

Habitat-dependent variation in motion signal structure between allopatric populations of lizards



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Habitat characteristics influence the efficacy of animal communication, and population differences in signal structure due to habitat variation are well known for sound and colour signals. However, this variation in signal structure has not been reported for motion-based signals. Here we tested the motion-based signalling displays of two populations of an Australian agamid lizard, *Amphibolurus muricatus*, in the context of their respective habitats. We employed a novel approach that calculates the distribution of motion speeds of lizard signals and environmental noise independently, before computing the difference in these distributions to obtain a measure of signal–noise contrast. Our results revealed variation in signal structure between the two populations and support the hypothesis that this variation can be explained by differences in the signalling environment. Signals from both populations showed similar contrast values at their respective habitats, but differed significantly when considered in the habitats of the allopatric population. These results are consistent with the hypothesis that habitat structure affects signal efficacy and causes population differences in motion signalling behaviour as a consequence of adaptations to enhance efficacy.

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Animal signals are constrained by the environment in which they are produced and by the sensory systems of the receivers for which they are intended (Bradbury & Vehrencamp, 1998; Lythgoe, 1979). For example, habitat-specific transmission properties are particularly important to auditory signals (Cocroft & Rodriguez, 2005; Hunter & Krebs, 1979; Morton, 1975; Slabbekoorn & Peet, 2003), as signal energy might be reduced through absorption, or redirected through reflection and diffraction by the air, ground or vegetation (Morton, 1975). This means that structurally distinct habitats will affect signals differently, and not all signals will perform equally well at a given habitat. Population differences in signal structure due to habitat variation are known for several species that utilize acoustic (Morton, 1975; Potvin & Parris, 2012; Ryan, Cocroft, & Wilczynski, 1990), vibrational (Cocroft, Rodriguez, & Hunt, 2010; McNett & Cocroft, 2008) and colour-based communication (Fuller, 2002; Leal & Fleishman, 2004; Ng, Landeen, Logsdon, & Glor, 2013; Seehausen, Alphen & Witte F, 1997). However, to our knowledge, variation in signal structure between allopatric populations as a consequence of habitat variation has not been reported for motion-based signals.

In addition to structural features of a given habitat, irrelevant sensory stimulation within the environment serves as noise that interferes with the reliable detection of a signal (Alberts, 1992; Fleishman, 1992; Morton, 1975; van der Sluijs et al., 2011). The degree to which a signal is correctly identified by a receiver after being distorted during the transmission process or masked by environmental noise determines the efficacy of that signal (Bradbury & Vehrencamp, 1998; Endler, 1992). Consequently, effective communication requires signallers to produce signals not only suited to a given habitat but also for the prevailing conditions (Bernard & Remington, 1991; Endler, 1992; Fleishman, 1992; Peters, Clifford, & Evans, 2002). In many species, this is essential for territorial defence (Carpenter, 1967, 1978), mating interactions (Hebets & Uetz, 1999) and even predator defence (Hasson, 1991). To achieve effective communication, some animals customize the properties of their signals to enhance transmission and facilitate detection in noisy environments (Brumm & Slabbekoorn, 2005; Brumm, Voss, Köllmer, & Todt, 2004; Cynx, Lewis, Tavel, & Tse, 1998; Ord & Stamps, 2008; Peters, Hemmi, & Zeil, 2007). Such moment-to-moment adjustments to signal structure represent contextual plasticity in signalling behaviour (Ord, Charles, Palmer, & Stamps, 2016). As this plasticity has been reported for motion-based signals within a population (Ord, Peters, Clucas, & Stamps, 2007; Peters et al., 2007), we predicted that species should also exhibit

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population differences if the signalling environments at the two locations are distinct.

Lizards are proving excellent models for understanding the evolution of motion-based visual signals (Losos, 1990; Ord, Blumstein, & Evans, 2001; Ord et al., 2016; Peters et al., 2002), just as they are for colour-based visual signals (Fleishman, Leal, & Persons, 2009; Fleishman & Persons, 2001; Ord, Blumstein, & Evans, 2002; Ord & Martins, 2006; Ord, Stamps, & Losos, 2013; Stuart-Fox & Johnston, 2005; Stuart-Fox & Ord, 2004). For these kinds of signals, the primary source of environmental noise comes from wind-blown plants (Eckert & Zeil, 2001; Fleishman, 1986, 1988; Peters et al., 2007). Environmental motion noise is site specific as local topography influences exposure to wind (Hannah, Palutikof, & Quine, 1995), and plants vary in their response to wind, both within and between species (Peters, 2013; Peters, Hemmi, & Zeil, 2008). This variation in motion noise environments is particularly relevant to widely dispersed species that occur in more than one habitat type because the signalling conditions might change dramatically. As such, allopatric populations exposed to very different environmental variables and noise conditions will require alternative signalling strategies. While it is possible that environmental differences lead to phenotypic variation as a result of genetic drift or sexual selection (Foster, 1999; Hill, 1994; Uy & Borgia, 2000), it is also likely that differences between populations, including behaviour, can arise from phenotypic plasticity and adaptive responses to the local environment (Dingemans et al., 2007; Ord et al., 2016; Stamps, 2016).

Some lizard species are known to differ between populations in several aspects of their signalling displays, such as body postures during push ups, number of head bobs per display and head bob duration (Ferguson, 1971; Martins, Bissell, & Morgan, 1998; Martins & Lamont, 1998). Furthermore, Bloch and Irschick (2006) observed temporal differences in the displays of the green anole, *Anolis carolinensis*, and suggested they are a result of differences in population density and habitat continuity between two populations. More detailed, fine-scale analyses were performed by Barquero, Peters, and Whiting (2015), who found evidence of temporal and structural variation in the core display of the jacky dragon, *Amphibolurus muricatus*, from three different populations, even though the components involved in the displays and their sequence remained consistent across populations. The differences observed in signalling behaviour were incongruent with genotypic differences between populations and might be a consequence of behavioural plasticity in response to concomitant variation in habitat structure (Barquero et al., 2015). Clearly, lizard motion signals show variation consistent with local adaptation explanations, but a direct link between habitat structure and motion signal structure has not been demonstrated.

The aim of the present study was to directly relate habitat and motion signal structure across populations of the same species. We assumed that the relative contrast between signal and plant movement is an important component of effective signalling and implemented a novel approach to compute relative signal contrast. We explicitly tested the hypothesis that variation in motion signal structure between populations of *A. muricatus* is attributable to differences in habitat characteristics, as suggested by Barquero et al. (2015). To support this hypothesis, we had to find variation in signal structure between populations, and provide evidence that this variation can be explained by differences in the signalling environment. If habitat does drive variation in signal structure, then we predicted first that signals, regardless of population differences, will be equally effective at their respective habitats on the assumption that signallers seek to optimize their signals for the existing context (Endler, 1992). Our second prediction was that relative signal contrast will change for a given signal when 'placed'

in a structurally distinct habitat featuring a different configuration of plants, as previously observed with acoustic signals (Dabelsteen, Larsen, & Pedersen, 1993; Gish & Morton, 1981). In bioacoustics, this is achieved by recording signals, broadcasting them in a different habitat and recording them again. This strategy is not possible with motion-based signals and we developed an alternative strategy. Our approach involved recording both the signal and relevant features of the noise environment (plants) independently, reconstructing signal motion in three dimensions (3D), and comparing it to the movement of wind-blown plants in the environment to determine the relative contrast of the signal. By reconstructing the displays in 3D and mapping the plant environment comprehensively we prevented any bias that might arise from camera position at the time of filming (Fig. 1). Importantly, this approach allowed us to place any signal we recorded in any habitat we mapped to calculate its contrast under different environmental circumstances. Thus, we could examine how the signals of lizards from one population perform in other habitats, both within and between populations, to directly consider whether differences in signal structure are a consequence of local adaptations to enhance signal efficacy within their specific noise environments.

METHODS

Data Collection

Amphibolurus muricatus (Fig. 2a) can be found in the woodlands and coastal shrublands ranging from southeast South Australia through most of nonarid Victoria, east New South Wales and southeast Queensland; excluding alpine areas (Wilson & Swan, 2013). We recorded displays at Croajingolong National Park ($N = 6$), in coastal Victoria, where the habitat is densely vegetated with tall grasses and shrubs (GPS coordinates: $37^{\circ}48.126'S$, $149^{\circ}16.541'E$; Fig. 2b). We also recorded displays at Avisford Nature Reserve ($N = 6$), near Mudgee, New South Wales. At this location, the habitat was mostly an open woodland with rocky outcrops, and

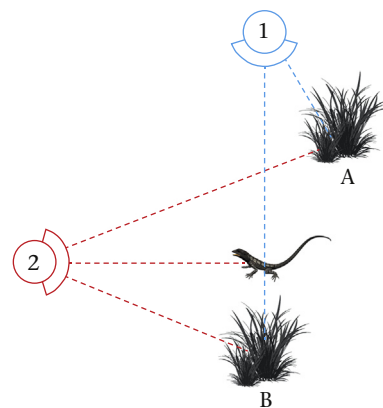


Figure 1. Studies on the effect of the noise environment on motion-based signals often utilize only one filming position, and assume it is the most appropriate position. However, motion signal contrast will vary with viewer position, even if all else remains the same. For example, at viewing position 1, both plants A and B are relevant sources of motion noise. If the physical movements of both plants are identical, plant A will provide stronger motion noise as angular speeds are dependent on viewing distance. Switching to viewing position 2, plant A is now further away and behind the lizard. Plant B is at the same depth plane as the lizard and, again, would provide more motion noise than plant A for the same physical movements. The extent to which the lizard display contrasts with plant motion is thus determined by the speed of the signal itself, the speeds of surrounding plant movements and, importantly, the position of the receiver. By recreating signal motion in 3D and mapping the habitat in detail, our approach ensures the filming location bias is no longer an issue.

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