elusive in this study, will ultimately lend important insight into the nature of circuits that integrate circadian and homeostatic cues to produce changes in sleep behavior.

References

1. Borbély, A.A. (1982). A two-process model of sleep regulation. Hum. Neurobiol. *1*, 195–204.
2. Goel, N., Basner, M., Rao, H., and Dinges, D.F. (2013). Circadian rhythms, sleep deprivation, and human performance. Prog. Mol. Biol. Transl. Sci. *119*, 155–190.
3. Saper, C.B., Fuller, P.M., Pedersen, N.P., Lu, J., and Scammell, T.E. (2010). Sleep state switching. Neuron *68*, 1023–1042.
4. Crocker, A., and Sehgal, A. (2010). Genetic analysis of sleep. Genes Dev. *24*, 1220–1235.
5. Liu, S., Lamaze, A., Liu, Q., Tabuchi, M., Yang, Y., Fowler, M., Bharadwaj, R., Zhang, J., Bedont, J., Blackshaw, S., *et al*. (2014). WIDE AWAKE mediates the circadian timing of sleep onset. Neuron *82*, 151–166.
6. Parisky, K.M., Agosto, J., Pulver, S.R., Shang, Y., Kuklin, E., Hodge, J.J., Kang, K., Liu, X., Garrity, P.A., Rosbash, M., and Griffith, L.C. (2008). PDF cells are a GABA-responsive wake-promoting component of the Drosophila sleep circuit. Neuron *60*, 672–682.
7. Kunst, M., Hughes, M.E., Raccuglia, D., Felix, M., Li, M., Barnett, G., Duah, J., and Nitabach, M.N. (2014). Calcitonin gene-related peptide neurons mediate sleep-specific circadian output in Drosophila. Curr. Biol. *24*, 2652–2664.
8. Jenett, A., Rubin, G.M., Ngo, T.T., Shepherd, D., Murphy, C., Dionne, H., Pfeiffer, B.D., Cavallaro, A., Hall, D., Jeter, J., *et al*. (2012). A GAL4-driver line resource for Drosophila neurobiology. Cell Rep. *2*, 991–1001.
9. Allada, R., and Chung, B.Y. (2010). Circadian organization of behavior and physiology in Drosophila. Annu. Rev. Physiol. *72*, 605–624.
10. Shafer, O.T., Kim, D.J., Dunbar-Yaffe, R., Nikolaev, V.O., Lohse, M.J., and Taghert, P.H. (2008). Widespread receptivity to neuropeptide PDF throughout the neuronal circadian clock network of Drosophila revealed by real-time cyclic AMP imaging. Neuron *58*, 223–237.
11. Cavanaugh, D.J., Geratowski, J.D., Wooltorton, J.R., Spaethling, J.M., Hector, C.E., Zheng, X., Johnson, E.C., Eberwine, J.H., and Sehgal, A. (2014). Identification of a circadian output circuit for rest:activity rhythms in Drosophila. Cell *157*, 689–701.
12. Seluzicki, A., Flourakis, M., Kula-Eversole, E., Zhang, L., Kilman, V., and Allada, R. (2014). Dual PDF signaling pathways reset clocks via TIMELESS and acutely excite target neurons to control circadian behavior. PLoS Biol. *12*, e1001810.
13. Choi, C., Fortin, J.P., McCarthy, Ev., Oksman, L., Kopin, A.S., and Nitabach, M.N. (2009). Cellular dissection of circadian peptide signals with genetically encoded membrane-tethered ligands. Curr. Biol. *19*, 1167–1175.
14. Jim, L., Han, Z., Platisa, J., Wooltorton, J.R., Cohen, L.B., and Pieribone, V.A. (2012). Single action potentials and subthreshold electrical events imaged in neurons with a fluorescent protein voltage probe. Neuron *75*, 779–785.
15. Benemei, S., Nicoletti, P., Capone, J.G., and Geppetti, P. (2009). CGRP receptors in the control of pain and inflammation. Curr. Opin. Pharmacol. *9*, 9–14.
16. Sink, K.S., Walker, D.L., Yang, Y., and Davis, M. (2011). Calcitonin gene-related peptide in the bed nucleus of the stria terminalis produces an anxiety-like pattern of behavior and increases neural activation in anxiety-related structures. J. Neurosci. *31*, 1802–1810.
17. Woods, I.G., Schoppik, D., Shi, V.J., Zimmerman, S., Coleman, H.A., Greenwood, J., Soucy, E.R., and Schier, A.F. (2014). Neuropeptidergic signaling partitions arousal behaviors in zebrafish. J. Neurosci. *34*, 3142–3160.
18. Donlea, J.M., Thimgan, M.S., Suzuki, Y., Gottschalk, L., and Shaw, P.J. (2011). Inducing sleep by remote control facilitates memory consolidation in *Drosophila*. Science *332*, 1571–1576.

[1]Cell and Molecular Biology Graduate Program, [2]Department of Neuroscience, University of Pennsylvania Perelman School of Medicine, Philadelphia, PA 19104, USA.
*E-mail: cavanaud@mail.med.upenn.edu

http://dx.doi.org/10.1016/j.cub.2014.10.020

Speciation: Frog Mimics Prefer Their Own

***Ranitomeya* poison frogs in the Peruvian Amazon are a rare example of Müllerian mimicry in vertebrates. These frogs also prefer to court same-coloured mimics. This suggests that divergence in mimicry plays a role in reproductive isolation.**

James Mallet

Had they been alive today, Henry Walter Bates and Charles Darwin would have enjoyed the recent finding that natural selection for mimicry in poison frogs (Figure 1) is involved in the origin of species, or speciation [1]. To understand why the new result is interesting today but also would have intrigued early Darwinians requires a little history. Darwin's 'Origin' [2] was long on logic and evidence for evolution, but short on convincing evidence for natural selection [3]. Henry Walter Bates supplied a key example: Batesian mimicry was the best and arguably the first clear case of natural selection [3]. Bates argued that edible butterflies in the Brazilian Amazon mimicked the colour patterns of inedible 'model' species avoided by predators. The patterns of both mimic and model switched every few hundred kilometres or so. The multiple convergences and rapid spatial turnover in mimetic colour schemes argued for natural selection on signalling rather than mere chance or inheritance from a common ancestor [4]. Fritz Müller later showed how mimicry between unpalatable butterflies could be mutualistic: similar-looking species benefit by sharing the costs of educating predators. This leads to a lower *per capita* mortality in each species, as predators need to learn to avoid only one colour pattern in several bad-tasting prey [5]. Mimicry between unpalatable species is today termed 'Müllerian mimicry'.

Neither Bates nor Müller noticed that on the mossy floors of the rainforests they knew so well there were tiny jewel-like dendrobatid frogs playing the same Müllerian games as the butterflies. Dendrobatid frogs are often known as 'poison arrow frogs' or 'poison dart frogs' due to their extreme toxicity. Extracts of some species are used by Amazon peoples on the tips of blowpipe darts to kill prey. When I first visited the Amazon of Eastern Peru in search of contact zones between mimicry races of butterflies, Rainer Schulte, a resident of Tarapoto, astonished me by demonstrating a rare case of Müllerian mimicry in a frog he had just described. His new species, the dendrobatid *Ranitomeya imitator* [6] mimics various other *Ranitomeya* species. Some *Ranitomeya*, according to Schulte, are so toxic that a single whiff can lead to a headache. As in butterflies, mimetic frogs in different places switch colour morphs in concert. In contrast to Bates' butterflies, however, these mimicry switches take place over tens instead of hundreds of kilometres. The narrower spatial scale of dendrobatid colour switching is easily explained: butterflies fly further than frogs hop.

In the new study, Evan Twomey *et al.* [1] found that local mimicry switches by *Ranitomeya* correlate with behaviour. Near Tarapoto, five distinct colour morphs of *R. imitator* are known, each mimicking a different model species in a different location. Two of these *R. imitator* morphs meet in a narrow zone of contact near the village of Varadero: a blotched “Varadero” morph mimicking *Ranitomeya fantastica* and a striped morph mimicking *R. variabilis* (Figure 1). Striped *R. imitator* from near the contact zone prefer to court fellow striped morphs than blotched morphs. Blotched morphs, meanwhile, as well as striped morphs farther away, do not exhibit a clear preference [1]. This courtship preference suggests an early and still incomplete form of reproductive isolation. Eleven microsatellite genetic markers show narrow allele frequency clines that switch together at the colour pattern contact zone, showing that gene flow across the contact is limited [1]. Naturally selected divergence in mimicry, therefore, may be catalysing the beginnings of so-called pre-mating reproductive isolation. There could also be post-mating isolation, perhaps caused by selection against poorly adapted immigrant morphs. The authors point out that the strongest premating isolation is shown by striped frogs nearest the Varadero contact zone, suggesting that ‘reinforcement’ of underlying hybrid unfitness is due to natural selection for assortative mating.

Figure 1. Mimetic forms of *Ranitomeya imitator* and its Müllerian co-mimics.

Top row, the mimic *Ranitomeya imitator*: left, “Varadero” blotched morph; right, striped morph. Bottom row, the models: left, the aptly named *R. fantastica*; right, *R. variabilis*. Photos courtesy of Evan Twomey.

That natural selection is driving speciation in poison frogs might not seem particularly novel at first sight: Darwin’s 1859 book was after all entitled “On the Origin of Species by Means of Natural Selection …” [2]. However, theories of speciation since then have often sidelined natural selection. By the 1890s, although most biologists accepted evolution, natural selection was less popular. Alfred Russel Wallace eloquently defended his and Darwin’s ground-breaking idea [7], but by then natural selection was becoming rejected as a major cause of evolution in favour of a plethora of other ideas, mostly now best forgotten. This period became known as the ‘Eclipse of Darwinism’ [8]. Natural selection was also, in this environment, likewise dismissed as a cause of the origin of species. The eclipse of natural selection lasted until the 1920s and 1930s, when Mendelian inheritance was shown to be consistent with Darwinian evolution by natural selection [9].

Even after natural selection was again understood to be important in evolution, speciation lingered on in eclipse phase. While natural selection had been rehabilitated in evolution generally, speciation was believed instead to require Lamarckian adaptation to local environments (especially in France and Germany), special *deus ex machina* intervention, such as macromutation [10], or geographic isolation [11]. Ernst Mayr, first writing in the 1940s on speciation, famously promoted the latter view, and by the 1960s evolutionary biologists mostly agreed with Mayr and Dobzhansky that geographic and reproductive isolation was the key to speciation, rather than natural selection. As late as 1999, Mayr put it thus: “… the crucial process in speciation is not selection, which is always present in evolution even when there is no speciation, but *isolation*”[12]: xix.

Mimicry was implicated in the origin of species from its earliest days, by Bates himself. Divergent natural selection, as Darwin knew well, could be reversed by “intercrossing” [2]. According to Bates, butterflies of the genera *Mechanitis*, *Hyposcada* and *Heliconius* displayed mimicry forms in the process of diverging into species. In these genera, Bates found that different colour forms within a lineage tended to mate assortatively, “coexisting in the same locality without intercrossing” (p. 501 [4]) as a result of which further divergence of the forms into species would be ensured.

The often sceptical Darwin was effusive in his praise of Bates. Not only had Bates found the clearest ever example of natural selection causing divergence, but he was now showing how the same kind of natural selection could lead to increased separation of incipient species, due to reduced intercrossing. Darwin was eager to get his hands on more information, and gently chided Bates for not providing the detailed evidence on which his assertions about lack of intercrossing rested [13]. Unfortunately, by this time Bates was back in England, never to return to the Amazon. No further data on the topic was forthcoming in Darwin’s lifetime.

By the 1930s, mimicry had again become a premier example of natural selection but had shed its earlier implications for speciation [9]. Much later, courtship behaviour was found to depend directly on divergent mimicry in *Heliconius* butterflies [14,15]. Males were more likely to court females of their own colour pattern rather than divergent patterns. The response was similar with coloured paper models, so this preference depended directly on colour pattern. Here at last was the result Darwin required. Mimicry can be a ‘magic’ trait that contributes both to species separation and to survival.

The recent evidence with poison frogs is similar. Courtship between adjacent forms considered members of the same species, but with different mimicry affiliations, tends to follow colour pattern [1]. Colour pattern is used in mate choice in other dendrobatids [16,17], so preference might here also depend directly on mimicry signals. Many more such cases might now be found among other mimetic butterflies, frogs and other species. In any case, taxa occupying different ecological niches are today well known to diverge in mating behaviour. There are now many examples of ecological speciation: insects that switch host plants, cuckoos and other birds that parasitize multiple bird host species, cichlid fish with divergent sexually selected colour patterns, and the famous Darwin’s finches feeding on different seed species in the Galápagos islands. As a result of this recent work, the key role of natural selection in speciation has to a large extent been rehabilitated (with or without geographic isolation) [18,19], in strong contrast to the beliefs of a few decades ago.

The current revival of the role of natural selection in speciation, it seems to me, still misses an important insight of Darwin’s. Even a hundred and sixty years later, we struggle to tune in to Darwin’s wavelength. In his “principle of divergence,” he argued that intermediates would be less fit because they are selected against, out-reproduced in the “struggle for existence” by competitive exclusion [2]. Avoidance of cross-mating and hybrid sterility or inviability (pre- and post-mating isolation) are usually cited as the main components of reproductive isolation[12], but almost any disruptive or divergent natural selection will yield poorly adapted intermediates. This reduced reproductive success hinders gene flow between divergent forms. Ecological genetic divergence may often be enhanced by hybrid sterility or inviability, or reinforcement of divergence through selective mating, but reproductive isolation also results more directly as a simple consequence of ecological divergence. For this reason, poison frogs in the rainforests of the Amazon — with their extraordinarily diverse and colourful mimicry patterns — show us not only beautiful examples of natural selection but also the very essence of speciation.

References

1. Twomey, E., Vestergaard, J.S., and Summers, K. (2014). Reproductive isolation related to mimetic divergence in the poison frog Ranitomeya imitator. Nat. Commun. *5*, 4749.
2. Darwin, C.R. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life (London: John Murray).
3. Gayon, J. (1998). Darwinism’s Struggle for Survival. Heredity and the Hypothesis of Natural Selection (Cambridge, UK: Cambridge University Press).
4. Bates, H.W. (1862). Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Trans. Linnean Soc. Lond. *23*, 495–566.
5. Müller, F. (1879). *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. Proc. Entomol. Soc. Lond. *1879*, xx-xxix.
6. Schulte, R. (1986). Eine neue *Dendrobates*-Art aus Ostperu (Amphibia: Salientia: Dendrobatidae). Sauria *8*, 11–20.
7. Wallace, A.R. (1889). Darwinism. An Exposition of the Theory of Natural Selection with Some of its Applications (London: Macmillan & Co.).
8. Bowler, P.J. (1992). The Eclipse of Darwinism, 2nd Edition (Baltimore, Maryland: Johns Hopkins University Press).
9. Fisher, R.A. (1930). The Genetical Theory of Natural Selection (Oxford: Clarendon Press).
10. Goldschmidt, R.B. (1940). The Material Basis of Evolution (New Haven: Yale University Press).
11. Dobzhansky, T. (1937). Genetics and the Origin of Species (New York: Columbia Univ. Press).
12. Mayr, E. (1999). Systematics and the Origin of Species, Volume Reprinted (Cambridge, Mass.: Harvard University Press).
13. Darwin, C.R. (1863). [Review of] Contributions to an insect fauna of the Amazon Valley. By Henry Walter Bates, Esq. Transact. Linnean Soc. Vol. XXIII. 1862, p. 495. Natural History Rev. *3*, 219–224.
14. Jiggins, C.D., Naisbit, R.E., Coe, R.L., and Mallet, J. (2001). Reproductive isolation caused by colour pattern mimicry. Nature *411*, 302–305.
15. Chamberlain, N.L., Hill, R.I., Kapan, D.D., and Kronforst, M.R. (2009). Polymorphic butterfly reveals the missing link in ecological speciation. Science *326*, 847–850.
16. Summers, K., Symula, R., Clough, M., and Cronin, T. (1999). Visual mate choice in poison frogs. Proc. R. Soc. Lond. B Biol. Sci. *266*, 2141–2145.
17. Reynolds, B.R., and Fitzpatrick, B.M. (2009). Assortative mating in poison-dart frogs based on an ecologically important trait. Evolution *61*, 2253–2259.
18. Coyne, J.A., and Orr, H.A. (2004). Speciation (Sunderland, Mass.: Sinauer Associates).
19. Nosil, P. (2012). Ecological Speciation (Oxford: Oxford University Press).

Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge MA 02138, USA.
E-mail: jmallet@oeb.harvard.edu

http://dx.doi.org/10.1016/j.cub.2014.10.001

Vision: Efficient Adaptive Coding

Recent studies show that perception is driven not only by the stimuli currently impinging on our senses, but also by the immediate past history. The influence of recent perceptual history on the present reflects the action of efficient mechanisms that exploit temporal redundancies in natural scenes.

David Burr[1,2,*]
and Guido Marco Cicchini[2]

Did you notice how Harry Potter’s T-shirt changes from a crewneck to a henley shirt in *The Order of the Phoenix*, or how Julia Roberts’ croissant inexplicably morphs into a pancake in *Pretty Woman*? Do not worry if you did not: such failure to notice blatant continuity errors may reflect the operation of our highly efficient perceptual systems, which adapt to the redundancies of the world. Recent work is showing how our perceptual systems exploit the temporal redundancies of natural scenes, particularly the fact that objects tend to be constant, rarely changing abruptly from one moment.

Many perceptual studies show how much detail in the world escapes our awareness. The most well known are the stunning demonstrations of ‘change blindness’ [1,2]: when motion transients are masked, subjects fail to see huge changes in successive scenes, such as the disappearance of aeroplane engines (see examples in http://www.gocognitive.net/demo/change-blindness). Another example is ‘motion silencing’ [3]: failure to see large changes in form or colour of groups of moving shapes. A newly developed approach complements these studies to shed more light on why changes may go unnoticed: the system seems to exploit temporal