



Evolving from static to dynamic signals: evolutionary compensation between two communicative signals



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Signals that convey related information may impose selection on each other, creating evolutionary links between different components of the communicative repertoire. Here, we ask about the consequences of the evolutionary loss of one signal (a colour patch) on another (a motion display) in *Sceloporus* lizards. We present data on male lizards of four species: two pairs of sister taxa representing two independent evolutionary losses of the static colour patch (*Sceloporus cozumelae* and *Sceloporus parvus*; *Sceloporus siniferus* and *Sceloporus merriami*). Males of the two species that have undergone an evolutionary loss of blue-belly patches (*S. cozumelae*, *S. siniferus*) were less active than their blue-bellied sister taxa (*S. parvus*, *S. merriami*), consistent with the suggestion that the belly patches were lost to reduce conspicuousness of species with high predation pressure. In contrast, the headbob display appears to have become more, rather than less, conspicuous over evolutionary time. The colour patch is exhibited primarily during aggressive encounters, whereas headbob displays are multifunction signals used in several different contexts, including aggressive encounters. Males of species that have lost the colour patch produced more motion displays, and the structure of those motion displays were more similar to those produced during combat. In both evolutionary episodes, a static colour signal appears to have been replaced by dynamic motion displays that can be turned off in the presence of predators and other unwanted receivers. The predominant pattern is one of evolutionary compensation and interactions between multiple signals that convey related information.

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Whenever animals use multiple signals, these signals can also be evolutionarily linked by the common demands of communication, such that shifts in one signal can influence the evolution of others (inter-signal interactions, sensu Hebets & Papaj, 2005). Many animals maintain repertoires of multiple communicative displays (e.g. Bro-Jørgensen, 2010; Higham & Hebets, 2013; Uetz, Roberts, Clark, Gibson, & Gordon, 2013). Multiple signals allow animals to convey information to different receivers or across different environments (e.g. Lyons, Goedert, & Morris, 2014; Uetz et al., 2013), to separate attention getting from information content (Endler, Gaburro, & Kelley, 2014; Preininger et al., 2013) or to provide the security of a backup signal for particularly important messages. Multiple signals with similar or related content may also

be evolutionarily maintained in the context of fluctuating frequency-dependent selection (Bro-Jørgensen, 2010), because of selection acting to increase the complexity and diversity of the repertoire (e.g. Akre & Ryan, 2011), or because of differential responses to natural and sexual selection (e.g. Chen, Symonds, Melville, & Stuart-Fox, 2013; Ord & Martins, 2006). Here, we make use of a replicated natural experiment in which male *Sceloporus* lizards have twice lost a conspicuous colour signal to ask whether evolution of a second signal, the headbob display, has been shifted via compensatory change.

Evolutionary interactions between signals, both trade-offs and positive relationships, have been reported in several comparative studies. In a now-classic example, birdsongs with broad frequency ranges tend to have lower trill rates, suggesting that there is a mechanical constraint imposed on the evolution of one aspect of the signal by the other (Podos, 1997). In contrast, there is a positive evolutionary relationship between the complexity of visual and

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seismic signals in wolf spiders, suggesting selection for increasing elaboration (Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013). Across *Sceloporus* lizards, there is evidence of evolutionary trade-offs between headbob display duration and complexity (Martins, 1993) and between visual and chemical markers of territory boundaries (Ossip-Klein, Fuentes, Hews, & Martins, 2013). Whereas loss of an aggressive colour signal in males of one species of *Sceloporus* lizards was accompanied by a compensatory increase in chemical behaviour (Hews & Benard, 2001; Hews, Date, Hara, & Castellano, 2011), there was no evidence of a compensatory shift in chemical cues for male crickets that have lost an acoustic signal (Gray, Bailey, Poon, & Zuk, 2014).

Evolutionary relationships between signals may be particularly important for signals that are functionally intertwined, such as signals that convey similar information (Ossip-Klein et al., 2013) or that modify the receiver's response to a second signal (e.g. Hebets, 2005; Rowland, Ruxton, & Skelhorn, 2013; Thompson, Bissell, & Martins, 2008). In many animals, selection has pushed signals to become more complex, carrying more information to more receivers (content-based hypotheses; Hebets & Papaj, 2005). In wood warblers, for example, sexual selection has shaped the evolution of more elaborate trills in some species and more complex songs in others (Cardoso & Hu, 2011). Male–male competition has similarly shaped an abundance of conspicuous colour, motion and chemical signals in lizards (e.g. Chen, Stuart-Fox, Hugall, & Symonds, 2012; Ord, Blumstein, & Evans, 2001; Pérez i de Lanuza, Font, & Monterde, 2013). Other forces shape signals that are easier or harder to detect in contrast to a particular environment (efficacy-based hypotheses; Hebets & Papaj, 2005). For example, male bowerbirds increase mating success by using multiple colour elements in their bowers to alter female perception (Endler et al., 2014).

Here, we ask whether the evolutionary loss of a colour signal (a male belly patch) in *Sceloporus* lizards has been accompanied by compensatory shifts in a motion signal (headbob display), particularly in aspects of the motion signal that are functionally similar to the colour signal. *Sceloporus* males actively show their colourful belly patches primarily during aggressive male–male combat (Carpenter & Ferguson, 1977), whereas headbob displays are a multifunction signal used primarily in long-distance broadcasts of individual, sex and species identity (Martins, 1991, 1994; Martins, Bissell, & Morgan, 1998). When headbob displays are produced during combat, they tend to be longer and are accompanied by postures that exaggerate male body size (Martins, 1993); these structural differences also elicit stronger responses from display receivers (Martins, Ord, & Davenport, 2005) than do broadcast headbob displays. In the current study, we focus on two evolutionary episodes in which the colour patch was lost, perhaps due to increased selective pressure from visual predators or to relaxed sexual selection from decreased male–male combat. For each episode, we ask whether male lizards of species that have lost the conspicuous colour patch also produce less conspicuous headbob displays, or whether the plain-bellied *Sceloporus* species have compensated for the loss of the colour signal by producing more aggressive headbob displays (i.e. more similar to those used during combat). We report comprehensive behavioural data from unmanipulated animals in the field, using the natural experiment of two independent evolutionary events to retain some generality while asking whether animals with multiple signals can compensate for signal loss.

METHODS

Subject Species

We collected data on two species pairs that represent independent evolutionary losses of the colourful belly patches typical of

male *Sceloporus* lizards. Clade A includes *Sceloporus parvus* and *Sceloporus cozumelae*; Clade B includes *Sceloporus merriami* and *Sceloporus siniferus*. Males of most of the 90+ species of *Sceloporus* lizards have colourful belly patches, and it is likely that males of the root ancestor of this genus also exhibited colourful belly patches (Wiens, 2001). In each of our two target clades, we chose one species (*S. parvus*, *S. merriami*) from among those in which males retain the colourful bellies typical of the genus, and a second species (*S. cozumelae*, *S. siniferus*) in which males have plain bellies that lack the colour patch (Fig. 1). The two species within each clade diverged and the colourful belly patch was probably lost a very long time ago: ~15 million years ago if we estimate times from a recent phylogeny (Wiens, Kuczynski, Arif, & Reeder, 2010) and place the root of the genus at the time of the oldest known fossil *Sceloporus* (Lawing, 2012; Yatkola, 1976). There are other extant and extinct *Sceloporus* species within each clade that are not represented in the current study; these four were chosen primarily for logistical reasons.

We sampled each species during the peak mating season (peak of male gonadal activity). In Clade A, Male *S. parvus* have blue belly patches (in the population we sampled, they are a pale blue), whereas female *S. parvus* and both male and female *S. cozumelae* have plain bellies (Fig. 1). We sampled male *S. parvus* in June 2013 in rocky outcrops of the desert scrub habitat near Querétaro, México. We collected behavioural data from male *S. cozumelae* on sandy beaches near Cancún, México in May 2013. For Clade B, we recorded behaviour of male *S. merriami* on the reddish-grey walls of a slot canyon in the Chihuahua desert Big Bend TX in May 2011 and 2012. We recorded male *S. siniferus* in the thick vegetation of a semi-deciduous tropical rainforest at the Huatulco National Park, MX in June and July 2012. *Sceloporus merriami* males have colourful belly patches that include blue and green elements, whereas the females have plain bellies (Fig. 1). Both male and female *S. siniferus* have plain bellies.

Procedure

We measured 21–51 males for each species using a Canon Elura 100 camcorder to record the undisturbed behaviour of each male from a distance of 2–10 m. The number of individuals we sampled from each species and viewing distances depended on local abundance and habitat conditions. Although we strived for 10 min focal animal samples, trials often ended sooner when the subject moved out of sight. For Clade A, we collected data from 21 male *S. parvus*, with trials ranging from 6 to 18 min in duration and summing to 4.9 h of observation time. We collected data from 23 male *S. cozumelae*, with trials ranging from 1 to 21 min in duration and summing to 3.9 h of observation time. We were able to collect more and longer behavioural samples from males of Clade B. We collected data from 51 male *S. merriami*, with trials ranging from 6 to 18 min in duration and summing to 10.1 h of observation time. We collected data from 34 male *S. siniferus*, with trials ranging from 2 to 23 min in duration and summing to 6.3 h of observation time.

Scoring

Afterwards, one observer (E.P.M.) scored each recording using an ethogram that categorized all behaviour that occurred during our samples while focusing on headbob displays. We scored 'activity' as the total number of behavioural acts, including chemical behaviour, visual displays and three types of movement. 'Motion displays' consisted primarily of headbob displays, but also included occasional shudder displays (typical of male courtship), full-shows (static postural displays including arched back, lateral flattening and gular extension) and tail wags. For each headbob display, we

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