



RESEARCH ARTICLE

THOUGHTS ON RECENT STUDIES ON ASYMMETRICAL INTROGRESSION VIA HYBRIDIZATION

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ABSTRACT

Gene flow from one population into another is facilitated by the migration of species resulting into genetic mix in the hybrids. The event of reproduction between different species is termed as hybridization which has been greatly reported in birds. The incorporation of species' genetic material into the gene pool of another via hybridization is called "genetic introgression" or simply "introgression." In the events where the genetic mix result in the exhibition of the characteristic of both parents is termed "symmetrical introgression" and when the characteristics of one parent is increasingly exhibited in the hybrids it is termed "asymmetrical introgression." Collating the recent studies on asymmetric introgression and presenting thoughts on the methods and interpretation from these studies is the main aim of this paper. Major findings include evidences for differential introgression, hybrid zones are semipermeable tension zones, absence of correlation evidence of mating advantage between manipulated males and natural males in nature, hindrance to introgression of song with the permission of asymmetrical introgression of plumage by male behavioural responses, environmental variables providing adequate explanation for variation in morphometric traits despite differences in distance between sites, lack of adverse effects of hybridization on survival and reproductive character in first generation hybrids, evidence for species collapse via hybridization and evidence for rivers not being a complete barrier to hybridization across taxon pairs. I recommend the incorporation of ecological niche of the species into the models considered for avian hybridization in addition to development of tools to incorporate climatic fluctuations into reconstructions of genetic diversification by evolutionary ornithologists.

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INTRODUCTION

The transfer of alleles from one population to another population is termed gene flow. This usually occurs due to migration of individuals from one population into another, which effects change in allele frequencies of the population and addition of genetic variants to the gene pool of the established population. When the strategies that support gene flow become sustainable it provides for effective combination of the two gene pools, thereby reducing the genetic differentiation between two populations. The outcome of this form of genetic mix is call hybrid and the geographic regions in which two genetically distinct taxa based on one or more heritable trait come into contact and interbreed resulting into genetic exchange is referred to as hybrid zones (Harrison 1990). It is theorized that several hybrid zones are semipermeable boundaries between genomes based on selective introgression within such zones. While *et al.* (2015) recognised hybridization as an essential driver for species diversification and adaptation.

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The occurrence of hybridization and backcrossing over several generations between two distinct taxa that results into the incorporation of alleles from one species into the gene pool of another species is considered as introgression. Backcrossing occurs when hybrids mate with one or both parents. Cases of interbreeding among hybrids have been reported (Coyne and Orr, 2004) which when may be so extensive that essentially all individuals become hybrids, leading to hybrid swarm or 'extinction through hybridization' (Taylor *et al.*, 2006). Introgression differs from simple hybridization as an effect of several generations of gene exchange and complex mixture of genes while simple hybridization is considered as an outcome of first generation of gene exchange with even mix of parental species. However, it is pertinent to mention that hybridization constitutes one of the vital mechanisms through which introgression can be effected in addition to backcrossing among many other possible factors and mechanisms. Successful hybridisation in which first-generation hybrids mate with parental species, producing backcrossed individuals often leads to the transfer of genetic material across species boundaries (Anderson 1949; Martinsen *et al.*, 2001; Kim *et al.*, 2008). The event of the backcrossed hybrids retain the full or

nearly full somatic complements of their parental species, we attribute that as symmetrical introgression. In this case we have the genes from the respective population being equally exchanged in both directions. On the other hand, when many of the backcrossed hybrids exhibit the full somatic complement of one parental species with little or none exhibition of the other parent, it is considered as asymmetrical introgression. This leads to greater manifestation of one or more traits from one species population in the population of another species in a more or less one direction.

Hypothesis of hybridization and introgression

It has been theorized that traits under positive selection introgress asymmetrically across a hybrid zone, with sexual selection considered as the potential driver (Baldassarre and Webster 2013). In their study they hypothesized that asymmetrical introgression may be facilitated by sexual selection on the condition of red males have a mating advantage over orange males (*ibid*). Some of the outstanding hypotheses on the occurrence and frequency of avian hybridization include those outline by Randler (2006) and summarized by Kleindorfer *et al.* (2014):

- A size-difference hypothesis of reduced hybridization in the presence of mechanical barriers to reproduction;
- A sexual selection hypothesis, with more hybridization in the absence of sexual dichromatism;
- Scarcity of conspecifics, which predicts hybridization is initiated by the rare species (Grant and Grant 1997);
- A paternal-care hypothesis, with more hybridization if females choose species that provide more paternal care; and
- A parapatric distribution hypothesis that predicts stronger female discrimination in sympatry with a reduction in hybridization in sympatric relative to parapatric species.
- Another interesting hypothesis on the occurrence and frequency of hybridization is that reviewed in Karvon and Seehausen (2012) which opined that parasite has the potential to mediate selection for hybrids. This is such that hybrid offspring possess immunological advantage achieved by genetic combination in defence against detrimental parasites coupled with reduced parasitic prevalence and/or susceptibility as reported by Tompkins *et al* (2006). Studies that supported this hypothesis include Rauch *et al.*, (2006) in sticklebacks, Tompkins *et al.*, (2006) in red-crowned parakeets, Wiley *et al.*, (2009) in collared and pied flycatchers, MacDougall-Shackleton *et al.*, (2005) in white-crowned sparrows, and in mice (Fritz 1999; Moulia 1999) in which the hybrid offspring had intermediate or reduced parasite prevalence and susceptibility (Karvonen and Seehausen 2012). On the other hand MacDougall-Shackleton *et al.*, (2002, 2005); Goldberg *et al.*, (2005) reported cases where hybrid showed lower viability in relation to disease. With the effects of environmental variables and geographic distance on sexual signals and morphometric traits, Baldassarre *et al* (2013) proposed two alternative hypotheses in continuation of the aforementioned hypotheses:
- That sexual signal and non-sexual morphometric traits are expected to correlate with environmental variables should

they have evolved via ecological selection;

- Alternatively, without taking environmental factors into consideration geographic distance should sufficiently explain the emergence of sexual signal so long as they are driven by sexual selection and genetic drift.

In the effort to explain the geographic patterns of trait divergence between subspecies, Baldassarre and colleagues (*ibid*) investigated the role of the Carpentarian Barrier and the plumage contact zone in divergence of traits as summarized in subsequent section in this paper.

Thoughts on the hypothesis

The debate on the role of hybridization in speciation and extinction still rages despite the wide acceptance of hybridization as being a common event. This is in addition to the question of whether hybrid offspring generally have lower fitness (Mallet 2007, 2008; Grant and Grant 2010). In the presence of compelling progress on hybridization studies, we are yet to accumulate sufficient examples of hybridization patterns under natural conditions with multiple sources of evidence on behavioural, molecular, and fitness measures platforms. The idea of separating geographic distance from environmental factors in explaining the emergence of sexual signals should such event be driven by sexual selection and genetic drift deserves a careful reconsideration as such discrimination may distort the explanatory strength of both factors. Two habitats could be relatively close and have very different environmental factors; greatly wide apart (several thousand km) and still have very similar environmental condition, coupled with high mobility of bird species and the contemporary effect of climate change which could force species to be displaced temporarily or permanently. Buying into the idea of sexual selection hypothesis, with more hybridization in the absence of sexual dichromatism needs to appreciate the fact plumage colour is just one out of very many other factors that may drive sexual selection such as morphological traits and multiple behavioural traits which in most cases are very difficult to control for in studies under natural conditions. The school of thought that scarcity of conspecifics predicts hybridization and hybridization is initiated by the rare species (Grant and Grant 1997) may force us to ask why several species go extinct in the midst of heterospecifics. Should this hypothesis be proved in nature, then it would contribute to our knowledge to attribute hybridization as a key factor in ecosystem stability based on species assemblages and/or composition.

Conditions that favour hybridization and introgression

The determinants of extent of introgression are fitness, genetic linkage status and reproductive isolation (Wu 2001; Morjan and Rieseberg 2004; Payseur 2010; Gompert *et al.*, 2013). With the abundance of genomic analyses, the semipermeable state of the hybrid zones has been demonstrated with highly variable introgression that allows only one directional recombination of the hybrids into the alternate genome. It has been theorized that traits under positive selection stand the chance to introgress across hybrid zone asymmetrically having sexual selection as its main driver (Baldassarre and Webster

2013). At an intermediate stage of divergence, reproductive isolation has been predicted to be asymmetrical within a hybridizing taxa as reported in golden- and white-collared manakins (*Manacus* spp.) where the asymmetrical introgression of a secondary sexual trait, male throat plumage colour (Parsons *et al* 1993; Brumfield *et al* 2001) has been driven by sexual selection (Stein and Uy 2006; Uy and Stein 2007). The prediction of Red Queen hypothesis is that genetic variance keeps organism just one step ahead of an evolutionary dead-end, in a never-ending cycle of competition (Bell 1982). Based on this premise introgression via hybridization can offer novel genetic solutions in a host-parasite cycle (Loker 2012). It is a common opinion to attribute reduced fitness to hybrid offspring (Templeton 1986) as reported across different organisms (Holtsford 1996; Hatfield and Schluter 1999; Fenster and Galloway 2000; Goldberg *et al.*, 2005). When subjected to different social and ecological parameters, Grant *et al.*, (2003) reported variation in fitness patterns between two interbreeding *Geospiza* ground finch species. Kleindorfer *et al.* (2014) argued that the novel genetic combinations through hybridization may confer an immunological advantage (Huber *et al.*, 2010) or parasite resistance (Loker 2012). In addition to the previously mentioned conditions such advantage over parasites by hybrids provide favourable conditions for hybridization and/or introgression.

Conditions that may impede hybridization

Sexual selection on multiple signals has the potential for differential rates of signal introgression across hybrid zones on the condition that some signals contribute to reproductive isolation but others facilitate gene flow (Greig *et al.*, 2015). Thus sexual selection may constitute a strong evolutionary force with the capability to restrict gene flow between diverging taxa upon secondary contact (Servedio *et al.*, 2007; Questiau 1999; Irwin and Price 1999). Other factors that may possibly impede hybridization include competition among males, behavioural responses to multiple traits (Greig *et al* 2015), rate of changes in environmental conditions (Kleindorfer and Webster, 2013) and physical barriers (Hayes and Seawall 2004) and host compatibility with parasite (Medeiros *et al.*, 2013).

Evidences of hybridization and its effects

Red-backed fairy-wren (*Malurus melanocephalus*) being at an early stage of speciation coupled with the exhibition of variation in both sexual and non-sexual traits, provides a great deal of opportunity as an ideal species in which to explore the events of hybridization and introgression. *Malurus melanocephalus cruentatus* and *Malurus melanocephalus melanocephalus* are recognized as subspecies based on variation in plumage color and tail length (Rowley and Russell, 1997) with *M. m. cruentatus* subspecies being crimson-backed, shorter-tailed and occurs in northern Australia while *M. m. melanocephalus* subspecies in eastern Australia is orange-backed and longer-tailed. The contact zone of the subspecies is attributed to occur in northern Queensland based on the presence of males with intermediate values for tail length and plumage colour (*ibid*). On the basis that Red-backed fairy-wren subspecies differ primarily in a sexual signal (red versus

orange male back plumage colour) used in mate choice, Baldassarre and Webster (2013) tested that asymmetrical introgression may be facilitated by sexual selection if red males have a mating advantage over orange males with correlational data and a plumage manipulation experiment where they reddened the back plumage of a subset of orange males to mimic males of the red subspecies. They found no correlational evidence of a mating advantage to naturally redder males in which reddened males were ascendant to similar amount of within-pair young and lost paternity at the same rate as orange males, but they sired significantly more extra-pair young, leading to substantially higher total reproductive success. They provided evidence for sexual selection via extra-pair mating driving the asymmetrical introgression of plumage colour in this system based on sensory bias for the red plumage signal.

Divergence in traits in several species exhibiting geographic variation in sexual signals may lead to speciation driven by differences in ecological conditions in situations where the environment constrains signal production or transmission. On the premise that sexual signals may diverge stochastically through sexual selection or genetic drift, with little environmental influence, Baldassarre *et al* (2013) proceeded on their studies on the red-backed fairy-wren (*Malurus melanocephalus*) investigating the role of ecological variation in driving divergence of sexual traits. They tested for associations between these traits and a number of environmental variables using generalized dissimilarity models. They showed that environmental variation explained morphometric traits; geographic distance explained variation in plumage colour, with the interpretation of lack of coincidence of plumage colour divergence in male with boundary between genetic lineages. They concluded that sexual plumage signal of one the red-backed fairy-wren subspecies has introgressed into the genetic background of the other, thereby adding to our knowledge of different mechanisms through which the signal evolution could exist within a species in addition to geographic patterns of signal variation that may occur under secondary contact. Still on the red-backed fairy-wren, using playbacks, mounts, and a reciprocal experimental design, Greig *et al* (2015) tested the hypothesis that male responses to song and plumage has the potential to explain patterns of differential signal introgression, in which plumage colour introgression occurs without the introgression of song trait. They reported symmetric discrimination of subspecies' songs at a long range in both subspecies and equal aggression at a close range in plumage and songs of both subspecies, with the suggestion of hindrance of song introgression by the behavioural responses of the males while allowing for plumage asymmetrical introgression. The present study provided insight for the consideration of behavioural responses as an important factor in signal evolution under secondary contact and the effect of responses to multiple signals on differential signal introgression. Furthermore on the red-backed fairy-wren studies, Baldassarre *et al.*, (2014) carried out genomic (genotyping-by-sequencing) and morphological (plumage reflectance spectrophotometry) analyses on the hybrid zone of the subspecies. Their findings included high variable pattern of differential introgression with a significant shift of the plumage cline into the genomic background of the orange subspecies

with the consideration of the hybrid zone as a semipermeable tension zone. The conclusion of the study was that sexual selection drives asymmetrical introgression of red plumage alleles across the hybrid zone, which is consistent with previous evidence that extra-pair mating drives asymmetrical introgression of a sexual trait. They opined the potential of sexual selection in eroding taxonomic boundaries with the promotion of gene flow mostly for species at an intermediate stage of divergence. In continuation of evidences of sexual selection constituting an important driver of asymmetric introgression, While *et al* (2015) showed how divergence in male secondary sexual characters between two lineages of the common wall lizard (*Podarcis muralis*) creates room for strong one-sided male competitive ability and mating success, resulting in asymmetric hybridisation under secondary contact. This they did by using an experimental approach to predict the direction of introgression based on the influences of natural and sexual selections. In addition to assessing the reproductive compatibility crosses between lineage, the survival and viability of the F1 hybrids, they also tested the validity of their predicted direction of introgression by employing mitochondrial DNA, microsatellites and phenotypic data across one native and two introduced locations of hybridisation. They found lack of adverse effect of hybridization on survival and fitness considered to be an indication of asymmetric introgression on the basis of displacement of sexual characters of the sub-dominant lineage. The present study provided an illustration on the mechanism behind the direction and extent of introgression being driven by divergence in sexually selected traits, which tends to shape the observed genetic and phenotypic diversity in space and time.

Rheindt and Edwards (2011) recommended contrasting phylogenetic signal or divergence among different population and taxa instead of among different loci as a more promising avenue for diagnosing introgression; with the hope of having this approach tested in birds due to the availability of genome-wide data in ornithology. This dream seemed to come through by the study of Weir *et al* (2015) coupled with assessing the occurrence of hybridization between taxa at geographic contact in headwater regions of the Rio Teles Pires and Rio Xingu as proposed by Haffer (1997) to be a suture zone where geographic contact was likely between many pairs of avian species or subspecies. Weir and colleagues focused on taxon pairs believed by Haffer (1992) to come into geographic contact in the stated regions: *Xiphorhynchus elegans* / *X. spixii*, *Rhegmatorhina hoffmannsi* / *R. gymnops*, *Willisornis poecilinotus* / *W. vidua*, and *Lepidothrix nattereri* / *L. iris*), as well as subspecies pairs in *Dendrocincla fuliginosa*, *G. spirurus*, and the species pair *Hypocnemis ochrogyna* / *H. striata*, which they found across the transect. They showed that seven taxon pairs that are distinct across Amazonian river come into geographic contact and hybridize in headwater regions based on large dataset of single nucleotide polymorphisms. They reported that all taxon studied possessed hybrids with low numbers of loci in which alleles were determined to be inherited from both parental species, suggestive of been backcrossed with the parents. This was considered as an indication of gene flow between parental populations. The authors concluded on incomplete

reproductive isolation irrespective of the taxon pairs are very old. They also challenged the generality that River-barrier drives *in situ* speciation in the Amazon.

Consequences of hybridization

Introgression through species hybridization can amount to reduction of individual fitness, collapse of biological species (Kleindorfer 2013), adaptive hybridization and hybrid speciation and novel evolutionary trajectories in changing environments (Grant and Grant 1996a, 1996b, 2002, 2010; Fritz 1999; Rieseberg *et al.*, 2003; Mallet 2007). Recent evidences of introgression being an integral part of evolutionary process address the early notion of introgression being an obstacle to understanding evolutionary processes (Rheindt and Edwards 2011). One of the major studies providing clear evidence on the consequence of hybridization is that of Kleindorfer *et al* (2013) on the collapse of Darwin's Tree Finches via hybridization. They tested the patterns of hybridization in three sympatric tree finch species (small tree finch *Camarhynchus parvulus*, medium tree finch *Camarhynchus pauper*, and large tree finch: *Camarhynchus psittacula*) on Floreana Island, Galapagos Archipelago based on genetic analysis of microsatellite data. They successfully showed two genetic populations and one hybrid cluster in two seasons (2005 and 2010) with hybrids coming from the small morphology population and large morphology population respectively considered to be genetically distinct. The trend of events they reported were that they found three morphological clusters in the historical tree finch sample between 1852–1906; two or three morphological clusters in 2005 with 19% hybridization and in 2010 they found two morphological clusters with increase in hybridization up to 41%. They concluded on the point that the rare and endangered species drove the observed hybridization suggestive of large rare females pairing with small common males and recognized that their results were in support of predictions by Grant and Grant (1996b) and Randler (2006).

Thoughts on the methods

Across the studies reported in this paper, little or no attention was paid to the specific differences in habitat characteristics among areas of sympatry, allopatry, contact zones and/or hybrid zones. Also, no mention of taking into account the differences in abundance of the resources directly dependent on by the species studied such as feed, nesting materials, potential competitors and presence of predators. These have great deal of effect to the overall dispersal/distribution and behaviour of the species. It will be of great interest to pay closer attention on the ecology of the species studied for hybridization purposes under natural condition on a species specific level instead of a general approach.

Conclusion

Having made some progress in our understanding of the roles and mechanisms behind hybridization, we still have more issues to take care of across taxa. It is pertinent to mention that our present methods of analysis and reconstruction of phylogeny may still stand the chance of advanced development

and growth as our knowledge of evolutionary processes increase. We also need to strive to see through the minds of the species as our current algorithms may be relatively too primitive in comparison to those used by the species studied which shapes their behaviours both in mate recognition and/or selection to otherwise.

REFERENCES

- Anderson, E. 1949. Introgressive Hybridization. Wiley, New York.
- Baldassarre, D. T. and Webster, M. S. 2013. Experimental evidence that extra-pair mating drives asymmetrical introgression of a sexual trait. *Proceedings of Royal Society B*, 280, 20132175. <http://dx.doi.org/10.1098/rspb.2013.2175>.
- Baldassarre, D. T., Thomassen, H. A., Karubian, J. and Webster, M. S. 2013. The role of ecological variation in driving divergence of sexual and nonsexual traits in the red-backed fairy-wren (*Malurus melanocephalus*). *BMC Evolutionary Biology*, 13:75.
- Bell, G. 1982. The masterpiece of nature: the evolution and genetics of sexuality. University of California Press, Berkeley.
- Brumfield, R. T., Jernigan, R. W., McDonald, D. B. and Braun, M. J. 2001. Evolutionary implications of divergent clines in an avian (*Manacus*: Aves. hybrid zone. *Evolution*, 55, 2070–2087.
- Coyne, J. A., Orr, H. 2004. Speciation. Sunderland (MA): Sinauer Associates, Inc. Fenster, C. B., and J. F. Galloway. 2000. Inbreeding and outbreeding depression in natural populations of *Chamaecrista fasciculata* (Fabaceae). *Conservation Biology*, 14, 1406–1412.
- Fritz, R. S. 1999. Resistance of hybrid plants to herbivores: genes, environment or both? *Ecology*, 80, 382–391.
- Goldberg, T. L., Grant, E. C., Inendino, K. R., Kassler, T. W., Claussen, J. E. and Philipp, D.P. 2005. Increased infectious disease susceptibility resulting from outbreeding depression. *Conservation Biology*, 19, 455–462.
- Gompert, Z., Parchman, T. L. and Buerkle, C. A. 2013. Genomics of isolation in hybrids. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367,439–450.
- Grant, B. R., and Grant, P. R. 1996a. High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology*, 77, 500–509.
- Grant, B. R., and Grant, P. R. 1996b. Speciation and hybridization in island birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 765–772.
- Grant, B. R., and Grant, P. R. 1997. Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences of the USA*, 94, 7768–7775.
- Grant, B. R., and Grant, P. R. 2002. Hybridization of bird species. *Science*, 256:193–197.
- Grant, P. R., and Grant, B. R. 2010. Conspecific versus heterospecific gene exchange between populations of Darwin's finches. *Philosophical Transactions of the Royal Society of London, Series B*, 365,1065–1076.
- Grant, P. R., Grant, B. R., Keller, L. F., Markert, J. A. and Petren, K. 2003. Inbreeding and interbreeding in Darwin's Finches. *Evolution*, 57, 2911–2916.
- Greig, E. I., Baldassarre, D. T., and Webster, M. S. 2015. Differential rates of phenotypic introgression are associated with male behavioral responses to multiple signals. *Evolution*, 69(10), 2602–2612.
- Haffer, J. 1997. Contact zones between birds of southern Amazonia. *Ornithological Monographs* 48, 281–305.
- Harrison, R. G. 1990. Hybrid zones: windows on evolutionary process. In: Futuyma D, Antonovics J, editors. Oxford surveys in evolutionary biology. Vol. 7. New York: Oxford University Press. pp. 69–128.
- Hatfield, T. and Schluter, D. 1999. Ecological speciation in sticklebacks: environment-dependent hybrid fitness. *Evolution*, 53, 866–873.
- Holtsford, T. P. 1996. Variation in inbreeding depression among families and populations of *Clarkia tembloriensis* (Onagraceae). *Heredity*, 76, 83–91.
- Huber, S.K., Owen, J.P., Koop, J.A., King, M.O., Grant, P.R., Grant, B.R. and Clayton, D.H., (2010). Ecoimmunity in Darwin's finches: invasive parasites trigger acquired immunity in the medium ground finch (*Geospiza fortis*). *PLoS One*, 5(1), p.e8605.
- Irwin D. E., and Price T. D. 1999. Sexual imprinting, learning and speciation. *Heredity*, 82, 347–354, doi:10.1038/sj.hdy.6885270.
- Karvonen, A., and Seehausen, O. 2012. The role of parasitism in adaptive radiations—when might parasites promote and when might they constrain ecological speciation? *International Journal of Ecology*, 2012.
- Kim, M., Cui, M.L., Cubas, P., Gillies, A., Lee, K., Chapman, M.A., Abbott, R.J. and Coen, E., 2008. Regulatory genes control a key morphological and ecological trait transferred between species. *Science*, 322(5904), 1116–1119.
- Kleindorfer, S., O'Connor, J. A., Dudaniec, R. Y., Myers, S. A., Robertson, J and Sulloway, F. J. 2014. Species Collapse via Hybridization in Darwin's Tree Finches. *The American Naturalist*, 183(3), 325–341.
- Loker, E. S. 2012. Macroevolutionary immunology: a role for immunity in the diversification of animal life. *Frontiers in Immunology*, 3, 25.
- MacDougall-Shackleton, E. A., Derryberry, E. P. and Hahn, T. 2002. Non-local male mountain white-crowned sparrows have lower paternity and higher parasite load than males signing local dialect. *Behavioural Ecology*, 13, 682–689.
- MacDougall-Shackleton, E. A., Derryberry, E. P., Foufopoulos, J., Dobson, A. P., and Hahn, T. P. 2005. Parasite-mediated heterozygote advantage in an outbred songbird population. *Biology Letters*, 1, 105–107.
- Mallet, J. 2007. Hybrid speciation. *Nature*, 446, 279–283.
- Mallet, J. 2008. Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 2971–2986.
- Martinsen, G. D., Whitham, T. G., Turek, R. J., and Keim, P. 2001. Hybrid populations selectively filter gene introgression between species. *Evolution*, 55, 1325–1335.
- Medeiros, M. C. I., Hamer, G. L., and Ricklefs, R.E. 2013. Host compatibility rather than
- Morjan, C. L., and Rieseberg, L. H. 2004. How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Molecular Ecology*, 13, 1341–1356.

- Moulija, C. 1999. Parasitism of plant and animal hybrids: are facts and fates the same? *Ecology* 80, 392–406.
- Parsons, T. J., Olson, S. L. and Braun, M. J. 1993. Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. *Science*, 260, 1643–1646.
- Payseur, B. A. 2010. Using differential introgression in hybrid zones to identify genomic regions involved in speciation. *Molecular Ecological Resources*, 10, 806–820.
- Questiau S. 1999. How can sexual selection promote population divergence? *Ethology Ecology and Evolution*, 11, 313–324, doi:10.1080/08927014.1999.9522816.
- Randler, C. 2006. Behavioural and ecological correlates of natural hybridization in birds. *Ibis* 148, 459–467.
- Rauch, G., M. Kalbe, and Reusch, T. B. H. 2006. Relative importance of MHC and genetic background for parasite load in a field experiment. *Evolutionary Ecology Research*, 8, 373–386.
- Rheindt, F. E., and Edwards, S. V. 2011. Genetic introgression: an integral but neglected component of speciation in birds. *The Auk*, 128(4), 620–632.
- Rowley, I., and Russell, E. R. 1997. Fairy-wrens and grasswrens: Maluridae. New York: Oxford University Press.
- Servedio, M. R., Saether, S. A., and Saetre, G. P. 2007. Reinforcement and learning. *Evolutionary Ecology*, 23, 109–123. doi:10.1007/s10682-007-9188-2).
- Stein, A. C., and Uy, J. A. C. 2006. Unidirectional introgression of a sexually selected trait across an avian hybrid zone: a role for female choice? *Evolution*, 60, 1476–1485, doi:10.1554/05-575.1
- Taylor, E. B., Boughman, J. W., Groenboom, M., Sniatynski, M., Schluter, D. and Gow, J. L. (2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*. species pair. *Molecular Ecology*, 15, 343–355.
- Templeton, A. R. 1986. Coadaptation and outbreeding depression. pp 105–116 in M. E. Soulé, ed. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, MA.
- Tompkins, D. M., Mitchell, R. A. and Bryant, D. M. 2006. Hybridization increases measures of innate and cell-mediated immunity in an endangered bird species. *Journal of Animal Ecology*, 75, 559–564.
- Uy, J. A. C., and Stein, A. C. 2007. Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone. *Journal of Evolutionary Biology*, 20, 1847–1858, doi:10.1111/j.1420-9101.2007.01378.x.
- vector–host–encounter rate determines the host range of avian Plasmodium parasites. *Proceedings of the Royal Society B*, 280, 20122947. <http://dx.doi.org/10.1098/rspb.2012.2947>
- While, G. M., Michaelides, S., Heathcote, R. J. P., MacGregor, H. E. A., Zajac, N., Beninde, J., Carazo, P., Lanuza, G. P., Sacchi, R., Zuffi, M. A. L. Horvathova, T., Fresnillo, B., Schulte, U., Veith, M., Hochkirch, A., and Uller T. 2015. Sexual selection drives asymmetric introgression in wall lizards. *Ecology Letters*, 18, 1366–1375, doi: 10.1111/ele.12531.
- Wiley, C., Qvarnström, A., and Gustafsson, L. 2009. Effects of hybridization on the immunity of collared Ficedula albicollis and pied flycatchers F. hypoleuca, and their infection by haemosporidians. *Journal of Avian Biology*, 40, 352–357.
- Wu C-I. 2001. The genic view of the process of speciation. *Journal of Evolutionary Biology*, 14, 851–865.
