

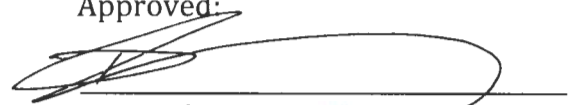
A phylogenetic approach to understanding the evolution of the rattlesnake rattle

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INTRODUCTION

One of the biggest questions of evolutionary biology is how novel traits arise and fixate in a population. Rattlesnakes (a monophyletic group within Viperidae) are equipped with a keratinized tail tip of overlapping hollow segments that makes sound when vibrated. This structure is unique to rattlesnakes, which use it for aposematic signaling (Greene 1988). A better understanding of how this novel structure evolved could shed light on how novel traits arise in general.

Though many researchers have postulated hypotheses about the evolutionary origins of the rattlesnake rattle (for example, Rowe et al. 2002; Klauber 1972; Young and Brown 1995), it is still unclear what exactly led to the evolution of this unique structure. Some authors support the idea that the rattle evolved to enhance the sound produced by tail-vibrating in an extinct rattlesnake ancestor (Klauber 1972; Rowe et al. 2002; Moon 2001). Tail-vibrating is a defensive signal where a snake vibrates its tail rapidly, often against a substrate, producing a buzzing sound. This widespread behavior almost certainly serves as a warning and/or distraction to a potential predator, though this has never been tested specifically. Tail-vibrating is used in a similar context as rattlesnake rattling, and the movement itself is strongly reminiscent of rattlesnake rattling, the major difference being that the rattlesnake tail is held vertically, while tail-vibrating snakes hold the tail horizontally. For these and other reasons, many researchers cite tail-vibration as the most likely signal precursor to rattlesnake rattling.

However, other researchers have speculated that the rattle signal could have evolved from a different snake tail behavior called “caudal luring” (Schuett et al. 1984). Caudal luring is a feeding behavior where a snake moves its (often brightly colored) tail in

a slow, wave-like manner in order to attract prey species that potentially mistake the tail for an invertebrate food source (Tiebout 1997; Sazima 1991; Leal and Thomas 1994). According to this hypothesis, an incipient rattle may not have increased sound production because of the high amount of structural specificity required for such a structure to function (i.e. a series of loosely overlapping hollow segments of keratin) in making noise. If that incipient structure did not increase sound production, then it would apparently have no function in enhancing tail-vibration (Schuett et al. 1984). Such an incipient rattle might, however, have increased the effectiveness of caudal luring if the tail modification resulted in more effective luring—for example, if the tail better resembled an arthropod head (though see Sisk and Jackson 1997). Selection for a modified tail to enhance caudal luring could have led to the evolution of further elaboration of the structure, eventually resulting in a sound-producing rattle.

However, this hypothesis runs into a number of problems, the most obvious being parsimony. Very few modern rattlesnakes caudal lure while all rattlesnake species use the rattle for defensive signaling (Moon 2001; Rowe et al. 2002). Thus, if caudal luring were the signal precursor for the rattlesnake rattle, the signal would have had to switch from an offensive to a defensive context. No such jump is required if tail-vibration were the signal precursor.

The second major problem with the caudal luring hypothesis is that both rattlesnakes and their closest relatives (the genus *Agkistrodon*) have elevated oxidative capacities in their tail musculature (Moon 2001). Rapid, sustained tail-vibration is a demanding movement for an ectotherm, especially compared to caudal luring, which almost certainly requires much less energy. With this in mind, it would seem more likely

that such specialized tail muscles in rattlesnakes and their closest relatives would have evolved to enhance a demanding movement like tail-vibration, not caudal luring.

Thus we are left with two hypotheses about the evolutionary origin of the rattlesnake rattle—the “tail-vibration as signal precursor hypothesis” and the “caudal luring as signal precursor hypothesis.” The purpose of this study is to use distributions of tail behaviors across modern species of New World pit vipers to better understand the tail behaviors that ancestral rattlesnakes might have had. This will inform the signal precursor debate and will more generally lead to a better understanding of rattle evolution. Such a phylogenetic approach to understanding rattlesnake evolution has not yet been published in the literature. The first step in this project was to map observations of caudal luring and tail-vibration in different New World pit viper species across the entire phylogeny. If one of these behaviors were clustered in close rattlesnake relatives while the other was concentrated in more distant relatives, it could suggest something about the likely behaviors displayed by ancestral rattlesnakes. If ancestral rattlesnakes did not display one of the tail behaviors, then it would of course be exceedingly unlikely that the rattlesnake rattle evolved to enhance that signal.

The second step in this project was more closely analyzing the specifics of one of the behaviors and how it changes across the New World pit viper phylogeny. Tail-vibrating was examined because there is wider support in the literature for that behavior being the signal precursor. Different New World pit viper species served as proxies for the evolutionary history of the rattlesnake, depending on how closely related each species is to rattlesnakes. In this way, if the behavior changed in any specific way in closer rattlesnake relatives, it could inform how that behavior changed along the ancestral rattlesnake lineage.

METHODS

First, a literature review was carried out in order to assess how widespread both tail-vibrating and caudal luring are in New World pit vipers. Data were obtained from journal articles, field guides, personal communication with researchers, and personal observations by the author. This information was then mapped onto ancestral state reconstructions created using Mesquite 2GB. The phylogenies used to build these ancestral state reconstructions were based on the phylogeny of Pyron et al. (2013), which is the most recent comprehensive phylogenetic reconstruction available for this clade.

With the knowledge of the general presence or absence of these traits in species within the clade, a more specific analysis of the behaviors was then carried out. This analysis compared the tail-vibration of species across New World pit vipers to examine whether it changed in any persistent way in closer rattlesnake relatives. Snakes from museums, zoos, and private collections were filmed with a high speed Casio Exilim EX-ZR700 camera at 480 frames per second. This high frame rate allowed for an analysis of the rattling speed of each individual. Tail-vibration was filmed for approximately 30 seconds to 2 minutes.

Tail-vibration was initiated by approaching the snake or, if that did not sufficiently provoke the animal to display defensively, a stuffed animal head mounted on a pair of tongs was presented to the snake. This was surprisingly successful in initiating a defensive response in the animals, potentially because of the toy's resemblance to a mammalian predator. Only maximum recorded rattle speeds were used in analyses to adjust for potential differences in the state of defensive arousal of each individual snake. No data was used in analyses for snakes being brumated or otherwise being kept at atypically low

temperatures, which has been shown to decrease rattling speed in rattlesnakes (Martin and Roland 1972). Videos were analyzed using Adobe Premiere Pro, which allowed for frame by frame analysis of the videos so that the number of tail vibrations per second could be recorded. One rattle/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.

RESULTS

Information was found on the tail behavior of nearly every genus of New World pit vipers (Appendix B), excluding rattling behavior in rattlesnakes. Both caudal luring and tail-vibration were widespread through the clade and neither behavior was significantly more concentrated in closer rattlesnake relatives (Figures 1 and 2). Thus, it appears likely that ancestral rattlesnakes exhibited both tail-vibration behavior and caudal luring behavior.

Tail-vibration was filmed in 65 individuals across 27 species and 11 genera. Snake groups filmed included Colubrids (outgroup), rattlesnakes, and non-rattlesnake New World pit vipers. This third group was further divided into close rattlesnakes relatives and more distant rattlesnake relatives (Figure 3) to see how tail-vibrating changed across the New World pit viper clade.

Maximum Likelihood Reconstruction of Caudal Luring in New World Pit Viper Genera

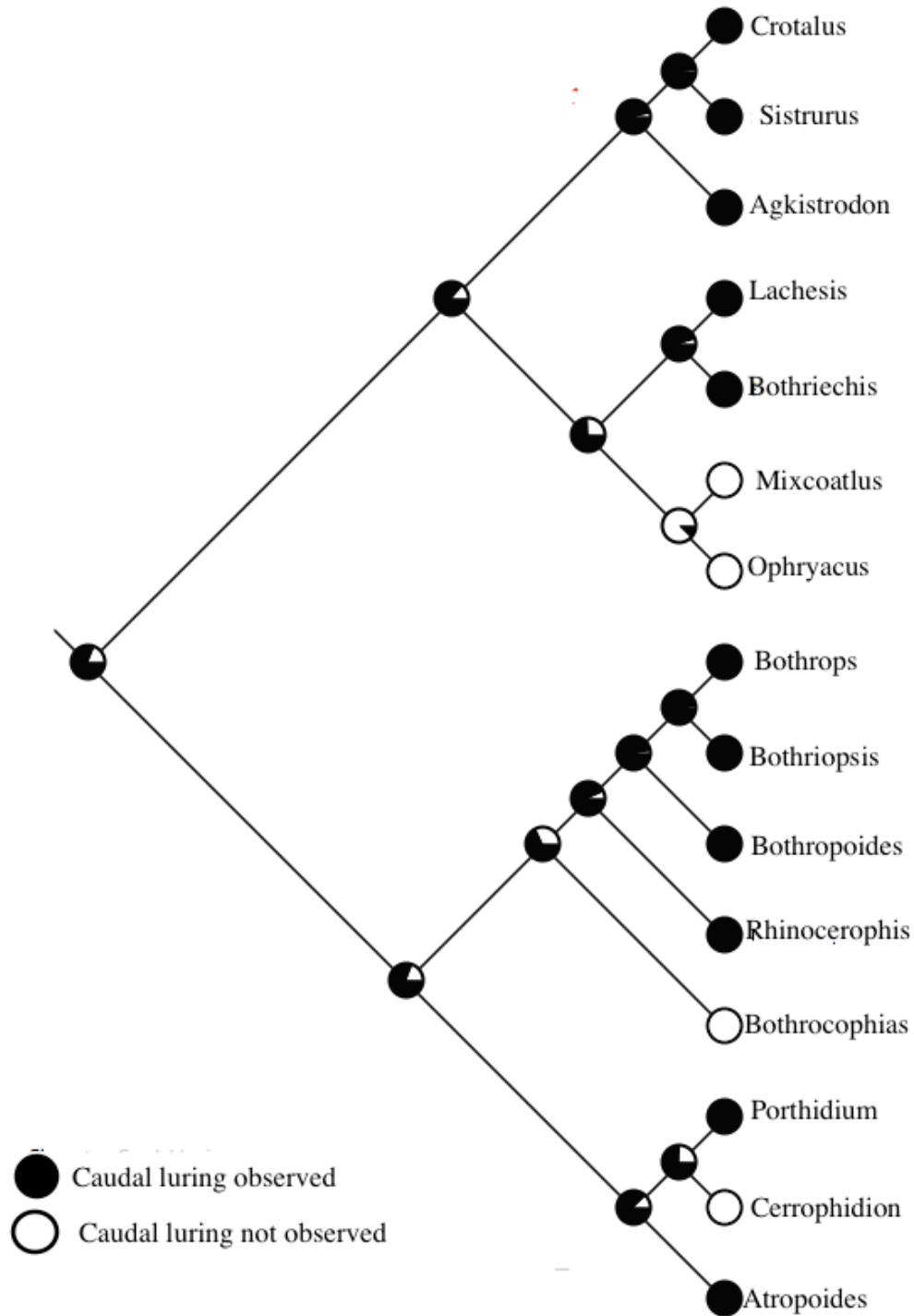


Figure 1: Genus-level ancestral state reconstruction of New World pit vipers. Black dots represent genera containing at least one species known to caudal lure. White dots represent genera without species known to caudal lure, though the absence of such an observation does not necessarily mean species in that genus do not perform caudal luring. Rattlesnakes comprise the two genera *Crotalus* and *Sistrurus*. This phylogeny is based on Pyron et al. 2013.

Maximum Likelihood Reconstruction of Tail-Vibrating in New World Pit Viper Genera

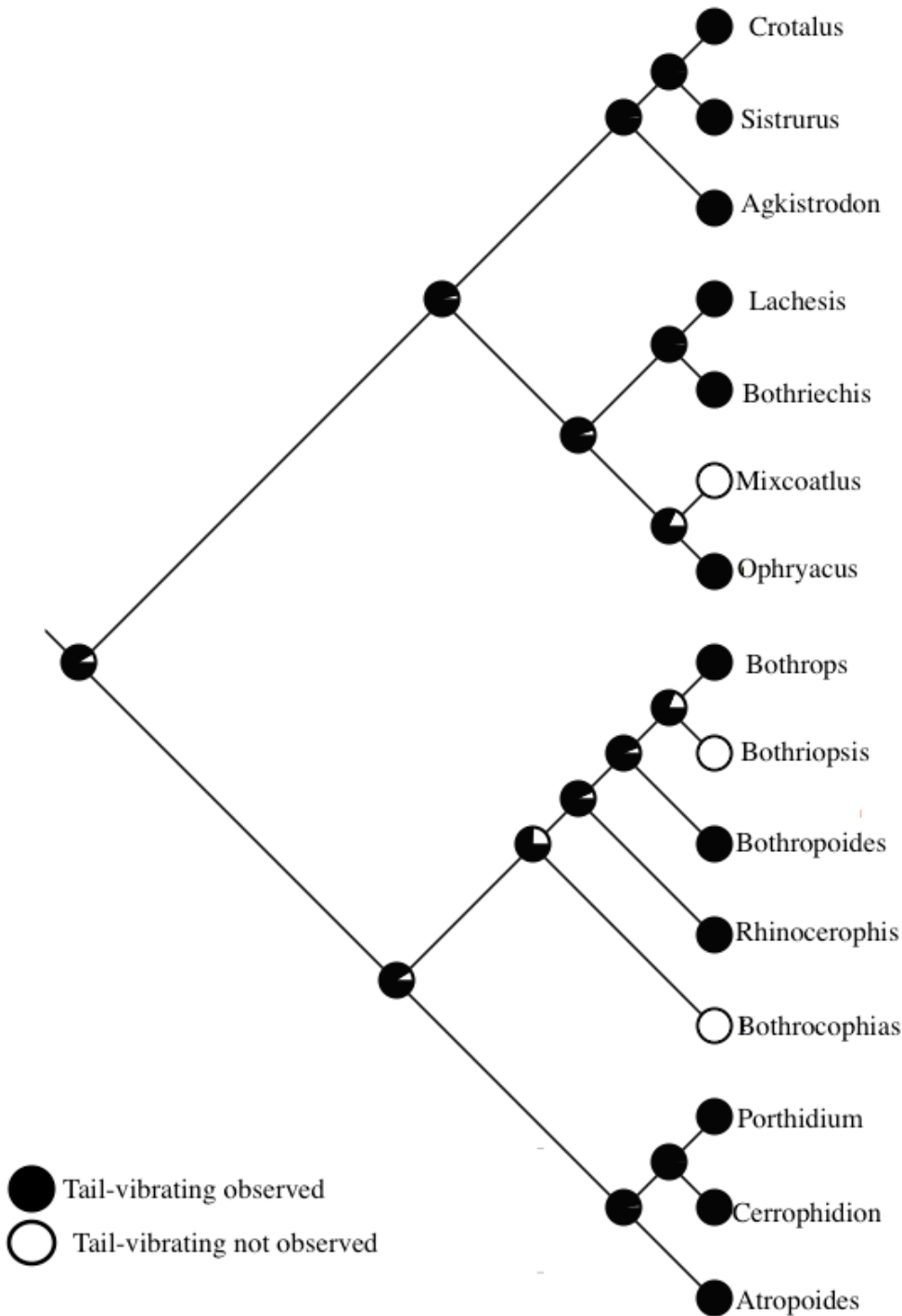


Figure 2: Genus-level ancestral state reconstruction of New World pit vipers. Black dots represent genera containing at least one species known to tail-vibrate (rattlesnake rattling was considered a form of tail-vibration in this figure). White dots represent genera without species known to tail-vibrate, though the absence of such an observation does not necessarily mean species in that genus do not perform tail-vibration. Rattlesnakes comprise the two genera *Sistrurus* and *Crotalus*. This phylogeny is based on Pyron et al. 2013.

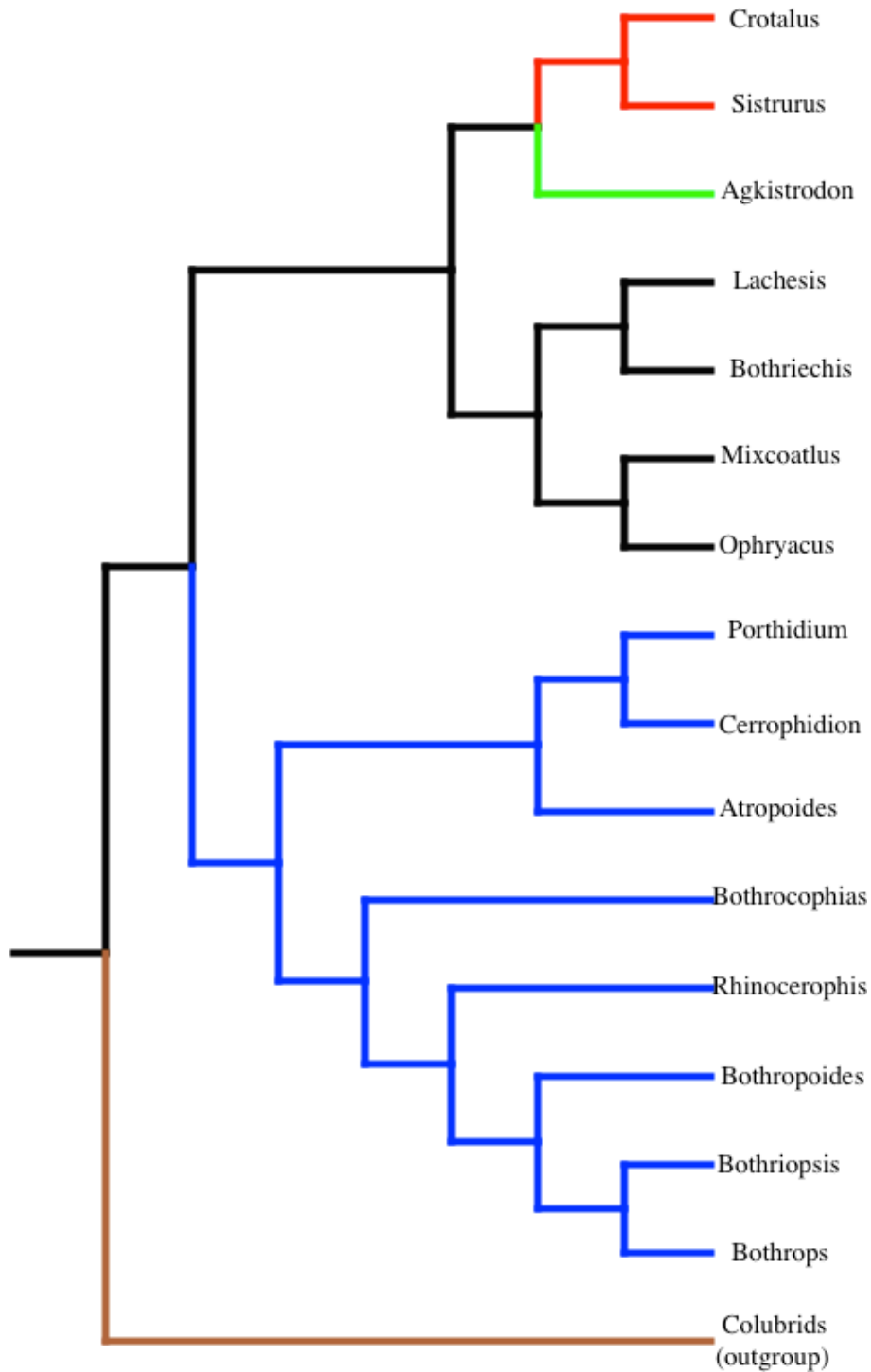


Figure 3: This figure shows how taxa are divided numerically in the analyses of rattling speed in the figures below. Rattlesnakes, the red taxa, represent group “0.” Group “1” represents the green genus Agkistrodon shown above. No data was obtained from taxa in the black genera. The blue taxa are the more distantly related New World pit vipers and are represented by group “2.” Importantly, tail-vibration was not filmed in all the genera in the blue clade (see Appendix A). The brown Colubrid outgroup will be represented by group “3.”

Average rattling/vibratory speeds among these groups were compared using a Tukey-Cramer means comparison. Rattlesnakes were found to rattle significantly faster than any other group tail-vibrated. The closer rattlesnake relatives (Group 1) tail-vibrated faster than Groups 2 and 3 on average (Table 1), but the Tukey-Cramer comparison did not find this difference to be significant (Figure 4).

Group	Number of individuals recorded	Average rattling/vibratory speed
0	23	58.74 rattles/second
1	12*	33.65 vibrations/ second*
2	22	21.91 vibrations/ second
3	8	21.04 rattles/ second

Table 1: Average tail-vibrating/rattling frequencies among the different groups of snakes outlined in Figure 3. (*) Indicates data that changes in Figure 5, with *A. piscivorus* data removed. Average vibratory speed increases to 37.11 rattles/second and the number of individuals recorded is reduced to 10.

However, one species in Group 1 is likely responsible for this—*Agkistrodon piscivorus*. The two outliers in Group 1’s data in Figure 4 that are dramatically lower than any other vibratory speeds in the group belong to the only two *A. piscivorus* individuals filmed. *A. piscivorus* is the only known aquatic pit viper in the world (Campbell et al. 2004) and it is possible that constraints from this habitat led to the loss of a fast tail-vibratory speed, perhaps due to morphological changes in the tail to make it a more effective swimming structure. If *A. piscivorus* is removed from the data, the rattling speeds from Group 1 become significantly higher than those of Groups 2 and 3 (Figure 5), while Group 0

remains significantly faster than any other group. Thus, according to this data rattling speed does increase in closer rattlesnake relatives.

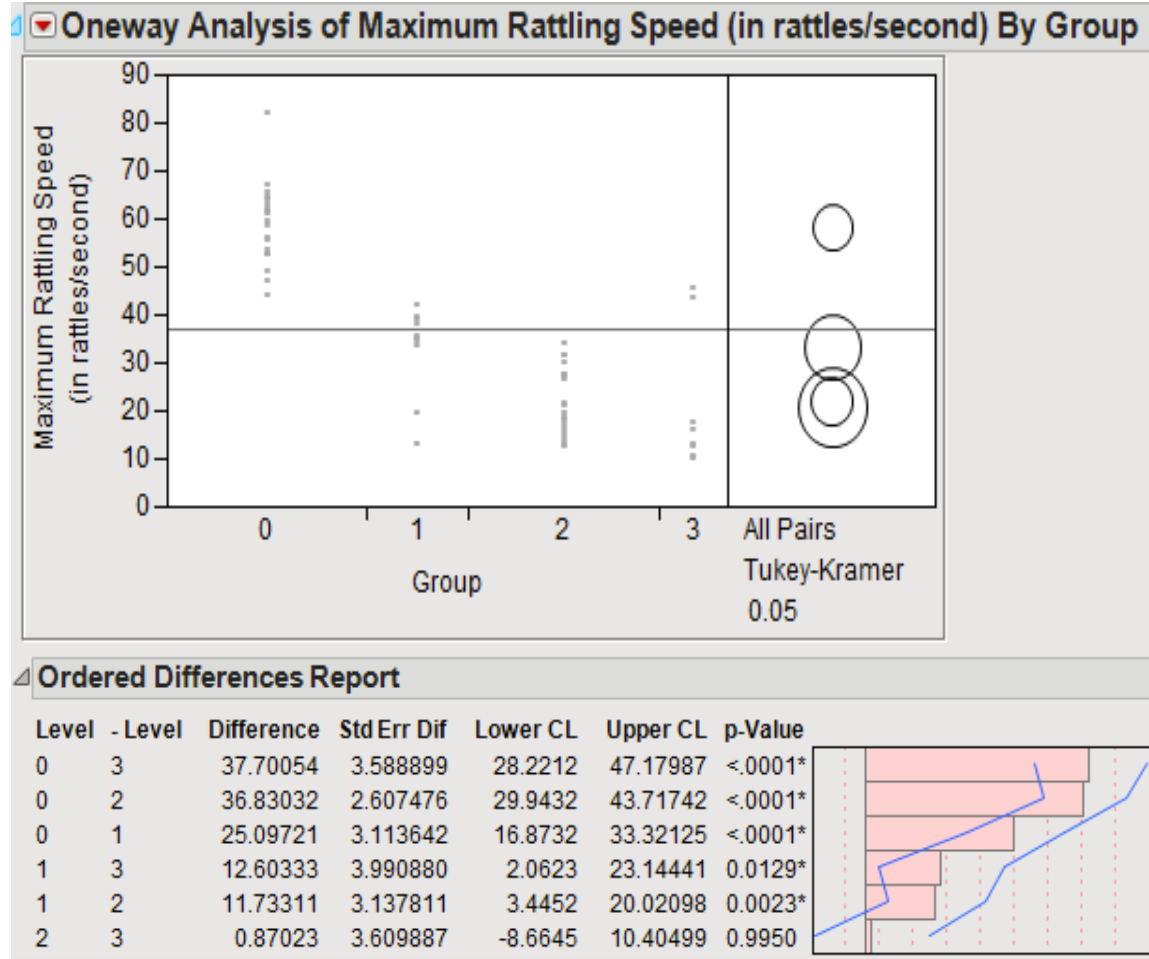
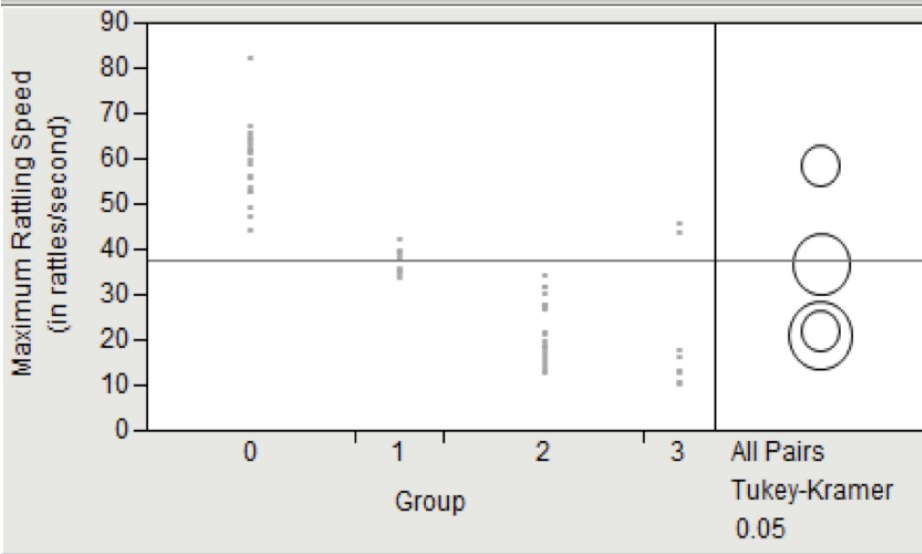


Figure 4: Tukey-Kramer comparison of tail-vibrating/rattling speed among the four groups of snakes outlined in Figure 3. Group 0 (rattlesnakes) rattle significantly faster than any other group. Group 1 (*Agkistrodon* sp.) tail-vibrates faster than Groups 2 and 3 but these results are not significant ($p= 0.0023$ and 0.0129 , respectively). Note the two *A. piscivorus* outliers in Group 1 that have rattling speeds dramatically lower than any other data points in the group.

Oneway Analysis of Maximum Rattling Speed By Group with *A. piscivorus* Data Removed



Ordered Differences Report

Level	- Level	Difference	Std Err Dif	Lower CL	Upper CL	p-Value
0	3	37.70054	3.347288	28.8510	46.55008	<.0001*
0	2	36.83032	2.431936	30.4008	43.25985	<.0001*
0	1	21.63604	3.088973	13.4694	29.80265	<.0001*
1	3	16.06450	3.868231	5.8377	26.29130	0.0006*
1	2	15.19427	3.110174	6.9716	23.41693	<.0001*
2	3	0.87023	3.366863	-8.0311	9.77152	0.9939

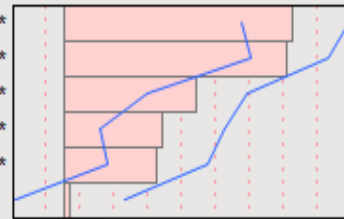


Figure 5: Tukey-Cramer comparison of the groups outlined in Figure 3, with *A. piscivorus* data removed. Groups 0 and 1 are both significantly different from all other groups and Group 1 is intermediary in rattling speed between Group 0 and Groups 2 and 3.

DISCUSSION

The ancestral state reconstructions obtained in this research suggest that ancestral rattlesnakes likely tail-vibrated and caudal lured. Had one of the tail behaviors been significantly more concentrated in closer rattlesnake relatives, it would have been particularly informative in the debate over what the signal precursor was to rattlesnake rattling. But because both behaviors are spread fairly evenly through the clade, this approach did not bolster either hypothesis.

However, the data obtained in the second part of this research supports the hypothesis that tail-vibration provided the signal basis for the evolution of the rattlesnake rattle. The data shows that rattlesnakes rattle faster than any other group tested. It also shows that, with the exception of *A. piscivorus*, species in the genus most closely related to rattlesnakes tail-vibrate faster than more distantly related pit vipers. This suggests that tail-vibration was modified in ancestral rattlesnakes during rattle evolution to become faster, as elevated vibratory speed is also a trait of extant rattlesnakes. One would not necessarily expect this stepwise modification of tail-vibration through evolutionary time if caudal luring were the signal precursor.

This research also suggests some potential hypotheses for the evolutionary pressures that led to the evolution of the rattle. With the exception of *A. piscivorus*, *Agkistrodon* species tail-vibrate significantly faster than more distantly related pit vipers. While it remains unclear *why* such an increased vibratory speed would be selected for in this genus, the results of this selection could have actually facilitated rattle evolution if this increased vibratory capacity led to tail damage. Rattlesnakes are thought to have originated in rocky outcrops in Central Mexico, and vibrating at high frequencies against such a hard substrate could have led to tail damage in fast-vibrating ancestral rattlesnakes. I know from personal communication with staff at the Kentucky Reptile Zoo that some individuals of the genus *Bothrops* in their collection have fractured their tails in the process of tail-vibrating. If a structure evolved in ancestral rattlesnakes that protected the tail during vibration—perhaps some sort of keratinous bulb at the end of the tail— it could have been selected for and then eventually modified into the unique sound-producing structure that modern rattlesnakes are equipped with. This hypothesis that the original purpose of incipient

rattles was for protection of the tail has been raised before (Tiebout 1997) but this is the first research to find potential support for the idea through an actual empirical study.

In moving forward, this hypothesis that incipient rattles first evolved to protect against tail-damage sustained during tail-vibration should be investigated more specifically. This could potentially be done by investigating whether faster tail-vibrating species have a higher incidence of tail breakage than slower vibrating species. One could also investigate whether tail fractures are more common in tail-vibrating species that live in habitats with hard substrates. Another potential way to move forward with this research would be to investigate why *Agkistrodon*, and for that matter rattlesnakes, evolved such elevated rattling speeds. Is a higher rattling speed indicative of healthier individuals more capable of delivering a toxic bite to a would-be predator? Are predators more likely to avoid faster-rattling individuals?

A more comprehensive examination of vibratory speeds across pit vipers would bolster the significance of this research. In particular, getting data for the one species of *Agkistrodon* (*A. taylori*) not included in the data is important in order to better substantiate the claim that vibratory speed is elevated in this genus compared to other non-rattlesnake pit vipers. Obtaining data from the clade containing *Lachesis*, *Ophryacus*, *Mixcoatlus*, and *Bothriechis* would also be informative in understanding where in the evolutionary sequence elevated vibratory speed began. It is also important to note that elevated vibratory speed is apparently not unique to rattlesnakes and the genus *Agkistrodon*. Two different species of Colubrid (*Pituophis melanoleucus* and *Elaphe obsoleta lindheimeri*) both vibrated at speeds typical of a slow rattling rattlesnake (Appendix A). Yet neither of these species are part of lineages that evolved any sort of modified tail structure. Why would a

rattle evolve in fast vibrating rattlesnake ancestors but not in fast vibrating Colubrid ancestors? Hopefully, future research will be able to address some of these questions in order to bring us closer to understanding how the rattlesnake rattle evolved and, thereby better understand how novel traits arise in populations in general.

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Appendix A: Rattling/ Vibratory Speeds of Snakes Filmed

Species	Maximum Rattles/ Second	Phylogenetic Group (according to Figure 3)
Othriophis taeniurus	10.20	3
Othriophis taeniurus	10.57	3
Bothrops colombiensis	12.28	2
Elaphe climacophora	12.31	3
Lampropeltis getula	12.87	3
Agkistrodon piscivorus	13.10	1
Bothrops caribbaeus	13.22	2
Bothrops moojeni	13.77	2
Bothrops moojeni	14.91	2
Bothrops colombiensis	14.91	2
Lampropeltis getula getula	16.00	3
Bothrops moojeni	16.17	2
Bothrops moojeni	16.82	2
Lampropeltis calligaster	17.27	3
Bothrops moojeni	17.98	2
Bothrops atrox	18.70	2
Bothrops moojeni	19.28	2
Bothrops colombiensis	19.51	2

Agkistrodon piscivorus	19.58	1
Bothrops matogrossensis	21.07	2
Porthidium ophryomegus	21.54	2
Bothrops moojeni	26.56	2
Rhinocerophus alternatus	26.67	2
Rhinocerophus alternatus	27.00	2
Rhinocerophus alternatus	27.40	2
Rhinocerophus alternatus	27.66	2
Rhinocerophus alternatus	29.99	2
Rhinocerophus alternatus	31.28	2
Rhinocerophus alternatus	31.54	2
Agkistrodon contortrix	33.35	1
Atropoides mexicanus	33.82	2
Agkistrodon bilineatus	34.67	1
Agkistrodon bilineatus	35.10	1
Agkistrodon bilineatus	35.56	1
Agkistrodon contortrix	35.56	1
Agkistrodon contortrix	37.93	1
Agkistrodon bilineatus	38.71	1
Agkistrodon contortrix	38.89	1
Agkistrodon contortrix	39.51	1

<i>Agkistrodon contortrix</i>	41.79	1
<i>Pituophis melanoleucus</i>	43.47	3
<i>Crotalus horridus</i>	43.79	0
<i>Elaphe obsoleta</i>	45.65	3
<i>Crotalus basilicus</i>	47.17	0
<i>Crotalus horridus</i>	49.18	0
<i>Crotalus atrox</i>	52.34	0
<i>Crotalus atrox</i>	52.63	0
<i>Crotalus cerberus</i>	53.22	0
<i>Crotalus durissus</i>	53.33	0
<i>Crotalus durissus</i>	55.43	0
<i>Crotalus durissus</i>	56.00	0
<i>Crotalus durissus</i>	56.22	0
<i>Sistrurus milairius</i>	58.34	0
<i>Crotalus lepidus</i>	59.65	0
<i>Crotalus mitchellii</i>	60.67	0
<i>Sistrurus milairius</i>	60.87	0
<i>Crotalus cerberus</i>	61.30	0
<i>Crotalus durissus</i>	62.02	0
<i>Crotalus durissus</i>	62.95	0
<i>Crotalus durissus</i>	63.05	0

Crotalus ornatus	64.10	0
Crotalus horridus	64.52	0
Crotalus lepidus	65.31	0
Crotalus adamanteus	66.95	0
Crotalus durissus	82.05	0

Appendix B: Recorded Instances of Tail-Vibrating and Caudal Luring in New World

Pit Vipers

Species	Tail-Vibrating	Caudal Luring	Reference
Sistrurus milairius	Yes (has rattle)	Yes	Pers. com. with TM Farrell (Stetson U.); Palmer 1993; Campbell and Lamar 2004
Agkistrodon bilineatus	Yes	Yes	Pers. com. with JA Campbell (U of Texas, Austin); Neill 1960
Lachesis sp.	Yes	Yes	Pers. com. with Tim Trout at Denver Zoo; pers. com. with Dean Ripa at Cape Fear Serpentarium.
Lachesis stenophrys	Yes		Pers. com. with Finn Spaeren of Rainforest Animals Rescue Group
Bothrops asper	Yes	Yes	Pers. com. with JA Campbell (U of Texas, Austin); Tryon 1985
Agkistrodon piscivorus	Yes	Yes	Heatwole and Davison 1976; Werler and Dixon 2000
Agkistrodon contortrix	Yes	Yes	Neill 1948; Pers. com. with CF Smith (Wofford U.); Moon 2001
Crotalus Lepidus	Yes (has rattle)	Yes	Kauffeld 1943
Porthidium hespere		Yes	Pers. com. with JR Velasco (U of Texas, Austin)
Sistrurus catenatus	Yes (has rattle)	Yes	Reiserer 2002
Bothropoides jararaca	Yes	Yes	Sazima 1991; Pers. Com. with Jim Harrison at Kentucky Reptile Zoo
Bothrops	Yes	Yes	Sazima 1991; Pers. comm with Jim

jararacussu			Harrison at Kentucky Reptile Zoo
Bothrops atrox	Yes	Yes	Sazima 1991; Pycraft 1925; Sisk and Jackson 1997
Bothriopsis bilineata		Yes	Green and Campbell 1972
Atropoides nummifer	Yes	Yes	Neill 1960; pers. com. with Jim Harrison at Kentucky Reptile Zoo; Pers. Com. with Gustav Eloy at Najil Kaan
Bothriechis schlegalii	Yes	Yes	Neill 1960; Pers. com. with Finn Spaeren of Rainforest Animals Rescue Group; Pers. com. with Adrian Acevedo of Southwest Florida Venom Farm
Bothriechis lateralis		Yes	Murphy and Mitchell 1984.
Bothriechis bicolor		Yes	Murphy and Mitchell 1984
Crotalus cerastes		Yes	Reiserer 2002
Bothrops moojeni	Yes	Yes	Martins et al. 2002; Andrade et al. 1996; pers. com. with Jim Harrison at Kentucky Reptile Zoo
Bothrops leucurus	Yes	Yes	Martins et al. 2002; Pers. com. with Vini Hansser from Bras Cubas University
Bothropoides neuwiedi	Yes	Yes	Martins et al. 2002; Pers. com. with Vini Hansser from Bras Cubas University
Bothriopsis taeniata		Yes	Martins et al. 2002
Crotalus willardi	Yes (has rattle)	Yes	Greene 1992
Rhinocerophis ammodytoides	Yes		Greene 1992
Bothrops colombiensis	Yes	Yes	Pers. com. with Jim Harrison at Kentucky Reptile Zoo
Bothrops caribaeus	Yes		Pers. com. with Jim Harrison at Kentucky Reptile Zoo; Pers. obs.
Rhinocerophus alternatus	Yes		Pers. com. with Jim Harrison at Kentucky Reptile Zoo; Pers. com. with Vini Hansser from Bras Cubas University
Cerrophidian godmani	Yes		Pers. com. with Jim Harrison at Kentucky Reptile Zoo; Pers. com.

			with Gustav Eloy from Najil Kaan
Atropoides mexicana/ nummifer	Yes		Pers. com. with Jim Harrison at Kentucky Reptile Zoo; personal observation
Rhinocerophus sp.		Yes	Pers. com. with Jim Harrison at Kentucky Reptile Zoo
Atropoides sp.		Yes	Pers. com. with Jim Harrison at Kentucky Reptile Zoo; Pers. com. with Gustav Eloy from Najil Kaan
Porthidium sp.		Yes	Pers. com. with Jim Harrison at Kentucky Reptile Zoo
Bothrops venezuelensis	Yes		Pers. obs.
Bothrops marmoratus	Yes		Pers. com. with Vini Hansser from Bras Cubas University
Atropoides olmec	Yes		Pers. com. with Gustav Eloy from Najil Kaan
Ophryacus undulatus	Yes		Pers. com. with Gustav Eloy from Najil Kaan
Porthidium ophryomegus	Yes		Pers. com. with Gustav Eloy from Najil Kaan; Pers. obs.
Bothrops matogrossensis	Yes		Pers. obs.
Bothropoides insularis		Yes	Andrade et al. 2010

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