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Microevolutionary change in mimicry? Potential erosion of rattling behaviour among nonvenomous snakes on islands lacking rattlesnakes

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Batesian mimics – harmless species that converge on the warning signals of a dangerous species – are spectacular examples of adaptation, but few documented cases involve acoustic signals. Even fewer studies have documented microevolutionary change in mimicry of any kind. Here, we describe a potential evolutionary change in acoustic mimicry. Many nonvenomous snakes vibrate their tail tip when threatened, making a sound resembling venomous rattlesnakes, which can vibrate their tail rapidly and for a long duration. When we compared this behavior between Gophersnakes from mainland California (where rattlesnakes are present) versus nearby derived island populations (where rattlesnakes are absent), we found that mainland snakes vibrated their tail for a longer duration, thereby producing a signal more similar to rattlesnakes. At the same time, we did not find evidence that island snakes differ from mainland snakes in the rate at which they vibrate their tails, or their propensity to vibrate their tails. Taken together, these data lend some support to the longstanding hypothesis that defensive tail vibration by nonvenomous snakes represents acoustic mimicry of rattlesnakes. These data further suggest that this mimetic signal may be undergoing erosion in populations where rattlesnakes are absent.

KEY WORDS: acoustic mimicry, Batesian mimicry, evolution on islands, Gophersnakes, microevolution, *Pituophis catenifer pumilis*.

INTRODUCTION

Batesian mimicry (Bates 1862) evolves when individuals of a palatable species (the “mimic”) gain the selective advantage of reduced predation by converging on the warning signals of a harmful species that predators avoid (the “model”). Although it has long been used to exemplify the power of natural selection to promote remarkable

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adaptation (Fisher 1930–1999; Malcolm 1990; Stevens 2013), most known cases of Batesian mimicry involve visual signals (Stevens 2013; Ruxton et al. 2018). By contrast, few examples involve “acoustic” signals (for exceptions, see Gans 1961; Rowe et al. 1986; Barber & Conner 2007; Aubret & Mangin 2014; Brejcha 2019; Vaughan et al. 2019).

Here, we tested for acoustic mimicry by focusing on a putative mimetic species that occurs in both sympatry – and in allopatry – with its model. Finding that such a species expresses a mimetic phenotype in sympatry – but not in allopatry (or that the phenotype expressed in allopatry resembles the model less) – would provide evidence that the species is, in fact, a Batesian mimic (Pfennig & Mullen 2010). This erosion of the mimetic signal in allopatry should take place because predators that do not co-occur with the model would not be under selection to recognize it, or any other species that resemble it, as dangerous (Waldbauer & Sternburg 1987; Pfennig et al. 2001, 2007; this prediction would not hold if predators migrate from sympatry into allopatry and thereby avoid the mimic in both locations). Moreover, because mimics resemble models that are typically aposematic and therefore conspicuous to potential predators (Stevens 2013; Ruxton et al. 2018), predation on these more apparent – but unprotected – allopatric mimics should be particularly intense (e.g., see Pfennig et al. 2001, 2007). Such erosion of visual signals has been demonstrated in butterflies (Prudic & Oliver 2008; Ries & Mullen 2008; Prudic et al. 2019) and snakes (Harper & Pfennig 2008). However, little is known about whether acoustic signals also degrade in allopatry. Testing for degradation of an acoustic signal in allopatry, therefore, provides an ideal opportunity to document not only a case of acoustic Batesian mimicry but also microevolutionary change in mimicry.

We tested for possible microevolutionary change in mimicry by studying defensive tail vibration in snakes, which has been postulated to represent acoustic mimicry of rattlesnakes (Klauber 1956; Kardong 1980; Brodie & Brodie 2004). As background, many snakes vibrate their tail tips when threatened (Allf et al. 2016), which can create a sound resembling a venomous rattlesnake’s rattle (Klauber 1956; Kardong 1980). Moreover, because rattlesnakes can vibrate their tail rapidly (for over 90 Hz) and for a long duration (for at least a minute in a single bout), presumably the more rapidly and longer a nonvenomous snake vibrates its tail the more likely it is to resemble a dangerous rattlesnake and thereby deter predation (Allf et al. 2016). Indeed, consistent with this rattlesnake mimicry hypothesis, nonvenomous snakes in the family Colubridae from the New World, which are sympatric with rattlesnakes (rattlesnakes evolved and occur exclusively in the New World; Klauber 1956), tail-vibrate faster and longer than Old World colubrids, which are allopatric (Allf et al. 2016).

We focused on a nonvenomous colubrid, the Gophersnake, *Pituophis catenifer*. Not only does this species frequently display defensive tail vibration (Kardong 1980), it also occurs in both sympatry with rattlesnakes (e.g., mainland California) and in allopatry (i.e., on nearby offshore islands where rattlesnakes are absent). We predicted that, if defensive tail vibration constitutes rattlesnake mimicry, then mainland snakes should sound more like a rattlesnake than island snakes. Specifically, mainland snakes should be more likely to vibrate their tail, vibrate their tail faster, and/or vibrate their tail longer. We based our prediction on the following rationale. Because rattlesnakes are present on the mainland only, selection should be more likely to favor rattlesnake mimicry among nonvenomous snakes on the mainland. In contrast, island populations should experience either relaxed selection for mimicry, or alternatively, if tail vibration makes snakes more conspicuous to predators or is energetically costly (as seems likely;

e.g., see Moon 2001), selection favoring the loss of tail-vibration behavior should be favored. Finding support for this prediction would point to possible microevolutionary change in an acoustic mimetic signal.

MATERIALS AND METHODS

We studied tail-vibration behavior among Gophersnakes from four populations and two general regions: two populations on the California mainland where one species of rattlesnake, the Western rattlesnakes (*Crotalus oreganus*), is present (near Santa Barbara and south of San Francisco), and two populations on two separate islands in the Pacific Ocean off of California, where rattlesnakes are absent: Santa Cruz Island and Santa Rosa Island (area: 249 and 217 km², respectively; distance to the mainland: 30 and 44 km, respectively).

Santa Cruz and Santa Rosa Islands are part of the California Channel Islands, which formed from tectonic activity and emerged above sea level around 5 mya (Atwater 1998). These islands were never connected to the mainland. However, until about 9,000 ya, Santa Cruz and Santa Rosa Islands, along with Anacapa and San Miguel Islands, formed a contiguous land mass, when, during the Pleistocene glacial period, sea level was much lower. The first fossil evidence of Gophersnakes on these islands is from 8,000 ya deposits on San Miguel Island (Guthrie 1993; Allen 2013). Presumably, Gophersnakes colonized the islands during the Pleistocene when sea level was lower and hence the distance to the mainland was shorter. It is unknown, however, whether Gophersnakes independently colonized Santa Rosa, Santa Cruz, and San Miguel Islands, or whether there was a single colonization event before the islands separated. Regardless, these populations share smaller body sizes, smaller relative head sizes, and reduced blood glucose (Sparkman et al. 2018). Recent gene flow between island and mainland populations is unlikely, owing to > 30 km of cold water separating the islands from the mainland (Fig. 1).

Unlike Gophersnakes, rattlesnakes do not currently occur on these islands (rattlesnake fossils have, however, been found in deposits dated to before 11,000 ya, before evidence of Gophersnake arrival; Guthrie 1993). On the nearby mainland, however, Western rattlesnakes (*Crotalus oreganus*) are common (this rattlesnake species can also be found on Catalina Island, 100 km from Santa Cruz Island and 135 km from Santa Rosa Island; Schoenherr et al. 1999). Island and mainland sites host similar vegetative communities throughout which Gophersnakes can be found – grassland, chaparral, coastal sage scrub, and oak woodland. Although the islands are less species rich than the mainland, similar types of predators are found on the islands as on the mainland. Although 12 species of mammals and 42 species of birds are found on Santa Cruz Island (including such potential snake predators as foxes, skunks, and six species of raptors), there is little, if any, migration between mainland and islands (Schoenherr et al. 1999).

To test our prediction that, compared to island snakes, mainland Gophersnakes should sound more like a rattlesnake (by being more likely to vibrate or to vibrate faster or longer; see Introduction), we recorded tail vibration in 18 mainland (7 males:11 females) and 15 island snakes (11 males:4 females) over 3 years (2017–2019). Snakes were captured between March and June under coverboards from field sites near Santa Barbara and south of San Francisco (mainland populations), and Santa Cruz Island and Santa Rosa Island (island populations). Upon capture, snakes' body size (snout-vent length, SVL) and cloacal temperature was immediately recorded and a small amount of blood was extracted from the caudal vein of island snakes (for a separate study). Snakes were then left undisturbed in a cloth bag for 2.5 hr at a working area close to the field capture location.

We removed each snake from its bag and placed it in a 28-L bucket. We then used similar procedures as a prior publication (Allf et al. 2016) to measure defensive tail vibration. Namely, each snake was briefly presented with a simulated predatory attack using a stuffed mammal head mounted on snake tongs. Defensive tail vibration was filmed with a Casio Exilim EXZR700 camera at 480 frames/sec. Each snake's behavior was filmed once for approximately 2 min. Rate (frequency) and duration of tail vibration were calculated by analyzing the slow-motion videos using Adobe



Fig. 1. — Study populations (stars) showing mainland (Santa Barbara and San Mateo counties: rattlesnakes present) and island (Santa Cruz and Santa Rosa Islands: rattlesnakes are absent) locations. Map: Wikimedia Commons.

Premiere Pro. Only maximum vibratory rate and duration were used in analyses to control for differences in snakes' states of arousal and for interruptions that occurred in some vibratory episodes during the trial (i.e. striking) that may have ended a vibratory episode prematurely.

For our analyses, we began by using an ANOVA to test whether there was a specific effect of year on either the rate or duration of tail vibration. Next, we constructed regression models to assess the relationship between a snake's location (i.e., island or mainland) and three dependent variables of interest: likelihood to vibrate tail, tail-vibration rate, and tail-vibration duration. To isolate the effect of location on each dependent variable, we adjusted for sex, SVL, body temperature and weight. For tail-vibration likelihood we used binary logistic regression and for vibration rate and duration we used linear regression models. Given that temperature data were not collected for eight mainland snakes (24% of our total sample) we also conducted sensitivity analyses excluding temperature as a covariate. Next, we tested whether an individual's temperature or body size was specifically associated with its rate or duration of tail vibration (temperature can affect tail vibration in rattlesnakes; Martin & Bagby 1972; similarly, size can influence antipredator behavior in snakes; Roth & Johnson 2004). Finally, we used a one-tailed Fisher's exact test and one-tailed *t*-tests to determine if (as predicted; see Introduction) mainland snakes were more likely than island snakes to tail vibrate and to vibrate faster and longer. All analyses were performed using JMP Pro 14.0.0 (SAS Institute).

RESULTS

There was no effect of year on either the rate or duration of tail vibration (ANOVA: rate: $F_{2,32} = 0.799$, $P = 0.459$; duration: $F_{2,32} = 0.396$, $P = 0.676$). Thus, for all subsequent analyses reported below, we pooled the data across all 3 years (2017–2019). There was no significant effect of location (i.e., island or mainland) on Gophersnakes' likelihood to tail vibrate or their tail-vibration rate or duration when accounting for sex, SVL, weight, and temperature as covariates in regression models ($N = 24$; Table 1). However, once temperature was removed as a covariate we found that island snake populations were associated with a 2.95 sec decrease in tail-vibration duration, adjusting for sex, SVL and weight ($P = 0.01$; $N = 32$; Table 1).

Although we did not record temperature for eight mainland snakes, the cloacal temperature for the remaining 10 mainland snakes was lower than that for the 15 island snakes (mean \pm s.e.m. temperature for mainland: 18.47 ± 1.37 °C, island: 22.43 ± 0.65 °C; t -ratio = 2.60, $P = 0.022$). This higher temperature on the island should have caused island snakes to tail-vibrate faster than mainland snakes, opposite of our a priori prediction (see above).

As expected (Sparkman et al. 2018), mainland snakes were larger than island snakes (SVL for mainland: 709 ± 60 mm, island: 488 ± 66 mm; t -ratio = 2.45, $P = 0.020$). However, an individual's body size did not affect its rate or duration of tail vibration (rate: $R^2 = 0.13$, $P = 0.121$; duration: $R^2 = 0.13$, $P = 0.176$).

Contrary to our a priori prediction, mainland Gophersnakes were no more likely to vibrate their tail than island snakes: 12 of 18 mainland snakes (67%) versus 7 of 15 island snakes (47%) vibrated [one-tailed Fisher's exact test, $P = 0.211$; snakes that vibrated did not differ from those that did not vibrate in sex, size, weight or temperature (Table 1)]. Also contrary to expectation, mainland snakes did not vibrate their tails faster than island snakes (mainland: 30.45 ± 5.79 Hz, island: 23.66 ± 7.11 Hz; t -ratio = 0.74, $P = 0.233$). This lack of relationship held when we excluded snakes that did not vibrate at all from the analysis (mainland: 45.68 ± 3.82 Hz, island: 50.70 ± 4.94 Hz; t -ratio = -0.80 , $P = 0.22$). However, consistent with our prediction, mainland snakes did tail vibrate longer than island snakes (mainland: 2.55 ± 0.57 sec, island: 1.10 ± 0.40 sec; t -ratio = 2.08, $P = 0.023$; Fig. 2). This difference between mainland and island snakes held even when we excluded snakes that did not vibrate at all (mainland: 3.83 ± 0.55 sec, island: 2.26 ± 0.56 sec; t -ratio = 1.87, $P = 0.041$). Likewise, the relationship held even when we excluded the eight mainland snakes whose temperature we were unable to record (mainland: 3.11 ± 0.83 sec, island: 1.10 ± 0.40 sec; t -ratio = 2.17, $P = 0.024$).

DISCUSSION

Our data suggest that Gophersnakes exhibit defensive tail vibration more similar to rattlesnakes in populations where rattlesnakes are present than in populations where rattlesnakes have long been absent. Specifically, prior studies have shown that rattlesnakes tend to vibrate their tail for a protracted duration (Allf et al. 2016), and we found that Gophersnakes from mainland California – where rattlesnakes are present – vibrated their tails for a longer duration than Gophersnakes from nearby islands – where rattlesnakes are absent (Fig. 2). We did not find a difference between the two populations in the rate at which Gophersnakes vibrate their tails, or their propensity to tail-vibrate.

Table 1.

Results of regression models predicting Gophersnake tail-vibration likelihood, rate and duration shown with and without temperature as a covariate.

*Indicates significant predictor variable ($P < 0.05$).

Outcome	All covariates ($N = 25$)		Temp. excluded ($N = 32$)	
Likelihood to tail-vibrate (1 = vibrated tail; logistic reg.)	$P = 0.26$, pseudo $R^2 = 0.19$		$P = 0.41$, pseudo $R^2 = 0.09$	
Covariate	Odds Ratio	P	Odds Ratio	P
Location (1 = island)	1.11	0.95	0.23	0.10
Sex (1 = male)	0.74	0.81	0.76	0.75
SVL	0.99	0.19	1.00	0.87
Weight	1.04	0.19	1.00	0.48
Temperature	0.87	0.55	N/A	N/A
Tail vibration rate (linear reg.)	$P = 0.90$, adj. $R^2 = -0.17$		$P = 0.49$, adj. $R^2 = -0.02$	
Covariate	Coef.	P	Coef.	P
Location (1 = island)	-0.41	0.98	-14.77	0.17
Sex (1 = male)	-1.70	0.91	-1.09	0.92
SVL	-0.07	0.41	-0.01	0.84
Weight	0.15	0.40	-0.03	0.63
Temperature	-0.37	0.86	N/A	N/A
Tail vibration duration (linear reg.)	$P = 0.12$, adj. $R^2 = 0.18$		$P = 0.04$, adj. $R^2 = 0.20$	
Covariate	Coef.	P	Coef.	P
Location (1 = island)	-2.54	0.07	-2.34	0.01*
Sex (1 = male)	-0.10	0.93	-0.06	0.94
SVL	0.00	0.53	0.00	0.54
Weight	0.00	0.94	0.00	0.64
Temperature	-0.08	0.64	N/A	N/A

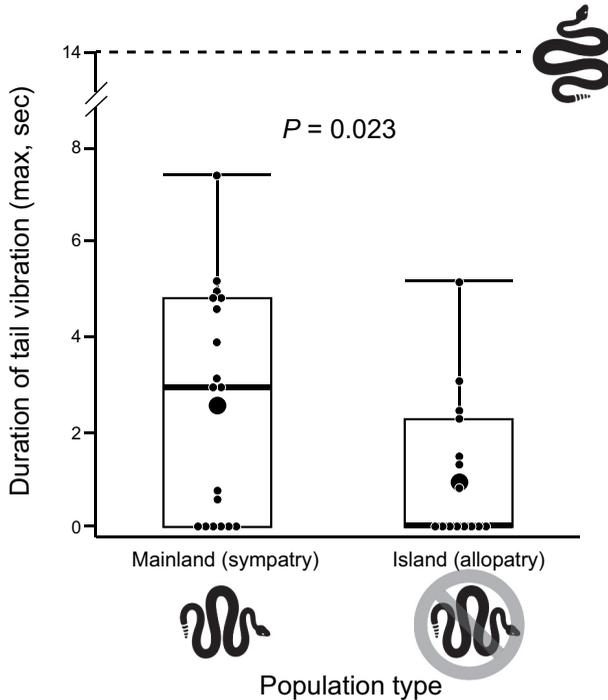


Fig. 2. — Maximum duration of tail vibration among Gophersnakes from mainland (where rattlesnakes are present) versus island (where rattlesnakes are absent) populations. Box plots show quintiles and median (bold horizontal line); large dots show mean (small dots show data for individual snakes). To visually contrast the putative mimic (Gophersnakes) with its model (rattlesnakes), the mean duration for rattlesnakes is shown by the horizontal-dashed line (based on data in Allf et al. 2016).

These data suggest that Gophersnakes produce an acoustic signal more similar to the aposematic signal of rattlesnakes where they actually co-occur with rattlesnakes. This evidence lends support for the long-standing hypothesis that Gophersnakes are acoustic mimics of rattlesnakes (Klauber 1956; Kardong 1980; Brodie & Brodie 2004). Because most known cases of Batesian mimicry involve visual signals, our study adds to the comparatively few studies investigating acoustic mimicry (for other examples of acoustic mimicry, see Gans 1961; Rowe et al. 1986; Barber & Conner 2007; Aubret & Mangin 2014; Brejcha 2019; Vaughan et al. 2019). Moreover, because one aspect of the mimetic signal – tail-vibration duration – appears to be undergoing erosion in derived populations (islands) where the model is absent, our data also provide evidence of possible microevolutionary change in mimicry. At the same time, it is unclear why the other two aspects of the signal we measured – rate and propensity to tail-vibrate – do not also appear to be undergoing erosion in the derived populations. One possibility is the difference in temperature between the two populations of Gophersnakes we measured. As discussed above, past work has shown that hotter snakes vibrate their tails more rapidly than colder snakes (Martin & Bagby 1972). Because the island snakes in our sample were nearly 4 °C warmer than the snakes from the mainland, it is possible that a difference in tail vibration rate between

the two populations was confounded by this difference in temperature. Future work using Gophersnakes with more similar body temperatures may reveal whether this is the case.

It might be contended that the signal produced by Gophersnakes is not likely to deter a predator, given how much it differs in duration from the aposematic signal of a rattlesnake (Fig. 2). Indeed, even mainland snakes (whose maximum tail-vibration bout length was only 2.5 sec) were poor at matching the prolonged tail vibration of a rattlesnake (which can tail vibrate for over 45 sec; Allf et al. 2016). However, imprecise mimicry abounds in nature (Kikuchi & Pfennig 2013; McLean et al. 2019), and theoretical and empirical studies suggest that even poor mimics can receive protection from predation (Lindström et al. 1997; Chittka & Osorio 2007; Kikuchi & Pfennig 2010; Penney et al. 2012; Kazemi et al. 2014). In the present case, potential predators may have avoided – and thereby selectively favoured – any mainland snake that vibrated its tail for a slightly longer duration if doing so caused the snake to sound (even slightly) more like a rattlesnake. This predator-mediated selection might have thereby favoured a tendency for mainland snakes to tail vibrate longer because of the fitness benefits of mimicking a model that is highly toxic (Campbell & Lamar 2004) and relatively abundant (Sullivan 1981).

A potential limitation of our study was that we compared just two island populations with two mainland populations (Fig. 1). Ideally, we would have also sampled Gophersnakes on Santa Catalina Island (which are sympatric with rattlesnakes) to evaluate whether the absence of rattlesnakes per se (as opposed to being derived from an insular population) drives the observed differences between insular and mainland behavior. Indeed, it is possible that the observed behavioral differences between populations arose because of differences other than the presence or absence of rattlesnakes, such as population differences in predation rates (leading to relaxed selection on antipredator behaviors), responses to stress, or resource availability (Sparkman et al. 2018). However, our conclusion that tail vibration by Gophersnakes represents acoustic mimicry of rattlesnakes is buttressed by earlier work showing that nonvenomous snakes from the New World (which are sympatric with rattlesnakes) vibrate their tails faster and longer than nonvenomous snakes from the Old World (which are allopatric; Allf et al. 2016). Nevertheless, future research is needed to clarify whether (and the degree to which) factors other than the presence versus absence of rattlesnakes could explain the observed differences in tail vibration between mainland and island populations.

Although island snakes are smaller than mainland snakes (Sparkman et al. 2018; confirmed in this study; see Results), we did not find that an individual's body size affected its rate or duration of tail vibration. At first glance, this lack of a size effect is surprising, given that body size affects antipredator behavior in other species of snakes (Roth & Johnson 2004). However, this absence of a relationship between body size and defensive tail vibration further reinforces our conclusion that mainland and island populations have diverged evolutionarily in defensive tail-vibration behavior.

Indeed, an important conclusion to emerge from our study was that this mimetic signal may be undergoing erosion in allopatry. As evidence of such a degradation of the signal, we found that snakes from island populations – which are derived from mainland populations (Schoenherr et al. 1999) – tail vibrated for a shorter duration (Fig. 2). Although the difference in duration of tail vibration between island and mainland snakes was small (a little more than 1 sec), it represented a greater than 40% reduction among island snakes. This possible erosion of

the mimetic signal might have been caused by either selection or random genetic drift. Selection might have disfavoured tail vibration among insular snakes if expressing this behavior is energetically costly (as has been suggested in rattlesnakes; Moon 2001) or if it alerts predators or prey (as has also been suggested in rattlesnakes; Klauber 1956; Avila-Villegas et al. 2007). Alternatively, even if selection does not act against the signal in allopatry, it might still be lost in allopatry owing to stochastic factors. Specifically, if the signal was not maintained by selection in allopatry, then random genetic drift might have resulted in its decay (Lahti et al. 2009). However, the fact that the mimicry signal has not been lost entirely suggests that some level of tail vibration is likely favoured by selection, even in allopatry. In support of this idea, defensive tail vibration is an ancestral trait in snakes (Allf et al. 2016). Presumably, defensive tail vibration has evolved to alert predators that the snake is annoyed and may therefore bite. Such a signal would benefit both parties: it reduces predation on the snake, and it allows the predator to avoid a bite.

In summary, our study adds to a growing number of studies documenting a possible microevolutionary shift in a mimetic signal (Harper & Pfennig 2008; Prudic & Oliver 2008; Akcali & Pfennig 2014; Katoh et al. 2017; Prudic et al. 2019). Because selection on these signals can be strong (Harper & Pfennig 2008), such investigations are ideal for studying microevolutionary change in contemporary populations.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

SUPPLEMENTAL DATA

Supplementary data for this article can be accessed at <https://doi.org/10.1080/03949370.2020.1837962>

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