

Historical contingency and behavioural divergence in territorial *Anolis* lizards

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Abstract

The extent that evolution – including adaptation – is historically contingent (dependent on past events) has often been hotly debated, but is still poorly understood. In particular, there are little data on the degree that behaviour, an aspect of the phenotype that is strongly linked to contemporary environments (social or physical), retains the imprint of evolutionary history. In this study, I examined whether differences in the design of the territorial displays among species of Caribbean *Anolis* lizards reflect island-specific selection regimes, or historically contingent predispositions associated with different clade histories. Adult males advertise territory ownership using a series of headbobs and dewlap extensions, bouts of which vary in duration among species. When display durations were mapped onto the *Anolis* phylogeny, prominent differences between species belonging to the Western and Eastern Caribbean radiations were apparent. Statistical analyses confirmed that species differences in the duration of headbob displays, and to some extent the duration of dewlap extensions, were historically contingent. The unique evolutionary histories of each clade have seemingly had a profound effect on the subsequent direction of display evolution among descendent taxa. These results combined with those from previous studies on these lizards show that past history can have an important impact on the type of behaviour exhibited by species today, to the point that adaptive evolution can proceed quite differently in lineages originating from different evolutionary starting points.

Introduction

The extent that present-day phenotypes are historically contingent or ecologically determined has been a point of contention. Some (most famously Gould, 1989) have argued that evolutionary outcomes are highly dependent on a complex sequence of innumerable – often chance – events that invariably leave an imprint in the phenotypes of descendent taxa. No distantly related taxa will therefore be alike. There is empirical support for this view from a variety of contexts. Experimental evolution studies have demonstrated a critical role for the type and order of genetic mutations on what and

when adaptations arise in evolutionary lineages (Blount *et al.*, 2008; Meyer *et al.*, 2012; see also Wischmann *et al.*, 2012). Ancestral starting points matter for similar reasons: different lineages have different evolutionary predispositions because evolution builds on past genetic and phenotypic changes. For example, distantly related species can evolve differently in common selection environments (Price *et al.*, 2000) or even ‘fail’ to reach optimal phenotypes because of evolutionary inertia (Travisano *et al.*, 1995). The alternative view is that natural selection can override historical effects; that phenotypic and species diversity is ecologically determined. Spectacular support for this argument comes from examples of adaptive convergence, in which distantly related species that occupy comparable ecological niches have converged on remarkably similar phenotypes [e.g. the replicated morphologies among the Caribbean *Anolis* lizards (Losos *et al.*, 1998) or three-spined sticklebacks (Taylor & McPhail, 2000) that

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reflect similarities in ecology; see also Melville *et al.*, 2006; Rosenblum, 2006].

Classically, the debate over the contribution of historically contingent vs. ecological deterministic processes in evolutionary diversification has been pitched from conflicting standpoints. Today, however, there is growing recognition that both probably play an important role (e.g. Schluter, 2009; Losos, 2010). The relevant question, then, is not whether one or the other accounts for the similarities or differences among extant species, but their relative contribution. Our knowledge of how historical contingency and ecological determinism interact is limited to a handful of studies, most of which focus on morphology (e.g. Huey *et al.*, 2000; Langerhans & DeWitt, 2004; Langerhans *et al.*, 2006; Melville *et al.*, 2006; but see Eroukhmanoff *et al.*, 2009). A broader understanding of the extent other aspects of the phenotype are dependent on past history, especially characteristics that are more sensitive to short-term environmental fluctuations (such as behaviour), is important for understanding when we might expect phenomena such as adaptive convergence to occur in different phenotypic characteristics. If historical contingency is strong, then the likelihood of convergence will decrease with increasing phylogenetic distance among species.

One system in which historical contingency and ecological determinism have been explicitly examined is the Caribbean *Anolis* lizards (e.g. Losos *et al.*, 1998; Langerhans *et al.*, 2006). Indeed, the group is one of the most well-known examples of how natural selection can largely erase the imprint of evolutionary history from ecological phenotypes. On each of the four islands of the Greater Antilles (Cuba, Jamaica, Puerto Rico and Hispaniola), replicate examples of the same set of ecomorphs (species that share ecological and morphological features; Losos, 2009) have evolved independently in species occupying comparable ecological niches. This adaptive convergence exhibits itself not only in numerous aspects of morphology but also in the behaviour of species (Losos, 2009). There has also been a second set of convergences in the design of the territorial advertisement displays among *Anolis* species living in similar environments, largely independent of ecomorphology (T.J. Ord, J.A. Stamps & J.B. Losos, in review). However, the evolution of the territorial display has not been as straightforward a case of ecological determinism as it has been in the evolution of the ecomorphs. In the case of ecomorphology, convergence has been so great that little difference exists among species within a given ecomorph class on different islands (Losos, 2009). By contrast, despite clear convergence in some aspects of display (T.J. Ord, J.A. Stamps & J.B. Losos, in review), major differences still remain between at least two islands (Ord *et al.*, 2010, 2011).

Much of the variation among species in the design of territorial advertisement displays is environment dependent. This is because the environment affects the

detectability of displays, and this in turn affects a male's reproductive success. Adult males vigorously defend territories that overlap female home ranges as a means of monopolizing access to those females (Jenssen & Nunez, 1998; Jenssen *et al.*, 2001). To advertise territory ownership and discourage territorial intrusions, males use a visual display consisting of an elaborate sequence of body movements – known as headbobs – and extension of a large and frequently colourful throat fan – a dewlap. Ambient light, the amount of distracting movement from windblown vegetation and the distance over which displays must travel have all been implicated in affecting display reception (Ord *et al.*, 2007, 2010; Ord & Stamps, 2008; Ord, 2012). To compensate, lizards exaggerate display movements or extend the duration of displays in visually noisy or poorly lit habitats, leading to predictable variation in display behaviour among species (Ord *et al.*, 2010).

Yet some of these same aspects of the *Anolis* territorial display exhibit prominent differences between islands. Among species on Jamaica and Puerto Rico, the duration of both headbob and dewlap displays increases with decreasing habitat light. These changes in display duration are, in a large part, the product of contextual plasticity (Ord *et al.*, 2010). Still, these plastic display durations also exhibited significant island effects: species on Puerto Rico generally performed headbob and dewlap displays of longer duration than species on Jamaica. The range of habitats occupied by lizards seems comparable on each island (Ord *et al.*, 2011), but this comparison is difficult because the identification and accurate measurement of all biologically relevant variables, plus their interaction, is nearly impossible. One known difference between the two islands is the evolutionary history of the *Anolis* communities: species on each island have originated from separate evolutionary radiations. Taken together, this suggests that display divergence between the Jamaican and Puerto Rican lizards could either reflect some island-specific selective regime [although occupying different selective environments within islands (Ord *et al.*, 2010), species tend to exhibit a broad island phenotype that reflects some form of island-wide stabilizing selection] or historically contingency (species on each island belong to separate radiations that originated from different evolutionary starting points and subsequently followed different evolutionary trajectories). The objective of this study was to separate these two alternative explanations by expanding the survey of species to include others found on different islands but still belonging to the same evolutionary radiations.

To this end, I compiled information on the headbob and dewlap durations of *Anolis* species and populations throughout the Caribbean. I then developed several evolutionary models to test the following hypotheses:

- The Contingency Hypothesis: evolutionary lineages that originated from a common ancestor share much

of their display behaviour through descent. The motor patterns and morphological structures affecting signal production that evolved in a species' ancestors have been conserved in their descendants today and have in turn affected the sorts of adjustments that can be made to suit current environmental conditions. This predicts broad, clade-specific behaviours among species independent of the particular island on which species were found. For example, *Anolis* species on Puerto Rico and Hispaniola belong to the Eastern Caribbean radiation and should differ in display behaviour to those species on Jamaica, the Caymans and Cuba that belong to the Western Caribbean radiation.

- The Selection Regime Hypothesis: evolutionary lineages – species or populations – found on different islands have experienced unique, island-specific selection regimes that have led to evolutionary divergence in behaviour between islands. Selection regimes might differ among islands in numerous ecological variables that interact in complex ways. Although the ranges of several habitat variables (e.g. habitat light, visual noise) on Jamaica and Puerto Rico do overlap (implying that there are a comparable range of habitats on each island; Ord *et al.*, 2010, 2011), these are only a subset of variables that could influence the trajectory of display evolution. Others might include social factors such as conspecific densities and sex ratios that affect the level of competition for territories and mates (Ord & Martins, 2006; Charles & Ord, 2012), predation pressure that targets conspicuous display behaviours (Stuart-Fox *et al.*, 2003; Stuart-Fox & Ord, 2004), or any combination of these or other factors. Taxa might still occupy different habitats within islands, and even express adaptations in display behaviour to those habitats, but there is an overarching selection pressure (or set of pressures) that has led species to be more similar in display within islands than closely related species found on other islands. For example, two species living on the same island will tend to share display characteristics (e.g. short bouts of headbob display that may still differ in the sequence of movements in species-typical ways), whereas populations of the same species on separate islands will tend to differ in display (e.g. shorter bouts of headbobbing on one island vs. longer bouts of headbobbing on another island, while still retaining species-typical elements in the display).
- The Random Change Hypothesis: a null model that describes differences among species in display behaviour as the outcome of Brownian motion. That is, display differentiation has occurred because of stochastic factors such as genetic drift and random mutation. Selection might have influenced the directional tendency of stochastic phenotypic changes in some evolutionary lineages, but the variance among

species in display duration is for the most part randomly distributed across the anole phylogeny. This predicts that neither island nor clade origin is associated with particular display durations. It differs from the Contingency Hypothesis in that it assumes incremental, random change over long periods of evolutionary time with similarities and differences among taxa detailed by the specific phylogenetic branching patterns and relative ages among taxa, and not an affiliation with any particular phylogenetic clade. Historical contingency (as investigated here) reflects evolutionary change that has been bracketed by past events and biased selective outcomes or stochastic differentiation along certain trajectories.

Materials and Methods

Data collection

Data on the average duration of headbob and dewlap bouts were obtained from two types of sources: (i) my own video library of display data and (ii) the published literature.

In the first instance, the majority of data for Jamaican and Puerto Rican taxa were obtained from an extensive library of video clips that depicted adult male lizards performing territorial advertisement displays in the field. Details on the recording protocol and recording locations are described in the study by Ord *et al.* (2007, 2010). In several cases, geographically separated populations were sampled for several species. I included these populations as separate taxa in my analyses because biologically relevant variance between populations in display behaviour has been demonstrated (Ord *et al.*, 2010; T.J. Ord, J.A. Stamps & J.B. Losos, in review) and was explicitly predicted by my Selection Regime Hypothesis (see Introduction). I also included new data on two additional Jamaican species not previously reported in earlier studies: *Anolis valencienni* and *Anolis garmani*. These species were video-recorded in the limestone forest around the Discovery Bay Marine Laboratory in the same manner as other species on Jamaica (Ord *et al.*, 2007, 2010). Sample sizes for these species were low (two adult males for each species; in comparison, the range of sample sizes for other Jamaican taxa was

35–41 male lizards and for Puerto Rican taxa, 8–40 male lizards), largely because of the limited opportunity to video-record lizards at the locations visited (densities were low). The uncertainty associated with my estimate of headbob and dewlap duration for *A. valencienni* and *A. garmani* was consequently higher than for other Jamaican taxa included in my study. This would in turn increase the overall variance in average display durations among the Jamaican taxa, reducing potential support for the Contingency or Selection Regime

hypotheses in favour of the Random Change Hypothesis (the null model). That is, low precision in the estimates of display duration will have increased the probability of type II error in my analyses.

In the second instance, I used the review of *Anolis* display behaviour by Ord & Martins (2006) to obtain data for additional populations of Jamaican species, several congeners of the same radiation found off Jamaica and other species from Hispaniola. This review compiled raw data from published display-action-pattern (DAP) graphs taken from various sources. These graphs are the traditional means of quantifying lizard visual displays (Carpenter & Grubitz, 1961; Jenssen, 1971) and depict the up and down movements of the head and extension and retraction of the dewlap over time for a given species. I supplemented these data with additional DAP graphs found in two studies that were overlooked by this review (Scott, 1984; Macedonia & Clark, 2003). The analyses of these supplementary DAP graphs were carried out in exactly the same manner as Ord & Martins (2006). The way in which the duration of headbob and dewlap displays was measured from videos and DAP graphs was also comparable (see Ord *et al.*, 2010 and Ord & Martins, 2006 for details on how these measures were taken). However, the sample size used for creating DAP graphs from published sources was difficult to determine, either because this information was vague or not reported at all. In most instances, the graphs were presented as representative display sequences for a given species, so presumably these were based on a single adult male. Sampling error associated with these estimates of average display durations would again tend to increase the variance among species, and bias support in favour of the Random Change Hypothesis.

All data used in this study, its sources and sample sizes have been deposited in the Dryad repository (see Acknowledgments).

Statistical analyses

I used the *SLOUCH* package version 1.1 (Hansen *et al.*, 2008) run in the *R* environment (R Development Core Team, Vienna, Austria) to fit three evolutionary models. Each model differed in the assumed process of how display duration had evolved along the anole phylogeny and corresponded to one of three hypotheses: the 'Contingency', 'Selection Regime' and 'Random Change' model.

The Contingency model assumed that the average duration of headbobs and dewlap displays was clade specific. In this model, the evolutionary starting points of the Western and Eastern Caribbean clades have set descendent taxa on different evolutionary trajectories. The result has been taxa within clades tending to cluster around a common display duration. This clustering might reflect some genetic, physiological or morphological constraint, or a lack of genetic variation (e.g. low

mutation rate), or mutations leading to only small, incremental changes in display duration over long periods of evolutionary time. In contrast, the Selection Regime model assumed that headbob and dewlap durations were the result of an adaptive response to a complex mix of island-specific selection pressures. Display durations are therefore particular to taxa living on the same island. Finally, the Random Change model assumed that variation among taxa in display duration reflects the outcome of a Brownian motion process of evolutionary change. This model was similar to the Contingency model in the sense that closely related taxa tend to share similar display durations more than distantly related taxa, but differs in the absence of a restraining force or some event that biased the trajectory of evolution in descendent lineages.

SLOUCH implemented these models based on an Ornstein–Uhlenbeck mode of phenotypic evolution. Phenotypes evolve towards some optimum value via Brownian motion and, if reached, are maintained at or near this optimum by stabilizing selection or some other restraining force. How quickly phenotypes evolve towards this optimum is summarized by its phylogenetic half-life, $t_{1/2}$, where values close to zero reflect rapid evolutionary change, whereas larger values reflect increasing phylogenetic inertia. An estimate of the amount of stochasticity in evolutionary differentiation, v_p , is also given by the program, with values close to zero reflecting little stochasticity in evolutionary change, whereas large values imply that the influence of stochasticity has been high.

I used the stationary 'optima' algorithm in *SLOUCH* to assess the fit of each of my models. The procedure relies on the reconstruction of a categorical, predictor variable onto the phylogeny and evaluates the extent that variable has selected for a discrete optimum value in a continuous phenotypic variable. For the Contingency model, the basal nodes of the Western and Eastern Caribbean radiations were used to assign those nodes and all descendent nodes to their respective radiations. The only node that was not assigned was the root node, which was reconstructed as 'ancestral'. For the Selection Regime model, nodes shared among taxa within a given island were reconstructed as belonging to that island radiation, whereas basal nodes deeper in the phylogeny were reconstructed as 'ancestral'. For the Random Change model, all nodes on the phylogeny were reconstructed as 'ancestral'. In doing so, phenotypic change was effectively modelled across the tips of the phylogeny as the outcome of Brownian motion.

I incorporated within-taxon variance in bout durations in these analyses as either a direct estimate of the variance computed for a given taxon – that is, those taxa for which data had been collected from video recordings – or the average of these computed variances when duration data for taxa had been compiled from the literature (e.g. Ord & Martins, 2006). My phylo-

geny was based on the tree constructed by Nicholson *et al.* (2005) and reproduced by Losos (2009) with branch length information. The phylogeny was generally well supported (e.g. most nodes with Bayesian posterior probabilities 90% or above) and has been confirmed in a recent phylogenetic analysis using an extended data set on a subset of species (Alföldi *et al.*, 2011). I trimmed the phylogeny to the species of interest using MESQUITE version 2.6 (Maddison & Maddison, 2010). Populations within species were positioned based on the minimum population divergence estimated for Jamaican *Anolis* species (see Jackman *et al.*, 2002). I also conducted other analyses that used the maximum estimate of population divergence (from Jackman *et al.*, 2002), but there was virtually no change to the outcome of analyses and are therefore not reported here.

I used Akaike's Information Criterion with a correction for sample size, AIC_c , to compare the relative support for each model. AIC_c reflects the likelihood that a given model fits the observed variation in display duration among taxa. The model with the lowest AIC_c value fits the data best, but any model within two units of this lowest value is essentially equally well supported (i.e. $\Delta AIC \leq 2.0$; Burnham & Anderson, 2002). I also computed model weights, AIC_w , to illustrate the level of support for a given model relative to all other models examined.

Results

Figure 1 illustrates the average duration of headbob and dewlap bouts across the anole phylogeny. Headbob duration among taxa from the Western Caribbean radiation was clearly shorter than the majority of headbob durations of taxa from the Eastern Caribbean radiation. Dewlap duration was more variable among taxa, but also appeared to exhibit some evidence of a clade effect: taxa from the Western Caribbean performed dewlap extensions that also tended to be shorter in duration than taxa from the Eastern Caribbean.

These patterns were mirrored in model support values. The Contingency model was by far the best-supported model for headbob duration. For dewlap duration, however, there was equal support for both the Random Change and Contingency models. The Selection Regime model was the least supported model in both cases and can be largely excluded as a viable explanation for the origin of variation among taxa in display duration.

Taken together, historical contingency does appear to have played an important role in the evolution of headbob duration. The evolutionary trajectories of descendent taxa from the Western and Eastern Caribbean radiations were highly divergent, nonrandom and independent of island origin. The evolution of dewlap duration was less clear, and this may have been affected by

taxon sampling. There were few data on the dewlap durations of taxa from islands other than Jamaica and Puerto Rico. Historical contingency may have affected the duration of dewlap extensions among taxa, but much of its variance was also consistent with the outcome of Brownian motion. Island selection regimes seemed not to have affected dewlap duration, but again the available information to test this model was limited.

Discussion

The contingent nature of evolution – descent with modification, with a certain amount of unpredictability in that modification – or the deterministic outcome of natural selection are classically viewed as alternative explanations for the evolutionary differentiation of species (Gould, 1989; Beatty, 2006, 2008). The assumed time scales over which historical effects and ecology affected phenotypic evolution probably complicated this early debate. It seems that Gould's position was that historical contingency showed its primary influence over palaeontological time scales, where he believed it would not be erased by the short-lived signature of selection (see Beatty, 2006). The discussion has since moved to one centred on the relative roles of history and ecological determinism (e.g. Langerhans & DeWitt, 2004; Langerhans *et al.*, 2006; Eroukhmanoff *et al.*, 2009). The emerging consensus seems to be that historical contingency and ecological determinism are not mutually exclusive, but instead two ends of the same continuum. My findings return to the notion of time scale and imply that this continuum has an important temporal dimensionality to it.

Both the duration of headbob and dewlap displays in *Anolis* lizards are dependent on the environment, and this has led to predictable differences among taxa in display duration according to the type of habitat occupied (Ord *et al.*, 2010). Yet the present study also highlights that – for the duration of headbob displays at least – there has been a major divergence among taxa from the Western and Eastern Caribbean radiations (Table 1; despite local adaptations to different environments within islands – Ord *et al.*, 2010). This split is obvious from the distribution of headbob durations across taxa in Fig. 1. This figure also shows considerable variance among taxa within the two clades, and it is this variance that has been shown to be the outcome of habitat-induced plasticity (see Ord *et al.*, 2010). At broad phylogenetic scales, historical contingency has set display evolution in the Western and Eastern Caribbean radiations along opposing evolutionary paths. At finer phylogenetic scales (within the clades), ecological determinism – in this case, from plasticity rather than evolutionary responses to selection – accounts for variation among closely related species. In fact, the magnitude of divergence between the two clades for the subset of species on Jamaica and Puerto Rico became even

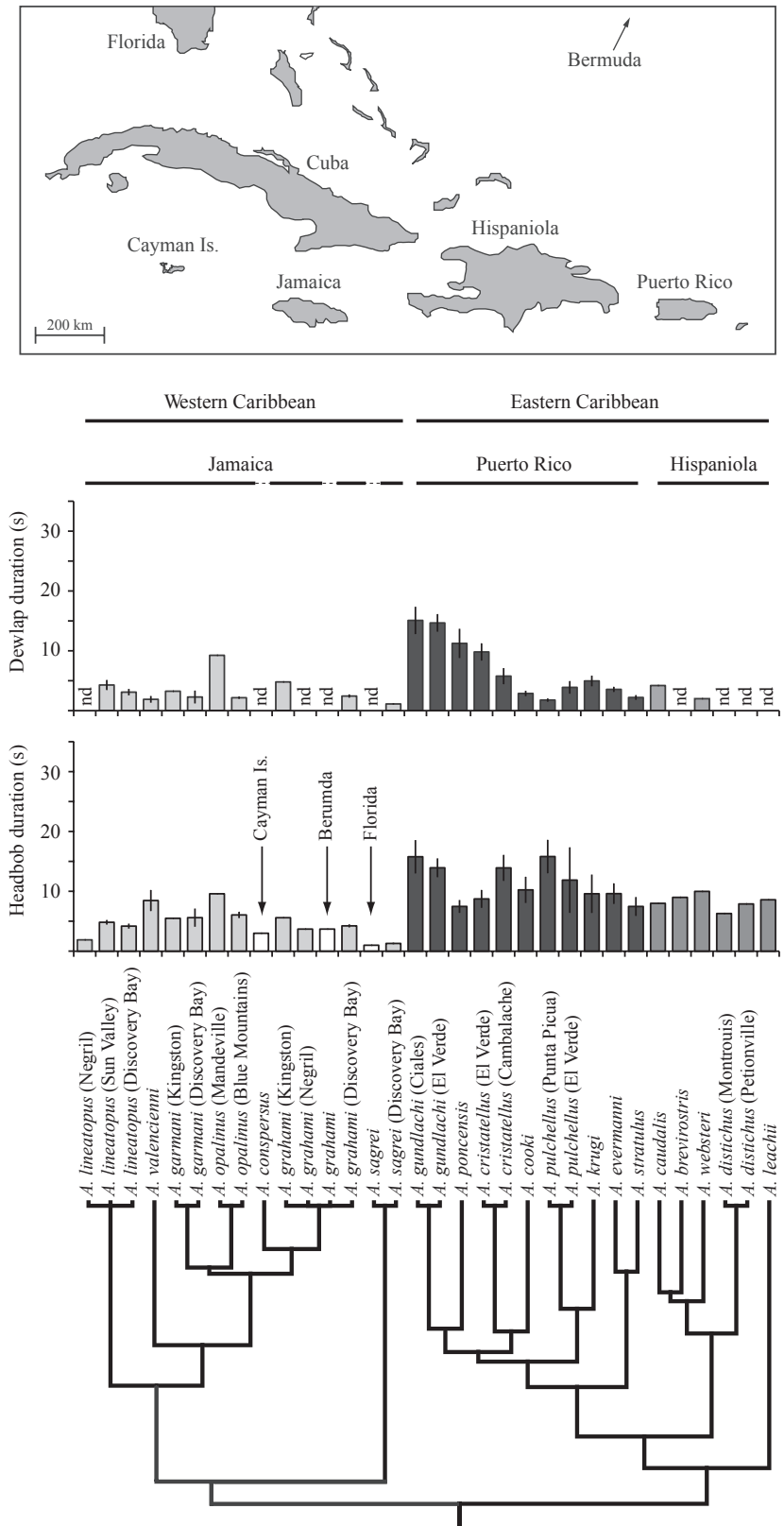


Fig. 1 Variation in headbob and dewlap duration contrasted with phylogenetic relationships among taxa. Error bars are 95% confidence intervals and indicate taxa for which data were compiled from display videos. Data for taxa lacking error bars were compiled from the literature ('nd' refers to no data). The tree is based on the mitochondrial phylogeny developed by Nicholson *et al.* (2005) and reproduced by Losos (2009) with branch lengths scaled proportional to time. Divergence among replicate populations of the same species was not represented in this species tree and was set here using the minimum level of population divergence reported among Jamaican species by Jackman *et al.* (2002).

Table 1 Support for alternative models of display evolution.

Model applied	AICc	Δ AICc	AICw	r^2	$t_{1/2}$ (support region)	v_y (support region)
Headbob duration						
Contingency	156.1	0.0	0.98	0.40	4.0 (0.5, 15.0)	6.0 (3.5, 12.5)
Selection regime	164.6	8.5	0.01			
Random change	166.5	10.4	0.01			
N_{taxa}	32					
Dewlap duration						
Random change	130.8	0.0	0.54	0.00	3.5 (0.5, 13.5)	14.0 (8.0, 30.0)
Contingency	131.8	1.0	0.33	0.08	3.0 (0, 12.5)	12.5 (8.0, 26.5)
Selection regime	133.7	2.9	0.13			
N_{taxa}	23					

Support regions for $t_{1/2}$ and v_y are the lowest and highest values within two log-likelihood units of the best estimate. The amount of variation explained by the most supported models is given by r^2 .

greater in a previous study that controlled for the plasticity of display duration (see fig. 4 in Ord *et al.*, 2010). This scale-dependent pattern is consistent with Gould's reputed position that historical contingency leaves its biggest mark over broad evolutionary time scales (Beatty, 2006).

It follows that the likelihood of adaptive convergence will be historically contingent as well: the more distantly related species are, the less likely they will respond in a similar manner to common selection pressures. Indeed, examples of convergent evolution are often among species of the same genus or closely related genera (e.g. Losos *et al.*, 1998; Taylor & McPhail, 2000; Blackledge & Gillespie, 2004; Rosenblum, 2006). The notion that convergent evolution is historically contingent is intuitive, but needs to be tested. One approach is a meta-analysis that plots the number of studies reporting convergence (or the number of phenotypic characteristics exhibiting convergence within taxa) against the phylogenetic distance between the taxa in question. If historical effects tend to constrain the likelihood of convergence, then the number of examples should decrease with phylogenetic distance. The present study shows that even aspects of the phenotype that respond quickly to short-term fluctuations in the environment (in this case behaviour that is plastic) can still be historically contingent, leading to the additional prediction that correlations between convergence and phylogenetic distance should be general, regardless of the type of phenotypic characteristic examined (morphology, behaviour, etc.).

A related question is the role that historical contingency plays in promoting the evolution of innovation and novelty. All the *Anolis* species examined in this study use displays to advertise and defend territories. For these displays to be effective, they must be readily detected by conspecifics, and detection is dependent on the type of environment in which displays are being viewed (e.g. Ord & Stamps, 2008). In noisy environ-

ments, extending the duration of those displays should enhance communication by increasing the chance that territorial neighbours will see the display (c.f. Wiley, 2006). Holding the dewlap open for longer periods will also allow conspecifics time to evaluate the dewlap more efficiently in dimly lit environments (Ord & Martins, 2006; NB: the colour and size of the dewlap probably conveys important information on species identity (Williams & Rand, 1977; Losos, 1985; Nicholson *et al.*, 2007) and potential fighting ability of males (Vanhooydonck *et al.*, 2005)). Some of the variance in display duration among Jamaican taxa does appear to be correlated with the type of habitat in which lizards advertise territories (Ord *et al.*, 2010), but Jamaican taxa and other members of the Western Caribbean radiation are generally predisposed to perform displays of short duration.

Rather than extend display durations, most Jamaican lizards rely on the rapid extension of the dewlap (Ord *et al.*, 2010, 2011). Robot playback experiments have shown that high-speed dewlapping is an effective means of maintaining a conspicuous display in low light (Ord & Stamps, 2008). I have no information on the speeds of dewlap extensions for other Western Caribbean species not found on Jamaica, but it appears that the innovation of alternative signal strategies in the ancestors of the two clades set the two clades on different evolutionary trajectories. Whether this innovation was initiated by a historical constraint on display duration in the ancestor of the Western Caribbean clade, or whether it subsequently negated changes to display duration in descendent taxa at the outset, is unknown (NB: in the latter scenario, ecological determinism led to historically contingent phenotypes). In either case, the effect of history appears to have prompted evolutionary innovation (here, the evolution of different ways of performing a conspicuous display).

The extent that adaptation occurs, and to what end, when organisms are predisposed to follow certain evo-

lutionary paths because of past selection and chance events, compounded by the additional stochastic element of mutation, is poorly understood. Both evolutionary history and contemporary selection regimes are predicted to generate or restrain phenotypic diversity (Gould, 1989; Losos, 2009), and both can be expected to interact in complex ways (Langerhans & DeWitt, 2004). Much research has been devoted to identifying the sources and strength of selection that might be acting on organisms today (Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001). We know much less about how an organism's evolutionary history can affect the extent organisms can respond to those selection pressures. This represents an important gap in our knowledge of how evolution unfolds.

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