

Behavioral Plasticity and the Origins of Novelty: The Evolution of the Rattlesnake Rattle

Bradley C. Allf,* Paul A. P. Durst, and David W. Pfennig†

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599

Submitted January 27, 2016; Accepted May 17, 2016; Electronically published July 28, 2016

Online enhancements: video, supplementary tables. Dryad data: <http://dx.doi.org/10.5061/dryad.c36k6>.

ABSTRACT: Environmentally induced behavior (behavioral plasticity) has long been hypothesized to promote the origins of novel morphological traits, but this idea remains controversial. One context in which this hypothesis can be evaluated is animal communication, where behavior and morphology are often linked. Here, we examined the evolution of one of nature's most spectacular communication signals: the rattlesnake rattle. We specifically evaluated whether rattlesnake rattling behavior—and, hence, the rattle—originated from a simple behavior: vibrating the tail when threatened. By reconstructing the ancestral state of defensive tail vibration, we show that this behavior is nearly ubiquitous in the Viperidae (the family that includes rattlesnakes) and widespread in the Colubridae (the largest snake family, nearly all of which are nonvenomous), suggesting a shared origin for the behavior between these families. After measuring tail vibration in 56 species of Viperidae and Colubridae, we show that the more closely related a species was to rattlesnakes, the more similar it was to rattlesnakes in duration and rate of tail vibration. Thus, the rattlesnake rattle might have evolved via elaboration of a simple behavior. These data thereby support the long-standing hypothesis that behavioral plasticity often precedes—and possibly instigates—the evolution of morphological novelty.

Keywords: behavioral evolution, phenotypic plasticity, ritualization, signal evolution, mimicry, *Crotalus*.

Introduction

Evolutionary biologists have long sought to explain how novel, complex traits originate (Mayr 1959; West-Eberhard 2003; Wagner and Lynch 2010). Although it is generally assumed that novel traits arise exclusively from changes in the genome (Carroll 2008), an alternative hypothesis holds that environmentally induced phenotypic change (i.e., phenotypic plasticity)—especially changes in behavior—can trig-

ger morphological novelty (Mayr 1959; Gottlieb 1992; West-Eberhard 2003; Moczek et al. 2011; Levis and Pfennig 2016). For example, a change in foraging behavior could expose diverse morphological variants (underlain by existing cryptic genetic variation) to novel selection pressures, such that individuals possessing any morphological feature that enhanced resource acquisition would be favored, thereby promoting the feature's spread (Price et al. 2003). In this way, behavioral plasticity can precede—and instigate—morphological evolution. However, this hypothesis remains controversial (e.g., cf. Laland et al. 2014; Wray et al. 2014). Indeed, as noted in a recent review (Futuyma 2015, p. 60), “More studies on the possibility that behavioral plasticity initiates evolutionary change would be desirable.”

An ideal context in which to evaluate whether behavioral plasticity promotes morphological novelty is the evolution of animal communication signals. Communication signals are among the most striking features of the natural world (Laidre and Johnstone 2013), and they often comprise a complex mix of behavioral and morphological traits. Not surprisingly, evolutionary biologists have long sought to understand how signals originate and diversify (Maynard Smith and Harper 2003). Generally, signals (and associated morphological traits) are thought to arise when simple behaviors that can be used by a receiver to predict the actor's future actions (or that happen to tap into a preexisting bias in receiver response) become elaborated over evolutionary time (Tinbergen 1952; Lorenz 1966). Thus, simple behaviors should precede more complex signaling behaviors. Moreover, simple behaviors should also pave the way for morphological traits that augment these complex signals.

We tested these predictions to evaluate the hypothesis that behavior precedes morphological evolution. We did so by examining the evolution of one of nature's most unique communication signals: rattlesnake rattling behavior and the rattle (fig. 1).

The rattlesnake rattle is a truly novel trait, having evolved only once in rattlesnakes (Klauber 1956), which consist of monophyletic sister genera *Crotalus* and *Sistrurus* (Pyron

* Present address: North Carolina Museum of Natural Sciences, Raleigh, North Carolina 27601.

† Corresponding author; e-mail: dpfennig@unc.edu.

ORCID: Allf, <http://orcid.org/0000-0003-1224-729X>; Pfennig, <http://orcid.org/0000-0002-1114-534X>.

Am. Nat. 2016. Vol. 188, pp. 475–483. © 2016 by The University of Chicago. 0003-0147/2016/18804-5675\$15.00. All rights reserved.
DOI: 10.1086/688017



Figure 1: Rattlesnakes possess one of nature's most spectacular signals: a vibrating rattle. Here, a western diamondback rattlesnake (*Crotalus atrox*) vibrates its rattle in response to a perceived threat (Portal, AZ).

et al. 2013). No other snake species (of more than 3,000 species) has evolved this feature. The rattle is composed of keratin, and it likely evolved from proliferative tissue of the outermost epidermal layer at the tail tip (Zimmerman and Pope 1948). The rattle on a mature snake consists of interlocking segments of keratin that fit loosely within one another (Klauber 1956). The contraction of highly specialized tailshaker muscles (Moon 2001) causes these segments to vibrate rapidly against one another, generating the rattle's distinctive sound. All rattlesnakes are venomous, and nearly all agree that the rattle functions as a deterrent signal to predators (Klauber 1956).

Because there are no obvious morphological precursors to the rattle (but see below), researchers have long sought to identify behaviors that might have preceded the rattle's evolution (Cope 1871; Garman 1889; Klauber 1956). One such behavior is tail vibration, a widespread reaction of snakes to a predatory threat (Garman 1889; Greene 1988). Because tail vibration is an environmentally induced trait (tail vibration is expressed only when a snake is threatened; Greene 1988), it represents a common form of behavioral plasticity (and therefore phenotypic plasticity) in snakes. Tail vibration is

particularly widespread in the families Viperidae and Colubridae (Young 2003; see also below). Moreover, tail vibration in distantly related species appears to be homologous (sensu Wagner 1989), as evidenced by the fact that this behavior is triggered by similar stimuli, expressed in a similar manner, and connected by a series of intervening intermediate forms (see below; for a discussion of the problems inherent in establishing behavioral homology, see Wenzel 1992).

Here, we sought to evaluate whether and how tail vibration behavior was elaborated over evolutionary time in a manner suggesting that this behavior might have preceded—and even facilitated—the evolution of rattlesnake rattling behavior and the rattle. To do so, we measured tail vibration in various species of snakes that differed in how recently they shared a common ancestor with rattlesnakes.

Material and Methods

Filming Tail Vibration Behavior

We measured tail vibration in 155 individual snakes from 56 species (table S1; tables S1, S2 available online). These

included 38 species of Viperidae (the family to which rattlesnakes belong) and 18 species of Colubridae (the largest snake family, nearly all of which are nonvenomous or have very weak venom). All snakes were held in captivity (museums, zoos, private collections) and were filmed under similar conditions (i.e., all were healthy, well fed, similarly habituated to humans, and maintained at roughly similar temperatures). By filming captive (as opposed to wild) snakes, we were able to control for variation in environmental factors (e.g., temperature) that can affect tail vibration behavior (Martin and Bagby 1972).

Snakes were filmed with a high-speed Casio Exilim EX-ZR700 camera at 480 frames/s. Defensive behavior was initiated by presenting each snake with a stuffed animal head (of the size/shape of a medium-sized mammalian predator) mounted on 40-inch Standard Midwest Tongs. One of us attempted to initiate defensive behavior by waving the stuffed animal in front of the snake for one minute. Snakes that did not vibrate their tail were scored as not vibrating their tail for the analyses. For snakes that did vibrate their tail, tail vibration was recorded for 30–60 s (while they were threatened by the stuffed animal). This was enough time to film multiple bursts of vibration in most individuals, from which the longest vibratory burst was determined for each individual. Because rattlesnakes are capable of sustained rattling for more than an hour (Klauber 1956), filming was sometimes stopped before rattlesnakes had finished an entire rattling sequence. In these cases, even if the longest vibratory sequence continued past the end of the video, duration was recorded as ending at the end of the video. Thus, our analyses of duration of tail vibration were conservative (we predicted prolonged tail vibration in rattlesnakes). Rate of tail vibration was calculated every 15–30 vibrations by playing back videos frame by frame using Adobe Premiere Pro. One tail vibration was defined as a full completion of the entire movement, whereby the tail flexes in one direction, flexes in the opposite direction, and then returns back to the original direction. Only maximum vibratory speeds were used in analyses. From these videos, we calculated three response measures for each species: (1) the probability of tail vibration (number of individuals that vibrated their tail divided by total number tested), (2) mean duration of tail vibration, and (3) mean rate of tail vibration. These data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c36k6> (Allf et al. 2016; video 1, available online).

Ancestral State Reconstruction of Tail Vibration Behavior

To determine how widespread defensive tail vibration behavior likely was among the ancestors of our focal species, we reconstructed the ancestral state of tail vibration behavior in our sample species on the basis of our video recordings, personal communication with snake authorities,



Video 1: Still image from video of examples of snakes vibrating their tails and summary of the results (video 1, available online).

and personal observations (table S2). Species observed to vibrate their tails were scored as such, and all others were scored as unclear (this conservative phrasing reflects the difficulty of definitively proving the lack of a behavior in a species). We pruned the phylogeny of all squamates from Pyron et al. (2013) using the ape package (Paradis et al. 2004) in R (R Development Core Team 2014) and reconstructed ancestral states across the tree using the phytools package (Revell 2012) in R.

Evaluating the Relationship between Tail Vibration Behavior and Phylogenetic Distance to Rattlesnakes

Next, to determine whether tail vibration behavior was elaborated over evolutionary time, suggesting that it preceded—and possibly facilitated—the evolution of rattlesnake rattling behavior and the rattle, we evaluated (1) the strength of the phylogenetic signal of each response measure and (2) the relationship between each response measure and the species' phylogenetic distance from rattlesnakes. First, to measure the strength of the phylogenetic signal, we calculated Pagel's λ across our pruned phylogeny for each measure, using the phytools package (Revell 2012) in R. Analyses were repeated for two subsets of the data: the full data set excluding New World colubrids (which are possibly rattlesnake mimics; see below) and a subset excluding New World colubrids and rattlesnakes (to determine whether the trends were driven solely by rattlesnakes). We also reconstructed the ancestral state for each response measure, again using the pruned phylogeny and the phytools package in R.

Second, to determine the relationships between our measures of tail vibration and phylogenetic distance to rattlesnakes, we calculated the distance between each species and the node containing all rattlesnakes, using the ape package in R (a distance of 0 was used for all rattlesnake species).

We then performed correlation tests in R to assess the relationship between the phylogenetic distance from the rattlesnake clade and each of the three response measures of tail vibration.

Results

Ancestral State Reconstruction of Tail Vibration Behavior

Our reconstruction of ancestral character states revealed that, regardless of whether we observed tail vibration behavior in our samples from each species, tail vibration behavior is widely distributed across the species in our data set (fig. 2). This is in agreement with previous work demonstrating that defensive tail vibration is nearly ubiquitous among viperids and widespread across colubrids (Young 2003), suggesting a shared origin for the behavior between the two families.

Evaluating the Relationship between Tail Vibration Behavior and Phylogenetic Distance to Rattlesnakes

An initial examination of the data revealed that certain colubrid species—specifically, those from the New World—vibrated their tails longer and faster than expected on the basis of their (distant) relatedness to rattlesnakes (fig. 3a, 3b). Indeed, these species (which are nonvenomous and sympatric with rattlesnakes; rattlesnakes are found exclusively in the New World; Klauber 1956) were more similar to rattlesnakes in rate of tail vibration than were other colubrids from the Old World (which are allopatric; ANOVA on rate of tail vibration: $F_{2,23} = 26.96$, $P < .0001$; rattlesnakes, New World colubrids, and Old World colubrids differed from each other: Tukey-Kramer honest significant difference test; $P < .05$). Thus, because New World colubrids appear to be rattlesnake mimics (see also Klauber 1956; Sweet 1985), we present all subsequent analyses with and without New World colubrids included.

We found little support for a phylogenetic signal in probability of tail vibration, regardless of whether we analyzed the full data set, the data set excluding New World colubrids, or that including just Viperidae ($\lambda = 0.34, 0.38, 0.37$; $P = .17, .20, .16$). By contrast, we found a significant phylogenetic signal in duration of tail vibration in both the full data set and that including just Viperidae ($\lambda = 0.47, 0.41$; $P = .04, .03$) and near support for the data set excluding New World colubrids ($\lambda = 0.52$, $P = .06$). For rate of tail vibration, we found an even stronger phylogenetic signal (full data set: $\lambda = 0.97$, $P < .0001$; excluding New World colubrids: $\lambda = 0.97$, $P < .0001$; within Viperidae: $\lambda = 0.94$, $P < .0001$).

In addition to a significant phylogenetic signal, there was a significant correlation between duration of tail vibration and phylogenetic distance from the rattlesnake clade (full

data set: $r = -0.41$, $P = .0101$; excluding New World colubrids: $r = -0.49$, $P = .0104$; fig. 3a), with species more closely related to rattlesnakes vibrating their tails longer. However, this trend was largely driven by the rattlesnake clade, because the relationship disappeared in the absence of rattlesnakes ($P = .34$). This is clearly seen in the ancestral state reconstruction of the trait (fig. 4a), where we found very high values within the rattlesnake clade (11.30 s for the ancestor of rattlesnakes; mean node value within clade = 15.01) and short durations for all ancestral nodes outside the rattlesnake clade (≤ 7.94 s for all other nodes; mean node value = 5.94). As with phylogenetic signal, we found a stronger relationship between rate of tail vibration and phylogenetic distance from the rattlesnake clade (full data set: $r = -0.52$, $P = .0007$; excluding New World colubrids: $r = -0.81$, $P < .0001$; fig. 3b), with species more closely related to rattlesnakes vibrating their tails more rapidly. Unlike duration of tail vibration, this relationship was not driven solely by the rattlesnake clade, because there was a nearly significant correlation between rate of vibration and distance from the rattlesnake clade when excluding rattlesnakes ($r = -0.43$, $P = .056$). Indeed, the relationship was highly significant within Viperidae, even when excluding rattlesnakes ($r = -0.66$, $P = .004$; fig. 3c). This was also seen in the ancestral state reconstruction (fig. 4b), with a more gradual decrease in ancestral node values with distance from the rattlesnake clade (55.25 Hz for the ancestor of all rattlesnakes; 35.94 Hz for the next oldest node; 33.61, 32.58, and 28.04 Hz going further toward the root of the tree). The data underlying figures 3 and 4 are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c36k6> (Allf et al. 2016). For a summary of the results, see video 1.

Discussion

We evaluated whether environmentally induced behavior might have preceded—and even facilitated—the evolution of one of nature's most unique signals: rattlesnake rattling behavior and the rattle. Our results suggest that tail vibration by rattleless ancestors of rattlesnakes might have served as the signal precursor to rattlesnake rattling behavior.

If ancestral tail vibration was a reliable cue to predators that a bite was imminent, then this behavior could have become elaborated as a defensive signal. In venomous species, where a stronger association existed between tail vibration and the threat (a bite accompanied by envenomation), this protosignal would have undergone increased elaboration; that is, snakes began to vibrate their tails longer and faster (as we found in modern-day pit vipers). Further signal elaboration would have been favored if predators could assess the threat level posed by a snake on the basis of, for example, how rapidly the snake vibrated its tail (as in modern-day rattlesnakes; Owings et al. 2002). Ultimately, to enhance

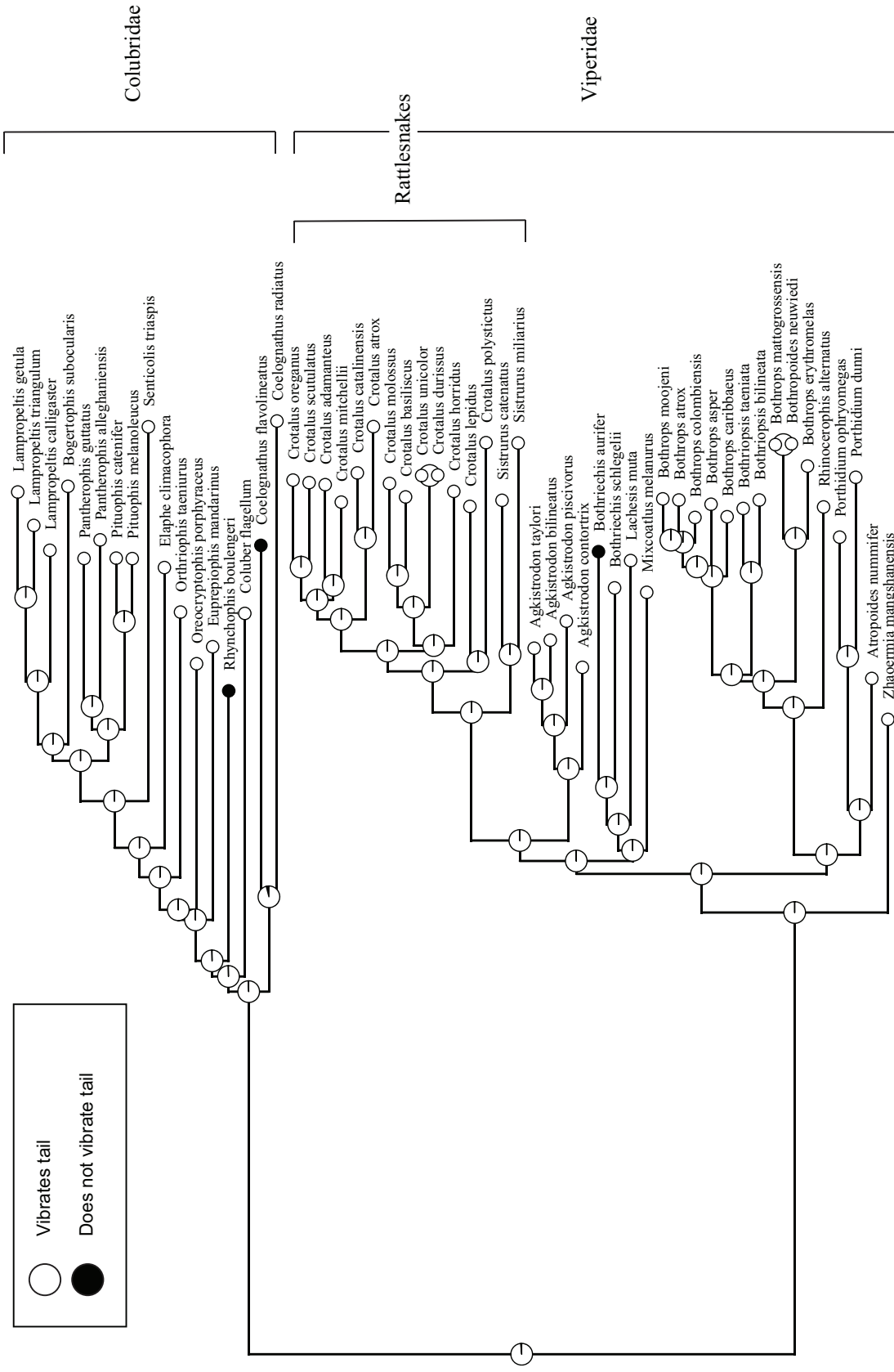


Figure 2: Ancestral character state reconstruction showing support for ancestral tail vibration behavior in the species of Colubridae and Viperidae examined in this study.

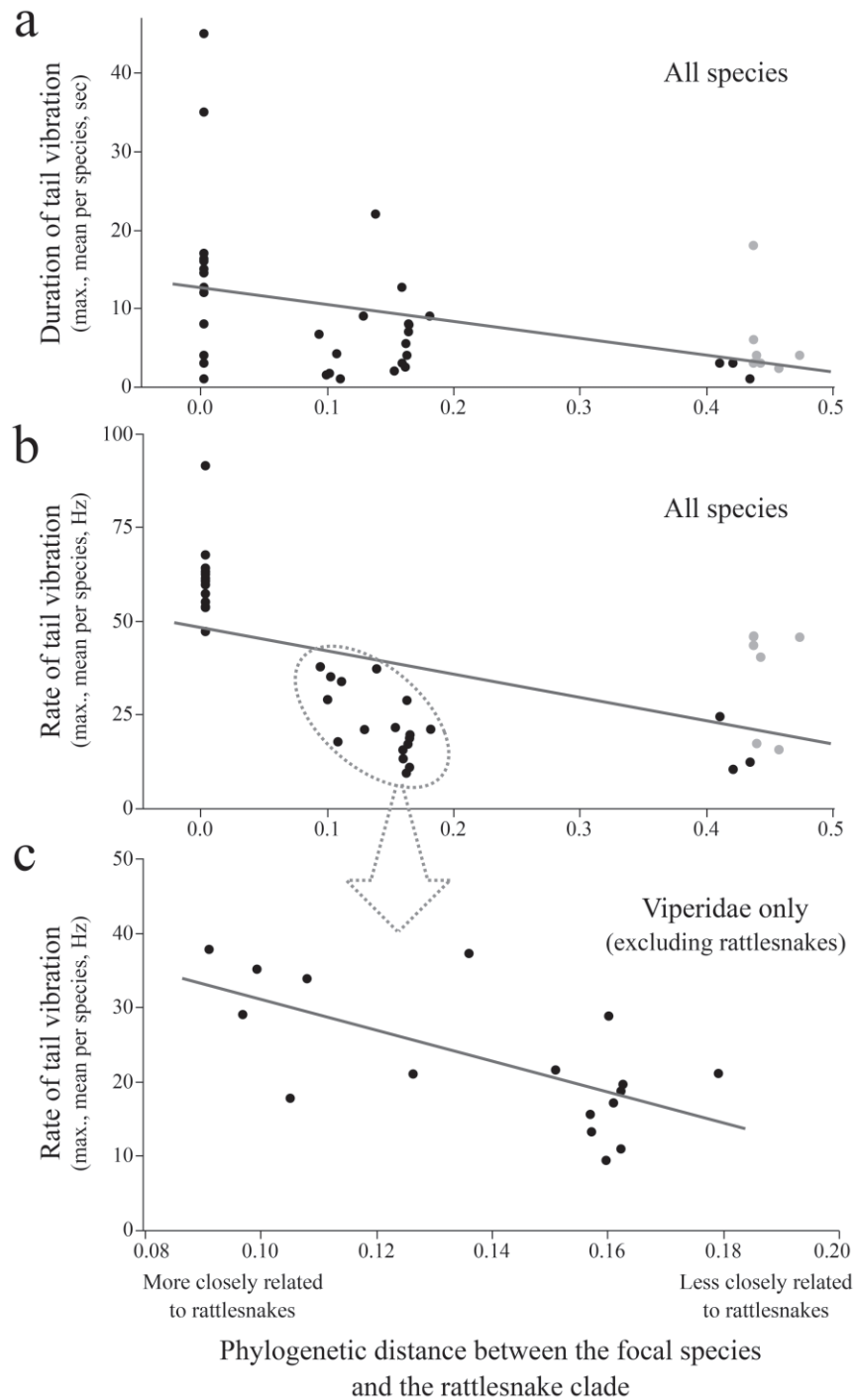


Figure 3: The more closely related a species was to rattlesnakes, the more similar that species was to rattlesnakes in duration (a) and rate that it vibrated its tail (b). Rattlesnakes have a phylogenetic distance of 0. Gray circles, New World Colubridae (included in analyses). c, Significant relationship for vibration rate held within Viperidae (the family containing rattlesnakes) even when excluding rattlesnakes, suggesting that this relationship was not driven solely by rattlesnakes.

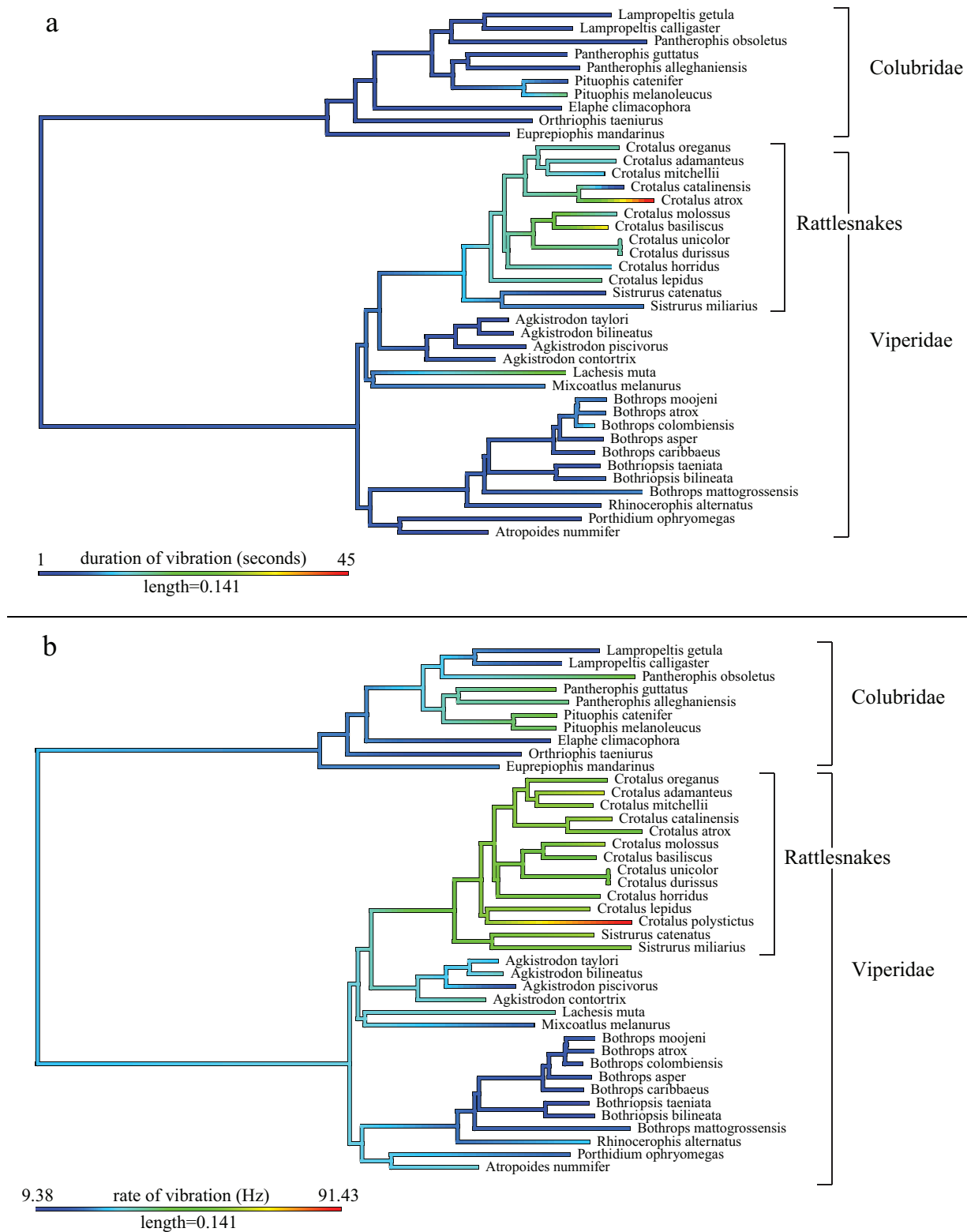


Figure 4: Ancestral character state reconstructions tracking values for duration (a) and rate of tail vibration (b) across the phylogeny. High values appear to be concentrated in the rattlesnake clade for duration of vibration, while a more gradual transition is observed between rattlesnakes and other species for rate of vibration.

the signal further, selection might have favored a rudimentary rattle (possibly analogous to the enlarged terminal scale in certain modern-day New World pit vipers; see Bellairs 1970; Greene 1992; Sisk and Jackson 1997). With continued directional selection for increasing signal efficiency, this rudimentary structure might have become the fully developed rattle.

Taken together, our results therefore suggest that rattlesnake rattling behavior—and, hence, the rattle—could have originated from the elaboration of a relatively simple behavior: tail vibration (but see Schuett et al. 1984 for an alternative—although controversial [Greene 1988; Tiebout 1997; Moon 2001; Young 2003]—behavioral precursor to the rattle). Thus, these data emphasize that changes in behavior might precede—and possibly even facilitate—the evolution of morphological novelty (Baldwin 1896; Mayr 1959; Odling-Smee et al. 2003; West-Eberhard 2003; Moczek et al. 2011). Our results therefore add to the growing number of comparative examples in which behavioral change has been shown to precede morphological evolution (Wcislo 1989).

Yet the origin of the rattle itself remains unknown. At least two evolutionary routes are consistent with our results. First, tail vibration behavior could have instigated rattle evolution by exposing existing morphological variants to novel selection pressures. For instance, certain ancestors of rattlesnakes might have been genetically predisposed to produce extra tissue on their tail (e.g., because of incomplete shedding; Klauber 1956). If, as a consequence, these individuals made more noise when vibrating their tail and were thereby better at startling predators, such features might have spread and undergone refinement into a rattle. Yet, in the absence of tail vibration, these features would have likely been lost. An alternative evolutionary route is that the rattle arose following genetic assimilation (*sensu* Waddington 1942) of callus-type formation wrought by repeated tail vibration. Specifically, snakes that vibrated their tail longer and faster when disturbed might have begun to facultatively develop a callus (Cope 1871), in which irritation causes the skin's outer layer to thicken into a mass of keratin (the same fibrous protein comprising the rattle). If genetic variation existed among individuals in propensity to produce a callus, and if individuals that were more prone to produce a callus were better at intimidating predators, then selection might have favored callus formation until, ultimately, this structure underwent genetic assimilation and was subsequently refined into a rattle (similar to how calluses might have undergone genetic assimilation in ostriches to form their distinctive callosities; Waddington 1953). Future studies are needed to identify the route that led to rattle formation.

In sum, communication systems offer rich opportunities to evaluate the role of behavior in the evolution of novel morphological features. Our data show that behavior might have preceded and possibly even contributed to the evolu-

tion of one of nature's most unique signals: the rattlesnake rattle.

Acknowledgments

We thank K. Arbuckle, H. Greene, N. Levis, C. Martin, M. A. McPeck, K. Pfennig, A. Pyron, M. Servedio, and an anonymous reviewer for comments and the individuals and institutions listed in table S1 for permission to film their snakes. This work was supported by National Science Foundation grant DEB-1019479 (to D.W.P.) and was completed in partial fulfillment of the requirements for an undergraduate honor's thesis at the University of North Carolina (to B.C.A.). The University of North Carolina's Institutional Animal Care and Use Committee approved all the procedures.

Literature Cited

- Allf, B. C., P. A. P. Durst, and D. W. Pfennig. 2016. Data from: Behavioral plasticity and the origins of novelty: the evolution of the rattlesnake rattle. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.c36k6>.
- Baldwin, J. M. 1896. A new factor in evolution. *American Naturalist* 30: 441–451.
- Bellairs, A. 1970. *The life of reptiles*. Vol. 2. Universe Books, New York.
- Carroll, S. B. 2008. Evo-devo and an expanding evolutionary synthesis: a genetic theory of morphological evolution. *Cell* 134:25–36.
- Cope, E. D. 1871. The method of creation of organic forms. *Proceedings of the American Philosophical Society* 12:229–263.
- Futuyma, D. J. 2015. Can modern evolutionary theory explain macroevolution? Pages 29–85 in E. Serrelli and N. Gontier, eds. *Macroevolution: explanation, interpretation and evidence*. Springer, New York.
- Garman, S. 1889. On the evolution of the rattlesnake. *Proceedings of the Boston Society of Natural History* 24:170–182.
- Gottlieb, G. 1992. *Individual development and evolution: the genesis of novel behavior*. Oxford University Press, New York.
- Greene, H. W. 1988. Antipredator mechanisms in reptiles. Pages 1–152 in C. Gans and R. B. Huey, eds. *Biology of the Reptilia: defense and life history*. Alan R. Liss, New York.
- . 1992. The ecological and behavior context for pitviper evolution. Pages 107–117 in J. A. Campbell and E. D. Brodie Jr., eds. *Biology of the pitvipers*. Selva, Tyler, TX.
- Klauber, L. M. 1956. *Rattlesnakes*. University of California Press, Berkeley.
- Laidre, M. E., and R. A. Johnstone. 2013. Animals signals. *Current Biology* 23:R829–R833.
- Laland, K. N., T. Uller, M. W. Feldman, K. Sterelny, G. B. Müller, A. P. Moczek, E. Jablonka, et al. 2014. Does evolutionary theory need a rethink? yes, urgently. *Nature* 514:161–164.
- Levis, N. A., and D. W. Pfennig. 2016. 'Plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends in Ecology and Evolution* 31:563–574.
- Lorenz, K. Z. 1966. *On aggression*. Methuen, London.
- Martin, J. H., and R. M. Bagby. 1972. Temperature-frequency relationship of the rattlesnake rattle. *Copeia* 1972:482–485.
- Maynard Smith, J., and D. Harper. 2003. *Animal signals*. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.

- Mayr, E. 1959. The emergence of evolutionary novelties. Pages 349–380 in S. Tax, ed. *Evolution after Darwin*. University of Chicago Press, Chicago.
- Moczek, A. P., S. E. Sultan, S. Foster, C. Ledon-Rettig, I. Dworkin, H. F. Nijhout, E. Abouheif, et al. 2011. The role of developmental plasticity in evolutionary innovation. *Proceedings of the Royal Society B: Biological Sciences* 278:2705–2713.
- Moon, B. R. 2001. Muscle physiology and the evolution of the rattling system in rattlesnakes. *Journal of Herpetology* 35:497–500.
- Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton, NJ.
- Owings, D. H., M. P. Rowe, and A. S. Rundus. 2002. The rattling sound of rattlesnakes (*Crotalus viridis*) as a communicative resource for ground squirrels (*Spermophilus beecheyi*) and burrowing owls (*Athene cunicularia*). *Journal of Comparative Psychology* 116:197–205.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Price, T. D., A. Qvarnstrom, and D. E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society B: Biological Sciences* 270:1433–1440.
- Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13:93.
- R Development Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Revell, L. J. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3:217–223.
- Schuett, G. W., D. L. Clark, and F. Kraus. 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. *Animal Behaviour* 32:625–626.
- Sisk, N. R., and J. F. Jackson. 1997. Tests of two hypotheses for the origin of the crotaline rattle. *Copeia* 1997:485–495.
- Sweet, S. S. 1985. Geographic variation, convergent crypsis and mimicry in gopher snakes (*Pituophis melanoleucus*) and western rattlesnakes (*Crotalus viridis*). *Journal of Herpetology* 19:55–67.
- Tiebout, H. M. 1997. Caudal luring by a temperate colubrid snake, *Elaphe obsoleta*, and its implications for the evolution of the rattle among rattlesnakes. *Journal of Herpetology* 31:290–292.
- Tinbergen, N. 1952. Derived activities: their causation, biological significance, origin and emancipation during evolution. *Quarterly Review of Biology* 27:1–32.
- Waddington, C. H. 1942. Canalization of development and the inheritance of acquired characters. *Nature* 150:563–565.
- . 1953. Experiments in acquired characteristics. *Scientific American* 189:92–99.
- Wagner, G. P. 1989. The origin of morphological characters and the biological basis of homology. *Evolution* 43:1157–1171.
- Wagner, G. P., and V. J. Lynch. 2010. Evolutionary novelties. *Current Biology* 20:R48–R52.
- Wcislo, W. T. 1989. Behavioral environments and evolutionary change. *Annual Review of Ecology and Systematics* 20:137–169.
- Wenzel, J. W. 1992. Behavioral homology and phylogeny. *Annual Review of Ecology and Systematics* 23:361–381.
- West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford University Press, New York.
- Wray, G. A., H. E. Hoekstra, D. J. Futuyma, R. E. Lenski, T. F. C. Mackay, D. Schluter, and J. E. Strassmann. 2014. Does evolutionary theory need a rethink? no, all is well. *Nature* 514:161–164.
- Young, B. A. 2003. Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. *Quarterly Review of Biology* 78:303–325.
- Zimmerman, A. A., and C. H. Pope. 1948. Development and growth of the rattle of rattlesnakes. *Fieldiana: Zoology* 32:357–413.

Natural History Editor: Mark A. McPeck



Pair of black-tailed rattlesnakes (*Crotalus molossus*) near Portal, Arizona. Photo credit: David W. Pfennig.