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# The Zebra Finch: the ultimate Australian supermodel

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**Abstract.** Today, the Zebra Finch is Australia's most studied bird and the focus of intensive multi-million dollar research projects throughout the world. Here we briefly summarise the history of the Zebra Finch in science and document the way in which studies of this species have proliferated and dominated a number of quite different fields within the biological sciences. The importance of the Zebra Finch is likely to increase still further after the recent publication of its genome sequence – only the second bird to be the focus of such an intensive research effort – and providing an amazing resource for understanding this species and genome evolution more generally. Finally, we highlight the contribution made by the late Richard Zann with his studies of the ecology, physiology and behaviour of the wild Zebra Finch and his tremendous enthusiasm for the species. Richard would have welcomed the status that the Zebra Finch currently enjoys in science, and looked forward to the many exciting research opportunities that this supermodel species will continue to provide in the future.

> 'The Zebra Finch is a small Australian Ploceid which is ideally suitable for laboratory observations. It will nest and rear young in small indoor aviaries. New birds, transported to the laboratory in small boxes, will begin to nest-build and court within minutes of their release into an aviary. There are no seasonal difficulties, as it breeds all through the year. The species is exclusively a seed-eater and the nestlings require no special diet in captivity. The birds are not disturbed by the presence of an unconcealed human observer.' Desmond Morris (1954; *Behaviour* **6**, 271–322).

With these words, written over half a century ago, Desmond Morris introduced the Zebra Finch (*Taeniopygia guttata*) to the scientific world as a highly amenable laboratory model. Over the past two decades in particular, the Zebra Finch has become established to the point where it is today the most important captive model passerine system, by a considerable margin. Indeed, for avian studies overall, it is only narrowly beaten in the total number of scientific studies devoted to it by the Great Tit (*Parus major*), which is studied in nest-box breeding populations throughout Europe with some long-term studies stretching back over half a century (Table 1). The pattern of increasing numbers of studies focussed on the Zebra Finch since the 1980s suggests that the importance of this small Australian finch is set to increase still further (Fig. 1). Here, we briefly consider the history of research into this species, the contribution that studies of Zebra Finches have made to several areas of scientific study, and the likely contribution that this species will make in the future. Richard Zann's contribution can be felt keenly in each of these areas. Richard was passionate about the bird and his lasting contribution was to make this species accessible to a wider audience. Richard achieved this through his excellent review of the species (Zann 1996), which communicated an enthusiasm for the bird, as well as providing a highly readable natural history of the species and summary of the key scientific findings across several important areas of research. One of Richard's main goals was to understand how the Zebra Finch managed to succeed in its natural environment, and the most important achievement of his book is arguably its provision of an excellent understanding of the environment in which the Zebra Finch lives and the selective pressures that have shaped the species over the millennia. This introduction to the arid Australian outback is important, as this environment is foreign to many of the researchers studying this species. So, to start with, we begin by trying to outline why so many people around the world spend so much time consumed with a curiosity for a bird that even most Australians have probably never seen in the field.

The work of Desmond Morris was conducted under the supervision of Niko Tinbergen in the Department of Zoology and Comparative Anatomy at the University of Oxford (UK), and was the first time that captive Zebra Finches were used to address scientific questions. Although Morris worked, and published, on several other species of estrildid finch at the same time (e.g. the Cut-throat Finch (*Amadina fasciata*) and Bronze Mannikin (*Lonchura cucullata*)), it was the Zebra Finch that was most readily suited to a life in the laboratory for the reasons that Morris (1954) described. In addition, throughout Europe and North America the Zebra Finch has always been widely available to scientists through the regular pet trade. Since it was first exported to Europe in the mid-1800s, domesticated breeding populations were readily established throughout the northern hemisphere and, to this day, the Zebra Finch remains probably the easiest bird to keep and breed in captivity (Zann 1996). Although Morris (1954) had demonstrated the practicality and relevance of addressing behavioural questions relating to reproduction in the Zebra Finch


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**Table 1. The number of publications for the years 1955–2010 returned in an ISI Web of Science search on different avian species**

The list, which is purely illustrative rather than analytical, comprises a selection of the most well-worked model systems worldwide, but specifically includes 14 Australian species so that the number of Zebra Finch studies can be benchmarked against other local birds, which have tended to have had less attention than those overseas as a result of larger scientific communities in Europe. The number given is the average number of papers from separate searches on the English name and the scientific name (i.e. $n=2$)

| English name | Scientific name | Average number of papers |
|---|---|---|
| Great Tit | *Parus major* | 1807 |
| Zebra Finch | *Taeniopygia guttata* | 1505 |
| Common Starling | *Sturnus vulgaris* | 1293 |
| House Sparrow | *Passer domesticus* | 999 |
| Pied Flycatcher[A] | *Ficedula hypoleuca* | 880 |
| Blue Tit | *Cyanistes caeruleus* | 756 |
| Barn Swallow | *Hirundo rustica* | 633 |
| Song Sparrow | *Melospiza melodia* | 609 |
| Budgerigar | *Melopsittacus undulatus* | 536 |
| Red-winged Blackbird | *Agelaius phoeniceus* | 488 |
| House Finch | *Carpodacus mexicanus* | 335 |
| Collared Flycatcher | *Ficedula albicollis* | 313 |
| Common Chaffinch | *Fringilla coelebs* | 248 |
| Common Canary[B] | *Serinus canaria* | 206 |
| Dunnock | *Prunella modularis* | 144 |
| Emu[B] | *Dromaius novaehollandiae* | 141 |
| Cockatiel | *Nymphicus hollandicus* | 134 |
| Greenfinch[C] | *Carduelis chloris* | 114 |
| Indian Peafowl | *Pavo cristatus* | 89 |
| Satin Bowerbird | *Ptilonorhynchus violaceus* | 81 |
| Bell Miner | *Manorina melanophrys* | 76 |
| Superb Fairy-wren | *Malurus cyaneus* | 70 |
| Silvereye[D] | *Zosterops lateralis* | 54 |
| Noisy Miner | *Manorina melanocephala* | 43 |
| Gouldian Finch | *Erythrura gouldiae* | 38 |
| Wedge-tailed Eagle | *Aquila audax* | 25 |
| Laughing Kookaburra | *Dacelo novaeguineae* | 20 |
| White-winged Chough | *Corcorax melanorhamphos* | 17 |
| Grey-crowned Babbler | *Pomatostomus temporalis* | 16 |
| Fairy Martin | *Petrochelidon ariel* | 13 |

[A]Search was restricted to European Pied Flycatcher.
[B]Search combined English name with ‘bird’ to remove spurious search results.
[C]Search was restricted to European Greenfinch.
[D]Search was restricted to Capricorn Silvereye.

it was several more decades before that line of research really began in earnest. Before further behavioural work began, pioneering work introduced the species to other fields of research. First, a team of researchers from Washington (USA) and the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) worked together on captive birds, and wild birds in the Western Australian desert and were interested in understanding the physiological basis of adaptation to the arid zone (Oksche *et al*. 1963). Their work showed that the Zebra Finch was an excellent subject for the detailed scrutiny of physiological and neurological processes. Such work depended on being able to catch, hold and conduct invasive work on a reasonable number of individuals and the Zebra Finch was fairly easy to catch and breed in large numbers. Of interest, although this work probably helped to establish the species as a good physiological model the specific questions addressed by this team (Oksche *et al*. 1963) were subsequently neglected for decades and, indeed, remain to be completely resolved (reviewed in this issue, Perfito 2010).

It was the scientific study of bird song that finally brought together the strands of ethology and physiology and made the Zebra Finch the important model that it is today. The work started by Morris (1954) was further developed by Klaus Immelmann who made a long and detailed study of the Zebra Finch in the wild and captivity throughout the 1960s and 1970s. As well as a variety of other important and largely neglected contributions (reviewed by Zann 1996), Immelmann (1969) characterised the development of the song in the Zebra Finch and therefore made this area accessible to further detailed work. Songbirds are an excellent model system for providing insight into learning and the acquisition of language and allow the detailed investigation of the associated neurological pathways that enable recognition, production and the learning of complex acoustic signals (reviewed in Brainard and Doupe 2002). The key work was conducted by a team at Rockefeller University in New York (USA) through the 1970s and started with Nottebohm and Arnold’s (1976) work that demonstrated a striking level of sexual dimorphism in the song-control areas of the brain in both the Common Canary (*Serinus canaria*) and Zebra Finch. This highly influential study was the first of an astonishing 24 papers focussed on the neurobiology of singing in the Zebra Finch to have been published, to date, in the two most influential scientific journals (*Nature* and *Science*), indicating the fundamental scientific importance of this work (see Table 2). Although similar neurological work is also conducted on other species, such as the Song Sparrow (*Melospiza melodia*), Common Starling (*Sturnus vulgaris*) and Common Canary, the Zebra Finch is the easiest of these species to hold and breed in captivity. Furthermore, the Zebra Finch provides a very useful contrast with these other species owing to several key features (Brainard and Doupe 2002). Firstly, the fixed and definable period for song learning allows complex questions to be asked concerning the process of learned communication. Second, the relatively simple structure of the song, compared with other species, allows the song to be easily analysed and compared to the putative tutor, even by automated means (Tchernichovski *et al*. 2000). The fundamental role the Zebra Finch has played in the study of song learning and production is reviewed by Hauber *et al*. (2010). By the late 1970s the Zebra Finch was a very well-established model system for the study of neuroscience and throughout the 1980s and 1990s the number of studies of Zebra Finches classified as neuroscience well outnumbered all other research areas combined (Fig. 2). Indeed, of the 10 most cited Zebra Finch papers, seven are in the area of neuroscience. In their review, in this issue of *Emu*, London and Clayton (2010) deal specifically with the most recent generation of studies in this important area of work, and summarise specifically the input that studies of gene expression have had on the neurobiology of song.

Over the past three decades, most of the non-neuroscience studies focussed on the Zebra Finch have been studies of animal behaviour. Such studies have concentrated on several areas, including signalling and communication, reproductive biology, sexual selection and parental care. Particularly important

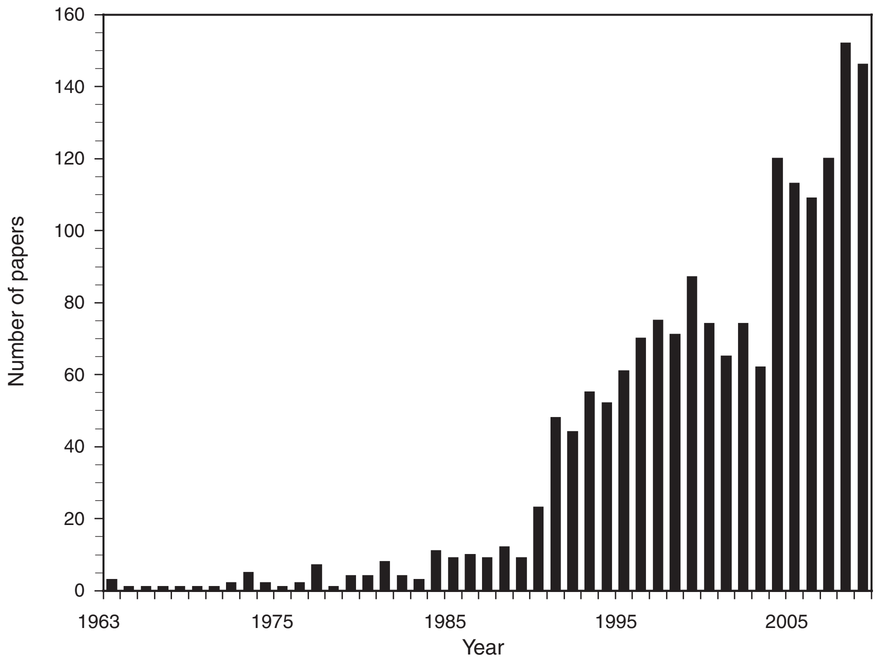


**Fig. 1.** The number of papers published annually from 1963 to the present returned by an ISI Web of Science search on 'zebra' and 'finch'.

contributions to the establishment of the Zebra Finch as a very useful and well-worked model system in animal behaviour were made independently by Nancy Burley in the USA and Tim Birkhead in the UK.

In the early 1980s Nancy Burley, a behavioural ecologist, was working on sexual selection in the domestic Zebra Finch and made several key findings, all of which subsequently became key areas of study within the broader field. Most importantly, Burley realised that the colour bands that researchers typically put on the legs of birds to identify individuals altered both the survival and mating prospects of males in a non-random way (Burley *et al*. 1982). Specifically, red bands made males more attractive to females and green bands made them less attractive. Burley believed that by manipulating just the bands that males wore (a very straightforward experiment to conduct), a researcher could create unattractive and attractive males and examine questions relating to female investment with respect to partner quality, and apparently not confounded by male quality. In the first such experiment, Burley (1981) provided intriguing evidence suggesting that females adjusted the sex of their broods in response to the attractiveness of their partner, a finding that was way ahead of its time and largely neglected until much later studies of other species, in which manipulations of natural traits demonstrated the same patterns (e.g. Sheldon *et al*. 1999; Pryke and Griffith 2009). The second experiment Burley conducted showed that females adjusted the level of reproductive investment in their offspring (measured by an estimate of parental care) in relation to the manipulation of colour bands, with females investing more when paired with red-banded males (Burley 1988). This finding prompted Burley to propose the differential allocation hypothesis, a model that has found support in several taxa (reviewed in Sheldon 2000) and is a very important component of our current understanding of sexual selection. Although it now appears that the manipulations of bands can affect the behaviour and physiology of males directly, and not just their appearance (Cuthill *et al*. 1997; Pariser *et al*. 2010), there is no doubt that the technique has continued to play a very important role in the development of other fields within the study of sexual selection, such as the more recent interest in maternal effects, and is perhaps the most-replicated experimental method in behavioural ecology (reviewed in this issue, Griffith and Buchanan 2010).

In the early 1980s, Tim Birkhead identified the domesticated Zebra Finch as an ideal model system to understand the mechanisms of fertilisation and sperm competition in birds, and he and his team have worked on the species continuously to date, providing a degree of insight into this area that is unparalleled in any avian system (reviewed in this issue, Birkhead 2010). The interest in sperm competition, a post-copulatory process in which the sperm of multiple males that have inseminated a female compete over the fertilisation of her eggs, naturally led Birkhead and his colleagues to broaden their work to embrace other areas of sexual selection. This group has continued to make other important contributions using the Zebra Finch, in areas such as condition-dependent sexual signalling and immunity (e.g. Birkhead *et al*. 1998).

The study of sexual selection increased through the 1990s, following Andersson's (1994) classic review, and the availability of new quantitative tools, such as molecular markers, spectrometers and methods for digital acoustic analytical comparison of songs allowing the accurate determination of the relationship between phenotypic variation and reproductive success. Throughout the expansion of the field of sexual selection, the Zebra Finch has been widely used. The use of

**Table 2. Articles based on empirical work conducted on the Zebra Finch that have been published in *Nature* ($n=21$) and *Science* ($n=15$) between 1979 and 2010**

| Authors | Year | Title | Journal | Volume | Pages |
|---|---|---|---|---|---|
| Neurobiology and development of song | | | | | |
| Nottebohm and Arnold | 1976 | Sexual dimorphism in vocal control areas of the songbird brain. | *Science* | 194 | 211–213 |
| Arnold and Saltiel | 1979 | Sexual difference in pattern of hormone accumulation in the brain of a songbird. | *Science* | 205 | 702–705 |
| Gurney and Konishi | 1980 | Hormone-induced sexual differentiation of brain and behaviour in zebra finches. | *Science* | 208 | 1380–1383 |
| Konishi and Akutagawa | 1985 | Neuronal growth, atrophy and death in a sexually dimorphic song nucleus in the zebra finch brain. | *Nature* | 315 | 145–147 |
| Williams and Nottebohm | 1985 | Auditory responses in avian vocal motor neurons: a motor theory for song perception in birds. | *Science* | 229 | 279–282 |
| Nordeen and Nordeen | 1988 | Projection neurons within a vocal motor pathway are born during song learning in zebra finches. | *Nature* | 334 | 149–151 |
| Yu and Margoliash | 1996 | Temporal hierarchical control of singing in birds. | *Science* | 273 | 1871–1875 |
| Chew, Vicario and Nottebohm | 1996 | Quantal duration of auditory memories. | *Science* | 274 | 1909–1914 |
| Fee, Shraiman, Pesaran and Mitra | 1998 | The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. | *Nature* | 395 | 67–71 |
| Dave, Yu and Margoliash | 1998 | Behavioural state modulation of auditory activity in a vocal motor system. | *Science* | 282 | 2250–2254 |
| Leonardo and Konishi | 1999 | Decrystallization of adult birdsong by perturbation of auditory feedback. | *Nature* | 399 | 466–470 |
| Brainard and Doupe | 2000 | Interruption of a basal ganglia–forebrain circuit prevents plasticity of learned vocalizations. | *Nature* | 404 | 762–766 |
| Dave and Margoliash | 2000 | Song replay during sleep and computational rules for sensorimotor vocal learning. | *Science* | 290 | 812–816 |
| Vogel | 2000 | Neuroscience – Death triggers regrowth of zebra finch neurons. | *Science* | 287 | 1381–1381 |
| Tchernichovski, Mitra, Lints and Nottebohm | 2001 | Dynamics of the vocal imitation process: how a zebra finch learns its song. | *Science* | 291 | 2564–2569 |
| Hahnloser, Kozhevnikov and Fee | 2002 | An ultra-sparse code underlies the generation of neural sequences in a songbird. | *Nature* | 419 | 65–70 |
| Kao, Doupe and Brainard | 2005 | Contributions of an avian basal ganglia–forebrain circuit to real-time modulation of song. | *Nature* | 433 | 638–643 |
| Deregnaucourt, Mitra, Feher, Pytte and Tchernichovski | 2005 | How sleep affects the developmental learning of bird song. | *Nature* | 433 | 710–716 |
| Long and Fee | 2008 | Using temperature to analyse temporal dynamics in the songbird motor pathway. | *Nature* | 456 | 189–194 |
| Aronov, Andalman and Fee | 2008 | A specialised forebrain circuit for vocal babbling in the juvenile songbird. | *Science* | 320 | 630–634 |
| Shank and Margoliash | 2009 | Sleep and sensorimotor integration during early vocal learning in a songbird. | *Nature* | 458 | 73–76 |
| Keller and Hahnloser | 2009 | Neural processing of auditory feedback during vocal practice in a songbird. | *Nature* | 457 | 187–190 |
| Feher, Wang, Saar, Mitra and Tchernichovski | 2009 | *De novo* establishment of wild-type song culture in the zebra finch. | *Nature* | 459 | 564–568 |
| Goodson, Schrock, Klatt, Kabelik and Kingsbury | 2009 | Mesotocin and nonapeptide receptors promote estrildid flocking behaviour. | *Science* | 325 | 862–866 |
| Ecology of song | | | | | |
| Miller | 1979 | Long-term recognition of father's song by female zebra finches. | *Nature* | 280 | 389–391 |
| Vignal, Mathevon and Mottin | 2004 | Audience drives male songbird response to partner's voice. | *Nature* | 430 | 448–451 |
| Sperm competition | | | | | |
| Birkhead, Pellatt and Hunter | 1988 | Extra-pair copulation and sperm competition in the zebra finch. | *Nature* | 334 | 60–62 |
| Birkhead, Fletcher, Pellatt and Staples | 1995 | Ejaculate quality and the success of extra-pair copulations in the zebra finch. | *Nature* | 377 | 422–423 |
| Birkhead, Pellatt, Brekke, Yeates and Castillo-Juarez | 2005 | Genetic effects on sperm design in the zebra finch. | *Nature* | 434 | 383–387 |

**Table 2.** (*continued*)

| Authors | Year | Title | Journal | Volume | Pages |
|---|---|---|---|---|---|
| Sexual selection | | | | | |
| Burley | 1982 | Reputed band attractiveness and sex manipulation in zebra finches. | *Science* | 215 | 423–424 |
| Swaddle and Cuthill | 1994 | Preference for symmetrical males by female zebra finches. | *Nature* | 367 | 165–166 |
| Bennett, Cuthill, Partridge and Maier | 1996 | Ultraviolet vision and mate choice in zebra finches. | *Nature* | 380 | 433–435 |
| Gil, Graves, Hazon and Wells | 1999 | Male attractiveness and differential testosterone investment in zebra finch eggs. | *Science* | 286 | 126–128 |
| Royle, Hartley and Parker | 2002 | Sexual conflict reduces offspring fitness in zebra finches. | *Nature* | 416 | 733–736 |
| Blount, Metcalfe, Birkhead and Surai | 2003 | Carotenoid modulation of immune function and sexual attractiveness in zebra finches. | *Science* | 300 | 125–127 |
| Optimal foraging | | | | | |
| Lemon | 1991 | Fitness consequences of foraging behaviour in the zebra finch. | *Nature* | 352 | 153–155 |

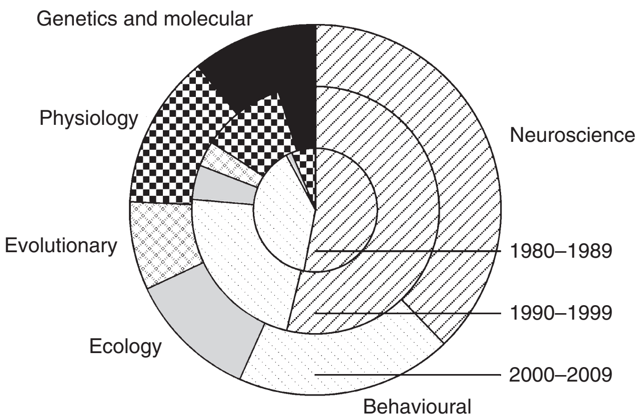


**Fig. 2.** The relative proportion of papers on Zebra Finches addressing different subject areas as classified on ISI Web of Science across the past three decades.

captive Finches has provided an opportunity to conduct imaginative manipulations and controlled observations that would not be possible with the classic wild ornithological models that researchers have worked on, such as the *Ficedula* flycatchers (European Pied Flycatcher (*Ficedula hypoleuca*) and Collared Flycatcher (*F. albicollis*)), the Great Tit and Blue Tit (*Cyanistes caeruleus*). Although studies in the wild of these other species have made a significant impact in their own right (see Table 1), the Zebra Finch has made a disproportinate contribution to this area of research, resulting in a total of nine papers in this field in *Nature* and *Science* (Table 2).

The different, and often more powerful, insights provided by studies of the Zebra Finch, compared to other avian model systems have resulted from the ability to conduct experiments that are not possible in free-living birds. For example, one of the key issues in the theory of sexual selection for a socially monogamous species is that mate-choice will affect reproductive success. In captive Zebra Finches, it has been possible to manipulate and study in detail the behaviour and cognitive processes underlying decisions that individuals make about alternative potential mates (reviewed in this issue, Healy *et al*. 2010), to an extent that is not logistically possible in wild birds. Furthermore, the ultimate experiment, in this area, is to manipulate the partner that an individual mates with, by randomly or deliberately allocating particular individuals to a breeding cage, thus constraining their ability to choose a partner. Although this is an almost standard procedure in many Zebra Finch studies, this extreme manipulation is probably impossible to achieve in the field in even the most amenable of the wild passerine model systems. The Zebra Finch, as such an amenable captive model, will probably always be utilised to address questions that are too difficult to investigate experimentally in free-living wild birds.

An additional bonus of the Zebra Finch is the remarkably short time in which it reaches sexual maturity (~70 days; Zann 1996). Certainly, all of the other passerine model species will not breed until they are ~1 year old. The rapid sexual maturation of the Zebra Finch has several benefits that have contributed to its use as a model system. Typically in evolutionary biology we are interested in the transmission of traits from one generation to the next. With a potentially shorter generation time in the laboratory, the Zebra Finch has been an excellent subject for studies of quantitative genetics, and is, arguably, still to reach its full potential in this area of research (reviewed in this issue, Tschirren and Postma 2010). The potentially high reproductive rate of Zebra Finches has also proved very useful in those studies that require large numbers of sacrificed birds, because these are fairly easy to produce and populations can be maintained effectively and efficiently within individual institutions, considerations that must have helped in the adoption of the species as the predominant avian model system for neurology. A new and growing field using this amenable model is the field of avian cognition. Although the traditional avian models in this area are pigeons (Columbiformes) or corvids (Corvidae), the Zebra Finch has shown it can be easily trained for simple tasks to test its cognitive abilities (reviewed in this issue, Healy *et al*. 2010).

This year, 2010, has seen the publication of the Zebra Finch genome (Warren *et al*. 2010), the result of an enormous investment in resources from the northern hemisphere, lobbied for and led by a team of neurologists based in the USA. The

Zebra Finch genome is only the second avian genome to be described after that of the Domestic Chicken (*Gallus gallus*). As well as being indicative of the importance of the Zebra Finch to the scientific community, this milestone will undoubtedly set the stage for a tremendous upsurge in the focus on this species, and open up new opportunities for neurologists, geneticists and evolutionary biologists alike (reviewed in this issue, Balakrishnan *et al*. 2010). It is interesting to see the dramatic increase in genetic and molecular studies over the past two decades (Fig. 2) and it would not be surprising to see that area of research involving Zebra Finches surpass all others in the next decade.

It is a great shame that Richard Zann is not alive to witness the publication of the Zebra Finch genome and the recognition of the importance of the bird to which he devoted his professional life, over some 34 years. One of the things that set Richard apart from many of those in the scientific world is that he revelled in sharing his chosen study organism with a wide community. Richard would have no doubt been delighted to have witnessed the publication of the Zebra Finch genome and the new opportunities that would have arisen and that would have encouraged others to take an interest in a bird he simply wanted to understand better. The importance of the Zebra Finch today as a model species owes a lot to Richard's professional generosity. Directly, he opened up his study system and field sites to several of those who have played a key role in the study of the species. Tim Birkhead, Nancy Burley, Nicky Clayton were all welcomed to join Richard in the field, where they gathered important data and developed a better understanding of the bird that they were studying in their far-off laboratories. Birkhead (2010) describes the personal generosity and enthusiasm that Richard afforded him and which was instrumental in accommodating his desires to begin his studies of the Zebra Finch. Over 20 years later, Richard's generosity remained the same, despite his frustrations at the lack of research support that he was able to attract. He continued to provide new generations of scientists with the benefit of his wealth of experience, access to his field sites, provision of blood samples, and even birds from his collection, and also encouraged and trained visiting students. We believe that Richard viewed all of those who wanted to work on the Zebra Finch not as competitors (as so many would), but as colleagues or members of an extended team, enthusiastic at the potential understanding that would be brought to bear by additional people coming at the species with new techniques and perspectives. This generous attitude and his obvious enthusiasm for everything that related to the Zebra Finch was widely recognised (Clarke 2009). This no doubt was instrumental in the establishment of the species as the model system it is today, and stands in marked contrast to many of the other potential model systems around the world that have been more closely guarded by one or two research groups.

The second major service that Richard provided to the wider community was his book, '*The Zebra Finch: A Synthesis of Field and Laboratory Studies*' (Zann 1996). This wonderful contribution provides the background that someone new to the species would need before embarking on their research. Through a combination of a fairly exhaustive literature review and the insight provided by his own years of direct work on the Zebra Finch in the field, the book paints an excellent picture of how the Zebra Finch operates in its natural environment. Even though there were many things that Richard did not formally study in the wild, the book contains many little hidden gems that demonstrate that he had a very deep understanding of the species. Our own recent work, on wild birds, using new methods that were not available to Richard is providing data that really only validates ideas and phenomena that Richard anticipated many years ago. To us, as to many others around the world, Richard's book is a treasure trove that is always within arm's reach of the desk.

The collection of reviews in this issue of *Emu* were designed to focus particular attention on the work on the Zebra Finch that has been published since Zann's (1996) book. The work reviewed, covering diverse areas of biology, along with the accelerating number of publications (Fig. 1), illustrates the prominence of the Zebra Finch in the biological sciences at the beginning of the 21st century. We feel that the position of the Zebra Finch is unlikely to change significantly in the foreseeable future. It is unlikely that another avian species will be found that provides access to so many interesting biological questions, and be as easy to maintain, breed and study in laboratory conditions, and that alone assures a vibrant future for this Finch. In addition, the publication of the genome and the rapidly advancing molecular technology paves the way for a generation of studies investigating gene expression across a variety of contexts – a very exciting prospect that promises further cutting edge, high-impact studies on this species.

There is no doubt that, as in the past, many of the exciting future studies focussing on the Zebra Finch will come from those working in the northern hemisphere. It is interesting that of the 36 papers focussed on the Zebra Finch and published in the two highest impact journals (*Nature* and *Science*) between 1976 and 2009, not one of the studies has an author based in Australia. It is intriguing to wonder how many of the authors of these papers – and the many hundreds published in other journals – have seen and experienced the species in the wild. We agree completely with Zann's view that it is important to understand how the species operates in its natural environment to aid in the interpretation of research conducted in the laboratory. The extent to which this is true will obviously vary across disciplines. For example, studies focussed on the mechanisms of song learning or the passage of sperm through the female reproductive tract will probably gain relatively little additional insight from studies of wild birds. However, studies focussed on areas such as parental care, sexual conflict and mate-choice will probably gain quite a lot from insights gained by a greater understanding of the selective pressures faced by wild birds. The recent establishment of nest-box breeding populations of free-living Zebra Finch in the semi-arid region of New South Wales (Griffith *et al*. 2008), will increase the ease with which wild populations can be studied, in the tradition of some of the classic model passerine species of the northern hemisphere.

Recent work has found that wild Zebra Finches differ from domesticated stocks in traits such as mate-choice behaviour (Rutstein *et al*. 2007), female infidelity (Griffith *et al*. 2010), body size (Tschirren *et al*. 2009), and the level of synchrony in hatching of broods (Mainwaring *et al*. 2010). These differences may relate to ecological differences in wild and captive conditions, selection on domestic stock or the significant genetic divergence seen in the domestic stocks from the wild types (Forstmeier *et al*. 2007). Reassuringly, some of these studies have also shown that the life-history trade-offs underlying the development of traits are fundamentally the same in captive and wild populations (Tschirren *et al*. 2009; Mainwaring *et al*. 2010).

Richard Zann published over 30 peer-reviewed publications concerning the biology of the Zebra Finch, six of which appeared in *Emu – Austral Ornithology* (Burley *et al*. 1989; Clayton *et al*. 1991; Zann and Rossetto 1991; Zann 1994; Zann *et al*. 1995; Rozman *et al*. 2003). Although his publications were not particularly well cited, this is certainly in part a result of the fact that he also published one of the most used ornithological books on a vitally important avian model species. Richard's legacy to the ornithological community is a significant body of work documenting the basic biology of a unique species that has now become a classic model for several fields of avian biology, including avian neurobiology, genetics, behaviour and physiology. He will be remembered fondly by those who were fortunate enough to have worked with him, and his work will continue to inspire a new generation of scientists in a whole range of fields who may employ his main study species to wrestle with fundamentals of avian evolution.

We are grateful to all of the authors who have contributed their excellent reviews of the many aspects of Zebra Finch biology that have been the recent focus of so much intensive study. We are all indebted to the immeasurable contribution that Richard Zann made to the study of this special bird. Thanks largely to his efforts, today we do have a very solid understanding of 'how this bird works' and have been infected by his enthusiasm for the species and a drive to learn more.

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