Animal Behaviour 85 (2013) 1415–1426

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards

Terry J. Ord [a,*], Judy A. Stamps [b], Jonathan B. Losos [c]

[a] *Evolution and Ecology Research Centre, and School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW, Australia*
[b] *Department of Evolution and Ecology, University of California at Davis, Davis, CA, U.S.A.*
[c] *Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.*

ARTICLE INFO

Article history:
Received 11 December 2012
Initial acceptance 4 February 2013
Final acceptance 15 March 2013
Available online 3 May 2013
MS. number: A12-00933

Keywords:
adaptation
Anolis lizard
contextual plasticity
convergence
signal detection
territorial display

To demonstrate adaptive convergent evolution, it must be shown that shared phenotypes have evolved independently in different lineages and that a credible selection pressure underlies adaptive evolution. There are a number of robust examples of adaptive convergence in morphology for which both these criteria have been met, but examples from animal behaviour have rarely been tested as rigorously. Adaptive convergence should be common in behaviour, especially behaviour used for communication, because the environment often shapes the evolution of signal design. In this study we report on the origins of a shared design of a territorial display among *Anolis* species of lizards from two island radiations in the Caribbean. These lizards perform an elaborate display that consists of a complex series of headbobs and dewlap extensions. The way in which these movements are incorporated into displays is generally species specific, but species on the islands of Jamaica and Puerto Rico also share fundamental aspects in display design, resulting in two general display types. We confirm these display types are convergent (the consequence of independent evolution on each island) and provide evidence that the convergence was driven by selection for enhanced signal efficiency. Our study shows how adaptation to common environmental variables can drive the evolution of adaptive, convergent signals in distantly related species.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Convergent evolution is the independent origin of similar phenotypes in distantly related species. When convergence results from natural selection, it provides some of the best evidence for adaptive evolution in nature because it represents replicated examples of the same, or at least very similar, adaptation arising from separate selection events. Most examples of convergent evolution involve morphological traits (e.g. Taylor & McPhail 2000; Rosenblum 2006; Losos 2009), but any aspect of the phenotype can be the target of selection and subsequently has the potential to exhibit convergence. Animal behaviour is no exception, and there are a number of compelling cases of behavioural convergence. Notable examples include strategies of maternal care shared between ungulates and macropods (wallabies, wallaroos and kangaroos; Fisher et al. 2002), the array of similar web patterns in distantly related Hawaiian spiders (Blackledge & Gillespie 2004), the common design of echolocation calls in diverse lineages of bats (Jones & Holderied 2007), and the high-pitched 'seet' alarm call produced by some songbirds (Marler 1955). Yet identifying behavioural examples of convergent evolution has been challenging: behaviour is often difficult to quantify because of its complexity and variability within individuals as compared to other phenotypic characteristics like morphology. Nevertheless, for these same reasons, behaviour can also provide valuable insights into the circumstances that promote convergent evolution in complex phenotypes that can vary within as well as across species.

An attractive candidate for the study of behavioural convergence is animal communication because it is a predictable target of selection from the environment. Indeed, how properties of the environment affect the propagation of animal signals has been a topic of long-standing interest to researchers of animal communication (e.g. Alexander 1962; Marler 1967; Morton 1975). There is now a strong body of signal detection theory (Wiley 2006) that outlines how animals should produce signals to maximize reception and assessment in difficult environments (e.g. habitats that are noisy). By extension these models also predict that the type of environment in which animals communicate should dictate the type of signals that the animals produce. This should lead to adaptations that drive signal convergence when distantly related species occupy very similar environments (Endler 1992). Habitat-dependent convergence in the design of animal signals should therefore be common, but few studies have investigated this

---

* Correspondence: T. J. Ord, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia.
E-mail address: t.ord@unsw.edu.au (T. J. Ord).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.03.037

phenomenon explicitly and robust examples are subsequently rare. Here, we provide a test of habitat-dependent convergence in the behavioural displays of 12 species of *Anolis* lizards from two separate island radiations on Jamaica and Puerto Rico.

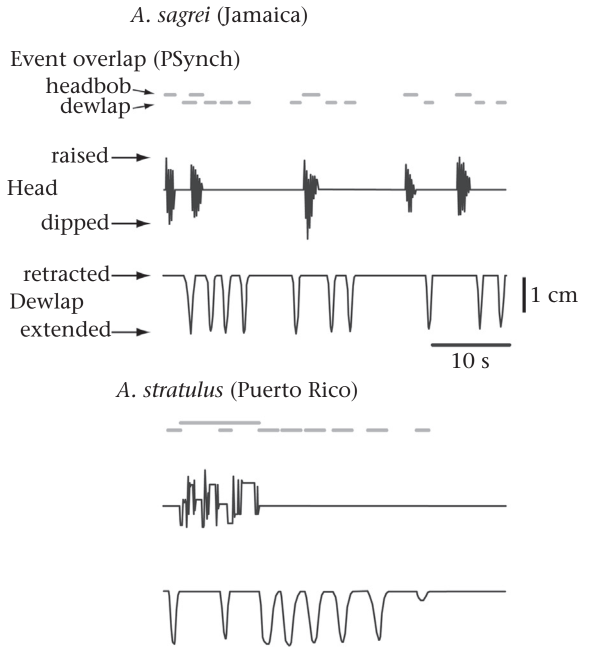
There are several important reasons why we might expect signal convergence in *Anolis* lizards. Anoles communicate using movement-based visual displays composed of two discrete components: vertical movements of the body, known as headbobs or pushups, and extensions of an expandable throat fan, called a dewlap. Males use these displays to advertise continued territory occupancy and to deter intrusions (Jenssen 1977; Ord 2008). As most potential receivers are located far from the signaller (Ord 2012), anole displays are particularly susceptible to environmental degradation (Ord & Stamps 2008). *Anolis* advertisement displays are therefore under considerable selection pressure to remain conspicuous. In particular, lizards living in poorly lit or windy environments in which there is frequent, distracting motion from windblown vegetation (high 'visual noise') compensate by enhancing the speed of display movements or extending the duration of displays (Ord et al. 2007, 2010). This predicts convergence in display characteristics among species living in comparable light and visual noise conditions between islands.

Another reason to anticipate convergence in the territorial displays of Jamaican and Puerto Rican anoles is the abundant evidence of the convergence of other traits among species on these and other islands. *Anolis* lizards of the Greater Antilles (which includes Jamaica and Puerto Rico) provide a classic example of convergent morphological evolution, in which the same set of ecomorphs has evolved independently on each island. These ecomorphs are named according to the area of the environment or microhabitat in which species are typically found and include grass-bush, trunk-ground and trunk-crown specialists (plus three other ecomorph types that are not the focus of this current study; see Losos et al. 1998). Much of the convergence within ecomorphs reflects adaptations that increase locomotor performance in a given microhabitat (reviewed in Losos 2009). However, there are indications that display rates may also have converged within ecomorphs (Losos 1990), in addition to the degree of overlap among male territories, which tends to increase from grass-bush (low overlap), trunk-crown (moderate overlap) to trunk-ground (high overlap; Johnson et al. 2010).

The current study focuses on a general aspect of communication: the extent to which animals with different signal components rely on each of those components for communication in the same functional context. Although all of the anoles on Jamaica and Puerto Rico use dewlaps and headbobs in their territorial advertisement displays, pilot studies suggested that species might differ in the extent to which they emphasize these two components. For instance, *Anolis stratulus* repeatedly 'pumps' the dewlap (many dewlap extensions of short duration), but rarely does so in conjunction with headbobs, while *Anolis gundlachi* performs a series of headbobs, while keeping the dewlap extended throughout the headbob display (Fig. 1). However, it was unclear whether these display types occur on both islands, and if so, whether they are related to ecomorphs or to differences in signalling conditions (light levels/visual noise).

We began by devising an index, PSynch, to quantify the nature of the relationship between the dewlap and headbob components in an anole's advertisement display, and then asked whether this index was correlated, across taxa, with other display characteristics. Next, we mapped these display phenotypes onto the phylogeny of Jamaican and Puerto Rican lizards to confirm that convergence was involved for at least one of the display types (the other display type could be ancestral). Finally, we tested two nonexclusive hypotheses to explain the convergence: (1) display phenotypes differed among ecomorphs, implying that morphological and behavioural traits evolved together in response to selection in different microhabitats; and (2) display phenotypes were associated with ambient light, visual noise and distance to receivers (Ord et al. 2010; Ord 2012), suggesting that certain types of displays have evolved to

(a) Asynchronous displayers



(b) Synchronous displayers

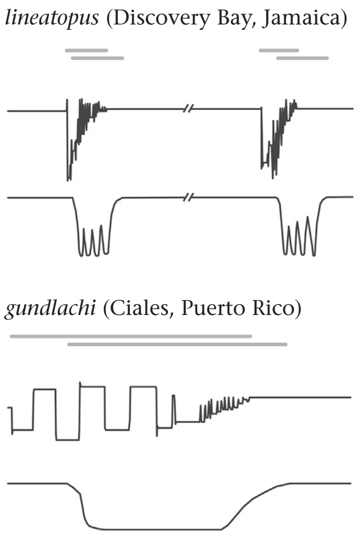


Figure 1. Convergent display types performed by male *Anolis* lizards on Jamaica and Puerto Rico. Lines in black are display-action-pattern graphs of representative displays that depict movement of the head up-and-down (top line) and the extension of the dewlap in-and-out (bottom line) over time. Lines in grey show the extent of headbob movements and dewlap extensions overlap. (a) Asynchronous displays were mostly made up of frequent extensions of the dewlap that rarely overlapped with headbob movements (proportion of synchronized dewlap and headbob movements, PSynch: μ_{taxon}: *A. sagrei* $= 1.7\%$; *A. stratulus* $= 15.9\%$). (b) Synchronous displays were made up of headbobs and dewlap extensions, but most movement was concentrated in the headbob portion of the display (PSynch: μ_{taxon}: *A. lineatopus* $= 68.9\%$; *A. gundlachi* $= 74.5\%$). Videos of these display sequences are provided in the Supplementary Material. These videos highlight that species that use asynchronous displays also tend to have small, colourful dewlaps, whereas species that use synchronous displays tend to have large, pale coloured dewlaps.

Download English Version:

https://daneshyari.com/en/article/10970766

Download Persian Version:

https://daneshyari.com/article/10970766

Daneshyari.com