



Listening carefully: increased perceptual acuity for species discrimination in multispecies signalling assemblages



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ARTICLE INFO

Article history:

Received 1 August 2014

Initial acceptance 23 September 2014

Final acceptance 11 November 2014

Published online

MS. number: 14-00625R

Keywords:

acoustic assemblages

acoustic communication

acoustic communication hypothesis

bats

echolocation

functional extension

habituation–dishabituation

receivers' perception acuity

Rhinolophus

species discrimination

Communication is a fundamental component of evolutionary change because of its role in mate choice and sexual selection. Acoustic signals are a vital element of animal communication and sympatric species may use private frequency bands to facilitate intraspecific communication and identification of conspecifics (acoustic communication hypothesis, ACH). If so, animals should show increasing rates of misclassification with increasing overlap in frequency between their own calls and those used by sympatric heterospecifics. We tested this on the echolocation of the horseshoe bat, *Rhinolophus capensis*, using a classical habituation–dishabituation experiment in which we exposed *R. capensis* from two phonetic populations to echolocation calls of sympatric and allopatric horseshoe bat species (*Rhinolophus clivosus* and *Rhinolophus damarensis*) and different phonetic populations of *R. capensis*. As predicted by the ACH, *R. capensis* from both test populations were able to discriminate between their own calls and calls of the respective sympatric horseshoe bat species. However, only bats from one test population were able to discriminate between calls of allopatric heterospecifics and their own population when both were using the same frequency. The local acoustic signalling assemblages (ensemble of signals from sympatric conspecifics and heterospecifics) of the two populations differed in complexity as a result of contact with other phonetic populations and sympatric heterospecifics. We therefore propose that a hierarchy of discrimination ability has evolved within the same species. Frequency alone may be sufficient to assess species membership in relatively simple acoustic assemblages but the ability to use additional acoustic cues may have evolved in more complex acoustic assemblages to circumvent misidentifications as a result of the use of overlapping signals. When the acoustic signal design is under strong constraints as a result of dual functions and the available acoustic space is limited because of co-occurring species, species discrimination is mediated through improved sensory acuity in the receiver.

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Communication plays a crucial role in almost all aspects of an animal's life (e.g. Maynard Smith & Harper, 2003) and is especially important for species discrimination (Bradbury & Vehrencamp, 2011; Ryan & Rand, 1993). It transmits information within a species as well as across species and may have evolved as a product of species coexistence (Li et al., 2013). Discriminating species is important in interactions with heterospecifics allowing identification of competitors, predators and prey, whereas the recognition of conspecifics is a prerequisite for any species-specific interactions, especially for mate choice (Jones, 1997; Sandoval, Méndez, & Mennill, 2013; Slabbekoorn & Smith, 2002; Wilkins, Seddon, & Saffran, 2013). Understanding how communication signals

originate and are modified over evolutionary time is therefore crucial to our understanding of the processes that generate biodiversity (Mendelson & Shaw, 2012). It is likely that communication systems evolved from systems used for other purposes (Monteiro & Podlaha, 2009; Tinbergen, 1952), such as the function of feathers first used for insulation being extended so that they also function as visual signals, for example in courtship displays (Cowen, 2005). Particularly, knowledge of processes involved in the evolution of dual functions for a single trait can provide insight into how phenotypic diversity in both form and function is generated from existing variation.

Echolocation may provide us with an opportunity to investigate such functional extension of a trait. Echolocation is primarily used for orientation and food acquisition in echolocating bats, birds and whales (Brinkløv, Fenton, & Ratcliffe, 2013; Schnitzler, Moss, & Denzinger, 2003; Thomas, Moss, & Vater, 2004) but there is increasing evidence that it also functions as a means of

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communication (Gregg, Dudzinski, & Smith, 2007; Jones & Siemers, 2010). In the context of species discrimination, communication cues have to be unambiguous and represent a reliable badge for the species. Such species-specific cues are present in the vocalizations of many animal groups including insects, anurans, birds and mammals (primates: Seyfarth, Cheney, & Marler, 1980; anurans: Duellman & Pyles, 1983; birds: Catchpole & Slater, 2008; insects: Pennetier, Warren, Dabiré, Russell, & Gibson, 2010). Vocalizations are often a crucial signal in mate choice (Anderson, Ambrose, Bearder, Dixon, & Pullen, 2000; Braune, Schmidt, & Zimmermann, 2008; Charlton, Huang, & Swaisgood, 2009; Vannoni & Mcelligott, 2007) as they can provide information about the sender which is used by the receiver to evaluate the mate's intention, compatibility and quality. The voice of mammals, for example, is often an honest cue which allows an individual to assess the body size or mass of the sender (Fitch, 2006; Liebermann & Blumstein, 1991). Among echolocating mammals bats are ideal candidates for studies on echolocation in the context of communication because most species form groups with complex social structures (Kulzer, 2005) in which many interactions are managed by acoustic signals (Altringham & Fenton, 2003; Fenton, 1985). The acoustic structure of their echolocation calls has a complex frequency–time contour and there are many different types of calls (Maltby, Jones, & Jones, 2010) providing sufficient variation to encode multiple cues. Furthermore, echolocation calls contain diagnostic information about the sender which can be useful for others and, as a frequently available signal, echolocation transmits information free of additional costs to a receiver (Dechmann, Wikelski, Noordwijk, Voigt, & Voigt-Heucke, 2013). In echolocating bats, the relationship between echolocation call frequency and body size is well established (Jacobs, Barclay, & Walker, 2007; Jones, 1999), and echolocation calls often carry species-specific signatures, individual signatures, population-specific signatures and sex-specific signatures (Jones & Siemers, 2010).

Several recent playback studies have provided evidence that conspecific bats are able to extract information encoded in the echolocation calls of other bats such as species membership, familiarity and sex (Dorado Correa, Goerlitz, & Siemers, 2013; Knörnschild, Jung, Nagy, Metz, & Kalko, 2012; Schuchmann, Puechmaile, & Siemers, 2012; Voigt-Heucke, Taborsky, & Dechmann, 2010) and have recently revealed a role in mate choice (Puechmaile et al., 2014). However, because echolocation has evolved primarily for orientation and food acquisition (Schnitzler et al., 2003) species assemblages that are composed of ecologically similar bat species, and which therefore have similar echolocation call structures (Denzinger & Schnitzler, 2013), should partition the acoustic characteristics of their echolocation calls so that the calls retain their species specificity (Duellman & Pyles, 1983; Heller & von Helversen, 1989). The concept of acoustic divergence of signals for species discrimination in multispecies assemblages to avoid misidentification as a result of the use of confusingly similar calls (Amézquita, Flechas, Lima, Gasser, & Hödl, 2011; Tobias, Planqué, Cram, & Seddon, 2014) is well established in animal communication (Grant & Grant, 2010; West-Eberhard, 1983). This idea was first advanced by Duellman and Pyles (1983) for anurans and Heller and von Helversen (1989) for bats and later named the acoustic communication hypothesis (ACH, Jacobs et al., 2007) which is similar to the spectral partitioning hypothesis coined by Amézquita et al. (2011). Both the ACH and the spectral partitioning hypothesis propose that sympatric animal species each uses a 'private frequency channel' to facilitate intraspecific communication and identification of conspecifics (Heller & von Helversen, 1989). This is supported by the divergence in the echolocation frequency of some bat species possibly as a consequence of the presence of other species (Heller & von Helversen,

1989; Jacobs et al., 2007; Kingston, Jones, Zubaid, & Kunz, 2000; Kingston & Rossiter, 2004; Russo et al., 2007). This acoustic divergence among signallers has also been found in morphologically cryptic species living in sympatry (Guillén, Juste, & Ibañez, 2000; Jones & Siemers, 2010; Jones & Van Parijs, 1993; Kingston et al., 2001; Thabab et al., 2006). However, a test of the ACH would also have to incorporate an investigation of the perception and discrimination ability of the receiver.

In this study we used the horseshoe bat, *Rhinolophus capensis*, to investigate the role of echolocation in communication in the context of the ACH. We chose a classical habituation–dishabituation experiment (Eimas, Siqueland, Jusczyk, & Vigorito, 1971) in which we exposed *R. capensis* to recorded calls of two sympatric horseshoe bat species (*Rhinolophus clivosus* and *Rhinolophus damarensis*) and different phonetic populations of *R. capensis*. In these assemblages we have populations of the same species using different echolocation frequencies as well as different hetero-specifics using overlapping frequencies. This natural system provides an excellent opportunity to test whether *R. capensis* discriminates between different species and populations on the basis of their echolocation calls. If acoustic divergence in the echolocation frequencies of *R. capensis* is a result of selection favouring the use of private frequency bands as proposed by the ACH, *R. capensis* should show increasing rates of misclassification with increasing overlap between its own calls and those used by sympatric heterospecifics. This concomitantly means that individuals of *R. capensis* from the different phonetic populations should have difficulty recognizing each other as belonging to the same species if they use calls of dissimilar frequency. In addition this system allows us to test whether peak frequency is the only parameter used by bats to discriminate between species.

METHODS

Study Animal

Rhinolophus capensis (Cape horseshoe bat) has a wide distribution along the coastal belt of South Africa's Cape (Monadjem, Taylor, Cotterill, & Schoeman, 2010). This species emits resting frequency echolocation calls (RF, calls emitted by rhinolophid bats when stationary and hunting from a perch; Neuweiler et al., 1987; Schnitzler, 1968) that vary by more than 10 kHz across its distribution range (Fig. 1; Odendaal, Jacobs, & Bishop, 2014). The lowest resting peak frequency, 75 kHz, is found in the northwestern part of its distribution, and the highest, 86 kHz, in the southeast. These phonetic populations co-occur with various other horseshoe bat species, namely *R. damarensis* (Jacobs et al., 2013) in the northwest and *R. clivosus* in the southern and eastern part (Jacobs et al., 2007). When both juveniles and adults are considered, *R. clivosus* calls at 87–92 kHz (Jacobs, n.d.) and *R. damarensis* at 79–87 kHz (Jacobs et al., 2013). In both cases *R. capensis* populations echolocate on average 2–9 kHz lower than the respective sympatric hetero-specific. This natural system provides an excellent opportunity to test the ACH.

Study Sites

The experiments were done at two sites in South Africa: De Hoop Nature Reserve on the southern coast of South Africa (March 2012 and October 2012) which represents a geographically central population with RFs at 85 kHz and a second more remote population at the Orange River near Lekkering in the extreme north-western corner of South Africa on the border with Namibia (November 2012). The latter population uses considerably lower RFs of 75 kHz.

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