

## Correspondence

# North American velvet ants form one of the world's largest known Müllerian mimicry complexes

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Color mimicry is often celebrated as one of the most straightforward examples of evolution by natural selection, as striking morphological similarity between species evolves in response to a shared predation pressure [1]. Recently, a large North American mimetic complex was described that included 65 species of *Dasymutilla* velvet ants (Hymenoptera: Mutillidae) [2]. Beyond those 65 species, little is known about how many species participate in this unique Müllerian complex, though several other arthropods are thought to be involved as Müllerian mimics (spider wasps [3]) and Batesian mimics (beetles, antlions, and spiders; see references in [2]). Müllerian mimicry is similarity in appearance or phenotype among harmful species, while Batesian mimicry is similarity in which not all species are harmful. Here, we investigate the extent of the velvet ant mimicry complex beyond *Dasymutilla* by examining distributional and color pattern similarities in all of the 21 North American diurnal velvet ant genera, including 302 of the 361 named species (nearly 84%), as well as 16 polymorphic color forms and an additional 33 undescribed species. Of the 351 species and color forms that were analyzed (including undescribed species), 336 exhibit some morphological similarities and we hypothesize that they form eight distinct mimicry rings (Figure 1A; Supplemental information). Two of these eight mimicry rings, red-headed *Timulla* and black-headed *Timulla*, were not documented in earlier assessments of mimicry in velvet ants [2–4], and are newly described here. These findings identify one of the largest known Müllerian mimicry systems worldwide and provide a novel system to test

hypotheses about aposematism and mimicry, especially those regarding the evolution of imperfect mimicry [4].

The existence of eight morphologically distinct mimicry rings was confirmed through non-metric multidimensional scaling (Figure 1B) and permutational analysis of variance based on 14 morphological characters. The overall effect of mimicry ring as a categorical variable was significant ( $F_{7,328} = 120.11$ ,  $R^2 = 0.719$ ,  $P = 0.001$ ; Supplemental information). As a complementary approach, latent class analysis confirmed the existence of distinct clusters without *a priori* assignment to mimicry rings [5] (Supplemental information). In addition, we compared the geographic distributions of each species to determine the extent of sympatry among visually similar individuals and to determine the spatial extent of each mimicry ring (Figure 1A; Supplemental information).

Of the 351 species that were analyzed, only 15 (~4%) did not fit into any mimicry ring (Supplemental information). Many of these had cryptic coloration and were small-bodied. Others appear to be aposematic, but did not clearly fit into any mimicry ring. In addition to the six rings that have previously been described [2], we identified two new mimicry rings, the red-headed *Timulla* mimicry ring and the black-headed *Timulla* mimicry ring (Supplemental information). Convergent evolution has been demonstrated in earlier assessments of mimicry in *Dasymutilla* [2], and is likely to play a major role in the expanded mimicry complex reported here, particularly given the taxonomic extent of participating species.

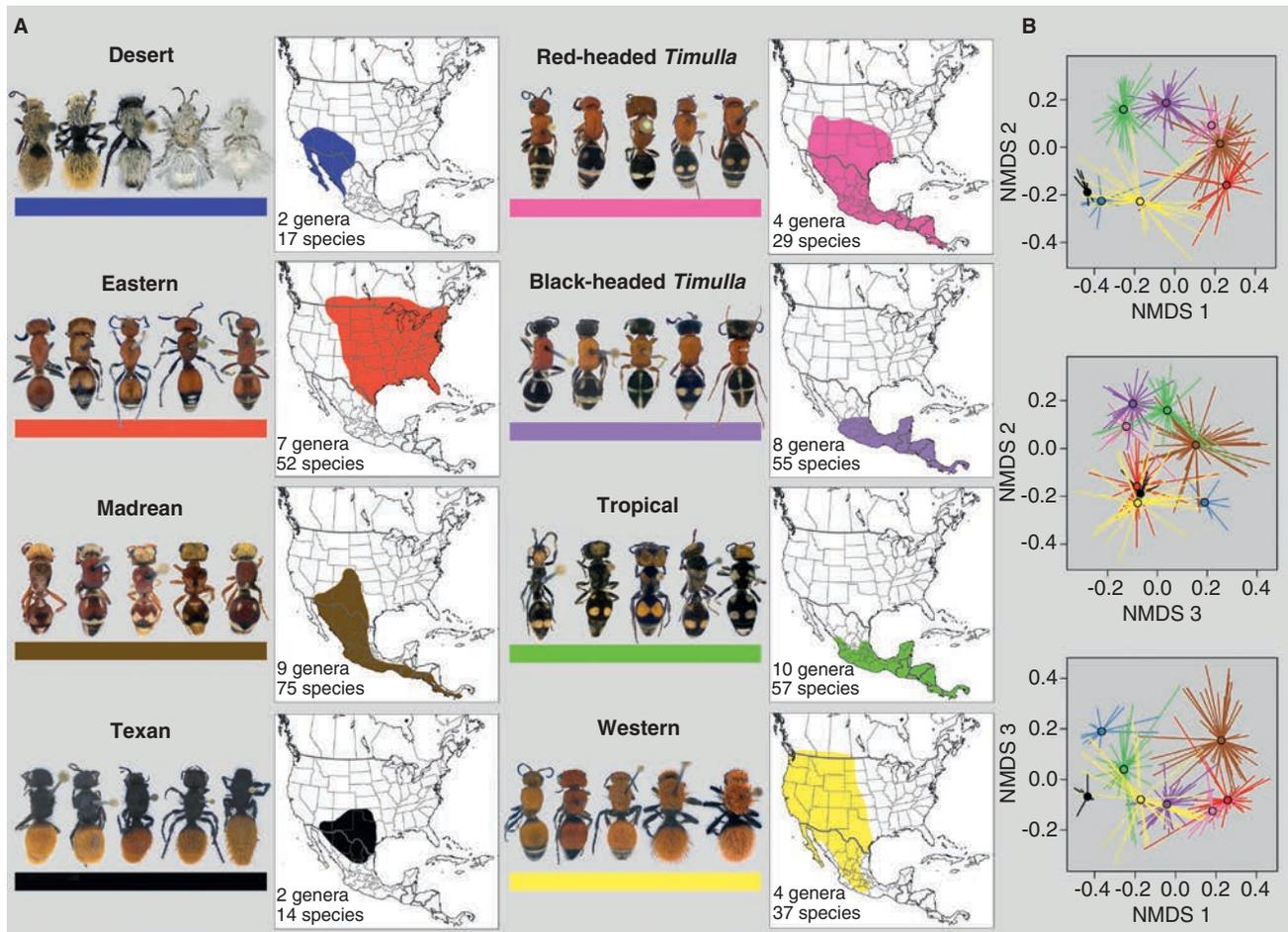
In addition to the number of species involved, several characteristics of this velvet ant mimicry complex make it an exceptional mimetic system. Velvet ants are protected by a suite of defenses that include pungent chemical secretions, aposematic coloration, auditory warning signals, a hard slippery cuticle, as well as a painful venom delivered by a sting nearly half the length of the insects body [2]. It has been shown that combinations of aposematic signals can accelerate predator learning [6]. The success of the velvet ant mimicry complex, both in terms of taxonomic diversity and geographic extent, could be explained at least in part by the rapid training of predators through the use of multisensory aposematism.

While birds are typically implicated as the predator driving the evolution of shared color patterns in mimicry systems [7], there is little evidence that birds regularly attack velvet ants. Instead, diurnal lizards may be the key selective agent in the evolution of mimicry in these animals [2]. This unique combination of predator and prey, and the fact that both can easily be kept in controlled laboratory settings, could allow for more experimentation than would be possible in systems driven by avian predation.

Yet another interesting feature of this system is that male velvet ants are relatively harmless compared to their female counterparts. However, the males often still have aposematic coloration but do not always resemble, or even participate in the same mimicry ring as their conspecific females. This phenomenon has been termed dual sex-limited mimicry [8], which is a form of automimicry. While relatively few velvet ant sex associations have been made (for example, fewer than 30% of *Dasymutilla* species are known from both sexes), the use of molecular techniques to improve taxonomy [9] will undoubtedly reveal additional synonymies and sex associations and will facilitate studies of automimicry in male velvet ants.

Finally, velvet ants exhibit a wide array of mimetic fidelity, with many species within a given mimicry ring being nearly indistinguishable and others being only vaguely similar [4], a phenomenon known as imperfect mimicry. Because the models (mimicry rings) and the mimics (individual members of each mimicry ring) are now relatively well defined in this vast velvet ant mimicry complex, hypotheses about mimetic fidelity and imperfect mimicry can be rigorously evaluated. For example, analyses of imperfect mimicry in the *Dasymutilla* mimetic system refuted the body size hypothesis (a.k.a. relaxed selection hypothesis [4]) that found support in hoverflies [10]. Instead, preliminary support in *Dasymutilla* was found for the community diversity hypothesis, which posits lower overall mimetic fidelity in geographic areas that harbor a high diversity of models [4]. We expect that other novel hypotheses will be generated and tested as more pieces of the velvet ant mimicry complex fall into place.

## SUPPLEMENTAL INFORMATION



**Figure 1. The eight mimicry rings found in North American velvet ants.**

The morphological and geographic ranges of the eight velvet ant mimicry rings. Each mimicry ring is represented here by five species. These species were selected because they are morphologically closest to the estimated mean for each mimicry ring (B). The estimated geographic range of each mimicry ring is presented based on distributional analyses that examined the known range of each species involved in each mimicry ring (Supplemental information). The number of genera and species involved in each ring is also given. (B) Velvet ant mimicry complexes are differentiated in ordinal space (NMDS). In each comparison of the three NMDS axes, the mean values for each mimicry ring are denoted by symbols, with lines drawn from the means to individual species values (Supplemental information).

Supplemental Information including experimental procedures, two tables and four figures can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.06.053>.

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