

Book Reviews

An Extended Review of *Speciation in Birds* by Trevor Price.

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An understanding of how new species come into being is a major issue in biology and it remains a profound question in philosophy. Few questions have caused more dissension in the history of ideas, and it remains the foremost bone of contention between the religious and the secular or scientific viewpoints. Some background into the controversies and issues surrounding speciation is essential to appreciate the significance of Trevor Price's *Speciation in Birds*. For most biologists, indeed for many scientists and philosophers, Charles Darwin's *Origin of Species* (Darwin 1859) is the most influential secular book published in the past millennium. It has had a profound influence on human thought and how humans view their place in nature. Some might argue that *Das Kapital* by Karl Marx (Marx 1867) is at least as influential, but they ignore Darwin's influence on Marx's thinking, indeed in *Das Kapital* Marx discusses Darwin, and even sent his seminal work to Darwin, though there is no evidence that Darwin read it. Furthermore, even a cursory consideration of the thinking and literature that has arisen from the two books quickly shows that Darwin is far more influential (e.g. Browne 2007). Darwin delayed publication because he wanted to spare the religious beliefs of his wife and he foresaw how his ideas would rock

establishment views on the immutable creation of life. It was only Alfred Russel Wallace's independent derivation of the ideas of natural selection and evolution that impelled Darwin to publish what was instantly an international best seller, which sold out on the first day (e.g. Quammen 2008). Though the word evolution is used only once in the book and Darwin largely avoids discussing human evolution, it was the issue that was seized upon by his many critics. Darwin did later write about human evolution and the potent force that sexual selection can be in evolution (Darwin 1871), but he largely left the public defence of his views to Huxley (Huxley 1863) and other champions. Extensive research and critical testing in the last 150 years overwhelmingly supports Darwin's theories, and the incorporation of genetics have shown that the Darwinian view is the only testable hypothesis of how life has evolved (e.g. Jones 2000).

The impact of the *Origin* is well known, yet few commentators mention two of the oddest things about Darwin's famous book. First, very few biologists, philosophers or indeed anyone else, has actually read the *Origin*, which despite its somewhat ponderous Victorian style is still fresh and staggeringly original. But the second issue overshadows this handicap, which is that the title of the *Origin of Species* is a complete misnomer. The book brilliantly provides an outline of the problem of variation in species, and despite pre-dating genetics it ingeniously provides a testable, now widely accepted, mechanism for evolution. Yet, despite its title, it never once deals with the actual origin of species. Darwin poses his "question of questions" and his "mystery of mysteries" and

while he deals with changes in existing species, he does not provide an answer to how species arise. Since Darwin there has been much work on the origin of species, but much of it is highly technical and overall the issue still remains a paradox.

This is why Trevor Price's book on *Speciation in Birds* is such a landmark event, for it tackles the question of how new species of birds arise, while providing a masterly overview of evolutionary processes. This synthesis is a huge task given the extensive scientific literature, and Price succeeds admirably in setting out the many ideas succinctly and with compelling logic. There are few books on speciation, but this book follows hard on the heels of two others: *Speciation* by J. A. Coyne and H. A. Orr that focuses on the genetics of speciation in both plants and animals (Coyne and Orr 2004); and the mathematical framework of speciation by S. Gavrilets in *Fitness Landscapes and the Origin of Species* (Gavrilets 2004). Yet Price's book stands up strongly to these two well-regarded books, as its main focus is behaviour and ecology and field tests of the underlying hypotheses, which makes it much more accessible to the general reader.

The study of speciation is beset with problems, including the fundamental question of how one defines a species. As birders we are familiar with seeing a bird and, in most cases, intuitively knowing that it belongs to a particular species and not another. Thus birders have a species concept for familiar birds, but it must be said it is based on the key features emphasised in the field guides. How was the species defined for the author and artist of the field guide, and are their criteria the ones by which the members of that species recognise each other? Modern biology and evolution are dominated by genetics and the view that a species must be genetically distinct from other species. Much of our understanding of the genetics of speciation comes from studies of organisms like *Drosophila* fruit flies, which are considered ideal because

they can be easily maintained in glass bottles and have a short time between generations. Unfortunately, virtually nothing is known about the ecology and behaviour of wild populations of *Drosophila*, and being so small they would be difficult to study in the wild (Mallet 2006). Conversely, in birds we know a great deal about their ecology and behaviour, but lack the sort of detailed genetic knowledge that is commonplace for *Drosophila*.

The key point is that species remain distinct because they have some sort of genetic, embryonic, geographical, ecological or behavioural barrier(s) to prevent interbreeding with others – a *reproductive isolating mechanism* (Poulton 1908; Dobzhansky 1937). Once reproductively isolated the species is an independent unit of evolution. This is the crux of the Biological Species Concept (BSC), which came about from the discovery that some species of *Drosophila* rarely interbreed despite having little genetic difference and being virtually indistinguishable in appearance (Dobzhansky 1937). Yet reproductive isolation does not tell us about the process of speciation; to understand speciation it is essential to know how the isolation came about and how it is fixed in the newly developing species (Coyne and Orr 2004; Mallet 2006). We need to distinguish between three types of reproductive isolation: (1) ecological separation of niches that keeps similar species apart and prevents a mixing of genes; (2) mate choice that ensures females usually do not select mates from the other species; and (3) natural selection against hybrids between the two species (Coyne and Orr 2004; Mallet 2006).

The BSC can be applied to species that geographically overlap, but the longstanding issue has been how to apply this criterion to geographically isolated populations that rarely, if ever, have a chance to interbreed. How can the BSC be used to determine whether these separate populations are within the same species or constitute different species? A recent

example has been the controversy over the splitting of the albatrosses into many more species (Robertson and Nunn 1998). These splits were on the grounds that the traditional species had separate populations that consistently breed on different islands and thus do not interbreed and consequently should constitute different species. These splits were rejected in the recent revision of the Australian list (Christidis and Boles 2008) because -while the populations may be geographically separate - there is no evidence that the populations from each island could not successfully interbreed, nor is there evidence that they have sufficient genetic divergence to be considered distinct species. There has been a spate of at least 25 new species concepts to try and resolve this sort of problem, together with other issues such as self-fertilizing plants and asexual organisms. Interestingly, all the recent reviews of speciation, including Price's book, define species with a modified BSC that allows some hybridisation between species that remain distinct (e.g. de Queiroz 1998; Helbig et al. 2002; see the extensive critical discussion in Coyne and Orr 2004).

Price makes no apologies for why birds are the focus of his book on speciation: they can be easily observed in the field, have varied behaviour, social systems and complex acoustic and visual communication. Consequently, birds have generated more ecological and evolutionary hypotheses than any other group of vertebrates, including mammals. Studies of birds have led to most of our current ideas about mate choice, territoriality, predation, ecological niches, species concepts, and the idea of species evolving both in geographical isolation and when geographically overlapping. Price uses the best field data and genetic evidence from birds to illuminate current thinking on speciation. Yet the book is not a dry academic treatise that will only appeal to the specialist - it is well written and beautifully illustrated with relevant graphs and fine photographs and paintings. Some topics are explained in the text and more detail is provided in appendices to prevent the book

becoming bogged down in the detail. There is even a fine glossary that will help explain the jargon that inevitably pervades the study of evolution and speciation.

This is a large and wide-ranging book with more than 1 300 references, so here I provide an overview and will then highlight a few illuminating sections. The first eight chapters are an excellent summary of the main two ideas on how species arise. The American ornithologist Ernst Mayr emphasized that new species arose when their populations were geographically isolated and the sub-populations could diverge in morphology, behaviour or song, until they were sufficiently distinct to be incapable of interbreeding (Mayr 1942). Conversely, the British ornithologist David Lack suggested that ecological factors were more important in shaping the morphology of species to match local conditions, until they were sufficiently distinct to form new species (Lack 1944). There is considerable evidence for both viewpoints and Price does much to differentiate their complementary roles. Price, like Lack and Darwin, worked on the Galápagos Islands where he studied Darwin's Finches, species that can show remarkable morphological and ecological differentiation on the same island, plus the geographical isolation model is supported by species that occur on different islands.

Price fully develops the many hypotheses and tests them with examples from around the world, and their implications are explored in understanding species concepts and the production of phylogenies. He describes how the Golden Whistler is the greatest "speciator" in the world with its many forms, particularly over the islands of Melanesia. He explains the conundrum of why South America has fully a third of all the bird species in the world, and twice as many species as Africa, despite being a slightly smaller continent. The geographical and ecological hypotheses for speciation find full support when comparing these two continents,

for South America has a greater range of latitude and altitude than Africa, plus there is more rainforest and rainfall within the forests. These effects are particularly noticeable in the northern Andes where there is extraordinary species diversity with closely related new species being found on different peaks and even on different aspects of the same mountain. Price explores the relationship between ecology and behaviour as well as the ways in which species arise on continents compared to remote oceanic islands. All this is highly relevant to Australian readers keen to unravel the controversies and confusion surrounding species concepts, allospecies, superspecies, and subspecies; or even just to make sense of taxonomic lists and phylogenies such as Christidis and Boles (2008). This book elucidates the apparently arbitrary decisions made by taxonomists and shows that while it is important to define a species, the endless discussion about various species concepts has been largely sterile and has generated little groundbreaking or even interesting biology.

Chapters nine and ten deal with social selection and the evolution of song, with all the constraints on songs as signals and how songs can be important isolating mechanisms in speciation. This includes a comparison of bird song with human language. Chapters eleven and twelve discuss sexual selection and its role in the divergence of populations that can lead to speciation. Sexual selection was proposed by Charles Darwin as an adjunct to natural selection to account for the evolution of competition between sexual rivals (usually males) and the choice of a mate (usually by females) from an array of suitable contenders (Darwin 1859, 1871). Sexual selection is less well known than natural selection and while male: male competition has always been accepted, the role of female choice was more or less rejected for over a hundred years, though in the last thirty years it has been a hot topic of research. It is becoming increasingly apparent that sexual selection can act as an extension to natural selection and lead to speciation, as I will discuss

below. Price even returns to one of Darwin's favourite themes when he examines the artificial selection of domestic animals that has led to very distinct forms, and compares it to the role of natural and sexual selection in producing new species in the wild.

Chapters thirteen to fifteen are an overview of how species recognise each other, which is vital in maintaining the integrity of a species and avoiding hybridisation, which usually has selective costs. Again sexual selection, especially mate choice, plays a pivotal role that has only recently been recognised. Hybridisation and hybrid zones are discussed together with the idea that hybridisation may play a creative role in the formation of new species. Price gives a brief description and interpretation of all the main bird hybrid zones around the world, including familiar Australian examples like the Australian Magpie, Varied Sittella, and Variegated Fairywren. In chapter sixteen there is a dissection of the role of genetic incompatibility as the final step in speciation, for once two populations of what was a single species are genetically incompatible they are clearly two species because they are unable to interbreed and therefore meet the criterion of the original BSC. This incompatibility generally takes 7 - 11.5 million years, though there is evidence it can be much quicker in some groups like finches and quail. Much further research is required on the interplay between ecological and behavioural factors with genetic incompatibility. Chapter seventeen is the final chapter, and rounds out the book with the overall conclusions, including showing why the principles derived from birds can be applied to other animals.

In a book full of highlights it has been difficult to select a few and naturally my choices reflect my own interests. First, there is the fascinating account of the interplay between natural selection and sexual selection. Due to changing ecological conditions the species barriers that have evolved through natural selection may be at variance with the preferences of

females for particular mates. Colleagues and I recently found this in our studies of the three species of Tree Finches that are supposed to be found on the island of Floreana in the Galápagos archipelago. Our morphological data suggest there are two species not three, yet our experiments in which we played back the songs of Small, Medium and Large Tree Finches showed responses as if there were still three species. Our preliminary thoughts are that while the species-isolating barrier of the three types of songs are still largely intact, there has either been sufficient hybridisation for the three species to merge into two; or recent extinction of one species followed by an early phase of speciation in the remaining two species to occupy the vacant niche. Thus there seems to be active speciation in a very short time, but this is the sort of anomaly that makes Darwin's Finches famously fascinating and the fastest evolving of all vertebrates (Grant and Grant 2007). These sorts of results would have been incomprehensible even two decades ago, but Price's book unravels how these processes can interact to produce apparent anomalies.

Another highlight is that Price does not dogmatically preach what he considers the correct view on controversial topics. Where there is controversy, Price states his position and briefly points the reader to the relevant literature to make up their own mind. Even better, he often provides an appendix that outlines the issues so that if interested the reader can decide if his approach is reasonable. This style underscores the limits of the field and how assumptions are made so that the field can progress - real science. How refreshing! For example, throughout the book Price dates evolutionary events by assuming a 2% sequence divergence of mitochondrial DNA per million years. He provides the references for how he chose this important clock for measuring the timing of evolution, and then also gives an excellent appendix on molecular dating that is a first-rate summary of the issues and assumptions. Another feature I like is that

Price in several chapters indulges in thought experiments to speculate how key features may have evolved or be developed. This type of speculation is unusual in such books and is often frowned upon, but to my mind it is perfectly clear when he does it and I found it added a new dimension to thinking about the issues. Similarly, Price does not simply quote from the existing studies, but uses the literature in novel ways to test new hypotheses that the original authors had not considered. This makes the book an extremely original review of well-known aspects of ornithology with the added bonus of many unique insights and interpretations.

A major highlight throughout the book is that Price stresses how social selection, especially social interactions and communication within and between the sexes, can drive speciation. He explores this extensively because it contradicts the prevailing view that the divergence of populations and subsequent speciation is due to either ecological factors or geographical separation. Many birds have bright colourful plumage they use for visual communication and many have simple calls and complex songs they use in acoustic communication. These are the signals by which birds recognise conspecifics and choose their mates as well as using the signals in everyday interactions. These social signals lead to different mating systems, differences in song acquisition, plumage dimorphism, moult patterns and other factors that do not fit under the usual umbrella of ecological factors in speciation. Variations in these social factors can lead to divergence of populations and eventually speciation. There are many examples such as the well-known case of female finches preferring males with novel ornaments, even if it is something as artificial as a coloured leg band. Thus female Zebra Finches prefer males that have red leg bands while female Double-barred Finches prefer males with blue leg bands. Females of both species also prefer males that have a tall white crest glued to the top of their head that has no resemblance

to normal males. Intriguingly these preferences can drive speciation even though the males with the preferred trait are not fitter than males that lack the trait.

Birds can display much unusual behaviour - a recent review identified 2,213 published records of novel behaviour, many of them observed by bird watchers and published as brief notes (Lefebvre *et al.* 2004). Some of these behaviours disappear when the avian originators die. Price gives the fascinating example of two Cactus Finches on a small island in the Galápagos that pecked the tails of larva lizards and if the lizards dropped their tails the two finches would eat it as if it were a caterpillar. When these two birds died their novel feeding behaviour apparently died with them. On the other hand there are many new behaviours that persist. Again on the Galápagos one finds the well-known and persistent behaviour of the 'vampire' form of Sharp-beaked Ground Finch, which on some islands drinks blood from the wounds they make on boobies. Similarly, the extraordinary innovation of some Blue Tits learning to pierce milk bottle lids and steal the cream started near Southampton in 1921 and rapidly spread to other populations around England. It is no coincidence that so many of these innovations concern feeding, and Price makes a compelling case that these behavioural changes can be the major impetus leading to genetic divergence and speciation. Recent research has found that the size of the forebrain of groups like the crows, parrots and falcons correlates with innovations in feeding behaviour and skills in learning novel tasks. Birds with small forebrains, such as the Emu, are notoriously difficult to train, are easily panicked and poor at solving problems. There is evidence that these differences in forebrain size and adaptability have an effect on speciation with the "smart" groups having more species than the "daft" groups.

Price extensively discusses acoustic signals, especially songs, because of their well known role in species recognition, though the songs

can be either highly variable in the space of a few kilometres, or unchanging over thousands of kilometres. Examples include the many local dialects of the Chaffinch in Europe, or the Chiffchaff superspecies that stretches right across Eurasia with many forms that appear similar, but have different songs. It seems that the most variability occurs in species where the young males learn their songs by listening to the songs of their father or neighbouring males. Similarly, the females of many species learn to prefer males that sound like their father or close neighbours. These are the species that are most likely to have dialects and clearly both sexes respond most strongly to their local dialect and less strongly to more distant dialects. Any mistakes made by young males while acquiring their song can lead to new dialects that can confuse local species recognition. To complicate matters, dialects are unknown in species in which the males do not learn their songs, yet there can also be considerable variation in the songs of these species. It is likely this variability arises from other mechanisms such as genetic mutations or ecological selection that optimises the attributes of the song to the acoustic characteristics of different habitats so as to avoid muffling or distortion. This acoustic adaptation to a variety of habitats is beautifully illustrated over the huge range of the Rufous-collared Sparrow in Argentina, where for different types of vegetation it has a distinct song dialect. If these ecological adaptations in the characteristics of the songs were reinforced by female preferences for particular variants, it would have a disproportionate effect on the attributes of male song that are implicated in species recognition. All these factors can lead to a large interbreeding population (a species) dividing into sub-populations each with their own songs. If song is the main cue used in species recognition and sexual selection, it is inevitable that song variability can drive speciation, as the subpopulations with different songs are unlikely to interbreed and mix their genes.

I will finish with the extraordinary case of “cultural speciation” in African indigobirds and the paradise and waxbill whydahs (all in the genus *Vidua*). Divergence and speciation in this group of 19 brood-parasitic finches is entirely due to learning. They lay their eggs in the nests of other species of finch, and 17 of them have specialised on a single host. Species recognition in these brood parasites depends on a learnt song, yet the young parasites do not hear the song of their father, they learn the song of their host. The females also learn to recognise the songs of their host and prefer them to other potential hosts. Experiments in which males and females were reared in captivity by hosts from another continent showed the males learnt the inappropriate host song and the females preferred the host song. Of course the problem is how do females distinguish the singing males of their own species from the males of their host? A mistaken choice would lead to an attempt to hybridise with the host species that is likely to fail or lead to sterile young. The cues used by females to correctly select a mate are unknown; perhaps they use other vocalisations, such as begging calls, in the final stages of mate choice. Having mated the female then has to find the nests of the correct host and it is thought she does this by following finches that resemble her foster mother. Females that choose the wrong host often have their eggs rejected, but in some cases they are accepted and reared, and the males and females from these incorrect hosts learn a different song and the characteristics of a different foster mother. New species can rapidly arise from these mistakes in selecting a host, and it is thought that the current overlap of the many species of indigobirds is due to this cultural speciation.

So there we have it: a wide-ranging book that comprehensively tackles huge topics and controversies, and provides a background for the big questions in biology, especially ornithology. It is that rare thing; a book that tackles difficult problems yet remains engaging and accessible, while transmitting the

excitement of the quest. I can't help thinking that, unlike *Das Kapital*, Darwin would have devoured *Speciation in Birds* with astonishment and joy. I certainly found it an enjoyable and exhilarating read, with new ideas and leads for future research popping off the pages. Having written this enthusiastic review I decided to find out what others have said about *Speciation in Birds*. Eminent biologists around the world have extensively reviewed the book, and all are effusive and positive. Many noted the book is essential reading for all undergraduate and graduate students in biology, plus professional biologists and ornithologists. What about members of the South Australian Ornithological Association? Well, I encourage you to read this fascinating book, it will give you an excellent overview of contemporary biology, it will clarify the main issues, sharpen your critical skills, and moreover it will change forever the way in which you look at birds. What more can one ask?

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