

LETTER

Deep-time convergent evolution in animal communication presented by shared adaptations for coping with noise in lizards and other animals

Terry J. Ord¹  | Danielle A. Klomp¹ | Thomas C. Summers¹ | Arvin Diesmos² | Norhayati Ahmad³ | Indraneil Das⁴

¹Evolution & Ecology Research Centre and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

²Herpetology Section, Zoology Division, National Museum of the Philippines, Manila, Philippines

³Department of Biological Sciences and Biotechnology, Universiti Kebangsaan Malaysia, Bangi, Malaysia

⁴Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Kota Samarahan, Malaysia

Correspondence

Terry J. Ord, Evolution & Ecology Research Centre and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia.
Email: t.ord@unsw.edu.au

Funding information

University of New South Wales (UNSW)

Editor: Greg Grether

Abstract

Convergence in communication appears rare compared with other forms of adaptation. This is puzzling, given communication is acutely dependent on the environment and expected to converge in form when animals communicate in similar habitats. We uncover deep-time convergence in territorial communication between two groups of tropical lizards separated by over 140 million years of evolution: the Southeast Asian *Draco* and Caribbean *Anolis*. These groups have repeatedly converged in multiple aspects of display along common environmental gradients. Robot playbacks to free-ranging lizards confirmed that the most prominent convergence in display is adaptive, as it improves signal detection. We then provide evidence from a sample of the literature to further show that convergent adaptation among highly divergent animal groups is almost certainly widespread in nature. Signal evolution is therefore curbed towards the same set of adaptive solutions, especially when animals are challenged with the problem of communicating effectively in noisy environments.

KEYWORDS

adaptive differentiation, contextual plasticity, historical contingency, repeated evolution, robotic playbacks

INTRODUCTION

Animals relying on signals for similar functions—for example, attracting mates or defending territories—and trying to communicate under similar environmental conditions are expected to converge in signal characteristics (Marler, 1967). This is because natural selection should only favour those strategies that maximise the detection and recognition of communicative signals in those environments (Endler, 1992). For example, communication theory (Dusenbery, 1992; Wiley, 2006) posits that animals should produce signals that maximise the signal-to-noise ratio with the environment through changes in the intensity of signalling or redundancy of information conveyed. Yet the convergent evolution of

common communicative strategies does not appear to be as likely as convergence in morphology (Ord & Summers, 2015; York & Fernald, 2017; these two studies examined over 120 examples of convergent, parallel and functionally redundant adaptations repeatedly arising from independent evolution). This is despite behaviour putatively being more evolutionarily labile than morphology (Blomberg et al., 2003) and efficient communication being central to the reproductive fitness of many animals (Bradbury & Vehrencamp, 2011). However, this could be because there are countless ways in which animals might maximise signal-to-noise ratios, making signal convergence improbable.

Of the examples of convergence in animal communication, most are between populations of the same species

(Kemp et al., 2018; Ng et al., 2013) or taxa that are otherwise closely related (Henry et al., 1999; Ord et al., 2013b). This in itself is not unusual for adaptive convergence (Ord & Summers, 2015; Vermeij, 2006). It could reflect adaptive outcomes being predisposed along common evolutionary trajectories because of shared genetic and developmental pathways between closely related taxa (Conte et al., 2012; Stern, 2013; these two studies examined over 40 cases of parallel evolution—i.e., instances of similar outcomes evolving independently through common genetic pathways). It might also reflect a systematic bias in studies being skewed towards documenting convergence in closely related taxa (Ord & Summers, 2015). This is an issue for our general understanding of the adaptive process, as it remains unclear whether a multitude of adaptive solutions exists for the same selection pressure—with adaptations only tending to converge among closely related taxa—or whether natural selection repeatedly produces the same set of adaptations

irrespective of the length of time taxa have evolved independently of one another.

To help resolve the issue, we examined lizards from the Old World iguanians (the family Agamidae) and New World equivalent (the family Iguanidae) that rely heavily on vision for social communication (Jenssen, 1977; Ramos & Peters, 2016). In these families, visual signals are vital for male lizards to establish and maintain territories (Jenssen et al., 2012; Ord, 2008). Signals are usually centred on the performance of an elaborate sequence of head and body movements that convey reliable cues on physical condition (Brandt, 2003; Perry et al., 2004) and, subsequently, their potential ability to aggressively defend territory (van Dyk & Evans, 2008). The detection of lizard territorial displays is also known to be acutely dependent on the properties of the environment. Previous work on male iguanid *Anolis* lizards in the Caribbean has shown that the speed (intensity) and duration (redundancy) of territorial displays are contextually plastic within some species (Table 1), and evolutionary differentiated across species, as a function of habitat light and background visual noise generated by windblown vegetation (Ord et al., 2010a, 2016). This is an adaptive outcome predicted by communication theory (Dusenbery, 1992; Wiley, 2006).

It is unknown, however, whether the distantly related species of the agamid family have converged on the same signal strategies in response to the same environmental conditions. An informal comparison between the Caribbean iguanid *Anolis* lizards (Ord et al., 2010a) and some Australian and Chinese agamid species (Peters et al., 2007; Peters et al., 2016; Ramos & Peters, 2017a) suggests this is not the case. However, the ecology of these particular agamid species is fundamentally different from the iguanid *Anolis*, making the comparison problematic. These agamids communicate in open, sunny environments and from locations close to (or on) the ground, where the visual environment is likely to be quite different to the arboreal, and often forested, environments occupied by the *Anolis* lizards. Visual noise from windblown vegetation does appear to be a masking agent for the displays of at least one agamid species (Peters, 2008), but these lizards rely on an intermittent series of rapid tail flicks for enhancing detection (Peters et al., 2007), a behaviour unlike anything seen in the iguanid lizards (including *Anolis*). More generally, the repertoire of signal components used in territorial advertisement display—and that could be modified to improve detection in visually difficult conditions—differs between the iguanids and agamids, at least on first examination (presented below).

On the opposite side of the world to the Caribbean iguanid *Anolis* lizards, and separated by over 140 million years of divergent evolution history (Kumar et al., 2017), are the Southeast Asian agamid *Draco* lizards (Figure 1). Unlike other agamid groups, *Draco* is a remarkable ecological analogue to the *Anolis*. Although

TABLE 1 Glossary of terms

Term	Definition
Contextual plasticity	Reversible changes in behaviour in response to fluctuations in external environmental stimuli (see Stamps & Groothuis, 2010). This has also been referred to as ‘activation plasticity’ (Snell-Rood, 2013) and ‘reversible phenotypic plasticity’ (Wright & Turko, 2016)
Contextual reaction norm	Behaviour described by the regression line computed from the response of behaviour to external environmental stimuli. The slope of the line reflects the contextual plasticity of behaviour as a function of fluctuations in environmental stimuli, whereas the intercept of the line represents the ‘baseline’ behaviour that would be expected at a specific value of the environmental stimuli
Within-taxon intercept	The ‘baseline’ behaviour that would be observed under a standard environmental condition, specifically when the external stimulus affecting behaviour has a value of zero. This intercept value can be used to identify the portion of behaviour that is not contextually plastic and potentially the product of evolutionary differentiation (see Ord et al., 2010a)
Within-taxon mean	The average phenotypic value (e.g., behaviour) or average environmental value (e.g., ambient light) exhibited or experienced by individuals of a given taxon
Within-taxon slope	The average contextual plasticity expressed by individuals of a given taxon in response to fluctuations in external environmental stimuli

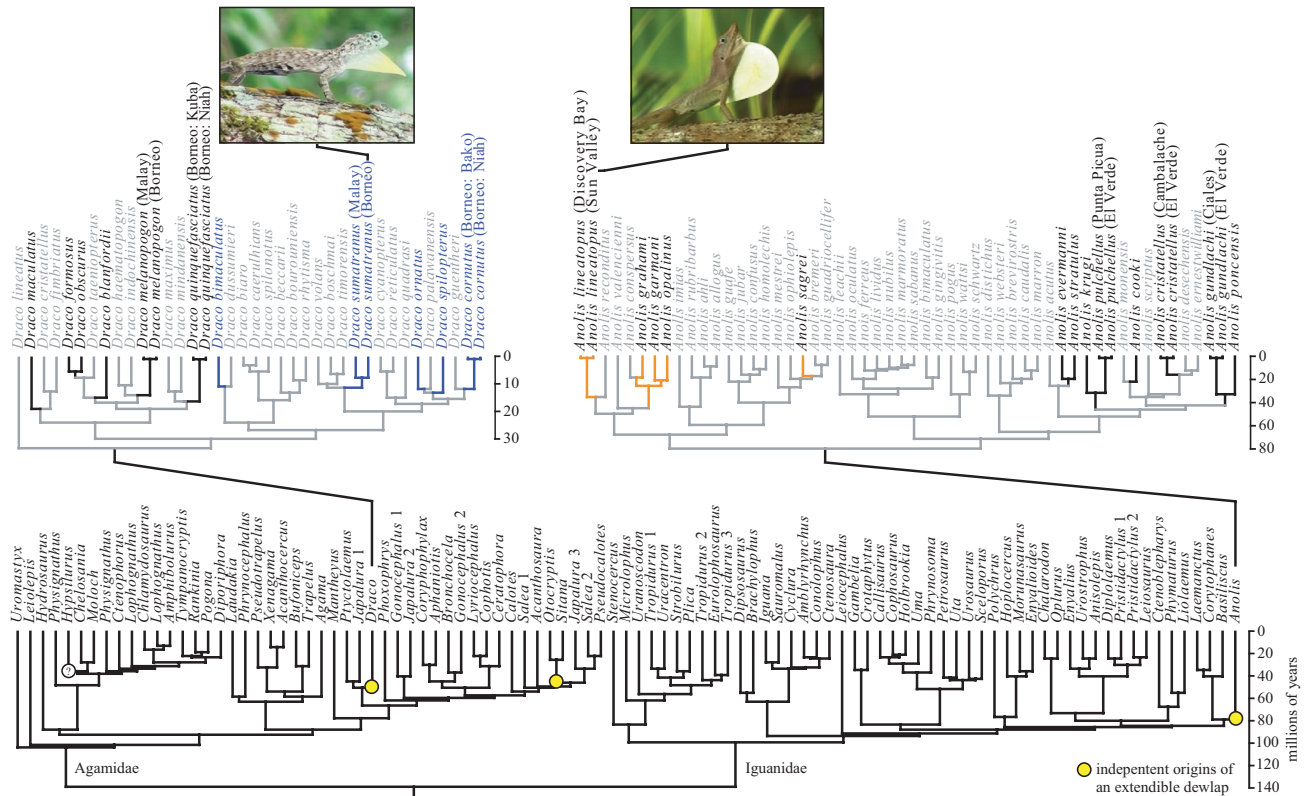


FIGURE 1 Phylogeny of agamids and iguanids highlighting the independent origin of the dewlap in Southeast Asian *Draco* and Caribbean *Anolis*. Territorial advertisement displays of free-ranging male lizards were investigated for species from the Malay and Philippine radiations of *Draco* (highlighted in blue and black, respectively) and the island radiations of *Anolis* on Jamaica and Puerto Rico (orange and black, respectively). The inset photos depict *Draco sumatranus* on Borneo and *Anolis lineatopus* on Jamaica in mid-display with the dewlap fully extended. Highlighted are the phylogenetic nodes identifying the historic origin of an extendible dewlap in *Draco*, *Anolis*, *Sitana*–*Otocyrtis* and possibly *Hypsilurus* (Ord et al., 2015)

there are obvious differences between the two groups—*Draco* is the only group to have evolved the ability to glide (Ord et al., 2020)—*Draco* and *Anolis* lizards are both arboreal, share key morphological adaptations to common structural environments (convergent limb lengths as a function of perch circumference as well as other aspects of ecomorphology; Ord & Klomp, 2014) and employ remarkably similar movements in their territorial displays (Mori & Hikida, 1994). In particular, both *Draco* and *Anolis* have independently evolved a large, conspicuous dewlap (Ord et al., 2015) that is extended and retracted as part of a main territorial display. Only one, or at most two, other lizard groups in the world exhibit this same extendible dewlap (Figure 1), which appears to have evolved to improve the efficiency of territorial displays in forested environments (Ord et al., 2015).

Moreover, both the complexity of headbob movements and the evolution of the dewlap (Figure 1) are characteristics that have independently—convergently—evolved in *Draco* and *Anolis*. Although the use of head movements for aggressive display is probably ancestral in iguanian lizards as a whole (Ord et al., 2001)—and has subsequently been retained in the signal repertoire of most agamid and iguanid genera—the similarity and

complexity in the design of the advertisement display between *Draco* and *Anolis* are unique and striking (Mori & Hikida, 1994). In contrast, the displays of other iguanids such as *Microlophus* (Clark et al., 2015), *Cyclura* (Martins & Lamont, 1998), *Sceloporus* (Martins, 1993) and *Liolaemus* (Martins et al., 2004; to mention only a subset of genera: see Carpenter, 1986 for a comprehensive list) are comparatively simple in design, consisting of fewer elaborations in the temporal sequence and amplitude of head movements. This is similarly the case for other agamid genera such as *Ctenophorus* (Ramos & Peters, 2017b), *Phrynocephalus* (Peters et al., 2016) and *Amphibolurus* (Peters & Ord, 2003). However, many agamids augment their territorial display with an extended repertoire of movements that include arm waves and a range of tail displays (see Ramos & Peters, 2016 for a comprehensive review of agamid signal repertoires).

Despite the similarities in the behaviour of male *Draco* and *Anolis* lizards, there are numerous alternative ways that these lizards might achieve an effective signal. This includes the addition of alert components such as rapid tail flicks (Peters et al., 2007) or other conspicuous movements (Ord & Stamps, 2008), an increase in signal repetition (Patricelli & Blickley, 2006), or the use of colour

or the exaggeration of other morphology (Klomp et al., 2016). It therefore remains unclear whether Southeast Asian *Draco* and Caribbean *Anolis* have similarly converged on the same set of communicative strategies for maintaining efficiency in the range of seemingly comparable environments occupied by both groups.

To determine convergence requires a method for quantifying the display behaviour of these lizards and the environments in which they communicate in a biologically meaningful way. A second method is then needed to experimentally manipulate the display movement of free-living animals to test hypotheses related to signal perception. Ideally, this experimental test should be done under the same conditions typically experienced by animals in the wild. Given the technical challenges on both of these fronts, it is perhaps not surprising that our understanding of animal movement in communication has lagged considerably behind animal colour (Cuthill et al., 2017) and bioacoustics (Wiley, 2015). Yet movement-based signals are ubiquitous in nature (Bradbury & Vehrencamp, 2011), and even taxa popularly known for their spectacular ornamentation usually rely on a movement display to present those ornaments effectively (e.g., birds-of-paradise: Ligon et al., 2018; peacocks: Yorzinski et al., 2013; and swordtail fishes: Rosenthal et al., 1996).

Motion analysis (Peters et al., 2002) has helped solve the first challenge of appropriately quantifying complex behaviour, although it is seldom used by communication biologists because it remains computationally demanding. Based on models of biological visual systems (Peters et al., 2002), computational motion analysis has proven highly effective at quantifying the movements and visual environments of free-living animals through the analysis of high-definition digital video recorded in the field. We combined this approach with conventional measures of ambient light to quantify the speed and duration of male *Draco* advertisement displays in relation to ambient light and visual background noise at the time displays were performed. Our goal was to use predictions from communication theory of how animals should maximise signal-to-noise ratios in their respective environments (Dusenbery, 1992; Wiley, 2006) as a framework for then identifying convergences in signal behaviour. Specifically, we wished to determine whether Southeast Asian *Draco* lizards and Caribbean *Anolis* lizards have converged on modifications to the speed (intensity) and duration (redundancy) of territorial advertisement displays according to the prevailing conditions experienced at the time of display (through contextual plasticity; Table 1) and the extent to which predictable evolutionary differentiation has occurred in displays along common environment gradients.

The development of robot playbacks (Martins et al., 2005; Ord & Stamps, 2009) that allow display movements to be manipulated in a realistic manner is technically difficult but offers a powerful solution for the second problem of experimentally testing the adaptive significance

of changes in communicative behaviour. Here, we used responses to robotic playbacks by free-ranging male lizards to experimentally confirm that the most prominent convergence in behaviour is adaptive because it improves the detection of displays under the same conditions lizards advertise territorial ownership to one another.

Finally, we supplemented our empirical study on *Draco* and *Anolis* with a targeted review of past reports of signal adaptation to noisy environments in other communication systems. Our goal here was to identify reports in phylogenetically diverse taxa to highlight other likely cases of signal convergence among major animal groups. All in all, the overarching motivation of our study was to determine whether convergent adaptation is generally less likely between species separated by vast periods of evolutionary time or whether natural selection in contemporary environments overrides the vagaries of evolutionary history to produce consistent adaptive solutions among taxa irrespective of the evolutionary time separating taxa.

MATERIALS AND METHODS

Our investigation involved three parts: (i) an evaluation of the extent to which *Draco* and *Anolis* lizards have converged on common communicative strategies in response to the same environmental conditions (ambient light and visual background noise); (ii) an experimental confirmation that convergence is adaptive by improving signal detection under the same visually challenging conditions experienced by lizards in the wild; and (iii) the identification of probable adaptive convergences in communication in response to environmental noise among major animal lineages (birds, lizards, mammals, frogs, fish and insects). A summary of methods is presented below, with full details provided in the supporting information.

Communicative strategies of *Draco* and *Anolis* in response to common environmental conditions

Field observations and recording

We studied multiple free-living territorial males of *Draco* (median per taxon = 14; range: 2–32) for 15 taxa (11 species, four of which were each represented by two geographically separated populations) from Peninsular Malaysia, Borneo and the Philippines. We combined these data with those previously published on free-living territorial males of *Anolis* (median per taxon = 36; range: 8–41) for 16 taxa (12 species, four of which were each represented by two geographically separated populations) from Puerto Rico and Jamaica (Ord et al., 2010b). The protocols used to observe lizards, videorecord behaviour and collect data on ambient habitat light were identical for both the Southeast Asian *Draco* and Caribbean

Anolis. Table S1 provides location details and sample sizes for each taxon surveyed.

Video and computational motion analysis

The protocols for processing and analysing videorecords follow those established by Ord et al. (2007) and were identical for the Southeast Asian *Draco* and Caribbean *Anolis*. We relied on estimates of maximum speed for display movements because this corresponds to bursts of rapid movement most likely to trigger orienting responses from inattentive receivers (Ord et al., 2007; Ord & Stamps, 2008). For consistency and ease of data presentation, maximum speed was similarly used to quantify the magnitude of visual noise occurring in image backgrounds (NB: maximum and mean background speed are highly correlated; see Ord et al., 2007). We examined display duration because this aspect of signal redundancy has been shown explicitly in *Anolis* to change in response to fluctuations in environmental conditions (Ord et al., 2010a), and our goal was to determine whether this was also the case in *Draco*. Increasing the rate of signal production might also function to increase redundancy, but this is not the case for *Anolis* (Ord et al., 2010a) where display rate is instead heavily dependent on air temperature (Ord & Stamps, 2017).

Statistical analyses

All statistical analyses were performed using R Version 3.5.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna).

Previous work (Ord et al., 2007, 2016) has shown contextual reaction norms (Table 1) of display behaviour as a function of light and visual noise can be computed across individuals for a given population to infer the average contextual reaction norm within individuals for that population. These within-taxon (average) contextual reaction norms were computed for territorial advertisement displays using the package ‘lme4’ Version 1.1-18-1 (Bates et al., 2015). A range of models was applied that considered various combinations of visual background noise, ambient habitat light and radiation history (lineages originating in Malaysia versus the Philippines for *Draco* or on Jamaica versus Puerto Rico for *Anolis*; see Table S2 for complete model list). The best supported contextual reaction norm model was identified by comparing values of a sample size corrected Akaike information criterion (AIC_c).

Two sets of evolutionary Ornstein–Uhlenbeck (OU) regression analyses were conducted to assess taxon differentiation in territorial advertisement displays using the package ‘phylolm’ Version 2.6 (Ho & Ane, 2014; NB: various other phylogenetic covariance models were also examined and found to produce congruent outcomes

to the OU option—see the supporting information for details). The first set was based on within-taxon mean values (the traditional species mean approach used by comparative evolutionary biologists; Table 1) and assessed mean visual background noise, mean ambient habitat light and radiation history in a comparable set of models to those used to compute contextual reaction norms (see previous paragraph; see Table S4 for complete model list). AIC_c was then used to identify the best supported evolutionary model accounting for display differentiation across taxa. The second set substituted taxon-mean display values with within-taxon intercept ‘baseline’ values (Table 1) extracted from the best supported contextual reaction norm model. These secondary analyses were limited to the best supported models found in the first set of OU regression analyses. They were designed to assess macroevolutionary relationships between display and habitat across taxa that were not the result of contextually plastic display changes (e.g., Ord et al., 2010a).

Ambient light, dewlap duration and headbob duration were log10-transformed prior to analysis to improve normality. For *Draco*, we focused on estimating the contextual reaction norms of the nine taxa with the largest within-taxon sample sizes (Table S1). This was further limited to three taxa for estimates of headbob display reaction norms because species from the Malay radiation were discovered to have lost this component entirely from their territorial advertisement displays. The evolutionary OU regression analyses using mean-taxon values included all 14 taxa for dewlap analyses and up to five taxa belonging to the Philippine radiation for the headbob analyses. Those based on within-taxon intercept values were necessarily restricted to those taxa included in the contextual reaction norm analyses. The phylogeny of *Draco* was taken from Ord et al. (2020), with populations within taxa inferred assuming the minimum intra-island population divergence reported for Philippine *Draco* by McGuire and Heang (2001). For *Anolis*, one species (*Anolis poncensis*) had a vastly reduced dewlap to the extent that it was functionally absent from the display (Ord et al., 2013a) and was not included in analyses of the dewlap display. The phylogeny of *Anolis* was taken from Nicholson et al. (2005), with populations within taxa extrapolated on both islands assuming the minimum intra-island population divergence that has been reported for Jamaican *Anolis* reported by Jackman et al. (2002).

Confirmation that increases in speed improve display detection

Robot playback experiment

In a previous experiment on *Draco melanopogon* (Klomp et al., 2017a), the role of dewlap colour on signal detection and species recognition was investigated by presenting

free-living lizards with a moving dewlap matched to the average size, spectral colour and temporal sequence of males in life. Colour was not found to influence display detection (Klomp et al., 2017a). Serendipitously, it was later discovered that two of the robots used in that experiment differed in the speed of the dewlap extension: one robot extended and retracted the dewlap at a speed that was equivalent to the slowest natural speed recorded for male *D. melanopogon*, whereas the other robot had a dewlap speed comparable with the upper quartile of natural dewlap speeds recorded for male *D. melanopogon*. Given this new information, we conducted a new set of analyses for the purposes of the current study using the published data of Klomp et al. (2017b) on the latency of *D. melanopogon* lizards to orient towards these two dewlapping robots. These robotic stimuli were presented to free-living lizards under the same environmental conditions these animals communicate with one another.

We focused our analyses on data obtained when robots were positioned within 5 m of the subject. This distance encompasses the natural quartile range of distances documented for surrounding male neighbours in this population (DAK unpublished data). We further limited our analyses to only those robot playbacks that presented a dewlap pattern within the natural range of male *D. melanopogon* lizards (specifically the two-coloured treatments reported in Klomp et al., 2017a).

Statistical analyses

Robot playback detection times were first log₁₀-transformed to improve normality and then evaluated using linear models that considered various combinations of lizard sex, robot, light (log₁₀-transformed) and their interactions (see Table S7 for full list of models applied). The best supported model was identified using AIC_c.

Identification of other deep-time convergences

We considered three common signal strategies that animals are known to adopt for enhancing the efficiency of communication in challenging environmental conditions. The first was centred on changing the intensity of signals and is frequently reported in acoustically communicating species: increasing the volume of vocalisations in order to be heard above acoustic background noise. The second was centred on increasing redundancy in signalling and was broadly applicable to many modes of communication: extending the duration of signal production to allow more time—and subsequently a greater probability—for detection to occur in noisy conditions. The third was centred on improving signal efficiency by simply waiting for lulls in environmental noise before

emitting signals and, in doing so, avoiding or reducing the impact of noise on signal detection.

We identified representative examples of each strategy reported in a bird, lizard, mammal, frog, fish or insect species, based on our general knowledge of the communication literature. Where an example was not immediately obvious, the datasets of two major meta-analyses (Kunc & Schmid, 2019; Roca et al., 2016) were consulted to identify possible examples for acoustically communicating animals. This was also supplemented with a general search of the ISI Web of Science online database. Our estimate of the time since the last common ancestor shared between groups was based on the median value extracted from the ‘TimeTree’ online database (www.timetree.org; see Kumar et al., 2017).

RESULTS

Communicative strategies of *Draco* and *Anolis* in response to common environmental conditions

We applied random regression models (also known as mixed-effects models or hierarchical regression models) to compute within-taxa contextual reaction norms, in which the parameter estimates for the slope measure contextual plasticity (Table 1): specifically, changes in display speed or duration as a function of fluctuations in ambient light, visual background noise or both. We found clear evidence that male *Draco* lizards have evolved the ability to contextually vary both the speed and duration of their territorial advertisement displays, depending on the amount of ambient light and background visual noise occurring at the time of display, and that this behaviour was statistically identical to that documented in Caribbean *Anolis* male lizards (Figure 2a,b; Figure S1 and Tables S2 and S3).

Likewise, remarkably similar convergences were apparent in how male display speeds have differentiated along parallel environmental gradients within *Draco* and *Anolis*. Taxon-mean display values were entered into evolutionary OU regression models (Figure S1; Table S4), and outcomes were again broadly consistent between *Draco* and *Anolis* (Table S6 also confirms that these findings were not dependent on the particular phylogenetic covariance model applied). Those species and populations advertising territory ownership in windier environments of high visual noise employed, on average, faster dewlap and headbob movements in their displays compared with other *Draco* or *Anolis* taxa defending territories in calmer, low visual noise environments (Figure 2c).

Nevertheless, the process by which this display differentiation has been achieved differs between the two groups. We used the intercept values from the within-taxa contextual reaction norms (Figure 2a,b) to compute ‘baseline’ display phenotypes (Table 1) that

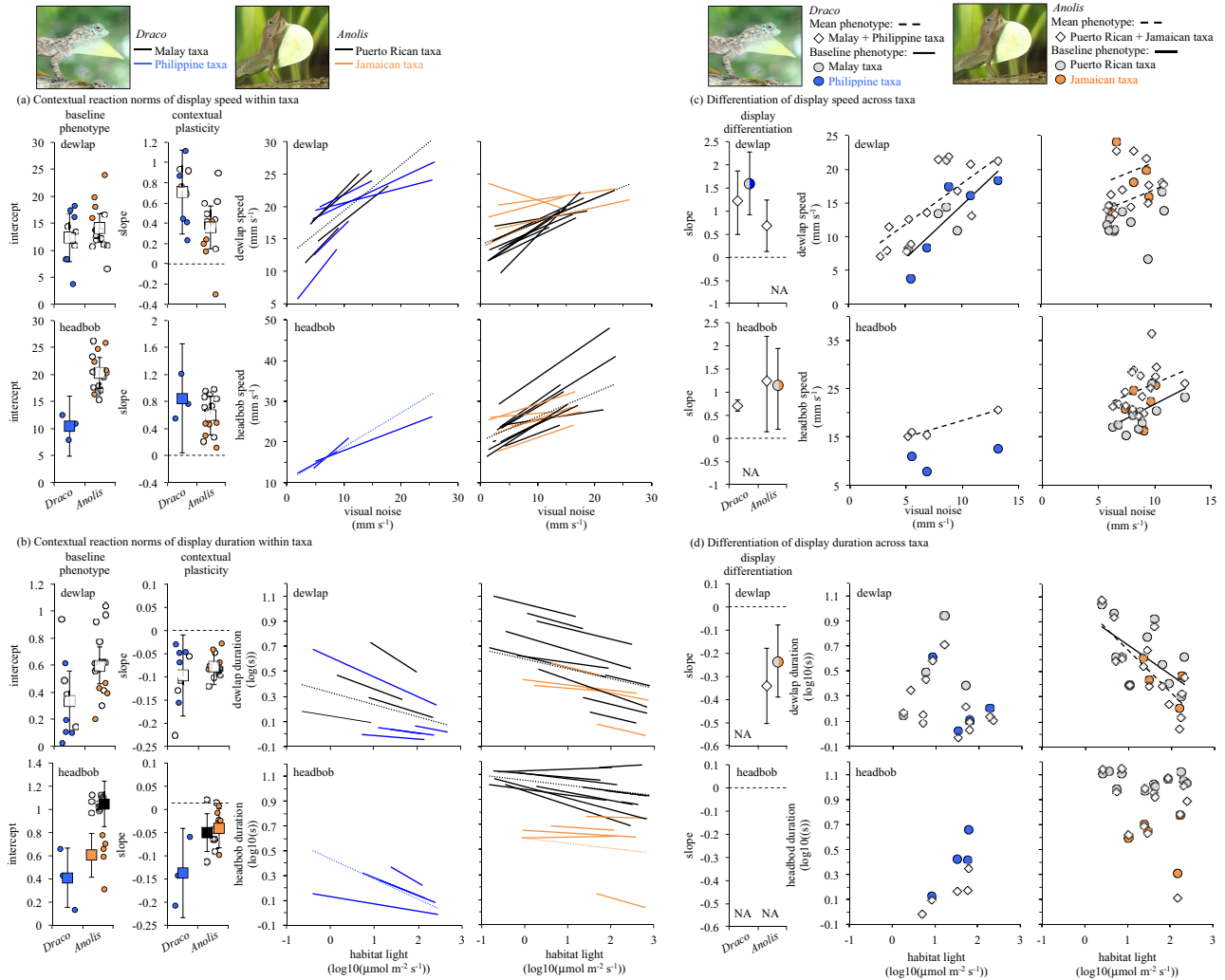


FIGURE 2 Multiple facets of convergence in territorial advertisement displays between male Southeast Asian *Draco* and Caribbean *Anolis* lizards in response to visual background noise from windblown vegetation and habitat light. Convergence is apparent in both the manner in which individual lizards tailored displays on a moment-to-moment basis to surrounding conditions (through contextual plasticity: a, b) and to some extent in how taxa differentiated the overall speed of displays when communicating in comparable noise environments (through a combination of contextually plastic and noncontextually plastic changes; c, b). The Malay *Draco* were discovered to have lost the headbob component entirely from their display and are therefore not represented in plots for headbobs. Parameter estimates and graphical representations of computed contextual reaction norms within taxa of (a) display speed and (b) duration (see also Table S3) show the baseline display phenotype (within-taxon intercepts) and the contextual plasticity of displays (within-taxon slopes) as a function of visual noise or ambient light at the time of display. Dot points and solid trend lines in (a) and (b) represent reaction norms for each taxon separately, computed over the range of environmental conditions experienced by that taxon, whereas the square points ($\pm 95\%$ confidence limits) and the dotted trend lines show the average computed reaction norm for the genus. Differentiation in (c) display speed and (d) display duration across taxa is reflected as on-average divergences in display (the ‘mean phenotype’; diamond symbols and dashed trend lines) that do not take into account contextual plasticity, and ‘baseline phenotype’ (within-taxon intercept values; circle symbols and solid trend lines; see also Table S5) taken from each taxon’s computed contextual reaction norm. These latter values effectively remove differences in display resulting from contextual plasticity and potentially represent evolutionary divergences in display. Trend lines are shown for slopes that were statistically distinguishable from zero. Both the mean phenotype (plastic) and the baseline phenotype (nonplastic) show the extent to which territorial advertisement displays have differentiated along common habitat gradients of visual noise and light

measure variation among taxa that is not the product of momentary fluctuations in environmental conditions (i.e., plasticity). These baseline display values were entered into the same evolutionary OU regression models used for taxon-mean display analyses (Table S5). In the case of male *Draco* lizards, baseline display speeds, for at least dewlap speed, have differentiation across taxa in a manner consistent with evolutionary changes in

behaviour (Figure 2c). In contrast, much of the variation across *Anolis* taxa in display speed can be attributed to within-taxon contextual plasticity, with only the speed of headbob movement likely exhibiting evolutionary differentiation across visual noise gradients (Figure 2c; Table S5).

There were other differences in communication behaviour between the two lizard groups as well (see

Figures S1 and S2; Tables S4 and S5). In particular, there were notable differences reflecting clad history within each group. We discovered male *Draco* lizards from one radiation appear to have lost the headbob from their display repertoire entirely (those from the Malay clade; Figure 2) and instead concentrate on the rapid deployment of the dewlap for territorial advertisements. The contingent effects of radiation history have been less extreme in *Anolis*, but our analyses reiterate past findings (Ord et al., 2010) that male Jamaican lizards use shorter territorial advertisement displays centred on the rapid extension of the dewlap. In contrast, male Puerto Rican lizards employ longer and more plastic displays overall (Figure 2; Figure S1). Both strategies are likely effective for signal detection (Ord & Stamps, 2008), but the dewlap display is presumably less costly in energy expenditure (Ord et al., 2013a). In this context, the switch to an exclusive dewlap-only territorial display in Malay *Draco* is intriguing.

Confirmation that increases in speed improve display detection

We experimentally confirmed that the speed of dewlap movements is important in the detection of territorial advertisements by male *Draco* lizards and in the same way as previously reported for male *Anolis* lizards (Ord & Stamps, 2008). A robotic system was used to 'play-back' displays to free-living *D. melanopogon* lizards, a dewlap-only species from the Malay radiation that advertises territory ownership in a deep-shade montane forest. Males detected the robot with the faster dewlap display more quickly than the robot with the slower dewlap display (Figure 3b; Table S7). These responses mirrored those to robot playbacks conducted on territorial male lizards of Caribbean *Anolis gundlachi* on Puerto Rico that similarly advertise territory ownership in deep-shade montane forest (Ord & Stamps, 2008).

Identification of other deep-time convergences

Evaluating a sample of past reports relating to the three most common signal strategies used by animals to maintain signal efficiency in noisy conditions shows probable convergences in behaviour among most major animal lineages (Table 2). Modifying the intensity, level of redundancy or simply concentrating communication during relative periods of quiet are strategies that appear to have repeatedly evolved among groups separated by 282 million years (e.g., between birds and lizards) and as much as 736 million years (e.g., between fish and insects). Furthermore, these convergences are not restricted to communicative systems of certain modalities but cross acoustic, visual and tactile sensory modalities (Table 2). The impact of environmental 'noise' on communication

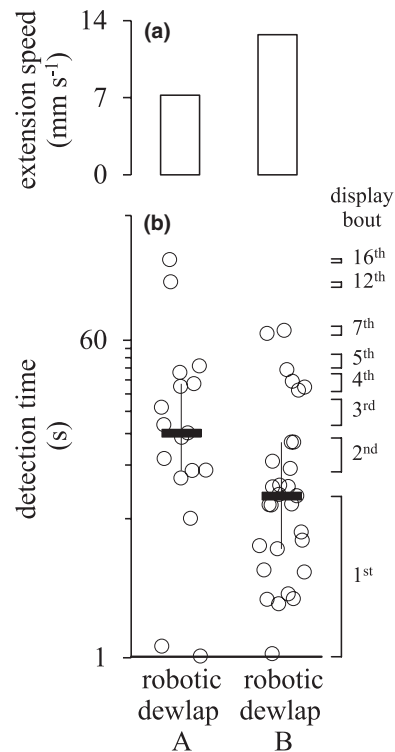


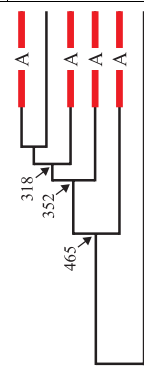
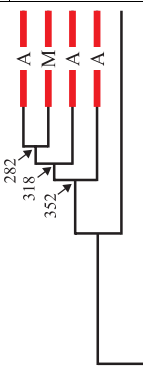
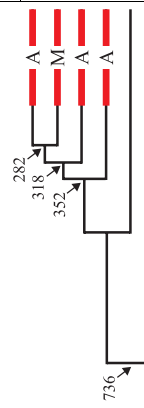
FIGURE 3 Detection of (a) robot territorial advertisement displays by (b) free-living male *Draco melanopogon* lizards. Males were presented with a robot that extended the dewlap either slowly (Robot A) or rapidly (Robot B; upper panel a). Most males detected the rapidly dewlapping robot by the end of its first display bout (approx. 8 s in duration), whereas most males detected the slowly dewlapping robot by the end of its second display bout (approx. 18 s later; lower panel b). Summary symbols for male detection times are the median \pm quartiles and are benchmarked against the timing of consecutive display bouts performed by the robot (42 males detected the robot within its first five display bouts, two males by its seventh display bout, one male by the 12th and the last male by the 16th)

is therefore ubiquitous in nature, and natural selection seems to have consistently produced a common set of signal strategies in animals faced with communication in such conditions.

DISCUSSION

All of the convergences uncovered in the speed and duration of territorial advertisement displays between Southeast Asian *Draco* and Caribbean *Anolis* are likely adaptive, irrespective of whether they reflect plasticity or an evolved display response to conditions typically experienced in a given habitat. The changes in signal intensity (speed) and redundancy (duration) found in both groups were predicted by communication theory (Dusenbery, 1992; Wiley, 2006) to enhance signal efficiency in 'noisy' conditions (here, low ambient light or high visual noise). We also confirm this adaptive function directly for both *Draco* (this study) and previously for *Anolis* (Ord & Stamps, 2008) in at least the speed of display movements,

TABLE 2 Deep-time convergences in animal communication in which the (a) intensity, (b) redundancy or (c) timing of signals have been reported to adaptively change in the same way to maintain efficacy in noisy conditions

		MYA since LCA	Lizard	Mammal (A)	Amphibian (A)	Fish (A)	Insect
(a) Increase call volume in noise		Bird (A)	no record as yet	318	352	465	no record as yet
		Lizard	-	no record as yet	no record as yet	no record as yet	no record as yet
		Mammal (A)	-	-	352	465	no record as yet
		Amphibian (A)	-	-	-	465	no record as yet
		Fish	-	-	-	-	no record as yet
		Insect	-	-	-	-	no record as yet
(b) Increase signal duration in noise		MYA since LCA	Lizard (M)	Mammal (A)	Amphibian (A)	Fish	Insect
		Bird (A)	282	318	352	no record as yet	no record as yet
		Lizard (M)	-	318	352	no record as yet	no record as yet
		Mammal (A)	-	-	352	no record as yet	no record as yet
		Amphibian	-	-	-	no record as yet	no record as yet
		Fish	-	-	-	-	no record as yet
		Insect	-	-	-	-	no record as yet
(c) Time signal production to exploit gaps in noise		MYA since LCA	Lizard (M)	Mammal (A)	Amphibian (A)	Fish	Insect (V)
		Bird (A)	282	318	352	no record as yet	736
		Lizard (M)	-	318	352	no record as yet	736
		Mammal (A)	-	-	352	no record as yet	736
		Amphibian (A)	-	-	-	no record as yet	736
		Fish	-	-	-	-	no record as yet
		Insect (V)	-	-	-	-	no record as yet

Notes: The signal mode affected: A, acoustic; M, movement; V, vibration. The remaining acronyms are as follows: MYA, millions of years ago; LCA, last common ancestor. Phylogenies to the left highlight lineages exhibiting convergent behaviour (in red) with time since LCA indicated at nodes. See Table S8 for species and associated sources of reports.

which increases detection of the territorial displays in visually difficult environments.

Such deep-time convergence—between groups separated by over 140 million years—is the first report for any movement-based visual communication system and the only confirmed example for any other form of communication involving species with such divergent evolutionary histories. This might imply that the adaptive convergence between Southeast Asian *Draco* and Caribbean *Anolis* documented here is extraordinary. But our study was unique in its phylogenetic perspective, and we argue that our findings have different ramifications from simply being a rarity of communicative convergence, which it is almost certainly not (see below).

Our broad synthesis of past reports of signal adaptation to noisy environments (Table 2; Table S8) implies that deep-time convergence—in general, not just animal communication—could be far more widespread than previously thought (Conte et al., 2012; Ord & Summers, 2015; Stern, 2013; York & Fernald, 2017; see also Vermeij, 2006). Furthermore, although the experienced communication biologist might recall the similar ways in which socially signalling animals seem to cope with environment noise, the extent to which this is the case among grossly disparate taxonomic groups is unlikely to be fully appreciated. This is now presented in Table 2 and has general implications for our understanding of both the magnitude of influence the environment has in steering the trajectory of signal evolution and the assumed precedence of evolutionary history in shaping contemporary adaptive evolution (reviewed by Ord & Summers, 2015).

First, acoustic communication appears to have evolved independently in birds, mammals and frogs (Chen & Wiens, 2020) and almost certainly in fish and insects as well. Excluding insects, all of the species so far examined in these lineages (Brumm & Zollinger, 2011) exhibit a common response of increasing the volume (intensity) of vocalisations to be heard above a noisy acoustic background (Table 2a). This is effectively the same strategy being used by visually displaying lizards reported here: *Draco* and *Anolis* lizards exaggerate the speed of display movements in order to be seen against a noisy visual background. Second, the strategy of increasing the duration (redundancy) of signals in noisy conditions is found in both acoustic and visual communication systems, with examples in birds, lizards, mammals and frogs (Table 2b). Finally, an alternative strategy is timing signal production to coincide with lulls in environmental noise, which is employed by various species of acoustically communicating birds, mammals and frogs, as well as visually communicating lizards and vibration-communicating insects (Table 2c). These examples almost certainly represent adaptive convergence in animal communication and among groups separated by at least 280 million years. Viewed in this context, our findings for *Draco* and *Anolis* lizards might be the first formal documentation of what is likely to be a widespread phenomenon of deep-time

convergence in animal communication when species are faced with communicating in noisy environments.

Descent with modification (Darwin, 1859) combined with the innumerable, often chance events that influence the evolution process (e.g., random mutation and other stochastic factors) has been argued (e.g., Gould, 1989) to place species on increasingly divergent evolutionary trajectories the longer those species have evolved independently of one another. Convergent adaptations should therefore be increasingly less likely among species separated by large amounts of evolutionary time. This position appeared to have been supported by previous evaluations of documented cases of convergence in the literature (Conte et al., 2012; Ord & Summers, 2015; York & Fernald, 2017). However, our findings, instead, show the considerable power that natural selection has in overriding the deep influence of evolutionary history to generate common adaptive solutions. This suggests there are a limited number of possible adaptive outcomes to any given selection pressure. Adaptation is, therefore, destined to repeat itself time and time again throughout history when distantly related taxa encounter common ecological challenges. The diversity in animal communication we observe in nature, as well as other aspects of organismal phenotypes, is subsequently the outcome of the unique balance of different selection pressures operating on taxa, rather than a reflection of the infinite adaptive possibilities available for the same selection pressure.

ACKNOWLEDGEMENTS

We thank Elizabeth Cassidy, Devi Stuart-Fox and Adnan Moussalli for their assistance in the field; Mae Diesmos for facilitating field visits in Rizal Province on Luzon; and Debadrita Guha, Marina Murashev, Christopher Allister, Phillipa Beale, Martin Coates, Kobe Martin, Charolette Mills, Rachael Schildkraut, Erin Hatch and Kate Montgomery for their help in processing footage for computational motion analysis. Permits for accessing field sites were provided by the Economic Planning Unit, Government of Malaysia (40/200/19/2689 and 40/200/19/3149), Sarawak State Planning Unit and Sarawak Forest Department (NCCD.907.4.4(V)-101; NCCD.907.4.4(Jld.7)-113; NCCD.907.4.4(Jld.11)-74; and NPW.907.4.4(V)-100), and entry permits to Sarawak's National Parks and Nature Reserves (54/2010; 21/2011; 65/2012; and 526/2014) and the Philippine Department of Environment and Natural Resources (especially PENRO Bohol). This work was funded by start-up funds to T.J.O. provided by the University of New South Wales (UNSW) School of Biological, Earth & Environmental Sciences (BEES) and the UNSW Evolution & Ecology Research Centre, a UNSW Science Faculty Grant (SFRGP) to T.J.O., separate Australian Postgraduate Awards to D.A.K. and T.C.S., and a School of BEES postgraduate research grant to D.A.K. The work described in this article was approved by the UNSW Animal Care and Ethics Committee under Protocols 11/33B and 15/39B.

AUTHORS' CONTRIBUTIONS

T.J.O. conceived the study, performed the computational motion analyses and statistical analyses, and wrote the manuscript. T.J.O., D.A.K. and T.C.S. conducted the fieldwork. D.A.K. performed the robot playback experiments. N.A., A.D. and I.D. facilitated permitting and provided logistic support for fieldwork. T.C.S., A.D., N.A. and I.D. contributed in manuscript editing.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13773>.

OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: <https://doi.org/10.5061/dryad.ncjxk5>

DATA AVAILABILITY STATEMENT

All data used in this study have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.ncjxk5>).

ORCID

Terry J. Ord <https://orcid.org/0000-0002-2608-2150>

REFERENCES

- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Blomberg, S.P., Garland Jr, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.
- Bradbury, J.W. & Vehrencamp, S.L. (2011) *Principles of animal communication*, 2nd edition. Sunderland: Sinauer Associates.
- Brandt, Y. (2003) Lizard threat display handicaps endurance. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1519), 1061–1068.
- Brumm, H. & Zollinger, S.A. (2011) The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, 148, 1173–1198.
- Carpenter, C.C. (1986) An inventory of the display-action-patterns in lizards. *Smithsonian Herpetological Information Service*, 68, 1–18.
- Chen, Z. & Wiens, J.J. (2020) The origins of acoustic communication in vertebrates. *Nature Communications*, 11, 1–8.
- Clark, D.L., Macedonia, J.M., Rowe, J., Stuart, M., Kemp, D.J. & Ord, T.J. (2015) Evolution of displays in Galapagos lava lizards: comparative analyses of signallers and robot playbacks to receivers. *Animal Behaviour*, 109, 33–44.
- Conte, G.L., Arnegard, M.E., Peichel, C.L. & Schluter, D. (2012) The probability of genetic parallelism and convergence in natural populations. *Proceedings of the Royal Society London, Series B*, 279, 5039–5047.
- Cuthill, I.C., Allen, W.L., Arbuckle, K., Caspers, B., Chaplin, G., Hauber, M.E. et al. (2017) The biology of color. *Science*, 357, 1–7.
- Darwin, C. (1859) *The origin of species*. London: Penguin Books.
- Dusenbery, D.B. (1992) *Sensory ecology: how organisms acquire and respond to information*. New York: W. H. Freeman and Company.
- Endler, J.A. (1992) Signals, signal conditions, and the direction of evolution. *The American Naturalist*, 139, S125–S153.
- Gould, S.J. (1989) *Wonderful life: the Burgess shale and the nature of history*. New York, NY: W.W. Norton.
- Henry, C.S., Wells, M.L.M. & Simon, C.M. (1999) Convergent evolution of courtship songs among cryptic species of the *Carnea* group of green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Evolution*, 53, 1165–1179.
- Ho, L.S.T. & Ane, C. (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63, 397–408.
- Jackman, T.R., Irschick, D.J., de Queiroz, K., Losos, J.B. & Larson, A. (2002) Molecular phylogenetic perspective on evolution of lizards of the *Anolis grahamsi* series. *Journal of Experimental Zoology*, 294, 1–16.
- Jenssen, T.A. (1977) Evolution of anoline lizard display behavior. *American Zoologist*, 17, 203–215.
- Jenssen, T.A., Garrett, S. & Sydor, W.J. (2012) Complex signal usage by advertising male green anoles (*Anolis carolinensis*): a test of assumptions. *Herpetologica*, 68, 345–357.
- Kemp, D.J., Batistic, F.-K. & Reznick, D.N. (2018) Predictable adaptive trajectories of sexual coloration in the wild: evidence from replicate experimental guppy populations. *Evolution*, 72, 2462–2477.
- Klomp, D.A., Ord, T.J., Das, I., Diesmos, A., Ahmad, N. & Stuart-Fox, D. (2016) Ornament size and colour as alternative strategies for effective communication in gliding lizards. *Journal of Evolutionary Biology*, 29, 1689–1700.
- Klomp, D.A., Stuart-Fox, D., Cassidy, E.J., Ahmad, N. & Ord, T.J. (2017a) Color pattern facilitates species recognition but not signal detection: a field test using robots. *Behavioral Ecology*, 28, 597–606.
- Klomp, D.A., Stuart-Fox, D., Cassidy, E.J., Ahmad, N. & Ord, T.J. (2017b). Data from: Color pattern facilitates species recognition but not signal detection: a field test using robots. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.dk565/1>.
- Kumar, S., Stecher, G., Suleski, M. & Heddes, S.B. (2017) TimeTree: a resource for timelines, timetrees and divergence times. *Molecular Biology and Evolution*, 34, 1812–1819.
- Kunc, H.P. & Schmid, R. (2019) The effects of anthropogenic noise on animals: a meta-analysis. *Biology Letters*, 15, 20190649.
- Ligon, R.A., Diaz, C.D., Morano, J.L., Troscianko, J., Stevens, M., Moskeland, A. et al. (2018) Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biology*, 16, e2006962.
- Marler, P. (1967) Animal communication signals. *Nature*, 157, 769–774.
- Martins, E.P. (1993) A comparative study of the evolution of *Sceloporus* push-up displays. *The American Naturalist*, 142, 994–1018.
- Martins, E.P., Labra, A., Halloy, M. & Thompson, J.T. (2004) Large-scale patterns of signal evolution: an interspecific study of *Liolaemus* lizard headbob displays. *Animal Behaviour*, 68, 453–463.
- Martins, E.P. & Lamont, J. (1998) Estimating ancestral states of a communicative display: a comparative study of *Cyclura* rock iguanas. *Animal Behaviour*, 55, 1685–1706.
- Martins, E.P., Ord, T.J. & Davenport, S.W. (2005) Combining motions into complex displays: playbacks with a robotic lizard. *Behavioral Ecology and Sociobiology*, 58, 351–360.
- McGuire, J.A. & Heang, K.B. (2001) Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean Society*, 72, 203–229.
- Mori, A. & Hikida, T. (1994) Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. *Copeia*, 1994, 124–130.
- Ng, J., Landeen, E.L., Logsdon, R.M. & Glor, R.E. (2013) Correlation between *Anolis* lizard dewlap phenotype and environmental variation indicates adaptive divergence of a signal important to sexual selection and species recognition. *Evolution*, 67, 573–582.

- Nicholson, K.E., Glor, R.E., Kolbe, J.J., Larson, A., Hedges, S.B. & Losos, J.B. (2005) Mainland colonization by island lizards. *Journal of Biogeography*, 32, 929–938.
- Ord, T.J. (2008) Dawn and dusk ‘chorus’ in visually communicating Jamaican anole lizards. *The American Naturalist*, 172, 585–592.
- Ord, T.J., Blumstein, D.T. & Evans, C.S. (2001) Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1468), 737–744.
- Ord, T.J., Charles, G.K., Palmer, M. & Stamps, J.A. (2016) Plasticity in social communication and its implications for the colonization of novel habitats. *Behavioral Ecology*, 27, 341–351.
- Ord, T.J., Collar, D.C. & Sanger, T.J. (2013a) The biomechanical basis of evolutionary change in a territorial display. *Functional Ecology*, 27, 1186–1200.
- Ord, T.J., Garcia-Porta, J., Querejeta, M. & Collar, D.C. (2020) Gliding dragons and flying squirrels: diversifying versus stabilizing selection on morphology following the evolution of an innovation. *The American Naturalist*, 195, E51–E66.
- Ord, T.J. & Klomp, D.A. (2014) Habitat partitioning and morphological differentiation: the Southeast Asian *Draco* lizards and the Caribbean *Anolis* lizards compared. *Oecologia*, 175, 651–666.
- Ord, T.J., Klomp, D.A., Garcia-Porta, J. & Hagman, M. (2015) Repeated evolution of exaggerated dewlaps and other throat morphology in lizards. *Journal of Evolutionary Biology*, 28, 1948–1964.
- Ord, T.J., Peters, R.A., Clucas, B. & Stamps, J.A. (2007) Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society B: Biological Sciences*, 274(1613), 1057–1062.
- Ord, T.J. & Stamps, J.A. (2008) Alert signals enhance animal communication in ‘noisy’ environments. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 18830–18835.
- Ord, T.J. & Stamps, J.A. (2009) Species identity cues in animal communication. *The American Naturalist*, 174, 585–593.
- Ord, T.J. & Stamps, J.A. (2017) Why does the rate of signal production in ectotherms vary with temperature? *Behavioral Ecology*, 28, 1272–1282.
- Ord, T.J., Stamps, J.A. & Losos, J.B. (2010a) Adaptation and plasticity of animal communication in fluctuating environments. *Evolution*, 64, 3134–3148.
- Ord, T.J., Stamps, J.A. & Losos, J.B. (2010b) Data from: adaptation and plasticity of animal communication in fluctuating environments. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.1619>.
- Ord, T.J., Stamps, J.A. & Losos, J.B. (2013b) Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards. *Animal Behaviour*, 85, 1415–1426.
- Ord, T.J. & Summers, T. (2015) Repeated evolution and the impact of evolutionary history on adaptation. *BMC Evolutionary Biology*, 15, 137.
- Patricelli, G.L. & Blickley, J. (2006) Avian communication in urban noise: causes and consequences of vocal adjustment. *The Auk*, 123, 639–649.
- Perry, G., Levering, K., Girard, I. & Garland Jr, T. (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour*, 67, 37–47.
- Peters, R.A. (2008) Environmental motion delays the detection of movement-based signals. *Biology Letters*, 4, 2–5.
- Peters, R.A., Clifford, C.W.G. & Evans, C.S. (2002) Measuring the structure of dynamic visual signals. *Animal Behaviour*, 64, 131–146.
- Peters, R.A., Hemmi, J.M. & Zeil, J. (2007) Signaling against the wind: modifying motion-signal structure in response to increased noise. *Current Biology*, 17, 1231–1234.
- Peters, R.A. & Ord, T.J. (2003) Display response of the Jacky Dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology*, 28, 499–506.
- Peters, R.A., Ramos, J.A., Hernandez, J., Wu, Y. & Qi, Y. (2016) Social context affects tail displays by *Phrynocephalus vlangalii* lizards from China. *Scientific Reports*, 6, 31573.
- Ramos, J.A. & Peters, R.A. (2016) Dragon wars: movement-based signalling by Australian agamid lizards in relation to species ecology. *Austral Ecology*, 41, 302–315.
- Ramos, J.A. & Peters, R.A. (2017a) Habitat-dependent variation in motion signal structure between allopatric populations of lizards. *Animal Behaviour*, 126, 69–78.
- Ramos, J.A. & Peters, R.A. (2017b) Motion-based signaling in sympatric species of Australian agamid lizards. *Journal of Comparative Physiology A*, 203, 661–671.
- Roca, I.T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R. et al. (2016) Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behavioral Ecology*, 27, 1269–1274.
- Rosenthal, G.G., Evans, C.S. & Miller, W.L. (1996) Female preference for dynamic traits in the green swordtail, *Xiphophorus helleri*. *Animal Behaviour*, 51, 811–820.
- Snell-Rood, E.C. (2013) An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85, 1004–1011.
- Stamps, J.A. & Groothuis, T.G.G. (2010) The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85, 301–325.
- Stern, D.L. (2013) The genetic causes of convergent evolution. *Nature Reviews*, 14, 751–764.
- van Dyk, D.A. & Evans, C.S. (2008) Opponent assessment in lizards: examining the effect of aggressive and submissive signals. *Behavioral Ecology*, 19, 895–901.
- Vermeij, G.J. (2006) Historical contingency and the purported uniqueness of evolutionary innovations. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 1804–1809.
- Wiley, R.H. (2006) Signal detection and animal communication. *Advances in the Study of Behavior*, 36, 217–247.
- Wiley, R.H. (2015) *Noise matters: the evolution of communication*. Cambridge, MA: Harvard University Press.
- Wright, P.A. & Turko, A.J. (2016) Amphibious fishes: evolution and phenotypic plasticity. *Journal of Experimental Biology*, 219, 2245–2259.
- York, R.A. & Fernald, R.D. (2017) The repeated evolution of behavior. *Frontiers in Ecology and Evolution*, 4, 143.
- Yorzinski, J.L., Patricelli, G.L., Babcock, J.S., Pearson, J.M. & Platt, M.L. (2013) Through their eyes: selective attention in peahens during courtship. *Journal of Experimental Biology*, 216, 3035–3046.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Ord TJ, Klomp DA, Summers TC, Diesmos A, Ahmad N, Das I. Deep-time convergent evolution in animal communication presented by shared adaptations for coping with noise in lizards and other animals. *Ecology Letters*. 2021;24:1750–1761. <https://doi.org/10.1111/ele.13773>