



Figure 3. A cone snail.

Conotoxins of cone snails (including *Conus miliaris*, shown here) show evidence of exceptional evolutionary diversification in areas without competitors, suggesting ecological release in venom evolution (Photo: Thomas Duda).

through genetic constraints that limit the diversity of classes produced or recruited through evolution is not yet clear.

At the same time, rapid evolutionary diversification and variability is the hallmark of venom evolution. Marine cone snails (*Conus*) are predatory mollusks that fire a venomous harpoon that almost instantly immobilizes target prey (Figure 3). These darts carry an astonishingly diverse blend of neurotoxins that block ion channels or disrupt neuronal receptors. Molecular genetic analysis demonstrates that these compounds are under strong diversifying selection. The rate of protein evolution in conotoxin genes is three to five times higher than the highest rates observed for other proteins. There is evidence for gene duplication and diversification leading to the radiation of toxin forms. Similar rapid diversification is also observed for snake venom proteins. In both cases, it is assumed that strong selection to subdue prey is driving such fast evolution. Cone snails tend to feed on a relatively limited range of prey within populations, but the group as a whole feeds on many groups of invertebrate and vertebrate prey. Snails that feed on different prey types diverge in venom blends, but the biochemistry of conotoxins is much more diverse than snail diets (an individual snail may have 50–200 distinct toxic components). Geographic variation in venom composition also correlates with diet diversity in some vipers. Among species of elapids (cobras and their relatives), the three-fingered neurotoxins diversify rapidly as do

diets of the venom producers. These examples all suggest that an arms race matching toxicity and resistance between predator and prey drives diversification of venoms. However, functional analyses that would more solidly confirm the existence of this process have yet to be conducted.

### Conclusions

The compounds that we recognize as toxins and venoms span an enormous diversity of pharmacological and ecological functions. The selection pressures driving the modification of venoms and toxins are fundamentally different from those of other proteins, and result in somewhat different evolutionary dynamics. Toxins often appear convergent because externally available compounds are used for defense, whereas venoms seem to evolve toward a rather constrained set of target functions and classes of compounds. At the same time, venoms diversify within lineages at least as fast as any known group of proteins. With more experimental tools for more diverse groups of organisms, we will begin to discover what general evolutionary pressures and constraints shape the landscape of natural poisons.

### Further reading

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## Correspondences

### Ants use the panoramic skyline as a visual cue during navigation

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Foragers of many ant species learn long, visually guided routes between their nest and profitable feeding grounds [1–3]. The sensorimotor mechanisms underpinning the use of visual landmarks are much studied [3], but much less is known about how ants extract reliable visual landmark information from a complex visual scene. For navigation, useful visual information should be reliably identifiable across multiple journeys in differing lighting conditions, and one such robust source of information is provided by the skyline profile generated where terrestrial objects contrast against the sky. Experiments with ants and bees [4–6] suggest that insects might use directional information derived from the skyline, and in the work reported here, we explicitly tested this hypothesis. Ants were trained to shuttle between their nest and a feeder. We then recreated the skyline profile as seen from the feeder using an artificial arena with variable-height walls. Ants returning from the feeder were captured near their nest entrance and released in the arena. Ants followed the direction given by the artificial skyline when it was aligned with their habitual homeward compass direction or rotated by 150°. This result indicates that a crude facsimile of a skyline can functionally mimic the natural panoramic scene.

We established an open access feeder 5 m from a *Melophorus bagoti* nest (Figure 1A) and the retinal elevation of the panoramic skyline (Figure 1B) from the feeder location was measured at 15° azimuthal intervals. At a distant test field an arena, 1 m in radius, was created using black plastic sheeting (Figure 1C). The height of the black plastic wall was varied so that from the centre of the arena the retinal elevation of the artificial

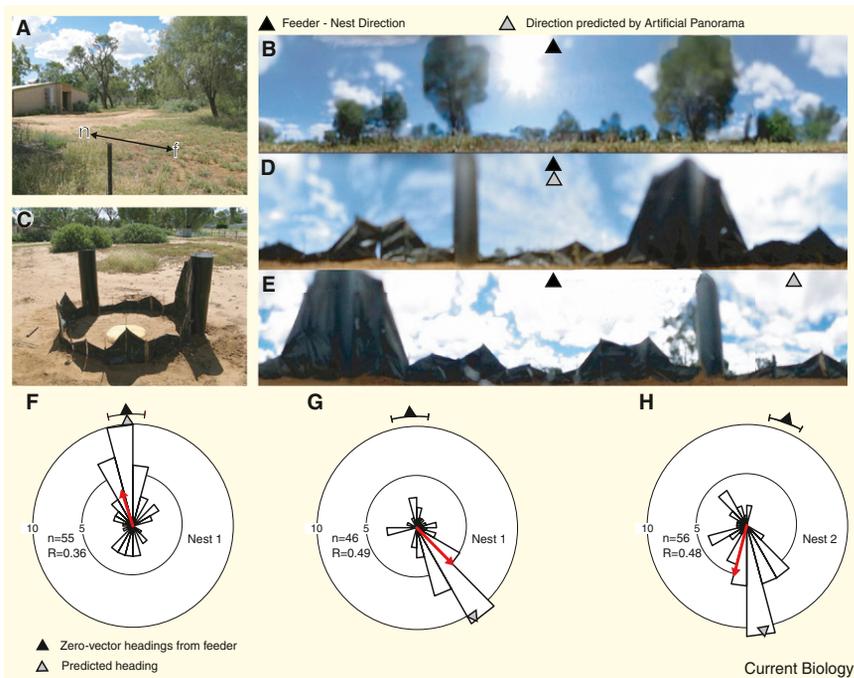


Figure 1. Headings of ants in response to artificial panoramic skyline.

(A) The nest (n) locale with an ad lib feeder (f) 5 m from the nest entrance. (B) The panoramic view from the feeder location. (C) 1-m radius panoramic arena with variable-height walls. (D,E) Panoramic views from the centre of the arena with the artificial skyline. The retinal height of the natural skyline was matched every 15° and linear interpolation used in between. (D) Skyline cues are aligned with habitual Feeder–Nest direction. (E) Test arena rotated clockwise by 150°. (F–H) Circular histograms of ants' headings after 15 cm in the test arena. Direction and length of the red arrow represent the direction and length of the mean vector for each distribution. All three distributions of headings (F–H) are significantly non-uniform (Rayleigh Test,  $p < 0.005$ ). Black arrows with ranges represent the mean compass bearing (with 95% confidence interval) of zero-vector ants from Nest 1 (F, G;  $n = 25$ ) and Nest 2 (H;  $n = 26$ ) returning home from the feeder at the training ground. The headings of Nest 1 and Nest 2 zero-vector ants are significantly different (Watson-Williams Test,  $p < 0.005$ ). Grey arrows represent predicted heading for ants using skyline cues. This heading is derived from the mean heading of zero-vector ants at the training ground (black arrows) and the orientation of the artificial arena. In all three cases (F–H) there is no significant difference (Watson-Williams Test) between the observed headings of zero-vector ants in the test arena and at the feeder, relative to the skyline profile. There is a significant difference (Watson-Williams Test,  $p < 0.005$ ) in the headings of Nest 1 and Nest 2 ants in the rotated arena (G,H).

skyline matched that of the natural panorama viewed from the feeder. In other respects the artificial panorama bore no resemblance to the natural scene. At the centre of the artificial panorama was a goniometer marked in 15° sectors. This was used to measure the departure bearing of ants released in the arena. Ants that had successfully foraged at the training feeder were captured just as they were about to re-enter their nest. So-called zero-vector ants have no idiothetic information available from path integration and are reliant on learnt route information for navigation. Ants in this state taken back to the feeder location and released showed an accurate homeward departure direction

(Figure 1F), demonstrating their familiarity with the visual environment. In tests with the artificial panorama, zero-vector ants were carried from the training field in a plastic tube and released at the centre of the artificial arena (more detailed information on the methods can be found in the Supplemental data).

In the first test, the artificial panorama was aligned with the natural panorama, relative to a global compass heading, and ants headed in a direction very close to the bearing taken by zero-vector ants from the normal training position. This may have been because the ants follow a global compass direction which they recall when they recognise a location [7], or because

they derive directional information from the skyline. To distinguish these possibilities, ants were also tested with a rotated artificial skyline. In this condition, ants also followed the directional information given by the rotated skyline (Figure 1G). This indicates that the crude arena, where the colour and distance to objects are radically different from the training situation, captures enough information in the skyline profile to functionally mimic a natural panoramic scene and give directional information independently of any compass mechanisms.

Fortuitously, during the experiment ants from a second nest, over 30 m from the feeder, began to forage at the experimental feeder. Zero-vector ants from Nest 2 departed the feeder in a significantly different direction to Nest 1 ants (Figure 1H) and when tested with the rotated arena, they also headed in the direction predicted by the artificial skyline rather than the habitual compass direction taken from the feeder (Figure 1H). Ants from Nest 2 did not take a direct route back to their nest (Figure S1 in Supplemental data), suggesting that multiple skyline views are needed to control their route, rather than a single skyline view being used at the feeder to set the overall route direction.

Taken together, these results suggest that the skyline, a high contrast boundary where terrestrial objects meet the sky, provides a characteristic signature from which ants can derive directional information. It further suggests that ants use an economical encoding of natural scenes, abstracting only simple features. That the skyline could be a strong source of directional information is an intuitive result backed up by theoretical studies [8,9]. The ant vision system is well suited to the extraction of the skyline contour using a UV-green opponent channel [8] and modelling work has shown how such a system could reliably extract a skyline profile in different light conditions. Further study is now required to address several open questions. Most pertinently: how do ants encode skyline information? And, how do ants derive a movement direction from the comparison of their current skyline view and their remembered view? Further

study is now required to address several open questions. Most pertinently: how do ants encode skyline information? And, how do ants derive a movement direction from the comparison of their current skyline view and their remembered view? Recent experiments, also with *M. bagoti* [10], have addressed the first question. By masking different portions of the visual panorama, it was possible to show that being able to view prominent skyline features at high retinal elevations was neither necessary nor sufficient for successful orientation. This suggests that *M. bagoti* derive information from a broad range of azimuthal directions rather than a small set of the most prominent features.

#### Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01585-1](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01585-1)

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## Evolutionary history of the Falklands wolf

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After visiting the Falkland Islands during the voyage of the *Beagle*, Charles Darwin remarked on the surprising presence of a wolf-like canid unique to the islands [1]. One hundred and forty years after its extinction [2], the evolutionary relationships of this unusual canid remain unresolved. Here, we present a phylogenetic analysis based on nuclear and mtDNA sequence data from the extinct Falklands wolf and find that its closest extant relative is the South American maned wolf. Molecular dating analyses suggest that the Falklands wolf and several extant South American canid lineages likely evolved in North America, prior to the Great American Interchange. The Falklands wolf was the sole representative of a distinct South American canid lineage that survived the end-Pleistocene extinctions on an island refuge.

The Falklands wolf (*Dusicyon australis*) was the only endemic terrestrial mammal inhabiting the Falkland Islands until its extinction in 1876 [1,2]. Since its description by Darwin, the occurrence of this large, wolf-like canid on a pair of islands 480 km from the eastern coast of Argentina has remained a mystery [1–4]. Although formerly abundant on the islands [1,4], few museum specimens of the species have been preserved. The Falklands wolf presents a puzzling combination of craniodental characteristics, resulting in controversial taxonomic alliances with domestic dogs (*Canis familiaris*) [2], the North American coyote (*Canis latrans*) [5], and South American foxes (*Pseudalopex* and *Cerdocyon*) [5,6]. Hypotheses for its presence on the islands, which have never been connected to the South American mainland [7], have ranged from dispersal by ice or logs [3,7], to domestication and subsequent transport by Native Americans [2].

We sequenced the complete *cytochrome oxidase II* mitochondrial gene and part of the *cytochrome b* gene from five museum specimens of Falklands wolf, including one specimen collected by Darwin himself (see Supplemental data published with this article online for details). We also sequenced four nuclear loci containing phylogenetically informative polymorphisms. Phylogenetic analyses of these datasets using neighbour joining, maximum likelihood and Bayesian inference do not recover a close relationship between the Falklands wolf and South American foxes (*Cerdocyon* and *Pseudalopex*) or *Canis* species, as suggested by morphological data [2,5,6]. In contrast, we found a surprising and well-supported sister group relationship to the South American maned wolf (*Chrysocyon brachyurus*) (Figure 1). Given our limited sequence data, we were unable to recover a monophyletic South American canid clade, or a clade comprising the maned wolf and bush dog (*Speothos venaticus*) in our unconstrained analyses. However, a topology constrained to include these well-documented relationships is not significantly less likely than the tree produced by unconstrained analyses (see Supplemental data). Furthermore, the monophyly of both the South American canids and the maned wolf/Falklands wolf/bush dog clade are independently supported by nuclear polymorphisms (Figure 1). Although the maned wolf is the closest extant relative of the Falklands wolf, a morphologically similar species, *Dusicyon avus*, survived in South America until the mid-Holocene [7]. This species may have an even closer relationship with the Falklands wolf and warrants further investigation.

Both Darwin [1] and Fitzroy [3] were surprised by the striking differences between the Falklands wolf and the canids of the South American mainland. We estimated the divergence time between the Falklands wolf and maned wolf as 6.7 million years ago (mya) (Figure 1; 95% highest probability density (HPD) = 4.2–8.9 mya). Such a long divergence time, coupled with subsequent ecological isolation on the Falkland Islands may account for the pronounced morphological