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Brief Communication

Evolutionary loss of complexity in animal signals: cause and consequence

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Abstract

We identified hypotheses for the cause and consequences of the loss of complexity in animal signals and tested these using a genus of visually communicating lizards, the Southeast Asian *Draco* lizards. Males of some species have lost the headbob component from their display, which is otherwise central to the communication of this genus. These males instead display a large, colorful dewlap to defend territories and attract mates. This dewlap initially evolved to augment the headbob component of the display, but has become the exclusive system of communication. We tested whether the loss of headbobs was caused by relaxed selection, habitat-dependent constraints, or size-specific energetic constraints on display movement. We then examined whether the consequences of this loss have been mitigated by increased signaling effort or complexity in the color of the dewlap. It appears the increased cost of display movement resulting from the evolution of large body size might have contributed to the loss of headbobs and has been somewhat compensated for by the evolution of greater complexity in dewlap color. However, this evolutionary shift is unlikely to have maintained the complexity previously present in the communication system, resulting in an apparent detrimental loss of information potential.

Keywords: animal signal, color signal, energetic cost, environmental noise, evolutionary loss, ornament

The term "complex" has been used to describe various forms of animal communication, including ornaments made up of many colors, acoustic signals consisting of many notes, stridulations or pulses, or signal systems that are multimodal (e.g., rely on both sound and visual components). In essence, complex signals are explicitly defined (or implicitly assumed) to be those that convey more information than simple signals, through the repetition and the use of different types of components (see Nelson et al., 2022). The origins of such complexity have been a classic focus of research for communication biologists (Freeberg et al., 2012). From this body of work, we know that complex communication can evolve to mediate an increasing number of social interactions among conspecifics (e.g., Freeberg, 2006), as a function of increasingly choosy mates (e.g., Choi et al., 2022), or to mediate aggressive encounters by improving opponent assessment among rivals (e.g., Ord et al., 2001). Less attention has been given to the causes (or consequences) of losses in signal complexity, despite such losses being widespread across many taxonomic groups (Maia et al., 2016; Miles & Fuxjager, 2019; Ödeen & Björklund, 2003; Ord & Stuart-Fox, 2006; Price et al., 2009; Romero-Diaz et al., 2021; Starrett et al., 2022). This presents a problem for our general understanding of signal evolution, as we know a reasonable amount about how communicative complexity evolves but not why complexity is often subsequently lost (Patricelli & Hebets, 2016). It is therefore difficult to fully account for the variation observed among species in the complexity of their signals, especially when those signals are used in the same context by closely related taxa (e.g., to attract mates or defend territories; Nelson et al., 2022).

Of what we do know, there are several potential scenarios in which we might expect the loss of complexity in animal signals. First, the need to have complex social signals could be reduced in instances where sexual selection on those signals has become relaxed. For example, the evolution of herbivory in iguanian lizards has been attributed to the relaxation of territoriality and the subsequent loss of complex territorial displays (Ord & Blumstein, 2002). Competition for mates and other resources can similarly be reduced with changes in conspecific density, obviating the need for complex, costly signals for mate attraction (Ödeen & Björklund, 2003; Rand & Ryan, 1981) or territorial defense (Price et al. 2009). Second, the ability of conspecifics to detect and assess complex signals can depend on environmental conditions and the distance over which signals are transmitted. For example, acoustic or visual background noise can limit the types of songs or visual displays that can be readily detected by conspecifics (Peters, 2008; Reed et al., 2021). There is also evidence that complex signals are more difficult to perceive with increasing

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