

so there may be systematic errors in the estimated field strengths. Despite this caveat, discoveries such as PSR J1846-0258 blur the division between pulsars and magnetars. It seems entirely possible that they represent extremes of the neutron-star population, depending on their original spin and magnetic field strength. So, for neutron stars, there may well be unity in their diversity. ■

Jim Cordes is in the Astronomy Department, Cornell University, Ithaca, New York 14853-6801, USA.

e-mail: cordes@spacenet.tn.cornell.edu

1. Gotthelf, E. V., Vasisht, G., Boylan-Kolchin, M. & Torii, K. *Astrophys. J. Lett.* **542**, 37–40 (2000).
2. Woods, P. M. *et al.* *Astrophys. J. Lett.* **519**, L139–L142 (1999).
3. Duncan, R. & Thompson, C. *Astrophys. J. Lett.* **392**, L9–L13 (1992).
4. Kouveletiou, C. *et al.* *Nature* **393**, 235–237 (1998).
5. Wheeler, J. C., Yi, I., Hoflich, P. & Wang, L. *Astrophys. J.* **537**, 810–823 (2000).
6. Baring, M. G. & Harding, A. K. *Astrophys. J. Lett.* **507**, L55–L58 (1998).
7. Manchester, R. N. *et al.* in *Pulsar Astronomy — 2000 and Beyond* ASP Conf. Vol 202 (eds Kramer, M., Wex, N. & Wielebinski, R.) 49–54 (2000).

Evolution

Speciation in the round

David B. Wake

‘Ring species’ occur when one species grades into two at the overlap of a circular population distribution. Good examples are rare, but one case has now passed some rigorous tests.

In principle, ring species should constitute “the perfect demonstration of speciation”¹. According to the classic model, such rings are composed of populations of an organism that started from a single ancestral population and are now distributed geographically in a circular manner. Neighbouring populations in the ring can interbreed, except for the two terminal, overlapping populations which cannot and behave as if they are distinct species. The process is a culmination of a gradual adaptation of the organism to a gradient of habitats around the ring such that, when populations meet at the terminus, species-level divergence has occurred. An especially attractive feature of ring species is that they represent a piece of history, in that various stages in the formation of species are preserved and can be studied.

For various reasons there may be no such thing as the perfect ring species. But on page 333 of this issue, Irwin *et al.*² describe how they have revisited one of the earliest putative examples — that of the greenish warbler (*Phylloscopus trochiloides*; Fig. 1), which is distributed around the margins of the Tibetan plateau in Asia and was first described over 60 years ago³. They conclude that, although this warbler ring is not perfect, it meets most of the requirements of the classic model.

Identifying ring species is complicated. First, the geographical conditions are critical: there needs to have been divergence from a single ancestral source population around some kind of barrier. An appropriate balance must be reached between the opposing forces of selection (which causes geographically neighbouring populations to diverge in their adaptations) and continuing gene flow through interbreeding (which maintains genetic continuity). Moreover, the ring of populations should be continuous, although it is almost impossible to satisfy this criterion. Ranges of species are subject to constant



Figure 1 On song — an east Siberian greenish warbler.

change — they expand and contract over time, with parts becoming separated then reconnecting to form secondary contacts. In other instances, populations become extinct, producing gaps. In the case of the greenish warbler, there is a gap in China, which seems to have been caused by human destruction of the bird’s forest habitat.

A further complication is that the two terminal populations are usually identified first, and are often named as different species. Given this initial taxonomic bias, subsequent studies may overlook the possibility that a ring species exists. In other instances, possible examples have fallen prey to changing concepts of what a species is; several former ring species are no longer treated as a single species taxonomically, but rather as groups of closely related species (circumpolar gulls are a classic example).

One of the best-studied cases is the salamander *Ensatina eschscholtzii*, which has populations around the Central Valley of California with sharply divergent forms coexisting in southern California⁴. But whether or not this is a genuine ring species is a matter of controversy. There is one break in

the distribution and another area where there is a ‘weak link’ in the chain of differentiated but intergrading forms. Also, there is debate over the most appropriate taxonomy because of different interpretations of genetic data^{5–9}.

From Irwin and colleagues’ work², however, it seems that greenish warblers satisfy most of the stringent requirements for a ring species. One form ranges from the Baltic region to western Siberia, where it spreads south and intergrades with another form along the western and southern slopes of the Himalayas (see Fig. 1 of the paper on page 334). Intergradation with other forms occurs to the east, then northward, until an eastern Siberian form meets the western Siberian form in the vicinity of the Yenisei River. There the two behave as distinct biological species, and do not interbreed. For instance, as Irwin *et al.* show, they have more complex songs than southern populations, and no longer recognize each other as potential mates — this is sexual selection as a driving force in speciation. The birds are thought to have originated in the south and moved around the Himalayas, the eastern and western populations coming into contact in the north, but remaining distinct, following the end of the last glacial epoch. This fulfils the geographical and biological requirements of a ring species.

Irwin *et al.* also collected mitochondrial DNA evidence from the various populations. The DNA sequences form two well-supported clades, one eastern and the other western. In the region of the putative ancestral populations, the clades are intermixed. Typical phylogeographic analysis^{10,11} would interpret these clades as historical entities: that is, that they arose from eastern and western isolates that diverged when they were geographically isolated, and subsequently expanded their ranges both north and south to reconnect. In the north, songs diverged such that coexisting populations behave as different species, whereas in the south birds remained sufficiently similar in song characteristics to merge and form an interbreeding unit.

This interpretation is considered, but rejected, by Irwin *et al.*². Instead, they have conducted simulations (not published) which show that antecedents of the two major clades of DNA sequences might have arisen within the same area. The sequences are not very divergent, and Irwin *et al.* argue that sorting of the two primordial lineages of sequences took place in the region in which they originated. One lineage came to dominate in the eastern region and the other in the western, as the populations expanded around the mountain mass. This interpretation runs counter to a central tenet of phylogeography, which sees history as having been recorded in the phylogeny of sequence lineages, and so is likely to be controversial.

Finally, the paper is notable for incorporating two different explanations for species formation. First, the authors take sexual

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selection to be responsible for the elaboration and divergence of songs in the greenish warbler. By contrast, they believe that the similarity in body size of the northern forms stems from natural selection acting on size. Both natural selection (especially in so-called ecological speciation)^{12,13} and sexual selection^{14,15} have been the subject of close recent interest. So the work of Irwin *et al.*² makes a multifaceted contribution to the current debate on species formation. ■

David B. Wake is in the Museum of Vertebrate Zoology and the Department of Integrative Biology, University of California, Berkeley, California 94720-3160, USA.

e-mail: wakelab@uclink.berkeley.edu

1. Mayr, E. *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963).

2. Irwin, D. E., Bensch, S. & Price, T. D. *Nature* **409**, 333–337 (2001).
 3. Ticehurst, C. B. *A Systematic Review of the Genus Phylloscopus (Willow-warblers or Leaf-warblers)* (Trustees of the British Museum, London, 1938).
 4. Stebbins, R. C. *Univ. California Publ. Zool.* **48**, 377–526 (1949).
 5. Moritz, C., Schneider, C. J. & Wake, D. B. *Syst. Biol.* **41**, 273–291 (1992).
 6. Jackman, T. R. & Wake, D. B. *Evolution* **48**, 876–897 (1994).
 7. Wake, D. B. *Proc. Natl Acad. Sci. USA* **94**, 7761–7767 (1997).
 8. Highton, R. *Herpetologica* **54**, 254–278 (1998).
 9. Wake, D. B. & Schneider, C. J. *Herpetologica* **54**, 279–298 (1998).
 10. Avise, J. *Phylogeography: The History and Formation of Species* (Harvard Univ. Press, Cambridge, MA, 2000).
 11. Riddle, B. R., Hafner, D. J., Alexander, L. F. & Jaeger, J. R. *Proc. Natl Acad. Sci. USA* **97**, 14438–14443 (2000).
 12. Orr, M. R. & Smith, T. B. *Trends Ecol. Evol.* **13**, 502–506 (1998).
 13. Schneider, C. J., Smith, T. B., Larison, B. & Moritz, C. *Proc. Natl Acad. Sci. USA* **96**, 13869–13873 (1999).
 14. Rice, W. R. in *Endless Forms: Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 261–270 (Oxford Univ. Press, New York, 1998).
 15. Gray, D. A. & Cade, W. H. *Proc. Natl Acad. Sci. USA* **97**, 14449–14454 (2000).

Water structure

Order and oddities

Srikanth Sastry

Water is a common but unusual liquid. Precise measures of the arrangement of molecules in water may help us to better understand some of its peculiar properties.

The structure of matter on microscopic scales is a pervasive theme in modern science. The successes of solid-state physics are built on exploiting the regularity of atomic arrangements in crystals. Chemists and materials scientists focus on relationships between the structure and properties of molecules and materials. Molecular biologists are concerned with the interplay of structure and function in bio-

logical molecules and their assemblies. Describing the crystalline order of solids is relatively straightforward, but the order found within ‘disordered’ materials, such as a liquid, glass or a protein molecule, is far more subtle and trickier to capture. On page 318 of this issue, Errington and DeBenedetti¹ show that combining two measures of the structural order in water — the most familiar of liquids but one that is notoriously peculiar

— reveals striking patterns of structural change, and also its relation to water’s unusual properties.

Perhaps the best-known peculiarity of water is its ‘density maximum’ at 4 °C (at atmospheric pressure); cooling or heating water from this temperature causes it to become less dense. An equally striking but less-known anomaly is that, as the density of water is increased, water molecules begin to move about — or diffuse — faster, but only up to a point known as the ‘diffusivity maximum’. At higher densities, the diffusivity decreases with increasing density, just as in normal liquids. By using computer simulations, Errington and DeBenedetti identify a ‘structurally anomalous’ region in the density–temperature phase diagram of water, in which order decreases with increasing density. They also find that all the unusual density and diffusivity behaviour occurs in this region, suggesting a precise link between anomalies in structure and behaviour.

In crystalline solids, atoms or molecules are arranged in a regular array. No such obvious order exists in liquids. A microscopic ‘snapshot’ of a liquid would reveal atoms in a disordered jumble, much like people packed during rush hour into a crowded subway in New York, or, even better, a local train in Mumbai. There is some form of order nevertheless, and it arises from what the English humorist P. G. Wodehouse describes as the law that “a given spot... at a given moment of time can be occupied by only one body”. From where one passenger stands, another passenger in any direction must be found a well-defined distance away, and the next at roughly twice that distance, and so on. But such order doesn’t persist over long distances.

Neuroscience

Cats, dogs and categories

Any child can tell a cat from a dog. But the difference has to be learned, and describing it is far from simple. Cats include cheetahs, lions and tabbies; dogs include Siberian huskies and dachshunds. How do we make the jump from recognizing a particular set of features to establishing a more general concept or category that will help us extrapolate to new situations?

Writing in last week’s *Science* (**291**, 312–315; 2001), David J. Freedman and colleagues describe how they have explored this question by training monkeys to distinguish between ‘catness’ and ‘dogness’. The authors used computer graphics to create blended images from a set of three dog and three cat images. An example of a cheetah, a Doberman and, in between, a blend of the two is

shown on the right. They then taught the monkeys to indicate, by releasing a lever, whether a sample image was of the same type as a test cat or a test dog. Monkeys, it turns out, are good at learning this distinction: even when the image was 60% cat and 40% dog, the monkeys reliably reported that it was like a cat. Furthermore, monkeys were not simply memorizing specific blends of cats and dogs as belonging to one category, because new blends were tested during the experiment.

To find out how these categories are represented in the brain, the authors recorded neural activity in the lateral prefrontal cortex — an area of the frontal lobes previously implicated in guiding complex behaviours — while the monkeys performed the task. Surprisingly, they found category



information represented at the level of single neurons. That is, regardless of whether the image was 60%, 80% or 100% dog, individual neurons responded in a similar way; but they responded differently for 60%, 80% or 100% cat.

Obviously, these category representations were the result of training — neurons in a monkey’s lateral prefrontal cortex probably don’t care about ‘dogness’ under normal circumstances. Indeed, the authors

went on to train one of their monkeys on a new, more abstract categorization of the same images, and showed that neurons no longer distinguished cats and dogs as they did previously, but now coded for the new categories. How these representations come to be formed rapidly and reversibly in this part of the brain is not going to be easy to answer. But it is clearly closely related to how we learn to categorize our world into meaningful concepts.

Hemai Parthasarathy