvenile distress vocalizations for species from 11 orders of mammals, three orders of birds, and one order each for non-avian reptiles, fishes and amphibians (Table A1). Calls made when an infant is separated from its mother, hereafter “isolation calls” (sometimes called “attraction” or “contact” calls in the literature) are widespread in vertebrates having parental care, with examples for mammals, birds and crocodylians. Mammalian, avian and crocodylian infants that are captured by predators or humans readily emit loud vocalizations, usually termed “distress calls”. For the sake of distinguishing these clearly from isolation calls, which are also termed “distress vocalizations” in the neuroscience literature (e.g., Panksepp, 1998), we will use the term “capture calls” in this review. Studies have confirmed that mothers, and often other conspecifics, approach quickly when hearing these vocalizations (Benedict, 2007; Chaiken, 1992; Lingle et al., 2007b; Vergne et al., 2011). Despite a large body of work on begging calls in neonatal birds (e.g., Leonard et al., 1997), and capture calls in adult birds (Aubin, 1987; Conover, 1994; Högstedt, 1983; Martin et al., 2011; Møller and Nielsen, 2010), we found comparatively few reports describing acoustic traits of isolation or capture calls in avian neonates (but see Baker and Bailey, 1987; Chaiken, 1992).

A general assumption is that infants from species that do not have parental care do not emit vocalizations equivalent to the distress vocalizations emitted by young animals that receive parental care. However, we found one example of a neonate having no parental care that vocalizes when prodded: the Argentine horned frog (*Ceratophrys ornate*, Natale et al., 2011) (Table A1). It is not clear whether the relative absence of reports of such vocalizations in other species lacking parental care is due to the absence of such vocalizations or the lack of investigations.

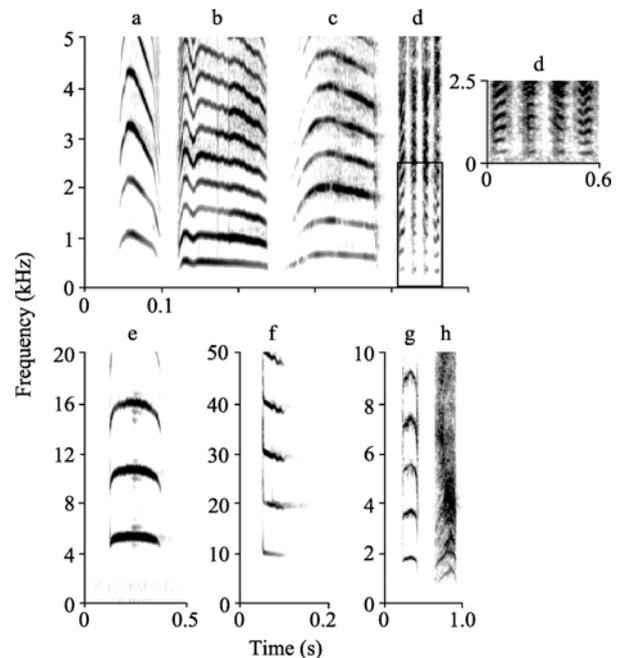
The isolation calls that female mammals emit when separated from their offspring, or that adults in general emit when separated from their social groups, have been nearly as well studied as the calls of infants for certain taxa such as pinnipeds and some artiodactyls, but have received comparatively little attention for other orders such as the chiropterans (but see Carter et al., 2012). Capture calls produced by adult bats (Russ et al., 2004),

birds (Martin et al., 2011) and, to a lesser extent, amphibians (Hödl and Gollman, 1986) have been closely-examined, perhaps reflecting the relative ease of handling these species without tranquilizers and considerable interest in vocal communication in these groups. For many taxonomic groups, there are no documented reports of capture calls in adults.

## 2.2 Acoustic structure

The reviewed literature (Tables 1, A1) revealed that the structure of distress vocalizations emitted by infants is remarkably similar across a wide taxonomic range and between the two behavioral contexts. We will therefore describe the structure of isolation and capture calls in the same section, drawing explicit contrasts as needed.

The most common form of vocalization reported for infants that are either separated from their mothers or captured by humans is a continuous tonal sound with a rich harmonic structure (Tables 1, A1; Fig. 1), as has been reported elsewhere (Newman, 2004; Newman, 2007). Our sample (Table 1) suggests this form of infant vocalization is even more widely distributed than described previously. In the context of isolation, tonal calls were emitted by neonates from nine of ten orders, 23 of



**Fig. 1 Spectrograms for distress vocalizations for neonatal mammals and adult birds**

**A.** Fallow deer capture call. **B.** human cry, unidentified context. **C.** fur seal isolation call. **D.** bighorn sheep capture call (with inset). **E.** Richardson's ground squirrel capture call. **F.** silver-haired bat isolation call. **G.** olive tanager capture call (adult), and **H.** black-striped sparrow capture call (adult). All neonatal mammals were less than four days old, except for the ground squirrel, which was <7 days post-emergence.

25 families and 35 of 38 species examined in this review (Table 1). In the context of capture, tonal calls were emitted by neonates from all of six orders, nine families and 17 species reviewed (Table 1). Such tonal sounds were the most common form of call made by infants in a context of isolation for artiodactyls, rodents, a manatee (*Trichechus inunguis*), three families of pinniped, a felid (*Felis catus*), a canid (*Lycaon pictus*), primates, bats, birds and crocodylians, and the same structure was observed in capture calls produced by neonatal artiodactyls, bats, a mongoose (*Mungos mungo*, Müller and Manser, 2008), and crocodylians (Table 1). However, we suspect that noisy broadband sounds have been underreported, as discussed below (Section 2c). It is also important to note that the distress vocalizations of the tadpoles of the Argentine horned frog *Ceratophrys ornate*, a species that does not have parental care, are also tonal with a rich harmonic structure (Natale et al., 2011). Most species that emitted mixed, soft or loud broadband sounds produced such sounds in addition to tonal and harmonically rich distress vocalizations. For example, neonates from four of five families (of 25 possible families) that produced loud broadband isolation calls did this in addition to tonal sounds, with the exception being the Macropodidae (Table 1).

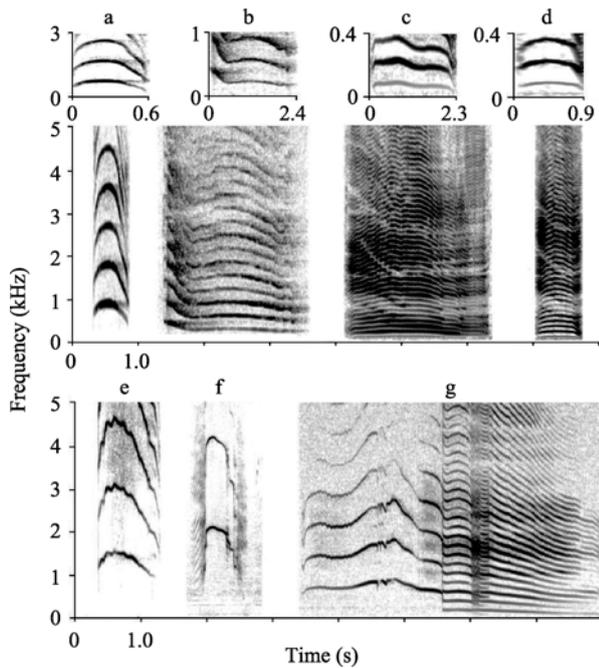
The pattern of frequency modulation was relatively simple in infant distress vocalizations, typically consisting of a chevron (rising then falling), flat (frequency change <10% of the mean F0; the F0 contour that was present usually had a chevron or descending shape) or descending shape (Fig. 1; Table A1). A chevron was identified for neonatal isolation calls in six of eight orders, 12 of 21 families and 14 of 30 species and for neonatal capture calls in four of seven orders, seven of 11 families and 15 of 20 species. However, there appears to be taxonomic variation in the relative frequency of modulation patterns. Although a chevron was the most common pattern of frequency modulation in artiodactyls (four of five species for isolation calls and 10 of 11 species for capture calls) and carnivores (five of six species for isolation calls), a flat or descending pattern was more common in bats (six and four of 11 species, respectively, with only two species having a chevron shape). Ascending patterns were observed in isolation calls of two species of rodents, primates and one bird. Across all orders, U-shaped or compound patterns of modulation were rare (Table A1; one case of a repeated U-shape and one of a U-shape followed by a descending frequency in neonatal bats). In addition to the overall pattern of frequency modulation, rapid inflections or

trills were observed in the capture calls of three distinct species including nestling European starlings (*Sturnus vulgaris*, Chaiken, 1992), neonatal banded mongoose (*Mungos mungo*, Müller and Manser, 2008) and juvenile capybaras (*Hydrochoerus hydrochaeris*, Barros et al., 2011).

Variation in the between call temporal pattern includes calls emitted in bouts, rather than singly, with the primary example being bats (Table A1, between call timing). We also looked at the timing of elements within a call. Although the majority of species produced one continuous sound, there were examples of pulsed or staccato calls in which voiced and unvoiced elements alternated (Table A1, within call timing: South American fur seal (*Arctocephalus australis*, Phillips and Stirling, 2000); black flying fox (*Pteropus alecto*, Van Parijs and Corkeron, 2002); and bighorn sheep (*Ovis canadensis*, Tables A1, B1).

The insertion of broadband noise, deterministic chaos and other nonlinear phenomena into calls having a primarily tonal structure is variable across taxonomic groups. There was no evidence of deterministic chaos or subharmonics in the isolation or capture calls of neonatal muroid rodents or the vast majority of bat species despite considerable research on these groups. These features are uncommon in the capture calls of neonatal cervids and bovids (Teichroeb et al., 2012; Table A1). In the case of the artiodactyls, the presence of nonlinear phenomena appears dependent on age. For example, whereas calls of neonatal fallow deer *Dama dama* and red deer *Cervus elaphus* are primarily tonal regardless of whether they are isolated or captured, isolation calls of older calves and adult females contain considerable deterministic chaos and subharmonics (Table A1; Fig. 2a,b).

However, deterministic chaos and subharmonics are intermittent in infant vocalizations made by two species of sciurid rodents when captured (yellow-bellied marmots (*Marmota flaviventris*, Blumstein et al., 2008); Richardson's ground squirrel (*Richardsonii spermophilus*, Table A1, B1). The presence of broadband noise and other nonlinear phenomena appears to vary across species of pinnipeds and does not coincide with divisions between the three families. For example, adult females and neonates from certain species such as the subantarctic fur seal *Arctocephalus tropicalis* and the walrus *Odobenus rosmarus* appear to emit entirely tonal isolation calls (Charrier et al., 2002; Charrier et al., 2010), although it is possible that the authors selected tonal calls for illustration of vocalizations for these species. In



**Fig. 2 Spectrograms for distress calls, contact calls and male courtship calls of red deer (top rows) and sika deer (bottom row)**

Top rows: **A.** capture call of neonatal red deer (<4 days) with inset. **B.** contact call of 7–9 month old red deer with inset. **C** and **D.** courtship calls of adult red deer male with insets. Bottom row: **E.** Distress call of neonatal sika deer (<4 day). **F.** Courtship “howl” of sika deer male, and **G.** courtship “moan” of sika deer male. Insets illustrate the harmonic structure of each of the red deer calls shown below the corresponding inset.

contrast, neonate and adult female isolation and contact calls have a mixed acoustic structure in the South American fur seal and in the northern elephant seal (*Miro-unga angustirostris*, Insley, 1992; Phillips and Stirling, 2000). Infant and adult South American fur seals are relatively unusual among placental mammals included in our review (Tables 1, A1) in that animals produce broadband as well as tonal isolation calls (Phillips and Stirling, 2000). We found no published data on pinniped vocalizations made when captured, but expect that neonates and adults that make noisy contact calls or isolation calls will emit considerable broadband noise when captured. Capture call data for terrestrial carnivores are also lacking although banded mongoose juveniles appear to make primarily tonal capture calls (Müller and Manser, 2008).

The presence of nonlinear phenomena such as deterministic chaos, subharmonics and frequency jumps is well-documented in vocalizations of young elephants (*Loxodonta africana*, Stoeger et al., 2011) and primates (Jovanovic et al., 2000; Rendall et al., 2009) including humans (Boero et al., 1998), and a correlation between

the level of distress and nonlinear features has been documented for each (Boero et al., 1998; Jovanovic and Gouzoules, 2001; Stoeger et al., 2011). Elephants produce sounds ranging from tonal to atonal when in relaxed circumstances; however nonlinear phenomena become more common when they are in more stressful circumstances such as when separated from the group (Stoeger et al., 2011). Although many primate infants are known to make tonal “coos” when separated from their mothers under natural conditions (Rendall et al., 2009), some will make a combination of tonal coos and harsh broadband screams when isolated in experimental conditions (Jovanovic et al., 2000). A decrease in tonality and increase in nonlinear phenomena has been correlated with the length of time a Rhesus macaque *Macaca mulatta* infant is restrained by conspecifics (Jovanovic and Gouzoules, 2001). Although it seems probable that neonatal primates or elephants would emit noisy screams if captured, one needs to be cautious about extrapolating results from socially stressful situations to the context of being attacked or captured. For example, adult little brown bats *Myotis lucifugus* are reported to emit harsh broadband sounds in socially antagonistic situations, but produce tonal distress vocalizations when captured (Barclay et al., 1979).

In the above paragraphs, we discuss species that emit isolation calls that are primarily tonal, although nonlinear phenomena may be intermixed or emerge with increased stress in certain groups such as elephants and primates. Although relatively uncommon, there are taxonomic groups that produce distress vocalizations with no tonal component. The main variant is a soft broadband click that is short in duration, low in amplitude and has a broad frequency range. This sound has been recorded in nocturnal strepsyrhine primates including bushbabies (*Galago* spp., Zimmermann, 1990), leading to the suggestion that this sound facilitates the location of infants by nocturnal primates (Newman, 2004). Indeed, gregarious diurnal strepsyrhines such as the gray mouse lemur *Microcebus murinus* emit tonal sounds that are more typical of mammals (Scheumann et al., 2007). The low amplitude click sound may be associated with a greater need to conceal infants, as it has been recorded in other species that have a solitary or a *cache* rather than *carry* parenting system. For example, neonatal short-tailed field voles *Microtus agrestis* usually emit the tonal calls that are typical of infant distress vocalizations, but also make soft clicking sounds during the first few days of life (Mandelli and Sales, 2004). Unlike many bats, infant eastern red bats *Lasiurus bo-*

*realis* are raised in seclusion and they seldom vocalize when their mother leaves the roost (Schmidt-French et al., 2006). When handled, they make clicking sounds, occasionally adding a tonal trill. In contrast to the young of this species, adult females produce tonal capture calls when handled (Table A1).

The isolation calls of young marsupials deviate from the tonal structure observed in other vertebrates. Infant kangaroos (*Macropus* spp.) that are in the pouch or have recently emerged emit a sound consisting of a series of three to four broadband pulses when isolated (Baker and Croft, 1993). These are longer in duration and louder in amplitude than the clicks described above. This deviation from the more typical vertebrate pattern may reflect the morphology of marsupials, for they have been reported to lack vocal folds substantial enough to modulate air flow as needed to produce a more tonal sound (Baker and Croft, 1993; Negus, 1962).

Similar to vertebrate infants, the capture calls of adult birds, bats and amphibians are most often tonal with a rich harmonic structure (Table 1, 23/36 species from 13/20 families; Fig. 1g), although some variation is evident (Table 1, 9/36 species from 6/20 families produced loud broadband sounds, Fig. 1h) (Conover, 1994; Hödl and Gollmann, 1986; Martin et al., 2011). We found only one published study in which adults appear to make a completely different type of call when captured than adults of the same species produce when isolated. Three species of vampire bats (*Desmodus rotundus*, *Diaemus youngi*, and *Diphylla ecaudata*) emit tonal isolation calls, but appear to emit loud broadband screams when captured (Carter et al., 2012). However, this interpretation may be premature as the focus of that study was adult isolation calls, with a single capture call illustrated for each species.

### 2.3 Have broadband sounds been under-reported?

Our review suggests that calls consisting primarily of broadband noise such as harsh screams, growls or snarls, are rare. We suspect calls of this type have been under-reported for two reasons: (1) the screening of calls to limit samples to sounds viewed as typical of either isolation or capture calls, and (2) fewer studies on capture vocalizations for infants from taxonomic groups that are more likely to respond aggressively or with noisy vocalizations (e.g., primates and carnivores).

In some studies, researchers may have screened recordings to select calls that are *a priori* viewed as typical of “isolation calls” or “distress calls”. For example, Lieblich et al. (1980) mentions that neonatal squirrel monkeys *Saimiri sciureus* produced a variety of sounds

in addition to the stereotypical isolation calls that were analyzed as isolation calls and Vergne et al. (2007) describe broadband hisses and higher-pitched screams that were produced by Nile crocodile *Crocodylus niloticus* neonates that were captured, in addition to the distress calls included in their analysis. Such screening is reasonable when investigators are interested in the structure and function of certain types of vocalizations. However, it is also important to understand the variety of sounds produced by young animals under distress. If distinct sounds are emitted during the same vocalization bout, one might expect these to be directed to different audiences – the infant’s mother and the adversary (Jovanovic and Gouzoulez, 2001; Rendall et al., 2009).

We can confirm that broadband screams or growls were not produced during lengthy recording of numerous species of neonatal artiodactyls that were captured (e.g., Table 1; Lingle et al., 2007a; Teichroeb, et al., 2012). However, we found very few examples of capture calls for taxa that might be expected to respond more aggressively to conditions of capture such as primates or carnivores. Recent conversations with researchers working with neonatal pinnipeds (B. Pitcher, personal communication) and adult bats (J. Nagel, L. McQuire, personal communication) suggest that broadband sounds, which tend to be viewed as more aggressive, may be more common than has been reported.

### 2.4 Acoustic transitions with increased distress

The range of taxonomic examples highlighted above reveal no qualitative differences in the acoustic structure of infant distress vocalizations made within or between the contexts of isolation or capture. Although we predicted the basic acoustic structure would be similar between isolation and capture contexts, we also anticipated that quantitative changes in certain acoustic traits that are associated with the infant’s level of arousal and the urgency of the context would occur in a consistent and graded fashion (Briefer, 2012; Mendl et al., 2010). To examine this transition, we include contact calls made by animals when they are within their normal social groups. Contact calls serve to regulate spacing and social relationships among individuals, and therefore should be rooted in the same social-affect system (Panksepp, 1998) as isolation and capture calls. In most situations, the level of arousal or stress is expected to increase as one makes the transition from a normal social situation (contact call) to isolation (isolation call) to capture (capture call).

The results of our review are consistent with recent work by Vergne et al. (2009, 2011) identifying three

acoustic changes associated with increased distress: (1) an increase in the maximum F0, (2) an upward shift in the energy distribution, and (3) an increase in amplitude. Increases in the maximum F0, the range of frequency modulation, and an upward shift in the energy distribution are evident when comparing contact calls with isolation calls in chickens (*Gallus gallus*, Marx et al., 2001), isolation calls with capture calls of neonatal fallow deer (Table A1), and pain cries with cries made in less-urgent circumstances by human neonates (Baeck and Souza, 2001<sup>1</sup>; Boero et al., 1998). A comparison of contact calls and isolation calls produced by Weddell seal pups *Leptonychotes weddellii* similarly reveals an increase in mean F0 and energy distribution, but not an increase in the overall extent of frequency modulation (Collins et al., 2011).

Call duration becomes longer for some species (Collins et al., 2011; Marx et al., 2001; Stoeger et al., 2011) but not all (Vergne et al., 2011). We did not examine call rate, which is known to increase with isolation (Christensson et al., 1995; Collins et al., 2011; Mandelli and Sales, 2004; Weary et al., 1997), and to decrease when animals are exposed to cues associated with the risk of predation (Pettijohn et al., 1977; Shair et al., 1999). As discussed above (Section 2), an increase in nonlinear phenomena such as deterministic chaos or subharmonics accompanies increases in arousal for some species (Boero et al., 1998; Rendall et al., 2009; Stoeger et al., 2011), but is unlikely to matter for species that do not exhibit these traits (Teichroeb et al., 2012).

The graded changes observed within the above species are also evident when reviewing data for the broader cross-section of species (Table A1). Animals that were captured consistently emit energy at higher frequencies than animals that were simply isolated or that were in social groups (e.g., Table A1, artiodactyl entries). This upward shift in energy has also been reported for the solicitation purrs of cats (McComb et al., 2009), for chacma baboon *Papio hamadryas ursinus* infants facing social adversaries (Rendall et al., 2009), and for the alarm calls of red-fronted lemurs (*Eulemur fulvus rufus*, Fichtel and Hammerschmidt, 2002). An increase in F0 and an upward shift in spectral energy may therefore be a general response to stress and, more generally, an increase in arousal (Briefer 2012), not a response restricted to infant distress vocalizations. In-

deed, physiological stress responses may elicit these acoustic shifts. For example, F0 may increase if elevated distress triggers certain vocal fold changes. Higher F0 can result from increased vocal fold elongation or tension due to associated increases in tissue stiffness, and possibly, a reduction in the proportion of oscillating tissue (Riede, 2010). Additionally, if higher states of distress cause increased muscle tension and shrinking of supralaryngeal cavities, emphasized frequency bands may shift upward (Fant, 1960; Titze, 1994).

Thus, the fundamental similarity in acoustic structure of isolation and capture calls, paired with small quantitative changes in parameters that have previously been associated with urgency (Baeck and Souza, 2001; Boero et al., 1998; Fichtel and Hammerschmidt, 2002; Vergne et al., 2009; Vergne et al., 2011), is consistent with our prediction that acoustic variation between these contexts involves a graded transition associated with the infant's level of arousal or urgency (Mendl et al., 2010), and may indicate that these vocalizations do not serve discrete functions.

### 3 Adaptive Function of Infant Distress Vocalizations

Morton's (1977) motivational-structural rules led to a basic dichotomy in which high frequency tonal sounds are predicted to attract or appease whereas low frequency broadband sounds are predicted to be hostile and to repel social or predatory opponents. Reports from the literature suggest that the tonal isolation calls emitted by infants universally serve to attract mothers or other conspecifics. Naturalistic observations and playback experiments with diverse vertebrate species confirm that mothers respond to calls emitted by their offspring by orienting, vocalizing, approaching, feeding, retrieving or simply accompanying the infant (artiodactyls, Briefer and McElligott, 2011; Espmark, 1971; Illmann et al., 2002; Torriani et al., 2006; Vaňková and Málek, 1997; Weary and Chua, 2000; pinnipeds, Charrier et al., 2002; Charrier et al., 2010; other carnivores, Haskins, 1977; Müller and Manser, 2008; primates, Jovanovic et al., 2000; Rendall et al., 2009; bats, Bohn et al., 2007; crocodylians, Vergne et al., 2011). Observations of naturally occurring predation attempts and playback experiments confirm that mothers, and often other conspecifics, rapidly approach when hearing the calls of infants that have been attacked or captured (Benedict, 2007; Chaiken, 1992; Lingle et al., 2007b; Vergne et al., 2011). Responses to the calls of an infant being attacked are more dramatic than responses to calls made when an

<sup>1</sup> Baeck HE, Souza MN, 2001. Study of acoustic features of newborn cries that correlate with the context. Papers from 23rd Annual International Conference of the IEEE Engineering in Medicine and Biology Society, October 25-28, 2001, Istanbul, Turkey. 3: 2174–2177.

infant is isolated. Animals hearing capture calls move quickly to the playback speaker where they often vocalize or show defensive behaviour (Benedict, 2007; Chaiken, 1992; Lingle et al., 2007b; Vergne et al., 2011).

An alternative hypothesis about the function of distress vocalizations made when an animal faces a predator or social adversary is that they startle or repel the opponent rather than attract help (Driver and Humphries, 1969; Rendall et al., 2009). This function has been proposed for the noisy atonal screams produced by baboon infants when faced with a social threat (Rendall et al., 2009). This hypothesis is not supported by data for macaque infants that were restrained by conspecifics (Jovanovic and Gouzoulez, 2001). The production of noisy screams did not influence the behaviour of the animal that was holding the infant as would be predicted if these vocalizations function to deter adversaries. However, mothers responded more quickly when the infant emitted a combination of tonal sounds and noisy screams.

But what about infants belonging to species that do not produce the typical tonal vertebrate distress vocalization, and instead emit broadband sounds including the low amplitude clicks of bushbabies or the atonal pulses (sometimes referred to as a cough) of kangaroos? Although we are not aware of playback experiments conducted with species making such broadband isolation calls, researchers have observed female marsupials respond to the calls of their infants with an approach (Croft and Eisenberg, 2006) or a vocal exchange (Aitkin et al., 1996). These examples of broadband sounds are unlikely to fit the traditional view, based on motivational-structural rules (Morton, 1977), that equates broadband sounds with harsh screams, growls or hisses emitted by animals with an underlying state of hostility.

Capture calls of adult birds and bats usually adhere to the tonal vertebrate pattern described above for infants (Tables 1, A1). These vocalizations are also known to attract conspecifics and heterospecifics, which frequently respond by intervening to attack the predator (Aubin and Bremond, 1992; Russ et al., 2004). The intervention of birds has been found to result in successful escape by the victim (Møller and Nielsen, 2010). Nonetheless, adults from many species of frogs (Hödl and Gollmann, 1986), and even tadpoles (Natale et al., 2011), also emit calls with a similar tonal structure when attacked by predators. Given the apparent absence of social antipredator tactics in these amphibians, it seems unlikely to serve as a call for help. Limited evidence suggests that the capture calls of amphibians can startle predators into dropping their prey, providing a

window of opportunity to escape (Hödl and Gollmann, 1986). From the perspective of motivational-structural rules (Morton, 1977), it is intriguing that calls that are tonal in structure (e.g., capture calls of adult amphibians, birds and neonatal birds) might serve a function in startling and repelling predators as well as a function in attracting conspecifics. Clearly, playback studies that test both functional hypotheses using a range of tonal and broadband acoustic stimuli are needed.

Taken together, the reports reviewed here provide strong evidence for a function of capture calls in recruiting help, but also suggest that distress calls emitted under the threat of capture may serve alternative or dual functions in different taxonomic groups.

## 4 What Acoustic Traits Make Infant Vocalizations So Evocative?

The vocalizations of infants have a powerful effect on their caregivers, one that has shaped their behaviour, physiology and anatomy. The sequence of hormonal, neural and chemical events that unfold in response to the cries of human infants is well known, resulting for example in the secretion of oxytocin in the female's brain and the release of milk from the mammary glands (McNeilly et al., 1983). But what specific aspects of the infant's call are responsible for the behavioral and physiological influence it exerts on caregivers? Our goal in this section is to consider the specific acoustic traits that are critical for caregivers to respond to infant distress vocalizations.

### 4.1 The power of frequency

Characteristics of the fundamental frequency, including mean, maximum, start or end F0, or the overall frequency modulation sweep, are usually listed among the top three variables in statistical discriminations of neonatal vocalizations made by different individuals or by different species. This is true for contact and isolation calls of neonatal pinnipeds (Charrier et al., 2002; Charrier et al., 2010; Collins et al., 2006; Job et al., 1995; Phillips and Stirling, 2000), ungulates (Briefer and McElligott, 2011; Espmark, 1975; Torriani et al., 2006; Volodin et al., 2011), manatees (Sousa-Lima et al., 2002), bats (Bohn et al., 2007; Carter et al., 2012; Van Parijs and Corkeron, 2002), and primates (Rendall et al., 2009). This is similarly true for vocalizations of neonates made when captured with examples for ungulates (Lingle et al., 2007a; Teichroeb et al., 2012), marmots (Blumstein et al., 2008), and crocodiles (Vergne et al., 2007).

Instead of F0, spectral peaks were included in a dis-

criminant analysis of vocalizations made by infant elephants with the lowest peak contributing most to the discrimination of individuals (Stoeger et al., 2011). This may still reflect the importance of energy being emitted in the range of the F0 given that the lowest spectral peak fell near to the F0 (F0=405 Hz, spectral peak=536 Hz). Other studies of infant isolation and capture calls report the dominant frequency rather than F0 as the most differentiated trait amongst individuals: however, the dominant frequency and F0 appear equivalent in these examples (bats, Bohn et al., 2007; flying foxes, Van Parijs and Corkeron, 2002; banded mongoose, Müller and Manser, 2008).

The individual distinctiveness or salience of emphasized frequency bands, which are assumed to be primarily filter-related traits (Fant, 1960), appears to increase with age. Even though F0 often remains the most important trait in the statistical discrimination of adult female isolation calls, characteristics of energy distribution start to carry more weight than in the corresponding vocalizations of infants (Charrier et al., 2003; Charrier et al., 2010; Phillips and Stirling, 2000).

Strictly temporal characteristics such as call duration were relatively unimportant in distinguishing individuals for most species, apart from a few examples including flying fox (Van Parijs and Corkeron, 2002) and certain pinnipeds (Insley, 1992). Temporal traits were the most discriminating variable for neonate isolation calls for only two species reviewed here: the broadband isolation calls produced by infants of two kangaroo species were discriminated most by call duration and inter-pulse interval (Baker and Croft, 1993).

In cases in which infants are attacked by predators, the individual distinctiveness of the sound may matter less than its ability to propagate over a long distance. Although the capture calls of individual mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* fawns are statistically distinctive (Lingle et al., 2007a), playback experiments reveal that females do not respond preferentially to the voice of their own fawn (Lingle et al., 2007b). In situations in which the infant's survival depends on immediate assistance, caregivers may not have the time needed to process subtle acoustic cues. Nevertheless, the F0 is well-suited for a role in recruiting help from a distance, as the harmonic intervals needed to identify this trait undergo less degradation than other spectral and temporal features when transmitted over long distances (Maciej et al., 2011).

As might be expected for a trait that has the potential to be used to distinguish individuals and species and can

also be transmitted reliably, playback tests have confirmed the salience of the fundamental frequency of infant vocalizations to adult caregivers. Maternal female mice *Mus musculus* show a strong attraction for tones played at the F0 of neonatal isolation calls (Ehret and Haack, 1981). Meerkat *Suricata suricatta* helpers feed pups as long as the pups are young enough to have a F0 falling within the range of the youngest juveniles (Madden et al., 2009); older pups continue to beg, but helpers are less likely to provision pups that emit calls with a lower F0. Significant variation in the F0 of human baby cries is one of the clearest predictors of the distress felt by adult listeners (reviewed by Esposito et al., 2012; Furlow, 1997; Zeskind and Marshall, 1988). Female mule deer and white-tailed deer also respond powerfully to the F0 of infants. When hearing capture calls falling within a certain species-specific frequency range – about 40% above or below the mean F0 of calls from conspecific fawns of their own species – females rapidly move to the speaker, showing defensive behaviour and often grunting, presumably to the apparent victim (Teichroeb et al., 2012). Once the F0 is shifted beyond these limits, the response of females is extinguished, even though the spectral envelope is kept essentially the same. Whether a response to the calls of heterospecific infants can similarly be turned on and off by a simple shift in F0 is under investigation (Lingle and Riede, unpublished data).

Frequency characteristics of infant vocalizations have left an indelible imprint on the anatomy of adults. A comparative study of bats found that the hearing of adults was most sensitive in the frequency range that corresponds to the F0 of neonatal isolation calls, which is equivalent to peak frequencies in most neonatal bats (Bohn et al., 2006). Similarly, the most sensitive adult hearing range in two marsupials, the adult northern quoll *Dasyurus hallucatus* and short-tailed Brazilian opossum *Monodelphis domestica*, corresponds to the dominant frequencies contained in the broadband isolation calls of their infants (Aitkin et al., 1996; Aitkin et al., 1997). Indeed, Aitkin et al. (1996, 1997) and Bohn et al. (2006) suggest the hearing of adults has been shaped specifically by the adaptive value of responding to neonatal isolation calls.

However, in many mammals, the frequency range at which adult hearing is most acute lies well above the F0 of conspecific infants. For example, the mean F0 of many of the medium to large mammalian groups included in our review varied from 100 Hz to 1,500 Hz (Table A1). The hearing of adult ungulates, carnivores,

primates and even subterranean rodents is generally most sensitive in the 2 to 8 kHz range (Heffner, 1998; Heffner and Heffner, 1990), substantially higher than the F0 of infants in these species. Our review suggests that the peak frequency of infant vocalizations shifts upward, into the range where adult hearing is most sensitive, as the infant's distress increases (see Section 2.4). The frequency range of 2 to 4 kHz is also known to be a sound window, below and above which sound attenuates more rapidly in the environment (Marten et al., 1977; Marten and Marler, 1977). Studies reveal that human mothers perceive infant cries as most urgent, arousing and disturbing when the energy is specifically concentrated in the 3 to 4 kHz range, and as least arousing when it falls within the 1 to 2 kHz range (Gustafson and Green, 1989). In cases of greater urgency, it should be advantageous for both neonates and their caregivers if the neonate emits more energy at frequencies that coincide with this sound window and with the peak in adult hearing sensitivity.

#### 4.2 What makes a cry a cry?

As described above, F0 is critical to the response of caregivers to the sounds of conspecific infants. However, females do not respond similarly to all sounds having a F0 similar to that of their infant. For example, mule deer move rapidly to a speaker when playing conspecific capture calls manipulated to have a F0 falling between 500 Hz and 1400 Hz, but not when hearing meadowlark *Sturnella neglecta* advertisement song shifted into this same frequency range (Lingle, unpublished data). This raises the question: what specific acoustic traits distinguish the distress vocalizations of infants from other vocalizations emitted in the same frequency range?

A rising and falling "chevron" pattern of frequency modulation is so widespread in certain groups including artiodactyls, carnivores (Table A1) and many birds (e.g., Aubin, 1987; Martin et al., 2011), that it might be thought essential for animals from these species to respond to distress vocalizations. Indeed, Aubin (1987) found that the removal of frequency modulation, so that the F0 contour was flattened, extinguishes the response of European starlings *Sturnus vulgaris* to capture calls of adult conspecifics. A time-reversed – but still chevron shaped – pattern of frequency modulation is sufficient to prevent female fur seals from responding to their infant's isolation calls (Charrier et al., 2002). In contrast to these examples, white-tailed deer and mule deer respond as strongly to capture calls of infants from which the F0 contour has been flattened as they do to the original calls (Teichroeb et al., 2012). These contradic-

tory results leave the importance of frequency modulation unresolved.

Charrier et al. (2002) also found that the harmonic structure was essential to elicit mutual recognition of isolation calls by mothers and infants, with the lowest three harmonics sufficient. The same result was obtained for the response of starlings to capture calls made by other adults (Aubin and Bremond, 1992). Recent work indicates that the harmonic structure is a second-order attribute that activates a distinct pathway in the auditory cortex (Lewis et al., 2009), providing neural evidence consistent with these behavioral findings.

Considerable attention has been devoted to nonlinear phenomena in recent years, with some researchers suggesting that these features are tied to the intensity of an animal's response to infant screams (Blumstein et al., 2008; Rendall et al., 2009; Riede et al., 2007). Although such features are correlated with both the infant's arousal (Boero et al., 1998; Jovanovic and Gouzoulez, 2001; Stoeger et al., 2011) and the mother's perception of distress (Gustafson and Green, 1989; Jovanovic and Gouzoulez, 2001) in certain taxonomic groups such as primates and elephants, our review shows that nonlinear phenomena are not a ubiquitous feature of calls made under duress in other taxa (e.g., Teichroeb et al., 2012; see Section 2.1). This result is consistent with Blumstein and Chi's (2012) suggestion that, in some species, urgency may alternatively be conveyed by a piercing loud tonal call.

Having reviewed these studies, we suggest that infant distress vocalizations that successfully elicit responses from caregivers will most likely have a tonal or mixed structure with a certain species-specific F0, a simple pattern of frequency modulation, and a rich harmonic structure. As the infant's distress increases, the basic acoustic structure remains the same; however, calls usually increase in amplitude and in maximum F0, resulting in a larger frequency modulation sweep. Additionally, the overall spectral envelope has consistently been found to shift upward (Baeck and Sousa, 2001; Marx et al., 2001; Vergne et al., 2009; Vergne et al., 2011) (see Section 2.4). Playbacks with black caimans (*Melanosuchus niger*, Vergne et al., 2011) reveal that caregivers respond to this set of traits when they are bundled together. Studies of human infant cries have confirmed that adults perceive upward shifts in maximum F0 and emphasized frequencies as reflections of greater distress (Baeck and Souza, 2001; Boero et al., 1998; Furlow, 1997; Gustafson and Green, 1989; Leger et al., 1996; Zeskind and Marshall, 1988).

## 5 Designed to Attract: The Evolution of Infant and Related Conspecific Vocalizations

Without question, the infant's need for assistance has led to a tightly-adapted system involving the structure of infant vocalizations and the anatomy (Aitkin et al., 1996; Aitkin et al., 1997; Bohn et al., 2006), physiology and behaviour of caregivers (Newman, 2007; Panksepp, 1998). The powerful effect of infant vocalizations on caregiver physiology and behaviour can easily lead to the hypothesis that other types of social vocalizations that serve to attract conspecifics have arisen as modifications of infant cries (Newman, 2007). Indeed, certain similarities in spectrographic structure, as illustrated between infant capture calls and male courtship calls for red deer *Cervus elaphus* and sika deer *Cervus nippon* (Fig. 2), may lead one to propose that aspects of adult vocalizations that attract conspecifics, including male courtship vocalizations, may mimic the sounds of neonates because of the adult female's sensory bias to respond to infant calls.

However, sexual interactions and communication existed in vertebrates long before parental care appeared. Neural pathways involved in communication in the context of sexual interactions should therefore have evolutionary primacy over the evolution of communication in the context of maternal-infant interactions (Panksepp, 1998; Panksepp and Biven, 2012). It is therefore more parsimonious to suggest that neural pathways and neurochemical structures involved in mother-infant and more general social interactions build on structures already in place for sexual interactions (Panksepp, 1998; Panksepp and Biven, 2012) rather than the reverse. For example, the role of oxytocin and vasotocin – which along with opioids inhibit the separation calls of infants – in maternal care suggests that social and maternal comfort are produced by the same brain chemistries that help to mediate sexual behaviour (Nelson and Panksepp, 1998; Panksepp, 1998; Panksepp, 2005; Panksepp and Biven, 2012). Tonal vocalizations that serve to attract females to infants or that maintain social cohesion probably share many similarities in acoustic structure because they take advantage of the same neural pathways as does communication in the context of sexual interactions.

A well-known example is that of an ancient species of fish, the plainfin midshipman *Porichthys notatus*. Females find the hum of a male highly attractive as long as it has a certain F0 (Bass and McKibben, 2003). Does

the important role of F0 in mother-infant and other forms of social communication hark back to the importance of F0 to the female's neural pathways in sexual interactions in early vertebrates such as this? Regardless of the answer to this question, Bass et al. (2008) have shown that the neural pathways underlying vocal social behaviour in teleosts have been conserved throughout vertebrates and are essential for any form of vocal communication in vertebrates from teleosts to higher primates. Once these mechanisms were in place, further evolutionary modifications would presumably have led to specializations for mother-infant communication.

However, it is possible that some male courtship vocal signals could secondarily have evolved to exploit the attractiveness of infant vocal signals. The acoustic parameters of male mating calls have the potential to encode reliable or 'honest' information about their quality (Reby and McComb, 2003; Wyman et al., 2008; Wyman et al., 2012), which can be used by females in the context of mate choice (Charlton et al., 2007; Reby et al., 2010). The ability to initially attract females using infant-like call elements may be an effective strategy when paired with other call elements that reflect male quality. This type of sensory exploitation has been suggested for certain visual displays of courting mule deer males, which sport facial patterns that are otherwise seen only in neonates and approach females with postures reminiscent of the suckling approaches of infants (Geist, 1981).

Many vocalizations serve to attract conspecifics, including contact calls, infant solicitations ranging from isolation to hunger to capture calls, male courtship calls and even mobbing calls that attract conspecifics to the location of a common enemy. Several studies have documented ontogenetic transitions of infant isolation calls into adult vocal displays, such as the contact calls of adult bobwhite quail (*Colinus virginianus*, Baker and Bailey, 1987) and the loud calls of primates (Zimmermann, 1990), revealing their underlying structural similarity. Animals may be responding primarily to cues of urgency when it comes to the critical differences among vocalizations that attract conspecifics in different contexts. For example, a recent study reported that chaffinch *Fringilla coelebs* do not respond to subtle structural differences between contact and mobbing calls, but instead to the rate at which the calls are presented (Randler and Förschler, 2011). When animals are together in a social group, the neurochemicals in the brain may be such that vocalizations are emitted in a maintenance mode needed to manage interactions with adja-

cent individuals (contact calls). When an infant becomes isolated (leading to isolation calls), when a predator is detected (mobbing calls), or when an infant is attacked by a predator (capture calls), vocalizations may be emitted with increasing cues of arousal and urgency that exert a more powerful influence on conspecifics.

## 6 Conclusion

The results of this review confirmed the predictions that; (1) infant distress vocalizations have a similar acoustic structure across species within the contexts of isolation and capture, and (2) infant distress vocalizations have a similar acoustic structure between these two contexts, as predicted if they share the same underlying motivation. Differences in acoustic structure between the two contexts involved graded changes in acoustic parameters – increases in amplitude, maximum F0 and an upward shift in spectral energy – that are associated with increased arousal. Evidence is overwhelming that vocalizations produced in both contexts attract caregivers, which approach and engage in forms of assistance appropriate to the specific context.

Two important conclusions follow from the results of this review. First, the great similarity in acoustic structure among species that are taxonomically and ecologically diverse, the similarity in acoustic traits associated with urgency in these different groups, and the similarity in response of caregivers from different species to these vocalizations and to cues of urgency, suggest that the same neural substrates are involved in the production and processing of infant distress vocalizations in different species. It is not reasonable to suggest that this degree of similarity in acoustic structure and caregiver response could have arisen through convergence in animals as diverse as the terrestrial, aquatic and volant mammals, birds and reptiles included in this review. Our results add support to the hypothesis that the production of distress vocalizations is part of a highly-conserved system of vocal behaviour in vertebrates (Newman, 2004; Newman, 2007; Panksepp, 1998; Panksepp and Biven, 2012), while also highlighting the essential relationship between the motivation underlying a vocalization, the structure of the vocalization and its influence on receivers (Morton, 1977; Owings and Morton, 1998; Owren and Rendall, 2001).

Second, our results support the idea that isolation calls and capture calls are functionally equivalent, differing only in urgency. This interpretation of animal distress vocalizations is consistent with the literature on human crying, which has shown that caregivers can distinguish the urgency of different cries and therefore

are motivated to respond more or less quickly, although they cannot reliably identify the specific context (e.g., hunger or pain) associated with the cry (Gustafson and Green, 1989). Research in this field may move forward by recognizing the acoustic commonality among different forms of infant vocalizations that attract caregivers, and the acoustic commonality of these solicitations with still other vocalizations that attract conspecifics in other behavioral contexts.

**Acknowledgements** Funding was provided by the Natural Sciences and Engineering Research Council of Canada and The University of Winnipeg (to S.L.). The work of R.K. was supported by long term institutional support from Czech University of Life Sciences, Prague and Ministry of Agriculture of the Czech Republic (grant number MZe 0002701404). We are grateful to Dan Mennill and the Mennill Sound Analysis Laboratory for providing us with recordings of bird distress calls; Dan Blumstein, Isabelle Charrier, Paul Faure, Elodie Briefer, Alan McElligott, Ben Pitcher, Ilya Volodin, Pavel Linhart, Joah Madden and Maddie Willis for sound recordings or information; Jim Hare, Jack Hogg, John Byers and his students, and Chris Enright, Charlene Berkvens, Robert Wrigley and other members of the animal care staff at the Assiniboine Park Zoo for recording vocalizations or for providing assistance with recording. We thank the Assiniboine Park Zoo, the Montana Bison Refuge, the Thrall family and McIntyre Ranching Company for permission to work at these field sites, Liam McQuire and Sergio Pellis for helpful discussions, and Jim Hare and two anonymous referees for their insightful comments on an earlier draft of this manuscript.

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**Appendix: Table A1 Acoustic traits of distress vocalizations (isolation calls and capture calls) made by neonates or juveniles, their mothers and other adults. Some calls made in other contexts (e.g., contact calls, calls made when in pain) are included for comparison (see explanatory note below table for definitions)**

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms): mean or range	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>Class Mammalia</b>										
<b>ARTIODACTYLA: Cervidae</b>										
Fallow deer <i>Dama dama</i>	Juvenile, 28–52 d Adult female	Isolation (NS) Isolation (NS)/ Contact	Tonal Mixed (primarily, tonal or BB Tonal)	150 350	Single (C) Single (C)	653 (598–699) 365	(653–2612) <sup>a</sup> No data	Chevron Chevron	No evidence DC	Torriani et al., 2006 Torriani et al., 2006
Red deer <i>Cervus elaphus</i>	Neonate, <4 d Juvenile, 7–8 mo.	Capture Isolation (E)	Tonal Tonal (primarily), mixed	550 1197	Single (C) Single (C)	910 (616–1024) 360 (290–474)	(1317–3803) EQ: 4661 (437–2256)	Chevron Chevron, descending	Uncommon DC, SH	See Table B1 See Table B1
Sika deer <i>Cervus nippon</i>	Neonate, <4 d	Capture	Tonal	270	Single (C)	108	(108–2880)	Chevron, flat	No data	Vánková and Malek, 1997
Mule deer <i>Odocoileus</i>	Neonate, <4 d	Capture	Tonal	590	Single (C)	747 (506–843)	(1238–3912) EQ: 4670	Chevron	Uncommon: SH, DC	Teichroeb et al., 2012
White-tailed deer <i>Odocoileus</i>	Neonate, <7 d	Capture	Tonal	980	Single (C)	1083 (723–1270)	(1898–5129) EQ: 5196	Chevron	Uncommon	See Table B1
Reindeer <i>Rangifer tarandus</i>	Neonate, 17–21 d	Capture	Tonal	600	Single (C)	615 (964–1069)	(1578–3814) EQ: 4736	Chevron	Uncommon: SH, DC	Lingle et al., 2007b; Teichroeb et al., 2012
Common eland <i>Taurotragus oryx</i>	Neonate, <4 d	Capture	Tonal	610	Single (C)	546 (419–586)	(1479–4406) EQ: 4607	Chevron	Uncommon: SH, DC	Teichroeb et al., 2012
Goitered gazelle <i>Gazella</i>	Neonate, Juvenile, 3–6 wk.	Isolation (E) Capture	Tonal	150	Single (C), Bouts (C)	(105–260)	(105–1880) <sup>a</sup>	Chevron	No data	Espmark, 1975
Markhor <i>Capra falconeri</i>	Neonate, <2 d	Capture	Tonal	180	Single (C)	148 (130–159)	(829–2025) EQ: 3881	Chevron, flat	Uncommon: SH, DC	Teichroeb et al., 2012
<b>ARTIODACTYLA: Bovidae</b>										
Common eland <i>Taurotragus oryx</i>	Neonate, <4 d	Capture	Tonal	1620	Single (C)	169 (127–191)	(837–2475) EQ: 4006	Chevron	Uncommon: SH, DC	Teichroeb et al., 2012
Goitered gazelle <i>Gazella</i>	Neonate, Juvenile, 3–6 wk.	Isolation (NS) or Hunger	Tonal	513	Single (C)	101	800 EQ: 1687	Flat	No evidence	Volodim et al., 2011
Markhor <i>Capra falconeri</i>	Neonate, <2 d	Capture	Tonal	730	Single (C)	487 (417–518)	(1524–4847) EQ: 5175	Chevron	No data	See Table B1

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms): mean or range	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, F)	Reference
<b>ARTIODACTYLA: Bovidae</b>										
Bighorn sheep <i>Ovis canadensis</i>	Neonate, <2 d	Capture	Tonal	640	Single (C, P)	329 (278–358)	(1036–3793) EQ: 4895	Flat/Chevron	No data	See Table B1
Goat <i>Capra hircus</i>	Neonate, 5–9 d	Isolation (E)	Tonal	300	Single (P)	588 (538–621)	EQ: 3002	Chevron (within pulse)	No evidence	Briefer and McElligott, 2011
	Juvenile, 34–39 d	Isolation (E)	Tonal	600	Single (P)	545 (493–573)	EQ: 2823	Chevron (within pulse)	No evidence	Briefer and McElligott, 2011
	Adult female	Isolation (E)	Tonal	700	Single (P)	223 (187–252)	EQ: 1951	Chevron (within pulse)	No evidence	Briefer and McElligott, 2011
Domestic cattle <i>Bos taurus</i>	Neonate, 0–4 d	Isolation (E)	Tonal	1150	Single (C)	116	464 <sup>a</sup>	Chevron	No evidence	Weary and Chua, 2000
	Adult female	Isolation (E)	Tonal	1253	Single (C)	152	197 <sup>a</sup>	Chevron	No evidence	Weary and Chua, 2000
<b>ARTIODACTYLA: Antilocapridae</b>										
Pronghorn <i>Antilocapra americana</i>	Neonate, <2 d	Capture	Tonal	470	Single (C)	385 (328–432)	(829–2025) EQ: 4760	Chevron	Uncommon: SH, DC	Teichroeb et al., 2012
<b>ARTIODACTYLA: Suidae</b>										
Domestic pig <i>Sus scrofa</i>	Neonate, 7–14 d	Isolation (E)	Tonal (prim- arily), mixed	340	Single (C)	500	(500–3500)	Chevron, U-shaped, ascending	No data	Xin et al., 1989; Tallet et al., 2010
	Neonate, 14 d	Capture	No data	900–1100 <sup>a</sup>	Single (C)	No data	(3000–8000) <sup>a</sup> EQ: 3400 <sup>a</sup>	Chevron	DC	Puppe et al., 2005 ("high-frequency calls")
<b>CETACEA: Delphinidae</b>										
Killer whale <i>Orcinus orca</i>	Juvenile, 3.2– 4.3 meters	Capture	Tonal, mixed	3000–16000 <sup>a</sup>	Single, Bouts (C)	No data	No data	Ascending, chevron	DC, SH	Van Parijs et al., 2004
Bottlenose dolphin <i>Tursiops truncatus</i>	Juvenile, 1–2 yr.	Capture	Tonal	250–1000 <sup>a</sup>	No data (C)	5000–15000 <sup>a</sup>	No data	Ascending, chevron, U-shaped	FJ	Savigh et al., 1990
<b>PERISSODACTYLA: Equidae</b>										
Horse <i>Equus caballus</i>	Juvenile, age not specified	Isolation (NS)	Tonal	500–2800	No data	400–2000	No data	No data	No data	Yeon, 2012

Continued Table A1

Class ORDER: Family (Genus species)	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>CARNIVORA: Canidae</b>										
African wild dog <i>Lycan pictus</i>	Neonate and Juvenile, 3–7 wk.	Isolation (NS)	Tonal	200–500	Bouts (C)	1100–2000	1100–2000	Flat/ Ascending	No evidence	Robbins and McCreery, 2003
<b>CARNIVORA: Felidae</b>										
Domestic cat <i>Felis catus</i>	Neonate, <2 d	Isolation (E)	Tonal	560–1000	Single (C)	1000 (1350 max)	4000 max <sup>a</sup>	Chevron	No evidence	Brown et al., 1978; Haskins, 1977, 1979
	Juvenile, 28–56 d	Pain	Tonal, mixed, BB	1600	Single (C)	900	8000 max <sup>a</sup>	Chevron	DC	Brown et al., 1978
<b>CARNIVORA: Herpestidae</b>										
Banded mongoose <i>Mungos mungo</i>	Neonate and Juvenile, 25–53 d	Capture	Tonal	338	Single (C)	5091 (3604–7331)	3604–7331	Descending/ Rapid inflections	No evidence	Müller and Manser, 2008
<b>CARNIVORA: Otariidae</b>										
Northern fur seal <i>Callorhinus ursinus</i>	Neonate, 0–28 d	Contact	Tonal	No data	Single (P)	No data	No data	No data	No data	Insley, 1992
	Adult female	Contact	Tonal, mixed	No data	Single (C)	No data	No data	No data	DC	Insley, 1992
Subantarctic fur seal <i>Arctocephalus tropicalis</i>	Neonate, <7 d	Isolation (NS)	Tonal	820	Single (C)	608	940	Chevron	No evidence	Charrier et al., 2002
	Adult female	Isolation (NS)	Tonal	No data	Single (C)	No data	No data	Chevron	No evidence	Charrier et al., 2003
South American fur seal <i>Arctocephalus australis</i>	Neonate, 8–28 d	Isolation (NS)	Mixed, tonal or BB	600	T: Single (C) BB: (C, P)	1030–1470	(1364–4143)	Chevron	DC	Phillips and Stirling, 2000
	Adult female	Isolation (NS)	Mixed, tonal or BB	1057	Single (C)	728–944	(871–2721)	Chevron	DC	Phillips and Stirling, 2000
<b>CARNIVORA: Phocidae</b>										
Weddell seal <i>Leptonychotes weddellii</i>	Neonate, 3–60 d	Contact	Tonal	350	Single (C)	305 <sup>a</sup>	No data	Chevron	No evidence	Collins et al., 2006, 2011
	Neonate, 3–60 d	Isolation (NS)	Tonal	600	Single (C)	335 <sup>a</sup>	No data	Chevron	No evidence	Collins et al., 2006, 2011
Northern elephant seal <i>Mirounga angustirostris</i>	Neonate, 0–28 d	Contact	Tonal, mixed	No data	Single (C)	No data	No data	Flat/Chevron	SH, DC	Insley, 1992
	Adult female	Contact	Tonal, mixed	No data	Single (C)	No data	No data	Flat/Chevron	SH, DC	Insley, 1992

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>CARNIVORA: Odobenidae</b>										
Walrus <i>Odobenus rosmarinus</i>	Neonate, 0–28 d Adult female	Contact	Tonal	139	Single (C)	400	420	Chevron	No evidence	Charrier et al., 2010
		Contact	Tonal	322	Single (C)	118	168	Chevron	No evidence	Charrier et al., 2010
<b>PROBOSCIDEA: Elephantidae</b>										
African elephant <i>Loxodonta africana</i>	Juvenile, 1–24 mo.	Mixed: suckling, separated, other distress	Mixed (primarily)	1340	Single (C)	405	(536–1378)	Chevron	Common: DC, SH, FJ	Stoeger et al., 2011
<b>SIRENIA:</b> <b>Trichechidae</b> Amazonian manatee	Juvenile, <135 cm	Isolation (E)	Tonal	235	Single (C, P)	3900 (3300–4900)	(5000–10000) <sup>a</sup>	Chevron/Flat	No evidence	Sousa-Lima et al., 2002
<i>Trichechus inunguis</i>	Adult female	Isolation (E)	Tonal	242	Single (C, P)	4800 (4200–5900)	(5000–10000) <sup>a</sup>	Chevron/Flat	No evidence	Sousa-Lima et al., 2002
	Unspecified age class (juvenile or adult)	Isolation (E)	BB	No data	No data	No data	No data	No data	No data	Sousa-Lima et al., 2002
<b>RODENTIA: Muridae</b>										
Domestic mice <i>Mus musculus</i>	Neonate, 7–8 d	Isolation (E)	Tonal	980	Single or bouts (C)	42000–90000	No data	No data	FJ	Branchi et al. 1998, 2004
<b>RODENTIA: Cricetidae</b>										
Short-tailed field vole <i>Microtus agrestis</i>	Neonate, 1–14 d Neonate, 1–8 d	Isolation (E)	Tonal	30–50	Single (C)	35000–50000	No data	Flat (primarily)	FJ	Mandelli and Sales, 2004
		Isolation (E)	Short BB	No data	Single (C)	NA	No data	NA	DC	
<b>RODENTIA: Sciuridae</b>										
Yellow-bellied marmot <i>Marmota flaviventris</i>	Neonate, <7 d post- emergence	Capture	Tonal, mixed	460	Single (C)	880–2260	No data	Chevron	DC, FJ, SH	Blumstein et al., 2008

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>RODENTIA: Scuridae</b>										
Richardson's ground squirrel <i>Spermophilus richardsonii</i>	Neonate, <7 d post- emergence	Capture	Tonal, mixed	187	Bouts (C)	4776 (4740–5332)	(5190–15104)	Chevron	SH, DC, FJ	See Table B1
<b>RODENTIA: Caviidae</b>										
Guinea pig <i>Cavia porcellus</i>	Neonate, 8 d	Isolation (E)	Tonal	200	Single (C)	2607	4352	Ascending	No evidence	Monticelli et al., 2004
Capybara <i>Hydrochoerus hydrochaeris</i>	Juvenile, < 20 kg Juvenile and Adult	Isolation (NS) Capture	Tonal Tonal	100 370	Single (C) Single (C)	2216–3353 597–2037	2868 1612	Ascending Flat/Rapid inflections	No evidence No evidence	Barros et al., 2011 Barros et al., 2011
<b>PRIMATES: Cheirogaleidae</b>										
Gray mouse lemur <i>Microcebus murinus</i>	Neonate, 11–31 d	Isolation (E)	Tonal	53	Single (C)	19700 (19300–20300)	22640	Ascending	No evidence	Scheumann et al., 2007
<b>PRIMATES: Galagidae</b>										
<i>Galago</i> spp.	Neonate, 0–2 mo.	Isolation (NS)	Short BB click	1.5–30	Single (C)	NA	No data	NA	NA	Zimmermann, 1990
<b>PRIMATES: Cebidae</b>										
Squirrel monkey <i>Saimiri sciureus</i>	Neonate, 7 d	Isolation (E)	1. Tonal	218–426	Single (C)	(7000–12000) <sup>a</sup>	No data	Chevron, ascending	No data	Lieblch et al., 1980; Newman, 2007
			2. Mixed, BB	No data	No data	No data	No data	No data	No data	
<b>PRIMATES: Cercopitheidae</b>										
Rhesus macaques <i>Macaca mulatta</i>	Neonate, 0.5–28 d	Isolation (E)	1. Tonal mixed	No data	Single (C)	No data	No data	No data	DC, SH, FJ	Jovanovic et al., 2000
			2. BB noise	No data	Single (P)	NA	No data	No data	NA	
<b>PRIMATES: Hominidae</b>										
Human <i>Homo sapiens</i>	Neonate, <30 d	Manipulation	Tonal, mixed or noisy	814	Single (C)	415	(1384–4881)	Chevron (58%), some flat or other	DC, SH	Baeck and Souza, 2001; Boero et al., 1998; Lieberman et al., 1971
	Neonate, <30 d	Pain (heel jab)	Tonal, mixed or noisy	908	Single (C)	458	(1620–4966)	Chevron (70%), some flat or other	DC, SH	Baeck and Souza, 2001; Boero et al., 1998; Lieberman et al., 1971;

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, F1)	Reference
<b>CHIROPTERA: Phyllostomidae<sup>b</sup></b>										
Seba's short-tailed bat <i>Carollia perspicillata</i>	Neonate, 0–21 d	Isolation (E)	1. Tonal 2. Tonal	7.7 35	Bouts (C) Bouts (P)	18000–44000 18000–44000	18000–44000 <sup>a</sup> 18000–44000 <sup>a</sup>	Descending U-shaped then descends	No evidence No evidence	Gould, 1975; Gould et al., 1973; Sterbing, 2002
Lesser long-nosed bat <i>Leptonycteris saborni</i>	Neonate, 0–21 d	Isolation (E)	Tonal	20 (minim.)	No data (C, P)	No data	No data	Flat/ Descending	No evidence	Gould, 1975; Gould et al., 1973;
Greater spear-nosed bat <i>Phyllostomus hastatus</i>	Neonate, 0–21 d	Isolation (E)	Tonal	No data	No data (P)	No data	No data	Flat/ Descending	No evidence	Gould, 1975; Gould et al., 1973;
California leaf-nosed bat <i>Macrotus californicus</i>	Neonate, 0–21 d	Isolation (E)	Tonal	No data	No data (P)	No data	No data	Descending	No evidence	Gould, 1975; Gould et al., 1973;
Common vampire bat <i>Desmodus rotundus</i>	Adult male/female	Isolation (E)	Tonal	9.1	No data (C)	19300–36200	25400	Descending	No evidence	Carter et al., 2012
White-winged vampire bat <i>Diaemus youngi</i>	Adult male/female	Isolation (E)	Tonal	18.6	No data (P)	17300–25700	22100	Descending	No evidence	Carter et al., 2012
Hairy-legged vampire bat <i>Diphylla ecaudata</i>	Adult male/female	Isolation (E)	Tonal	11.5	No data (C)	12600–20800	16400	Descending	No evidence	Carter et al., 2012
Jamaican fruit bat <i>Artibeus jamaicensis</i>	Adult male/female	Capture	Tonal	84–139	Bouts (C)	1000	(1000–14000)	Chevron	No evidence	August, 1985
<b>CHIROPTERA: Phyllostomidae<sup>b</sup></b>										
Greater spear-nosed bat <i>Phyllostomus hastatus</i>	Adult male/female	Capture	Tonal	83–93	Bouts (C)	1000	(6000–15000)	Chevron	No evidence	August, 1985
Common vampire bat <i>Desmodus rotundus</i>	Adult male/female	Capture	BB	50–100 <sup>a</sup>	No data	NA	No data	NA	NA	Carter et al., 2012
White-winged vampire bat <i>Diaemus youngi</i>	Adult male/female	Capture	BB	50–100 <sup>a</sup>	No data	NA	No data	NA	NA	Carter et al., 2012
<b>CHIROPTERA: Phyllostomidae<sup>b</sup></b>										
Hairy-legged vampire bat <i>Diphylla ecaudata</i>	Adult male/female	Capture	BB	No data	No data	NA	No data	NA	NA	Carter et al., 2012
<b>CHIROPTERA: Vespertilionidae<sup>b</sup></b>										
Pallid bat <i>Antrozous pallidus</i>	Neonate, 0–21 d	Isolation (E)	Tonal	No data	No data (C)	No data	No data	Flat/ Descending	No evidence	Gould, 1975; Gould et al., 1973;

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>CHIROPTERA: Vespertilionidae<sup>b</sup></b>										
Big brown bat <i>Eptesicus fuscus</i>	Neonate, 0–21 d	Isolation (E)	Tonal	20–60	Bouts (C)	No data	No data	Flat/ Descending	No evidence	Gould, 1975; Gould et al., 1973;
Little brown bat <i>Myotis lucifugus</i>	Neonate, 0–21 d	Isolation (E)	Tonal	21	Bouts (C, P)	22000–39000	No data	Descending	No evidence	Gould, 1975; Gould et al., 1973; Barclay et al., 1979
Eastern red bat <i>Lasiurus borealis</i>	Neonate, age not specified	Isolation (NS)	Tonal	1.2	Single (C)	No data	71700	Descending	No evidence	Schmidt-French et al., 2006
	Neonate, age not specified	Capture	1. BB	2.8	Single (C)	No data	49000	NA	NA	Schmidt-French et al., 2006
	Adult female	Isolation (NS)	2. BB w/ tonal trill	No data	Single (P)	No data	No data	Repeated U-shaped	No evidence	
			Tonal	2.6	Single (C)	No data	16300	Descending	No evidence	Schmidt-French et al., 2006
Nathusius' pipistrelle <i>Pipistrellus nathusii</i>	Adult male/female	Capture	Tonal	4.4	Single, Bouts (C)	22200	22200 <sup>a</sup>	Descending elements	No evidence	Russ et al., 2004
	Adult male/female	Capture	Tonal	2.4	Single, Bouts (C)	22200	22200 <sup>a</sup>	Descending elements	No evidence	Russ et al., 2004
Soprano pipistrelle <i>Pipistrellus pygmaeus</i>	Adult male/female	Capture	Tonal	2.1	Single, Bouts (C)	28200	28200 <sup>a</sup>	Descending elements	No evidence	Russ et al., 2004
<b>CHIROPTERA: Molossidae<sup>b</sup></b>										
Black mastiff bat <i>Molossus ater</i>	Neonate, 0–21 d	Isolation (E)	Tonal	No data	No data	No data	No data	Flat	No evidence	Gould, 1975; Gould et al., 1973;
<b>CHIROPTERA: Rhinolophidae<sup>b</sup></b>										
Greater horse-shoe bat <i>Rhinolophus ferrumequinum</i>	Neonate, <7 d	Isolation (NS)	Tonal	No data	Single (C)	No data	No data	Chevron	No evidence	Liu et al., 2007
<b>CHIROPTERA: Pteropodidae</b>										
Black flying fox <i>Pteropus alecto</i>	Neonate, <21 d	Isolation (NS)	1. Tonal	3000–4500	Single (C)	5000–6000	5000–6000 <sup>a</sup>	Chevron	DC	Van Parijs and Corkeron, 2002
			2. Tonal/BB	5500–7100	Single (P)	2500–4000	2500–4000 <sup>a</sup>	Chevron/Flat	DC	
			3. BB	1000–2500	Single (P)	NA	(6000–8000)	NA	NA	

Continued Table A1

Class ORDER: Family ( <i>Genus species</i> )	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>CHIROPTERA: Pteropodidae</b>										
Greater short-nosed fruit bat <i>Cynopterus sphinx</i>	Adult male/female	Capture	Tonal	2260–3360	Bouts (P)	No data	(5000–10000) <sup>a</sup>	Chevron	No evidence	Ganesh et al., 2010
<b>DIPROTODONTIA: Macropodidae</b>										
Eastern grey kangaroo <i>Macropus giganteus</i>	Juvenile, (in pouch or at foot) 165–295 d	Isolation (E)	BB	354 (pouch), 250 (foot)	Single (P)	NA	(2000–5000)	NA	NA	Baker and Croft, 1993
Red kangaroo <i>Macropus rufus</i>	Juvenile, (in pouch or at foot) 150–230 d	Isolation (E)	BB	276 (pouch), 170 (foot)	Single (P)	NA	(2500–6500)	NA	NA	Baker and Croft, 1993
<b>DASYUROMORPHIA: Dasyuridae</b>										
Northern quoll <i>Dasyurus hallucatus</i>	Juvenile, (in pouch) 35–65 d	Isolation (E)	No data	100–200	Single (No data)	No data	(8000–11000)	No data	No data	Aitkin et al., 1994, 1996
<b>Class Aves</b>										
<b>PASSEIFORMES: Sturnidae</b>										
European starling <i>Sturnus vulgaris</i>	Neonate, 15–17 d	Capture	Tonal, mixed	439	Single (C)	1253–1604	No data	Flat/Rapid inflections	No evidence	Chaiken, 1992
<b>GALLIFORMES: Phasianidae</b>										
Domestic chicken <i>Gallus gallus domesticus</i>	Neonate, 6–7 d Neonate, 6–7 d	Contact Isolation (E)	Tonal Tonal	23–93 100–250	Bouts (C) Bouts (C)	2500–5500 2000–6500	No data No data	Ascending Descending	No evidence No evidence	Marx et al., 2001 Marx et al., 2001
<b>GRUIFORMES: Odontophoridae</b>										
Northern bobwhite quail <i>Colinus virginianus</i>	Neonate, 1 d	Isolation (E)	Tonal	135	Single (C)	3700 (max)	No data	Chevron, descending, ascending	No evidence	Baker and Bailey, 1987
<b>Class Reptilia</b>										
<b>CROCODYLIA: Crocodylidae</b>										
Nile crocodile <i>Crocodylus niloticus</i>	Neonate, 7–14 d Neonate, 7–14 d	Contact Capture	Tonal 1. Tonal 2. BB (hiss)	195 184 900 <sup>a</sup>	No data Single (P) Single (C)	211–506 253–733 NA	912 3564 No data	Descending, chevron Descending, chevron NA	No data No evidence NA	Vergne et al., 2007, 2009 Vergne et al., 2007, 2009 NA

Continued Table A1

Class	Family	Age	Context	Call structure	Call duration (ms)	Timing: between (within)	F0 (Hz): mean and/or range (min-max)	Dominant frequency (Hz)	Frequency modulation pattern	NLP (DC, SH, FJ)	Reference
<b>CROCODYLIA: Alligatoridae</b>											
	Black caiman	Neonate, 10–30 d	Contact	Tonal	80	Single (C)	144–292	EQ: 540	Descending	No evidence	Vergne et al., 2011
	<i>Melanosuchus niger</i>	Neonate, 10–30 d	Capture	Tonal	100	Single (C)	133–418	EQ: 988	Descending	No evidence	Vergne et al., 2011
<i>No parental care below</i>											
<b>Class Amphibia</b>											
<b>ANURA: Ceratophryidae</b>											
	Argentine horned frog	Neonate, 72 hr.	Physical	Tonal	38	Single (P)	No data	2900	Flat	No data	Natale et al., 2011
	<i>Ceratophrys ornata</i>	post-hatching	contact								
<b>Class Actinopterygii (ray-finned fishes)</b>											
<b>SILURIFORMES: Callichthyidae</b>											
	Armoured catfish	Juvenile, <4 mo.	Capture	No data	13.6	Single (C)	No data	4082	No data	No data	Pruzsinszky and Ladich, 1998
	<i>Corydoras paleatus</i>	Adult	Capture	No data	male/fem.: 19.9/15.7	Single (C)	No data	male/fem.: 1465/1235	No data	No data	Pruzsinszky and Ladich, 1998

**Explanatory note:** "Isolation" includes natural separation (NS) and experimental isolation (E). Acoustic traits include the structure (tonal, mixed or broadband (BB)), call duration, between-call timing (single or bouts) and within-call timing (continuous (C) or pulsed (P)), fundamental frequency (F0), dominant frequency, frequency modulation pattern, and nonlinear phenomenon (NLP, including DC = deterministic chaos, SH = subharmonics, FJ = frequency jumps). "No data": no relevant data or illustrations available in source. "No evidence": no indications of NLP although relevant data or figures are included in the source. "NA": not applicable. When not specified in a paper, frequency modulation patterns and the presence of nonlinear phenomena were based on data or spectrograms presented in the source.

<sup>a</sup> Specific values for these traits were not identified in the source. Estimated values were instead based on other available data included in the study or estimated visually from the spectrograms.

<sup>b</sup> For bats other than the Pteropodidae, "continuous" or "pulsed" calls refer to single-note and double-note calls, respectively.

**Age categories.** Animals less than one month in age were considered neonates. The term "juvenile" was applied to animals beyond one month in age that were sexually immature, still in a group with their mother and probably reliant on maternal care. The upper age range of "juvenile" extends much further for groups such as primates and dolphins that mature slowly.

**Dominant frequency.** This column includes reported traits that vary from (i) the frequency of maximum amplitude as identified by a spectral peak or dominant harmonic; (ii) a range of frequencies for a single dominant harmonic, usually the F0, shown without parentheses, e.g., min-max; or (iii) a range of spectral peaks, formants or dominant harmonics, shown in parentheses. EQ: the 50<sup>th</sup> percentile energy quartile was also shown when available (the frequency at which 50% of the energy of a call falls above and below).

**Frequency modulation pattern.** *Chevron:* F0 (or peak frequency or other harmonics if there is no F0) rises and then falls so that the maximum F0 usually falls within the middle half of the call duration. *Ascending:* F0 rises throughout the call. *Descending:* F0 declines throughout the call; *Flat:* F0 does not vary by more than 10% of the mean F0 during the call. *U-shaped:* F0 falls and then rises. A comma (e.g., Chevron, descending) indicates that different patterns were observed for different calls. A slash (e.g., Chevron/descending) indicates that the pattern is intermediate between two forms.

**Appendix: Supplementary Acoustic data**

The following acoustic traits were scored from calls for fallow deer, sika deer, red deer, bighorn sheep and Richardson's ground squirrels (Table B1) following methods described in Lingle et al., 2007a and Teichroeb et al., 2012: between and within call timing; call duration; mean, maximum and minimum F0; the three harmonics of dominant amplitude; the frequency modulation pattern; presence of deterministic chaos, subharmonics or frequency jumps.

**Table B1** Calls other than those obtained from published sources that were included in the data presented in Tables 1 and A1.

Species	Age and type of call	Number of Individuals	Number of calls
Fallow deer	Neonate, capture call	5	25
Sika deer	Neonate, capture call	1	3
Red deer	Juvenile, isolation call	4	10
Bighorn sheep	Neonate, capture call	3	12
Richardson's ground squirrel	Neonate, capture call	3	13