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The snake hiss: potential acoustic mimicry in a viper–colubrid complex

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Examples of acoustic Batesian mimicry are scarce, in contrast to visual mimicry. Here we describe a potential case of acoustic mimicry of a venomous viper model by harmless viperine snakes (colubrid). Viperine snakes resemble vipers in size, shape, colour, pattern, and anti-predatory behaviours, including head flattening, false strikes, and hissing. We sought to investigate whether hissing evolved as part of, or separately to, the viper mimic syndrome. To do this, we recorded and analysed the hissing sounds of several individual asp vipers, viperine snakes, and grass snakes (a close relative of viperine snakes that hisses but does not mimic the asp viper). Frequencies consistently ranged from 40 to 12 000 Hz across species and individuals. All vipers (100%) and most viperine snakes (84%) produced inhalation hissing sounds, in comparison to only 25% of grass snakes. Inhalation hissing sounds lasted longer in vipers than in viperine snakes. The hissing-sound composition of grass snakes differed significantly from that of both asp vipers and viperine snakes; however, the hissing-sound composition between viperine snakes and asp vipers was not statistically distinguishable. Whilst grass snake hissing sounds were characterized by high frequencies (5000–10 000 Hz), both vipers and viperine snake hissing sounds were dominated by low frequencies (200–400 Hz). A principal component analysis revealed no overlap between grass snakes and vipers, but important overlaps between viperine snakes and vipers, and between viperine snakes and grass snakes. The likelihood that these overlaps respectively reflect natural selection for Batesian mimicry and phylogeny constraints is discussed. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 1107–1114.

ADDITIONAL KEYWORDS: Batesian mimicry – hissing – *Natrix* – *Vipera*.

INTRODUCTION

Batesian mimicry is a form of mimicry in which an innocuous species has evolved to imitate the warning signals of a potentially harmful species directed at one or several common predators (Bates, 1862). Warning signals may be (or combine) patterns, colours, shape, behaviour, odours, and sounds (Tooke, 1886; Rothschild, Moore & Brown, 1984; Joron & Mallet, 1998; Mallet & Joron, 1999; Golding & Edmunds, 2000). Although visual mimicry has been extensively researched, acoustic mimicry has received much less attention (Pickens, 1928; Brower & Brower, 1965; Rowe, Coss & Owings, 1986; Barber & Conner, 2007). Here we describe a potential case of warning sound mimicry by an innocuous colubrid snake of its venomous viper model.

The asp viper (*Vipera aspis*; Linnaeus, 1758) is a venomous European snake (Ursenbacher *et al*., 2006). Asp vipers usually display a black dorsal zigzag over a lighter background, although, in some populations, lined, melanistic, or concolour individuals may occur in various proportions (Mebert *et al*., 2011; Ducrest *et al*., 2014). The black dorsal zigzag is thought to act as a warning signal to potential predators (e.g. Wüster *et al*., 2004; Niskanen & Mappes, 2005; Valkonen *et al*., 2011a). There is also some experimental evidence that predators can recognize the triangular head shape, typical of vipers, as a warning signal (Valkonen, Nokelainen & Mappes, 2011b). When threatened, asp vipers will adopt a defensive posture (s-shape positioning of the body) and produce a loud hissing sound (Pough *et al*., 2004). Such anti-predatory displays are presumably used to deter potential predators (such as birds of prey and mammals; Greene, 1988; Pough *et al*., 2004) and, in

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*Corresponding author. E-mail: faubret@gmail.com the case of hissing, probably also to reveal the snake's presence to larger herbivorous animals and avoid trampling (Moon, 2001).

A colubrid species (the viperine snake, *Natrix maura*; Linnaeus, 1758) is a close copy of all sympatric vipers throughout its distribution range (Brodie & Brodie, 2004). *N. maura* resembles vipers in size, shape, colour, and pattern, and displays the entire anti-predatory behavioural panel seen in vipers. When threatened, *N. maura* will flatten its head in a triangular shape, strike repeatedly at the intruder (usually with its mouth closed), and produce a loud hiss (Werner & Frankenberg, 1982; Greene, 1988; Dell'Aglio *et al*., 2012). The viper mimicry observed in the viperine snake is fine-tuned to the point that inexperienced human observers will almost systematically mistake it for a genuine viper (F. Aubret, pers. observ.).

Deciphering the evolutionary origin of anti-predatory traits can be a challenging task, however. For instance, in viperine snakes, head triangulation has been interpreted as mimicry of sympatric vipers (Werner & Frankenberg, 1982; Werner, 1983) but will also make any snake appear more formidable (Young, Lalor & Solomon, 1999). Even more questionable is the evolutionary significance of acoustic signals such as hissing. The low information content in the hissing sounds produced by snakes suggests that these sounds are not suitable for intraspecific communication (i.e. hissing in snakes was described as being little more than forced ventilation; Young *et al*., 1999) and may have evolved primarily as an anti-predatory display (Young, 2003).

Not only snakes hiss. Several studies have investigated the evolutionary significance of hissing in other taxa. For instance, some Paridae birds (titmice and chickadee) have evolved a defensive reaction to predators in the form of a display that mimics a hissing snake (Pickens, 1928; Sibley, 1955). Ducks, crocodiles, badgers, skunks, cats, etc., also use hissing (Garrick & Lang, 1977; Lartviere & Messier, 1996; Theroux, 2006; Curtis, 2008; Medill, Renard & Larivière, 2011) but in no way do so in an attempt to impersonate a venomous snake. Along the same line of thought, the vast majority of snakes are capable of hissing (Greene, 1988; Young, 2003), but not all snakes mimic poisonous snakes. Nevertheless, it seems reasonable to think that a harmless snake will have more chance of deceiving a predator if it not only looks and behaves like a poisonous snake, but also sounds like one. Thus, one may wonder whether hissing has evolved as part of, or separately to, the panel of anti-predatory behaviour exhibited by snakes mimicking poisonous snakes (i.e. the viper mimic syndrome). In order to answer this question, we recorded and analysed the hissing sounds of sympatric asp vipers (*V. aspis*), viperine snakes (*N. maura*), and grass snakes (*Natrix natrix*), a close relative of *N. maura* that hisses when threatened but does not mimic the asp viper in coloration and patterns.

MATERIAL AND METHODS

ANIMAL AND SOUND COLLECTION

Viperine snakes ($N = 12$ females), grass snakes ($N = 12$; 11 females and one male) and asp vipers ($N = 10$; five females and five males) were caught along the banks of the Lez River and surrounding pasture and woodland in south-west Ariège (France) in May and June 2013. Snakes were captured by hand, placed in individual calico bags, and brought back to the laboratory (CNRS à Moulis). Testing was performed as follows. Snakes were left undisturbed and allowed to acclimate to the laboratory ambient temperature (25 °C) for at least 2 h before testing. Snakes were then individually placed in a translucid 60 cm × 40 cm × 40 cm plastic container with an open top. Several identical containers were used on days when more than one snake was tested. Containers were always cleaned with a solution of Virkon, washed with clean water, and dried before use. Two observers were in full view of the snake. In such an exposed position, all snakes readily adopted a defensive posture and started hissing at the observers.

Hissing sounds were recorded using a Sennheiser ME66/K6 Super-cardioid microphone (sensitivity 40 Hz to 20 kHz, ±2.5 dB) and MZW66PRO wind shield (Hanover, Germany) plugged into a Marantz Professional PMD620 solid-state recorder. The microphone was directed at the snake's head and moved gently from side to side approximately 10 cm in front of the snake's snout. The recording lasted no longer than 2 min for each individual, after which snakes were placed back in their calico bag and returned to their exact site of capture within 24 h.

The Audacity software was used to visualize, isolate, and export hissing sounds, as WAV files, into Matlab for numerical signal analysis. The Audacity software was also used to plot (as in Fig. 1) and manually extract exhalation and inhalation hissing durations for each individual of each species. Single factor ANOVAs were used to compare body mass and snout-vent length amongst species. Hissing durations were analysed using General Linear Models with (1) species, (2) snout-vent length, and (3) body mass as explanatory variables and the mean durations of inhalation and exhalation as response variables, for each individual. Wilcoxon matched pair tests were used to compare the duration of inhalation and exhalation hissing sounds within each species. Data were log-transformed before analysis.

SOUND ANALYSIS

Hissing is produced in snakes by using an exhalant airstream that can be characterized by its intensity and frequency. Acoustic signal analysis traditionally operates via spectral analysis, in which each frequency is first identified and then measured in intensity using fast Fourier transform (Cooley & Tukey, 1965). Because snake acoustic signals were nonstationary in the first and second orders (i.e. they changed in both intensity and variability through time), as well as extremely noisy, we followed the analysis procedure described by Max (1980) based on the Wiener–Khintchine theorem, in which the fast Fourier transform is calculated using a correlogram. This procedure yielded an acoustic spectrum for each hissing sound and each individual [three exhalation hissings per animal ($N = 69$ in total) for eight asp vipers, eight viperine snakes, and seven grass snakes). We analysed each spectrum by computing a scalogram using continuous Morlet wavelet transforms (Grossmann, Kronland-Martinet & Morlet, 1989; Arneodo, Bacry & Muzy, 1995). This technique allowed the identification of frequency components that are consistently present over the entire acoustic signal so that frequency confounding noise could be eliminated.

A total of ten frequency components were isolated using orthogonal wavelet analysis (Mallet & Joron, 1999). We then calculated a mean amplitude value for each frequency component [i.e. spectrum maximum graded on a normalized scale from 0 (no energy) to 100 (maximum value)] based on three exhalation hissing sounds extracted for each individual (see Fig. 2). For example, where an individual hissing sound yielded peak values of 25, 28, and 31 (out of a maximum of 100) for the 5513-Hz component of the acoustic signal, its average amplitude value for this frequency was reported as 28 (mean value). Extreme components 1 (frequencies located in the very-short-term range) and 10 (located in the very-long-term range) were discarded because of their lack of significance, as these components reflect signal noise and signal tendency, respectively (see the Shannon sampling theorem for details on the method; Jerri, 1977). Because spectrograms were normalized, amplitude values were directly comparable across individuals and species. These data were then used to run (1) a repeated measure ANOVA with species as factors and the average amplitude values for the successive frequencies components as the repeated measure and (2) a mean centred principal component analysis (PCA).

RESULTS

HISSING PATTERNS

Snake hissing was described as quadriphasic (Young, 2003): exhalation (hissing), pause (silence), inhalation (hissing), and breath-holding pause (silence). Because exhalation hissing was substantially louder than inhalation hissing, we focused on the former for the purpose of the current study (see Fig. 1 and Audio Clips S1–S3). Nevertheless, inhalation as well as exhalation hissing lengths (in seconds) were calculated for each individual of each species (on average $N = 10.5 \pm 5.1$ exhalations and $N = 6.5 \pm 3.3$ inhalations).

Grass snakes were larger than viperine snakes and asp vipers in body mass and snout-vent length (Table 1). There was no significant difference in exhalation hissing duration amongst species [General Linear Model (GLM); $P = 0.70$; Table 1] and no effect of body mass ($P = 0.99$) or snout-vent length ($P = 0.50$).

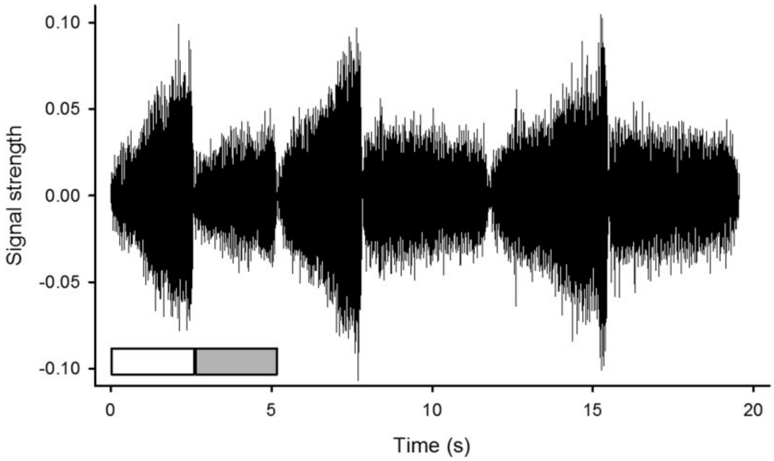

Figure 1. Hissing sounds recorded in an asp viper (*Vipera aspis*). Exhalation hissing (see example above the white bar; white bar indicates duration) is substantially louder but shorter on average than inhalation hissing (example above grey bar; grey bar indicates duration).

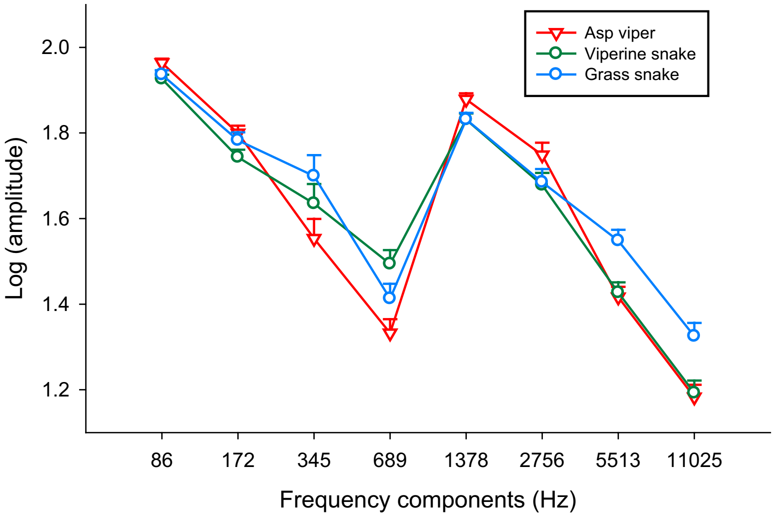

Figure 2. Mean amplitude values were calculated for eight frequency components of the sound spectrum of hissing sounds (three per individual; $N = 69$ in total) recorded in eight asp vipers (model), eight viperine snakes (mimic), and seven grass snakes (control – three; see the text for details). Log-transformed amplitude values were used to perform a repeated measures ANOVA with species as factors and the average amplitude values for the successive frequencies components as the repeated measure. Sound composition (i.e. energy distribution) significantly differed across species ($F_{2, 20} = 9.07$; $P < 0.0016$) and frequency components ($F_{7, 140} = 207.85$; $P < 0.0001$; interaction term $F_{14, 140} = 3.90$; $P < 0.0001$).

Table 1. Comparison of body size and hissing sound duration in asp viper, viperine snake and grass snake. Mean values and statistical results obtained with single factor ANOVAs and General Linear Models are given (see text for details on statistics)

	Asp viper ($N = 10$)	Viperine snake ($N = 12$)	Grass snake ($N = 12$)	F d.f.	P
Body mass (g)	60.55 ± 16.06	75.66 ± 21.51	275.32 ± 156.12	37.104; 2, 31	0.0001
Snout-vent length (cm)	45.00 ± 3.58	55.81 ± 9.36	82.21 ± 10.17	55.13; 2, 31	0.0001
Exhalation hissing (s)	2.16 ± 0.75	2.30 ± 0.68	2.25 ± 0.91	0.37; 2, 29	0.70
Inhalation hissing (s)	2.46 ± 0.93	1.60 ± 0.40	–	6.69; 1, 16	0.019

d.f., degrees of freedom.

Although all snakes tested produced exhalation hissing sounds, not all were observed to produce inhalation hissing sounds. All asp vipers produced inhalation sounds compared with 10 (84%) of 12 viperine snakes, but only three (25%) of 12 grass snakes (Pearson $\chi^2 = 16.10$; $P < 0.0032$). The duration of inhalation significantly differed between asp vipers and viperine snakes (grass snakes were excluded from the analysis as a result of the small sample size; GLM; $P < 0.019$). Inhalation hisses were, on average, longer than exhalation hisses in the asp viper (Wilcoxon matched pairs test; $P < 0.007$) but shorter than exhalation hisses in the viperine snake ($P < 0.009$).

SIGNAL ANALYSIS

Frequencies consistently ranged from 40 to 12 000 Hz across species and individuals (Table 2). Sound

Table 2. Component to frequency correspondence table (In order to compare hissing sound characteristics amongst snake species, ten frequency components were identified using orthogonal wavelet analysis. See the text for details on the method.)

Components	Frequency (Hz)
1	11 025
2	5 513
3	2 756
4	1 378
5	689
6	345
7	172
8	86

composition (i.e. energy distribution) significantly differed across species ($F_{2,20} = 9.07$; $P < 0.0016$) and frequency components ($F_{7,140} = 207.85$; $P < 0.0001$; interaction term $F_{14,140} = 3.90$; $P < 0.0001$; Fig. 2). Post-hoc analysis revealed that grass snakes significantly differed in sound composition from asp vipers and viperine snakes ($P < 0.0021$ and $P < 0.0078$ respectively; Tukey's HSD test). Asp vipers and viperine snakes were, however, statistically indistinguishable regarding sound composition ($P = 0.81$). Additionally, a mean centred multiple component analysis generated two main factors that explained 46.5% of the total variance (26.7% and 19.8% for factors 1 and 2, respectively; Fig. 3A). Factor 1 opposed component 7 (345 Hz; low range) and C5 (1378 Hz; middle range). Factor 2, on the other hand, was inversely proportional to both C2 and C3 (11 025 Hz and 5513 Hz, respectively; high range). Whilst grass snake hissing sounds were mostly characterized by high frequencies (5000–10 000 Hz; Fig. 3B), both asp viper and viperine snake hissing sounds were dominated by low frequencies (200–400 Hz).

DISCUSSION

The analysis of hissing sounds (i.e. duration, patterns, and frequency composition) in the asp viper (model), the viperine snake (alleged mimic), and the grass snake (control) confirmed that hissing in snakes contained little structure, and hence little potential information (Young *et al.*, 1999). Nevertheless, detailed signal analysis revealed subtle, but significant, differences amongst species. Only 25% of grass snakes produced inhalation hissing sounds compared with 100% of asp vipers and most viperine snakes (84%). Furthermore, inhalation hissing sounds were significantly longer in duration in asp vipers than in viperine snakes. The hissing-sound composition of grass snakes significantly differed from that of both asp vipers and viperine snakes. Viperine snake and asp viper hissing sounds, on the other hand, could not be statistically differentiated. Plotting individual snakes using a PCA revealed almost no overlap between grass snakes and asp vipers. However, there was an important overlap between viperine snakes and asp vipers on the one hand, and between viperine snakes and grass snakes on the other (see Fig. 3B). The broader distribution of viperine snake hissing characteristics may reflect both phylogeny constraints and natural selection. That is, grass snakes and viperine snakes are closely related species that diverged between 18 and 27 Mya (Guicking *et al.*, 2006a). Hence, the possibility that the hissing characteristics overlap between grass snakes and viperine snakes may reflect that phylogeny cannot be excluded. Consideration of hissing sounds of a grass snake sister species, the dice snake, (*Natrix tessellate*; divergence with *N. natrix* 13–22 Mya) may provide insights into this possibility. On the other hand, viperine snakes and asp vipers share a long biogeographical history. Both species evolved in the early Miocene within the Mediterranean basin, colonizing southern Europe back and forth in favour of cold and warm spells. There is also evidence that both species used common refuges during glaciation events (Ursenbacher *et al.*, 2006; Guicking *et al.*, 2006a). Hence, this model/mimic complex may have first evolved as early as 22 Mya. This ancient evolutionary history has provided the Batesian mimicry complex with many opportunities for reinforcement; that is, fine tuning of shape, colour, pattern, behaviour, and even hissing-sound characteristics in which both species were, or became, sympatric (Werner & Frankenberg, 1982; Brodie & Brodie, 2004; Wüster *et al.*, 2004).

When considering the evolution of various forms of mimicry it may be prudent to consider the threat form (visual predation, acoustic predation, accidental harm) faced by the possible mimic. Animals that may predate on or harm (i.e. accidental trampling of basking snakes) European snake species include birds such as falconidae, accipitridae, corvidae, and ardeidae, and mammals such as mustelidae, canidae, felidae, cervidae, and suidae, as well as domestic ungulates (Schwartzkopff, 1955; Heffner & Heffner, 1983, 1985; Calford, Wise & Pettigrew, 1985). Specialized snake predators, such as birds of prey, often rely on sight (movement detection) to detect ground-dwelling prey, such as snakes, and often attack by surprise, with speed and violence (Schwarzkopf & Shine, 1992; Niskanen & Mappes, 2005). Visual, rather than acoustic, warning signals would therefore presumably be more effective at deterring such predators. On the other hand, one may question the visual accuracy of cows and sheep when it comes to detecting small ground-dwelling animals. Detecting a motionless snake basking in the grass may occur by chance visually, whereas an attention-drawing display may be perceived by the grazing animal and act to alert and divert the animal to avoid injury. This highlights the potential importance of threat type (predation or accident) and the way in which harm is inflicted (surprise attack or accidental trampling) in the evolution of visual, acoustic, or a combination of visual and acoustic, Batesian mimicry.

In conclusion, whether snake predators (birds of prey and mammals) can discern species based on hissing-sound differences (i.e. the presence of inhalation hissing, or the relative duration of inhalation hissing compared with exhalation hissing) remains an open question. Nevertheless, the occurrence of hissing pattern differences between innocuous and harmful snake species renders two processes possible:

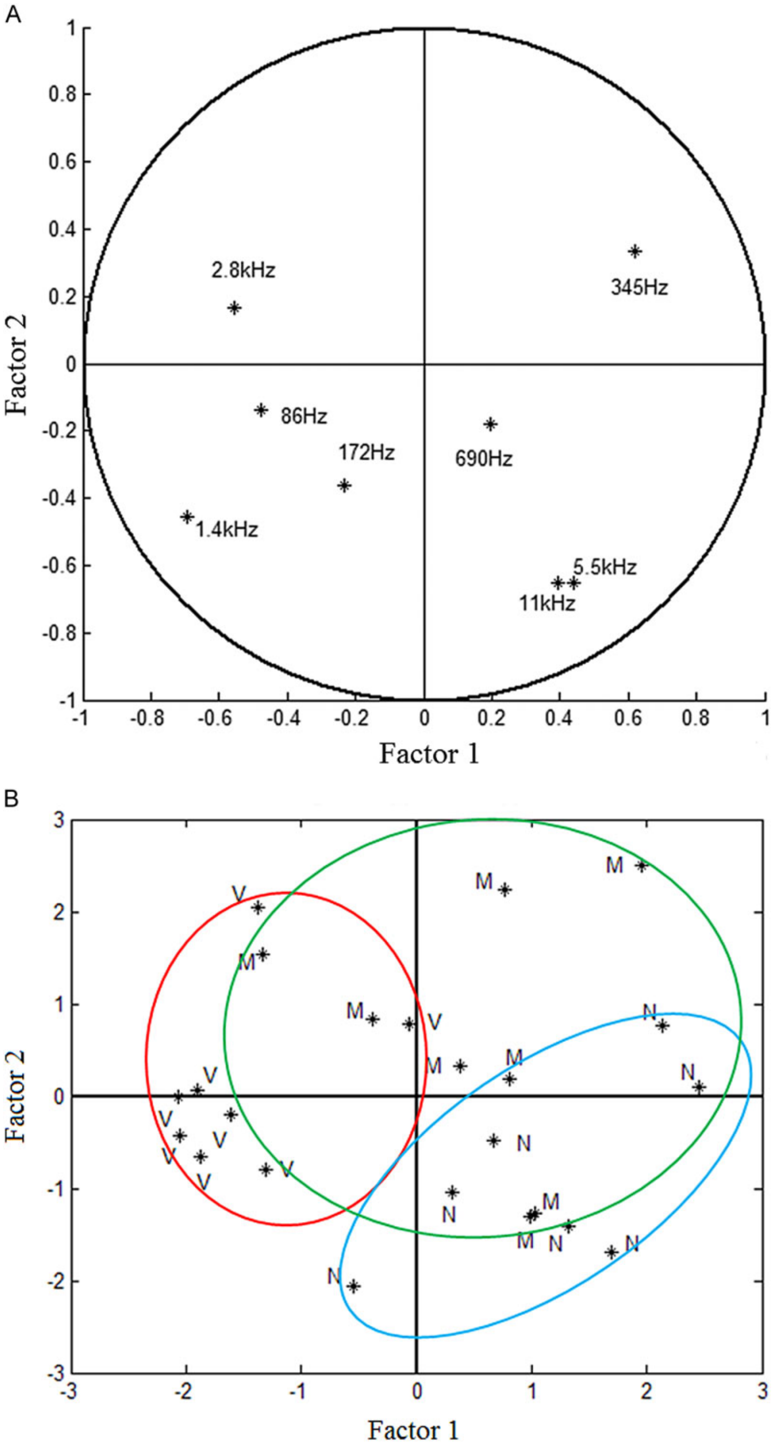

Figure 3. A mean centred Principal Component Analysis was performed using mean frequency components (i.e. spectrum maximum) of exhalation hissing sounds in eight asp vipers, eight viperine snakes, and seven grass snakes. A, two main factors explained 46.5% of the total variance (26.7% and 19.8% for factors 1 and 2 respectively). B, whilst grass snake hissing sounds are mostly characterized by high frequencies (5000–10 000 Hz), both asp viper and viperine snake hissing sounds are dominated by low frequencies (200–400 Hz). The broader distribution of viperine snake hissing characteristics may reflect both phylogeny constraints and natural selection (see the text).

(1) positive selection for closer mimics by predators that consistently avoid potentially harmful snakes (Smith, 1975, 1977; Pough, 1988); and (2) learning processes that occur in naïve predators to distinguish harmless copies from genuine vipers (Czaplicki, Borrebach & Wilcoxon, 1976; Goodale & Sneddon, 1977). Both of these processes may be tested experimentally and warrant further research. Future studies may also investigate the possibility of local accents in snake populations across species' latitudinal, longitudinal, or altitudinal distribution, as seen in human populations, and the potential matching of such accents between models and copies across their range. Finally, a possibility exists that under particular conditions, allopatric snake populations (for instance on islands where there are no vipers, such as Mallorca, Spain; Guicking *et al*., 2006b) may benefit from distant model/mimic complexes (Pfennig, Harcombe & Pfennig, 2001; Pfennig & Mullen, 2010). Provided that some predators regularly migrate between areas of viper–colubrid sympatry and areas of allopatry, selection might occur for hissing-sound patterns (as well as for other morphological and behavioural traits): Batesian copies of vipers may be selected for and evolve in areas where no vipers occur or have ever occurred. Future studies may also address this exciting possibility.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Audio Clip S1. Asp viper.
Audio Clip S2. Viperine water snake.
Audio Clip S3. Grass snake.