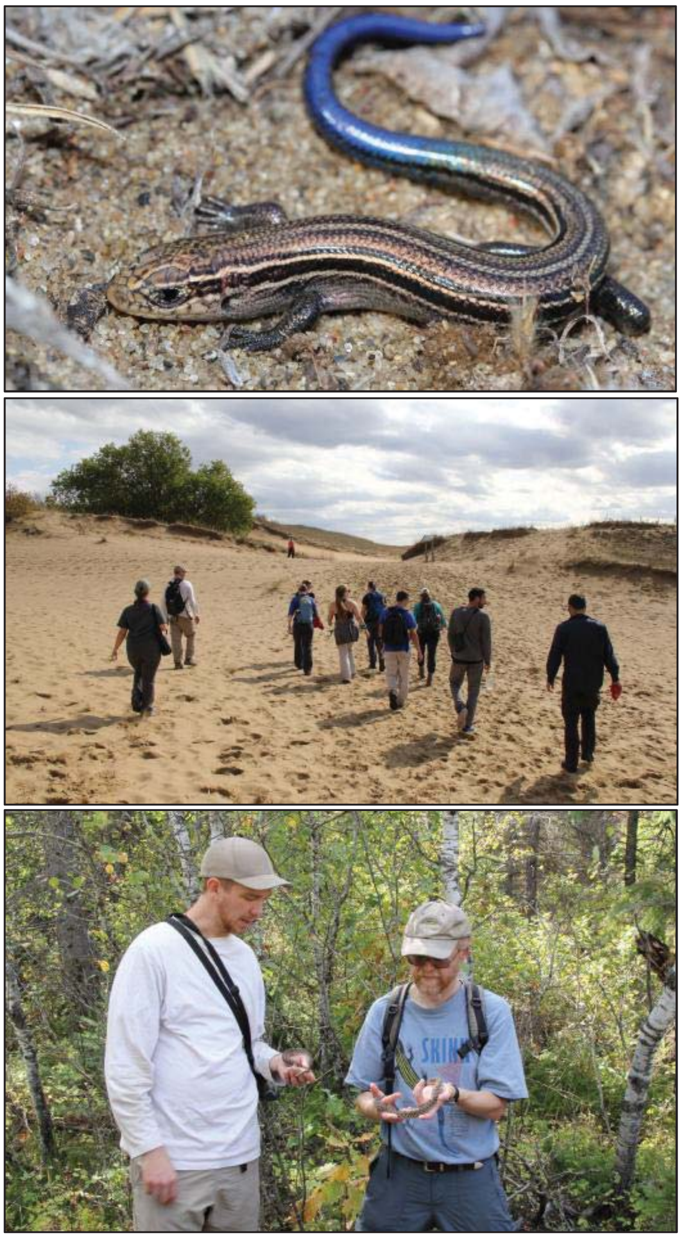
perfect, and participants were able to see the beauty of this region and appreciate all of the unique plants and animals that are in this habitat. Throughout the afternoon, folks were able to find most of the amphibians and reptiles in this region, including Red-bellied Snakes, baby Common Snapping Turtles, and Red-sided Garter Snakes. Everyone returned to the vehicles exhausted and thirsty but with many stories to tell. It was a treat to be part of this field trip and showcase this wonderful region in Canada. Many thanks to our tour guides and field trip organizers: Nick Cairns, Neil Gushulak, Allison Krause Danielsen and Pamela Rutherford.



A Prairie Skink that was observed during the CHS field trip (top); field trip participants exploring Spirit Sands (middle); field trip participants inspecting (admiring!) two Plains Hog-nosed Snakes (bottom) (photos by Joe Crowley)

A final thank you to Brandon University, the local organizing committee, CHS Board members, sponsors and participants. And, of course, big thanks go to all the presenters who took the time to share their work and experiences over the weekend. It was a successful conference, full of wonderful and inspiring people. Keep up the great work and we hope to see you next year in British Columbia!

FEATURE ARTICLES

Better Red than Dead?

Peter B. Mills
Trent University and Algonquin Park
peter.b.mills@hotmail.com

Even casual observations of the Common Gartersnake (*Thamnophis sirtalis*) reveal this species comes in a wide variety of appearances. Dark snakes with longitudinal, cream-coloured stripes may be considered the standard colouration (Fig. 1), but other individuals can be brown, tan, checkered, missing their dorsal stripe, or even all black. Several sub-species have prominent red bars above the lateral stripes; others have bright yellow-orange dorsal stripes; and the Puget-sound Gartersnake is often tinged with blue. Dashes of red, blue, or green hues may show on the membrane between the scales and become visible if the snake inflates in self-defense. One explanation for various colour morphs within a species is that different appearances offer different adaptive advantages. That is, one particular appearance may increase survival in one environment, while another appearance is more superior in a different environment. As a result, both colour morphs are maintained by positive selection for these appearances in the environments for which they are best suited. By contrast, the existence of different colour morphs may be driven by random genetic processes. In these cases, colour morphs may only represent the individual's random inheritance of a particular set of genes, and the resulting appearance coded by these genes confers no adaptive advantage to the individual. Are the forces maintaining this diversity of colour morphs within *T. sirtalis* rooted in adaptation (are certain appearances better in some situations?) or in random processes (do mutations coding for appearance simply get bounced around within the gene pool with no influence on survival)?

Studies designed to address exactly these questions have been carried out along the coast of Lake Erie, where populations of Common Gartersnakes include a mix of "normal" looking individuals and a melanistic, or all-black, morph. The black phenotype is caused by a recessive mutation, but black individuals are more common in many of these coastal populations than would be expected for a recessive trait. As such, it is presumed that being black has unique benefits in this environment. One benefit might include being able to warm up faster in the spring when the cold lake creates an exaggeratedly cool environment compared to inland areas (see Rowell 2013, and references within, for a more thorough review). Many of the places these black garter snakes occur are on isolated islands or sand spits connected to the mainland by a narrow isthmus—a fact that may be important to the persistence of melanism. Because such narrow or non-existent connections to the mainland severely reduce access to mainland mates, the recessive melanistic trait may be less likely to be swamped by non-melanistic mainland genes. All this considered, this example elucidates that natural selection across different environments, and connectivity among these different environments, plays a strong role in dictating colour patterns in organisms.

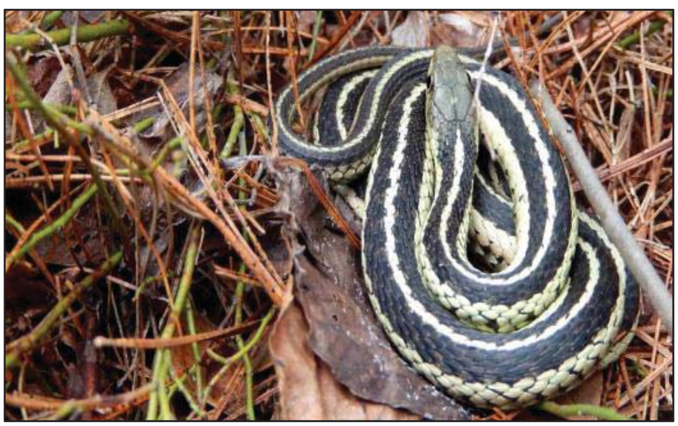


Figure 1. “Standard” colouration of the Common Gartersnake.

A paper by Mooi et al. (2011) addresses the "remarkable variation and frequency of colour morphs" of the Common Gartersnake in central Canada; their work includes thorough coverage of the striking erythristic morph—a phenotype comprised of profoundly red individuals (Fig. 2). These red snakes are noted from the Abitibi region of northern Ontario, westward to south-central Manitoba, and the Montréal area (Bleakney 1959). These “flame” Gartersnakes typically sport crimson flanks, blackish upperparts, and a well-defined, cream-coloured vertebral stripe running the length of the body. Why such a conspicuous, intensely red morph of *T. sirtalis* persists in this region remains unknown. Presuming diet as an unlikely mechanism because neonates can be born intensely red, the authors suggest that gene flow, random genetic drift, and/or natural selection must explain the origin and persistence of the mutations(s) that produce these red individuals.

Figure 2. Erythristic Common Gartersnakes are striking animals. Their faces and flanks are crimson red, while the upper surface is charcoal-black with red interstitial dashes on the skin among the scales. The dorsal midline is delineated by a sharply-defined cream-coloured stripe.

Erythrism and random genetic drift

The gartersnakes at Mooi *et al.*'s study site and in the rest of Canada are relatively recent arrivals that expanded their range following the Wisconsin Glaciation episode (Barnett 1992). Is this red colour morph somehow associated with gene sorting during this northward range expansion? Mutations can "ride the wave" at the leading edge of a range expansion and such mutations may "reach a larger spatial distribution and a much higher frequency than would be expected in stationary populations" (Klopfstein et al. 2006; Hallatschek et al. 2007). Such a phenomenon can be considered "the founder effect in motion", whereby individuals at the edge of the frontier will produce offspring that will further the front of invasion, populating and establishing that frontier-genotype in new populations along the advancing wave. If a mutation coding for erythrism appeared in frontier-breaking garter snakes during their northward range expansion, these genes might have an exaggerated representation in populations that followed as the wave of colonization advanced. This perception might help to explain why erythristic individuals are noted in the north, but not the southern part of *T. sirtalis'* range. Although Placyk et al. (2007) considered *T. sirtalis* from a phylogeographic perspective within the Great Lakes basin, their work did not sample from regions where the erythristic morph is known, and they did not measure signatures of genetic drift. That this erythristic morph is anecdotally described from the Montréal Island lends support that random genetic drift may play a role in its persistence because gene flow should be restricted in such an isolated place. However, the presence of erythrism in the Abitibi region of Ontario westward to central Manitoba may be more difficult to ascribe to this mechanism given the gene flow that would be expected to occur across the apparently-contiguous range of garter snakes in this region.

Erythrism and non-random natural selection

Because bright red hues are generally conspicuous to predators (Ruxton et al. 2004), it is surprising that these profoundly red garter snakes were not snubbed out of the gene pool given that predators should find them more often than cryptically-coloured morphs. This may suggest natural selection works to keep erythristic individuals in the gene pool. With the exception of anecdotal reports from the Montréal area, these intensely erythristic *T. sirtalis* appear limited to boreal climates. A reasonable presumption that follows this observation is that life in boreal environments might be what promotes the presence of erythrism (Fig. 3). Gartersnakes operating relatively farther north might be expected to face greater challenges with growth and reproduction given their thermally-limited environment. In their work on the plains garter snake (*T. radix*), Tuttle and Gregory (2012; 2014) demonstrated that northern snakes did not necessarily underperform southern snakes—a fact that they partially attributed to "effective thermoregulation". That is, these northern garter snakes may rearrange their time-energy budgets to permit more basking than would a more southerly snake, and by extension arrive at equivalent achievements. While an increase in basking may allow northern garter snakes to achieve similar levels in reproduction and growth to more southerly snakes, it would also lead to a lifestyle where a high level of exposure was a necessity. If exposure is unavoidable, such snakes might be pressed to develop ways that mitigate the increase in predation attempts that result from an increase in exposure. Many North American snakes mitigate predation attempts through a Batesian Mimicry strategy, whereby mimetic species of snakes look very similar to a truly venomous model, such as the coral snakes of the genus *Micrurus* (Davis Rabosky et al. 2016).

It may seem outlandish to consider these erythristic gartersnakes as mimetic of coral snakes since gartersnakes are generally longitudinally striped, rather than banded like *Micrurus*. Some gartersnakes may appear loosely banded when the skin is stretched to reveal angularly-arranged dashes of colour, but even in this context, *T. sirtalis* can hardly be considered truly banded. However, findings from Kikuchi and Pfennig (2010) demonstrate this may not particularly matter since limitations to predator cognition permit imperfect mimicry and that in some scenarios imperfect mimics may be under little or no selective pressure to improve. Potential pattern mismatches between *T. sirtalis* and *Micrurus* aside, it may also seem outlandish that red gartersnakes from boreal North America could be coral snake mimics given that *Micrurus* is only found in sub-tropical and tropical regions. However, studies analyzing sympatry between mimics and their models reveal counter-intuitive results which demonstrate mimics are most similar to their model where their model is rare or absent (Pfennig and Mullen 2010). Grasping why this occurs is rooted in considering the probability that a given predator might encounter the truly venomous model. Where the model occurs, mimics can afford to be crude because a high encounter rate with the model selects for extreme avoidance of even the most approximate lookalikes in a would-be predator. In areas where the model is rare or absent, the encounter rate with the model is low or zero so predators are under very low selective pressure to avoid any semblance of the model's patterning. Accordingly, only the very best mimics—by bearing extreme resemblance to the model—are afforded *any* protection in places where the model is rare or absent (Harper and Pfennig 2007). This phenomenon received stunning support when Akcali and Pfennig (2014) demonstrated that mimicry improved in a mimetic species after its sympatric model became locally extirpated. That three species of mimetic *Lampropeltis* are found various distances between 600 and 1500 km from the closest populations of *Micrurus* also lends strong support for this concept. In summary, the absence of a venomous model is not reason to discount a mimetic lifestyle in snakes, and resemblance to a model should be highest where the model is rare or absent.

It may not matter that there are no coral snakes in the boreal forest since Broad-winged Hawks (Fig. 4), Northern Harriers, Red-tailed Hawks, American Kestrels, Sandhill Cranes, and Great Blue Herons are migratory birds that breed in boreal regions, eat snakes, and spend their winters in tropical areas within the range of *Micrurus* (Powell et al. 2016; Sibley 2014). Presumably these birds' fear of red or banded snakes would be transferable across landscapes. Assuming the former, it is not so unlikely that these migratory birds of prey would apply a selective pressure on gartersnakes that would leave more erythristic individuals alive than more cryptically-coloured individuals. This could lead to exaggeratedly redder individuals in cold climates where an increase in snake basking combined with selectivity by the birds could lead to a red morph of *T. sirtalis* that was effectively mimetic of *Micrurus*. Though a far cry from some of North America's incredibly precise *Micrurus* mimics, these erythristic gartersnakes could be best mimetic phenotype *T. sirtalis* can manage given a contiguous range and gene flow with southern snakes under different selective pressures.

Figure 3. Does life in a colder environment promote erythrism? With the exception of the Montréal area, profoundly erythristic gartersnakes are known from boreal regions in northeast Ontario and [probably continuously to?] central Manitoba. Erythristic snakes appear absent from the southern range, but "standard" morphs are present in northern regions where erythrism is present. Erythrism may also be clinal, given that some mid-latitude snakes show red-orange colouration that is more intense than that of southern snakes but less so than true erythristic snakes from the far north. The green scale bar represents average annual temperature in degrees Celsius.

Adaptive or random?

Speculations on genetic drift and natural selection need not be considered exclusively; the origin of erythrism may be rooted in random genetic drift and maintained by natural selection, or vice versa. In fact, rapid phenotypic changes are associated with range expansions and both random genetic drift and directed natural selection have meaningful roles in this regard (Bittner and King 2003; Swaegers et al. 2015; Noguerales et al. 2016).

Could an exaggerated need for basking in boreal regions leave gartersnakes more susceptible to predation? If at least some of these predation pressures were inflicted by migratory birds with a fear of red snakes, might that be a cause for the high-latitude red-morph *T. sirtalis*? Speculation aside, the only way to truly assess this would be through a series of tests of exacting design. Do northern gartersnakes spend more time basking than southern gartersnakes? Or in more exposed positions? If so, does this lead to an increase in predation attempts compared to more southerly populations? If so, do redder snakes receive fewer predation attempts than less red snakes? Is avoidance of red snakes biased toward migratory birds that spend winters in landscapes with *Micrurus*? If so, which bird species encourage red morphs most? The tools needed to address some of these questions could include time-energy budget analyses, outdoor cages to observe basking tendencies, snake models made of artificial materials of varying colour, motion-sensor remote cameras to capture predator-model interactions, and even computer-generated niche models that elucidate range overlap among red morph gartersnakes and different bird species. If these tests don't receive support, mechanisms investigating genetic drift and its role in the northward post-glacial expansion of *T. sirtalis* might be investigated. Genomic samples paired with simulations of range expansion might elucidate if areas with erythristic gartersnakes match areas expected to exhibit significant carryovers from genetic drift.

Figure 4. Broad-winged Hawks (*Buteo platypterus*) breed in temperate and boreal regions of eastern Canada, eat snakes, and spend their winters in landscapes where venomous coral snakes (genus *Micrurus;* shown) can be found. If they have a fear of red snakes and exert selective pressures on snakes while hunting on their breeding grounds, could this elicit a mimetic strategy in Canadian gartersnakes?

Figure 5. "Hudson Bay Toads" (bottom) are well-marked by definition, and some individuals display red, orange, yellow, white, and black markings that could be taken as aposematic. Many tropical anurans (like *Atelopus varius*; shown at top) exhibit these same universally-recognized colours to warn predators of their toxicity.

Better red than dead?

Given the questions outlined above, collecting evidence to support or refute the ideas herein would be arduous and time-consuming. Before committing to the time and effort needed to test these ideas, one might look to build confidence on the matter by looking for an analogous system where this same string of logic would predict a similar outcome. The gartersnake complex on the Pacific coast (e.g. Janzen et al. 2002) include *T. s. concinnus* and *T.s. infernalis* which qualitatively look like *Micrurus* mimics and might offer more support that *Thamnophis* can indeed achieve mimetic phenotypes. Another such system might occur with American Toads (*Anaxyrus americanus*) in the Hudson Bay regions of Ontario and Quebec (Fig. 5). This local "morph" has been described as the subspecies "*Bufo americanus copei"* (Ashton et al. 1973; Yarrow and Henshaw 1878), though Green (1996) points out that species-species distinctions in this group are difficult enough to formalize, let alone colour morphs within a species. Regardless, these "Hudson Bay Toads" are distinctively marked with black, red, and white blotches and stripes and recall an aposematic appearance—colours that predators of tropical anurans universally avoid (Richards-Zawacki et al. 2013). Tests similar to the ones described above for gartersnakes might elucidate if an increased need for these boreal toads to bask elicits a Batesian (or even Müllerian!) Mimicry strategy that emulates toxic models from the tropics.

Canada's herpetofauna has a recent, post-glacial origin. The distributions of Canadian species reflect their post-glacial invasion of this landscape, and their genomes have been shaped and sorted by this history and these journeys. The Common Gartersnake may be an ideal organism to investigate how genetic drift and natural selection interplayed across this saga since this snake's distribution spans Carolinian and high-Boreal landscapes, and it displays a multitude of phenotypes. Questioning what forces explain the origin and persistence of erythristic gartersnakes may offer insight into how genotypes and phenotypes relate across regions, time, range expansions, and contractions —and, it just may clear up if, at least in some cases, it is better to be red than dead.

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Secrecy or Transparency with Herpetological Data

Stephen J. Hecnar
Lakehead University
Thunder Bay, ON
shecnar@lakeheadu.ca

A contemporary trend in most governmental and non-governmental agencies is to be as transparent as possible with information and data while respecting personal privacy. That being said, we live in a time where we are often under video surveillance and our electronic communications are monitored. This activity no doubt promotes public safety but it is somewhat uncomfortable knowing that “Big Brother is watching” (Orwell 1949). A similar dilemma exists in scientific communications. We are expected to be honest and accurate so that readers can completely understand, scrutinize, and replicate our work. However, scientific publications can also help poachers to locate wildlife (Stuart et al. 2006, Lindenmayer et al. 2017). The