Avian introgression patterns are consistent with Haldane’s Rule

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Abstract

According to Haldane’s Rule, the heterogametic sex will show the greatest fitness reduction in a hybrid cross. In birds, where sex is determined by a ZW-system, female hybrids are expected to experience lower fitness compared to male hybrids. This pattern has indeed been observed in several bird groups, but it is unknown whether the generality of Haldane’s Rule also extends to the molecular level. First, given the lower fitness of female hybrids, we can expect maternally inherited loci (i.e. mitochondrial and W-linked loci) to show lower introgression rates than biparentally inherited loci (i.e. autosomal loci) in females. Second, the faster evolution of Z-linked loci compared to autosomal loci and the hemizygosity of the Z-chromosome in females might speed up the accumulation of incompatible alleles on this sex chromosome, resulting in lower introgression rates for Z-linked loci than for autosomal loci. I tested these expectations by conducting a literature review which focused on studies that directly quantified introgression rates for autosomal, sex-linked and mitochondrial loci. Although most studies reported introgression rates in line with Haldane’s Rule, it remains important to validate these genetic patterns with estimates of hybrid fitness and supporting field observations to rule out alternative explanations. Genomic data provide exciting opportunities to obtain a more fine-grained picture of introgression rates across the genome, which can consequently be linked to ecological and behavioral observations, potentially leading to novel insights into the genetic mechanisms underpinning Haldane’s Rule.

Keywords: cline theory, coalescent modelling, genetic incompatibilities, genomics, hybridization, sex-biased dispersal
Introduction

Haldane (1922) observed that ‘When in the F1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is always the heterozygous [i.e. heterogametic] sex.’ This observation applies to many groups of animals, regardless of whether the male or the female is the heterogametic sex (Orr, 1997; Schilthuizen et al., 2011). In birds, where the sex is determined by a ZW-system, females are the heterogametic sex and hybrid females are thus expected to show greater fitness reductions compared to hybrid males. This expectation has been confirmed for birds in general (Price & Bouvier, 2002) and for specific bird groups, such as ducks (Tubaro & Lijtmaer, 2002), wildfowl (Arrieta et al., 2013), and pigeons and doves (Lijtmaer et al., 2003). Despite the generality of Haldane’s Rule, the underlying mechanisms are still a matter of debate (Delph & Demuth, 2016).

An often invoked explanation for Haldane’s Rule relies on dominance theory, which is based on the Dobzhansky-Muller incompatibility model (Presgraves, 2010; Wu & Ting, 2004). This theory states that hybrid sterility and unviability arise because of interactions between two or more genetic loci that have developed incompatible alleles during an allopatric phase. If these alleles are recessive and located on the Z-chromosome, their effect is expected to be more pronounced in female birds. This expectation is based on the fact that females lack another Z-chromosome that could carry a dominant version of the incompatible allele, which would nullify the negative effect of the recessive allele. The same reasoning applies to organisms with XY-chromosomes, where males carry the hemizygous Y-chromosome.

Another explanation for Haldane’s Rule can be traced back to work on Drosophila where substitutions on the X-chromosome have a larger impact on hybrid sterility and unviability than autosomal substitutions (Coyne & Orr, 1989). This ‘Large X-effect’ might be due to faster evolution of X-linked genes compared to genes on the autosomes. Accelerated evolution on the X-chromosome has been reported in several Drosophila species and certain mammals, but the overall evidence is mixed (Meisel & Connallon, 2013). In birds, several studies have reported faster evolution of genes on the Z-chromosome (Mank et al., 2007; Wang et al., 2014), which has mainly been attributed to strong genetic drift due to its lower effective population size compared to autosomes and the accelerated fixation of non-dominant beneficial alleles which are exposed to selection on the hemizygous sex-chromosome (Hayes et al., 2020; Mank et al., 2010; Wright et al., 2015). In some bird species, the direct effects of selection have been invoked to explain faster sequence
divergence on the Z-chromosome (Hogner et al., 2012; Lavretsky et al., 2015). Particularly, a study on *Luscinia* nightingales suggested that strong postcopulatory sexual selection on males (with ZZ-chromosomes) might lead to lower levels of genetic diversity on the Z-chromosome. The consequent lower effective population size of the Z-chromosome will then render it more susceptible to random processes, such as genetic drift (Janoušek et al., 2018). In addition, the Z-chromosome experiences less recombination compared to autosomes, which could contribute to the accumulation of incompatible alleles on this sex-chromosome due to the divergence of non-recombining sections (Butlin, 2005; Wright et al., 2016). It is thus likely that multiple independent evolutionary processes can explain the ‘Faster Z-effect’ in birds.

The initial observations of Haldane (1922) and the possible explanations for these patterns (e.g., dominance theory, Faster Z-effect) lead to several expected patterns on a molecular level, specifically with regard to the introgression rates of different genetic loci. First, because female bird hybrids are generally less fit than male hybrids, we can expect that maternally inherited loci (i.e. mitochondrial DNA and W-linked loci) will show lower levels of introgression compared to biparentally inherited loci. However, it is important to keep in mind that reduced introgression of maternally inherited loci can also be due to other processes, such as the stronger effect of drift (because of the smaller effective population size of mtDNA and W-linked loci compared to nuclear loci), the lack of recombination, or sex-specific differences in behavior or physiology (Ballard & Whitlock, 2004; Evans et al., 2021; Patten et al., 2015). Therefore, it is crucial to also provide estimates of hybrid fitness before attributing lower introgression rates of maternally inherited loci to reduced fitness of female hybrids.

Second, the faster evolution of Z-linked loci compared to autosomal loci might speed up the accumulation of incompatible alleles on this chromosome. Moreover, if genes involved in premating and postzygotic isolation become physically linked on the Z-chromosome, they can facilitate the evolution of reproductive isolation. This situation has been suggested for *Ficedula* flycatchers where genes for low hybrid fitness and female preference seem to be located on the Z-chromosome (Backström et al., 2010; Saetre et al., 2003). The potential pivotal role of the Z-chromosome in reproductive isolation might thus result in lower introgression rates of Z-linked loci compared to autosomal loci (Irwin, 2018). To investigate if (1) introgression rates of maternally inherited loci are lower compared to biparentally
inherited loci due to reduced fitness of female hybrids, and if (2) introgression patterns of Z-linked loci are consistent with dominance theory as an explanation for Haldane’s Rule, I conducted a literature review in which I focused on papers that quantified and compared introgression rates for autosomal, sex-linked or mitochondrial loci.

**Ninety percent of avian studies adhere to Haldane’s Rule**

The literature search was done in three stages (Figure 1). First, I performed an extensive search on Web of Science™, using several broad keywords. The resulting set of 511 papers was subsequently scanned based on title and abstract to limit the number of studies with potentially useful information with regard to introgression rates and Haldane’s Rule. The remaining 185 studies were examined in more detail to extract data on introgression rates of autosomal, sex-linked or mitochondrial loci. I applied a strict filter by only considering studies that provided direct estimates of introgression rates, using at least one of the following methods: coalescent modelling, cline analyses, or calculation of introgression from population genetic summary statistics. This search strategy uncovered 30 studies that directly compared introgression rates for autosomal, sex-linked or mitochondrial loci (Table 1, Figure 2), using coalescent modelling (14 studies, 47%), geographic and genomic cline analyses of hybrid zones (10 studies, 33%), and calculating migration rates from genetic differentiation (3 studies, 10%). The majority of these studies documented introgression patterns in line with Haldane’s Rule (Table 1, 28 out of 30 studies, 93%). Specifically, 21 out of 23 studies (91%) reported introgression patterns of maternally inherited loci in line with Haldane’s Rule and 11 out of 11 studies (100%) reported lower introgression rates of Z-linked loci compared to autosomal loci (Figure 2).

Most studies applied coalescent modelling to quantify introgression rates for different genomic markers. This approach allows researchers to calculate introgression rates between populations or species within the framework of an Isolation-with-Migration (IM) model. These models use a Bayesian Markov chain Monte Carlo (MCMC) method to estimate population size, migration rate and splitting time parameters (Hey & Nielsen, 2004). By running IM-models for different sets of genetic loci, it is possible to directly compare the resulting introgression rates for several genomic classes. For example, Carling and Brumfield (2008) used IM-models to estimate introgression rates between lazuli bunting (*Passerina amoena*) and indigo bunting (*P. cyanea*) for autosomal, Z-linked and mitochondrial loci. The results were in accordance with Haldane’s Rule, showing higher levels of introgression for
autosomal loci compared to Z-linked and mitochondrial ones. In general, most of the studies that applied coalescent modelling reported introgression patterns in line with Haldane’s Rule: six studies (out of 14, 43%) found higher introgression rates for autosomal loci compared to Z-linked loci, and eight studies (57%) estimated higher introgression rates for autosomal loci than for mitochondrial loci.

Ten studies relied on cline analyses to estimate introgression rates for different genomic classes. Cline analyses quantify the changes in allele frequencies occurring along a geographic transect of a hybrid zone. According to cline theory, there is a straightforward relationship between selection against hybrids and cline width, namely that stronger selection against introgression results in a narrower cline (Slatkin, 1973). Genomic loci with narrower clines might thus be more important in maintaining reproductive isolation between the hybridizing taxa than genomic loci with wider clines. With regard to Haldane’s Rule, it is expected that Z-linked and mitochondrial loci should exhibit narrower clines than autosomal loci. In total, seven studies (out of 10, 70%) reported narrower clines for mitochondrial loci compared to autosomal loci, and three studies (30%) found that clines for Z-linked loci were narrower than clines for autosomal loci.

Another approach to estimate introgression rates relies on calculating \( N_m \) from genetic differentiation statistics, where \( N_m \) is the product of the effective population size (\( N \)) and the rate of migration (\( m \)) among populations (Slatkin, 1985). In two out of three studies that applied this method, the introgression patterns followed the expectations from Haldane’s Rule. Bensch et al. (2002) found low mitochondrial introgression (\( N_m = 0.065 \)) and high nuclear introgression (\( N_m = 4.9 \)) between the common chiffchaff (\( Phylloscopus collybita \)) and the Iberian chiffchaff (\( P. brehmi \)). Similarly, introgression of nuclear loci (\( N_m = 1.1 \)) was higher compared to mitochondrial loci (\( N_m = 0.11 \)) for greater spotted eagle (\( Aquila clanga \)) and lesser spotted eagle (\( A. pomarina \)) (Helbig et al., 2005). However, \( N_m \) might be a less reliable proxy for introgression, because the calculation of this parameter depends on relative genetic differentiation, which can be influenced by other evolutionary processes.

Finally, three studies applied alternative methods to compare introgression rates between genomic classes. Using AFLP-markers, Secondi et al. (2006) assigned individuals of icterine warbler (\( Hippolais icterina \)) and melodious warbler (\( H. polyglotta \)) to different parental and hybrid classes. This assignment exercise revealed introgression of autosomal loci, but
indicated no exchange of mitochondrial loci. A similar approach in a hybrid zone between black-capped chickadee (Poecile atricapillus) and Carolina chickadee (P. carolinensis) revealed the same pattern: autosomal introgression, but no mitochondrial introgression (Davidson et al., 2013). A third study used data from whole genome sequencing to quantify introgression patterns between different Gallus species. Analyses based on D-statistics indicated lower introgression rates on the Z-chromosome compared to autosomal chromosomes (Lawal et al., 2020).

**Few studies directly estimate hybrid fitness**

The literature search revealed that most avian studies (90%) were in accordance with dominance theory as an explanation for Haldane’s Rule, confirming the generality of this pattern on the molecular level. However, just because a molecular pattern is in line with the expectations of Haldane’s Rule does not necessarily mean that reduced introgression of particular loci is due to the lower fitness of female hybrids. Other mechanisms, such as mate choice, local selection pressures or sex-biased dispersal, can account for these patterns (Petit & Excoffier, 2009). To confidently invoke Haldane’s Rule, one has to provide convincing evidence for reduced fitness of female hybrids (see for example, Neubauer et al., 2014). Across all studies that reported genetic patterns in accordance with Haldane’s Rule, only two studies explicitly referred to direct estimates of hybrid fitness (Table 1). Storchova et al. (2010) mentioned that captive crosses between thrush nightingale (Luscinia luscinia) and common nightingale (L. megarhynchos) yielded sterile females and fertile males (Stadie, 1991). Similarly, a study on a hybrid zone between saltmarsh sparrow (Ammodramus caudacutus) and Nelson’s sparrow (A. nelsoni) indicated that hybrid females had lower survival rates than hybrid males (Walsh et al., 2016). Hence, most studies reported genetic patterns in line with Haldane’s Rule, but did not confirm the underlying mechanism with additional data on hybrid fitness.

The lack of hybrid fitness estimates is not surprising as this parameter can be extremely difficult and cumbersome to measure in wild populations (Linnen & Hoekstra, 2009). Moreover, hybrid individuals might be rare (Taylor et al., 2012) or only occasionally observed in the field (Galla & Johnson, 2015). Some exceptions include study systems where researchers can rely on long-term population data to connect introgression rates with fitness parameters (Grant & Grant, 2016; Lamichhaney et al., 2020) or species that can be bred in captivity to quantify the fertility of male and female hybrids (Campagna et al., 2018; Lijtmaer
et al., 2003; Stadie, 1991). Given the difficulty of estimating hybrid fitness, some researchers might be tempted to turn to genomic data because methods to infer introgression and selection are constantly improving (Ottenburghs et al., 2017; Setter et al., 2020). However, solely relying on genomic data can potentially lead to wrong conclusions, which was nicely illustrated by a recent study on Darwin’s Finches. Genomic analyses of the medium ground finch (Geospiza fortis) and the cactus finch (G. scandens) pointed to reduced introgression on the Z-chromosome in comparison with autosomal loci. This pattern might be due to genetic incompatibilities on the Z-chromosome (which would support Haldane’s Rule), but detailed field observations showed that particular mating patterns – unrelated to female fertility – could explain the introgression rates (Lamichhaney et al., 2020). This example highlights the value of field observations and indicates the importance of combining different lines of evidence to determine whether Haldane’s Rule holds for a particular study system.

Exceptions to Haldane’s Rule: Sex-biased dispersal and ancient introgression

Only two studies reported introgression patterns that were not in line with Haldane’s Rule. Kulikova et al. (2004) found that hybridization between mallard (Anas platyrhynchos) and spot-billed duck (A. zonorhyncha) resulted in higher introgression rates for mitochondrial loci compared to autosomal loci. This pattern can be explained by asymmetrical mating patterns and sex-biased dispersal between these duck species. Male spot-billed ducks tend to disperse more than the philopatric female spot-billed ducks. Hence, male spot-billed ducks are more likely to come into contact with female mallards. Consequently, most hybridization events involved a male spot-billed duck and a female mallard. When the resulting hybrids return to the breeding grounds of spot-billed ducks, they carry the mallard mtDNA with them, leading to asymmetrical introgression of mtDNA from mallards into spot-billed ducks. In contrast, nuclear introgression is mediated by both males and females, so nuclear loci are not expected to reflect dispersal differences between the sexes. In this case, the introgression rates for nuclear loci were lower than for mitochondrial ones, although still primarily from mallards into spot-billed ducks. This exception to Haldane’s Rule emphasizes the importance of understanding the life history and behavioral characteristics of the study system.

The second exception concerns high levels of mitochondrial introgression between black-browed tit (Aegithalos bonvaloti) and sooty tit (A. fuliginosus) compared to negligible exchange of autosomal and Z-linked loci (Wang et al., 2014). The authors attributed this pattern to ancient introgression of mtDNA, potentially in combination with a selective sweep.
or strong genetic drift. Ancient introgression events have been uncovered in several avian families (Fuchs et al., 2013; Ottenburghs et al., 2017; Zhang et al., 2021), sometimes even involving extinct lineages (Ottenburghs, 2020; Zhang et al., 2019). In addition, mtDNA is known to easily cross species boundaries and quickly spread throughout a population (Funk & Omland, 2003; Toews & Brelsford, 2012). The fixation of a mitochondrial variant can often be explained by genetic drift as the effective population size of mtDNA is only one quarter of that of nuclear DNA (Ballard & Whitlock, 2004). In some cases, the introgressed mtDNA might confer an adaptive advantage on the receiving species, speeding up the fixation process (Morales et al., 2017). Regardless of the underlying mechanism, ancient introgression of mtDNA can lead to introgression patterns that deviate from Haldane’s Rule.

**Haldane’s Rule in the genomic era**

Despite the increasing availability of genomic data for birds, only one study used a genomic approach to directly estimate introgression rates (Lawal et al., 2020). The lack of genomic studies in this literature review can be explained by (1) my strict search strategy and (2) the focus of recent genomic studies on finding loci involved in reproductive isolation instead of estimating introgression rates. First, my literature search only included studies that directly quantified introgression rates, using approaches such as coalescent modelling and cline analyses. Most genomic studies indirectly inferred introgression by comparing levels of genetic divergence between different genomic regions. For example, Stryjewski & Sorenson (2017) suggested autosomal introgression in *Lonchura* munias based on a limited number of divergent autosomal regions, while mitochondrial introgression was deemed less likely based on the observation of distinct mitochondrial haplotypes. Although these patterns are consistent with Haldane’s Rule, they could also be explained by the higher mutation rates in mtDNA (Ballard & Whitlock, 2004) or selective sweeps on autosomal loci (Hejase et al., 2020). In addition, methodological issues in assembling sex-chromosomes from genomic data – which often have lower coverage – might result in biased estimates of genetic differentiation and consequent inferences of introgression rates (Okuno et al., 2021). Based on these theoretical and methodological uncertainties, I decided to omit studies that infer introgression patterns from genetic divergence, resulting in the removal of several genomic studies from the literature search.

A second explanation for the lack of genomic studies concerns the recent focus in speciation genomics on detecting barrier loci that might contribute to reproductive isolation (Campbell et al., 2018; Ravinet et al., 2017). The comparison of genomes between closely related species has revealed a heterogenous genomic landscape in which genetic differentiation is
often distributed in particular genomic regions (Wolf & Ellegren, 2017). These ‘genomic islands of differentiation’ might contain loci involved in reproductive isolation, shielding them from the homogenizing effects of introgression (Ravinet et al., 2017; Turner et al., 2005). However, other evolutionary processes, such as linked selection, can also explain the formation of genomic islands (Battey, 2019; Rettelbach et al., 2019). Consequently, recent research efforts have been mainly aimed at understanding the evolutionary forces underlying this heterogenous genomic landscape (Bourgeois et al., 2020; Ottenburghs et al., 2020; Sendell-Price et al., 2021; Stryjewski & Sorenson, 2017), rather than directly estimating introgression rates for particular genomic regions (but see Schield et al., 2021). In addition, most genomic studies that did quantify introgression rates between hybridizing species provided a genome-wide estimate instead of comparing genomic classes (Ottenburghs et al., 2020; Pulido-Santacruz et al., 2019; Sadanandan et al., 2020). Future genomic studies could focus more on relating introgression rates of certain genomic regions to particular fitness components, potentially providing more insights into the genetic mechanisms underlying Haldane’s Rule.

Finally, no study included W-linked loci in the analyses. The W-chromosome is notoriously difficult to sequence due to its haploid nature and high repeat content (Tomaszkiewicz et al., 2017). However, the development of new sequencing technologies for non-model organisms will allow researchers to explore the evolutionary history of this sex-chromosome (Rogers et al., 2021; Xu et al., 2020) and its connection to Haldane’s Rule. For example, a recent study reported an excess of endogenous retroviruses (ERVs) on the W-chromosome, which could contribute to genetic incompatibilities between species due to mismatches in ERV-repressor mechanisms in hybrids (Peona et al., 2021). Quantifying introgression patterns of W-linked loci provides exciting avenues for future research.

These knowledge gaps – estimating local introgression rates across the genome and studying the W-chromosome – can be addressed as genomic resources and methods to quantify introgression are constantly improving (Bravo et al., 2021; Hibbins & Hahn, 2021). A more fine-grained picture of introgression rates across the genome will lead to important insights into the evolutionary processes and genomic features that determine whether introgressed loci will be retained or removed from the population (Moran et al., 2020; Runemark et al., 2019). Linking these introgression patterns to fitness estimates and field observations might results in novel insights on the mechanistic basis of Haldane’s Rule.
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Data Availability
All the data associated with this paper can be found in Table 1.
References

Arrieta, R. S., Lijtmaer, D. A., & Tubaro, P. L. (2013). Evolution of postzygotic reproductive isolation in galliform birds: Analysis of first and second hybrid generations and backcrosses. *Biological Journal of the Linnean Society, 110*(3), 528–542. https://doi.org/10.1111/bij.12153

Backström, N., Palkopoulou, E., Qvarnstrom, A., & Ellegren, H. (2010). No evidence for Z-chromosome rearrangements between the pied flycatcher and the collared flycatcher as judged by gene-based comparative genetic maps. *Molecular Ecology, 19*(16), 3394–3405. https://doi.org/10.1111/j.1365-294X.2010.04742.x

Backström, N., & Väli, U. (2011). Sex− and species−biased gene flow in a spotted eagle hybrid zone. *BMC Evolutionary Biology, 11*(1), 100. https://doi.org/10.1186/1471-2148-11-100

Ballard, J. W. O., & Whitlock, M. C. (2004). The incomplete natural history of mitochondria. *Molecular Ecology, 13*(4), 729–744. https://doi.org/10.1046/j.0962-1083.2003.01455.x

Battey, C. J. (2019). Evidence of linked selection on the z chromosome of hybridizing hummingbirds. *Evolution, evo.13888*. https://doi.org/10.1111/evo.13888

Bensch, S., Helbig, A. J., Salomon, M., & Seibold, I. (2002). Amplified fragment length polymorphism analysis identifies hybrids between two subspecies of warblers. *Molecular Ecology, 11*(3), 473–481. https://doi.org/10.1046/j.0962-1083.2001.01455.x

Bourgeois, Y. X. C., Bertrand, J. A. M., Delahaie, B., Holota, H., Thébaud, C., & Milá, B. (2020). Differential divergence in autosomes and sex chromosomes is associated with intra–island diversification at a very small spatial scale in a songbird lineage. *Molecular Ecology, 29*(6), 1137–1153. https://doi.org/10.1111/mec.15396

Bravo, G. A., Schmitt, C. J., & Edwards, S. V. (2021). What Have We Learned from the First 500 Avian Genomes? *https://Doi.Org/10.1146/Annurev-Ecolsys-012121-085928*, 52(1), 611–639. https://doi.org/10.1146/ANNUREV-ECOLSYS-012121-085928

Brumfield, R. T., Jernigan, R. W., McDonald, D. B., & Braun, M. J. (2001). Evolutionary implications of divergent clines in an avian (Manacus : Aves) hybrid zone. *Evolution, 55*(10), 2070–2087. https://doi.org/10.1111/j.0014-3820.2001.tb01322.x
Butlin, R. (2005). Recombination and speciation. *Molecular Ecology, 14*(9), 2621–2635. https://doi.org/10.1111/j.1365-294X.2005.02617.x

Campagna, L., Rodriguez, P., & Mazzulla, J. C. (2018). Transgressive phenotypes and evidence of weak postzygotic isolation in F1 hybrids between closely related capuchino seedeaters. *PLOS ONE, 13*(6), e0199113. https://doi.org/10.1371/journal.pone.0199113

Campbell, C. R., Poelstra, J. W., & Yoder, A. D. (2018). What is Speciation Genomics? The roles of ecology, gene flow, and genomic architecture in the formation of species. *Biological Journal of the Linnean Society, 124*(4), 561–583.

Carling, M. D., & Brumfield, R. T. (2008). Haldane’s Rule in an Avian System: Using Cline Theory and Divergence Population Genetics to Test for Differential Introgression of Mitochondrial, Autosomal, and Sex-Linked Loci across the Passerina Bunting Hybrid Zone. *Evolution, 62*(10), 2600–2615. https://doi.org/10.1111/j.1558-5646.2008.00477.x

Carling, M. D., Lovette, I. J., & Brumfield, R. T. (2010). Historical Divergence and Gene Flow: Coalescent Analyses of Mitochondrial, Autosomal and Sex-Linked Loci in Passerina Buntings. *Evolution, 64*(6), 1762–1772. https://doi.org/10.1111/j.1558-5646.2010.00954.x

Cheviron, Z. A., & Brumfield, R. T. (2009). Migration-Selection Balance and Local Adaptation of Mitochondrial Haplotypes in Rufous-Collared Sparrows (Zonotrichia Capensis) Along an Elevational Gradient. *Evolution, 63*(6), 1593–1605. https://doi.org/10.1111/j.1558-5646.2009.00644.x

Cicero, C. (2004). Barriers to sympatry between avian sibling species (Paridae: Baeolophus) in local secondary contact. *Evolution, 58*(7), 1573. https://doi.org/10.1554/03-272

Coyne, J. A., & Orr, H. A. (1989). Patterns of speciation in Drosophila. *Evolution, 43*(2), 362–381. https://doi.org/10.1111/j.1558-5646.1989.tb04233.x

Davidson, B. S., Sattler, G. D., Via, S., & Braun, M. J. (2013). Reproductive isolation and cryptic introgression in a sky island enclave of Appalachian birds. *Ecology and Evolution, 3*(8), 2485–2496. https://doi.org/10.1002/ece3.604

Delph, L. F., & Demuth, J. P. (2016). Haldane’s Rule: Genetic Bases and Their Empirical Support. *Journal of Heredity, 107*(5), 383–391. https://doi.org/10.1093/jhered/esw026
Evans, B. J., Peter, B. M., Melnick, D. J., Andayani, N., Supriatna, J., Zhu, J., & Tosi, A. J. (2021). Mitonuclear interactions and introgression genomics of macaque monkeys (Macaca) highlight the influence of behaviour on genome evolution. Proceedings of the Royal Society B, 288(1960). https://doi.org/10.1098/RSPB.2021.1756

Fuchs, J., Pons, J.-M., Liu, L., Ericson, P. G. P., Couloux, A., & Pasquet, E. (2013). A multi-locus phylogeny suggests an ancient hybridization event between Campephilus and melanerpine woodpeckers (Aves: Picidae). Molecular Phylogenetics and Evolution, 67(3), 578–588. https://doi.org/10.1016/J.YMPEV.2013.02.014

Funk, D. J., & Omland, K. E. (2003). Species-Level Paraphyly and Polyphyly: Frequency, Causes, and Consequences, with Insights from Animal Mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics, 34, 397–423. https://doi.org/10.1146/ANNUREV.ECOLSYS.34.011802.132421

Galla, S. J., & Johnson, J. A. (2015). Differential introgression and effective size of marker type influence phylogenetic inference of a recently divergent avian group (Phasianidae: Tympanuchus). Molecular Phylogenetics and Evolution, 84, 1–13. https://doi.org/10.1016/J.YMPEV.2014.12.012

Gowen, F. C., Maley, J. M., Cicero, C., Peterson, A., Faircloth, B. C., Warr, T., & McCormack, J. E. (2014). Speciation in Western Scrub-Jays, Haldane’s rule, and genetic clines in secondary contact. BMC Evolutionary Biology, 14(1), 135. https://doi.org/10.1186/1471-2148-14-135

Grant, P. R., & Grant, B. R. (2016). Introgressive hybridization and natural selection in Darwin’s finches. Biological Journal of the Linnean Society, 117(4), 812–822. https://doi.org/10.1111/BIJ.12702

Haldane, J. B. S. (1922). Sex ratio and unisexual sterility in hybrid animals. Journal of Genetics, 12, 101–109.

Hayes, K., Barton, H. J., Zeng, K., & Slotte, T. (2020). A Study of Faster-Z Evolution in the Great Tit (Parus major). Genome Biology and Evolution, 12(3), 210–222. https://doi.org/10.1093/GBE/EVAA044

Hejase, H. A., Salman-Minkov, A., Campagna, L., Hubisz, M. J., Lovette, I. J., Gronau, I., & Siepel, A. (2020). Genomic islands of differentiation in a rapid avian radiation have
been driven by recent selective sweeps. *Proceedings of the National Academy of Sciences*, 202015987. https://doi.org/10.1073/pnas.2015987117

Helbig, A., Seibold, I., Kocum, A., Liebers, D., Irwin, J., Bergmanis, U., Meyburg, B., Scheller, U., Stubbe, W., & Bensch, S. (2005). Genetic differentiation and hybridization between greater and lesser spotted eagles (Accipitriformes : Aquila clanga, A-pomarina). *Journal of Ornithology, 146*(3), 226–234.

Hermansen, J., Saether, S., Elgvin, T., Borge, T., Hjelle, E., & Saetre, G. (2011). Hybrid speciation in sparrows I: phenotypic intermediacy, genetic admixture and barriers to gene flow. *Molecular Ecology, 20*(18), 3812–3822. https://doi.org/10.1111/j.1365-294X.2011.05183.x

Hey, J., & Nielsen, R. (2004). Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of Drosophila pseudoobscura and D. persimilis. *Genetics, 167*(2), 747–760. https://doi.org/10.1534/genetics.103.024182

Hibbins, M. S., & Hahn, M. W. (2021). Phylogenomic approaches to detecting and characterizing introgression. *Genetics*. https://doi.org/10.1093/GENETICS/IYAB173

Hogner, S., Saether, S. A., Borge, T., Bruvik, T., Johnsen, A., & Saetre, G.-P. (2012). Increased divergence but reduced variation on the Z chromosome relative to autosomes in Ficedula flycatchers: differential introgression or the faster-Z effect? *Ecology and Evolution, 2*(2), 379–396. https://doi.org/10.1002/ece3.92

Irwin, D. E. (2018). Sex chromosomes and speciation in birds and other ZW systems. *Molecular Ecology, 27*(19), 3831–3851. http://doi.wiley.com/10.1111/mec.14537

Jacobsen, F., & Omland, K. E. (2012). Extensive introgressive hybridization within the northern oriole group (Genus Icterus) revealed by three-species isolation with migration analysis. *Ecology and Evolution, 2*(10), 2413–2429. https://doi.org/10.1002/ece3.365

Janoušek, V., Fischerová, J., Mořkovský, L., Reif, J., Antczak, M., Albrecht, T., & Reifová, R. (2018). Postcopulatory sexual selection reduces Z-linked genetic variation and might contribute to the large Z effect in passerine birds. *Heredity, 1*. https://doi.org/10.1038/s41437-018-0161-3
Kingston, S. E., Jernigan, R. W., Fagan, W. F., Braun, D., & Braun, M. J. (2012). Genomic variation in cline shape across a hybrid zone. *Ecology and Evolution*, 2(11), 2737–2748. https://doi.org/10.1002/ece3.375

Kulikova, I., Zhuravlev, Y., & McCracken, K. (2004). Asymmetric hybridization and sex-biased gene flow between Eastern Spot-billed Ducks (Anas zonorhyncha) and Mallards (A-platyrhynchos) in the Russian Far Eas. *The Auk*, 121(3), 930–949.

Lamichhaney, S., Han, F., Webster, M. T., Grant, B. R., Grant, P. R., & Andersson, L. (2020). Female-biased gene flow between two species of Darwin’s finches. *Nature Ecology & Evolution*, 1–8. https://doi.org/10.1038/s41559-020-1183-9

Lavretsky, P., Dacosta, J., Hernandez-Banos, B., Engilis, A., Sorenson, M., & Peters, J. (2015). Speciation genomics and a role for the Z chromosome in the early stages of divergence between Mexican ducks and mallards. *Molecular Ecology*, 24(21), 5364–5378.

Lawal, R. A., Martin, S. H., Vanmechelen, K., Vereijken, A., Silva, P., Al-Atiyat, R. M., Aljumaah, R. S., Mwacharao, J. M., Wu, D.-D., Zhang, Y.-P., Hocking, P. M., Smith, J., Wragg, D., & Hanotte, O. (2020). The wild species genome ancestry of domestic chickens. *BMC Biology*, 18(1), 13. https://doi.org/10.1186/s12915-020-0738-1

Lijtmaer, D. A., Mahler, B., & Tubaro, P. L. (2003). Hybridization and postzygotic isolation patterns in pigeons and doves. *Evolution*, 57(6), 1411–1418.

Linnen, C. R., & Hoekstra, H. E. (2009). Measuring Natural Selection on Genotypes and Phenotypes in the Wild. *Cold Spring Harbor Symposia on Quantitative Biology*, 74, 155–168. https://doi.org/10.1101/SQB.2009.74.045

Mank, J. E., Nam, K., & Ellegren, H. (2010). Faster-Z Evolution Is Predominantly Due to Genetic Drift. *Molecular Biology and Evolution*, 27(3), 661–670. https://doi.org/10.1093/molbev/msp282

Mank, Judith E., Axelson, E., & Ellegren, H. (2007). Fast-X on the Z: Rapid evolution of sex-linked genes in birds. *Genome Research*, 17(5), 618–624. https://doi.org/10.1101/gr.6031907

Manthey, J. D., & Spellman, G. M. (2014). Increased differentiation and reduced gene flow
in sex chromosomes relative to autosomes between lineages of the brown creeper Certhia americana. *Journal of Avian Biology*, 45(2), 149–156. https://doi.org/10.1111/J.1600-048X.2013.00233.X

Martínez-Cruz, B., & Godoy, J. A. (2007). Genetic evidence for a recent divergence and subsequent gene flow between Spanish and Eastern imperial eagles. *BMC Evolutionary Biology* 2007 7:1, 7(1), 1–8. https://doi.org/10.1186/1471-2148-7-170

Meisel, R. P., & Connallon, T. (2013). The faster-X effect: Integrating theory and data. In *Trends in Genetics* (Vol. 29, Issue 9, pp. 537–544). Elsevier Current Trends. https://doi.org/10.1016/j.tig.2013.05.009

Miller, M. J., Lipshutz, S. E., Smith, N. G., & Bermingham, E. (2014). Genetic and phenotypic characterization of a hybrid zone between polyandrous Northern and Wattled Jacanas in Western Panama. *BMC Evolutionary Biology*. https://doi.org/10.1186/s12862-014-0227-7

Morales, H. E., Sunnucks, P., Joseph, L., & Pavlova, A. (2017). Perpendicular axes of differentiation generated by mitochondrial introgression. *Molecular Ecology*, 26(12), 3241–3255. https://doi.org/10.1111/mec.14114

Moran, B. M., Payne, C., Langdon, Q., Powell, D. L., Brandvain, Y., & Schumer, M. (2020). The genetic consequences of hybridization. *ELife*, 10, e69016. https://doi.org/10.7554/ELIFE.69016

Neubauer, G., Nowicki, P., & Zagalska-Neubauer, M. (2014). Haldane’s rule revisited: Do hybrid females have a shorter lifespan? Survival of hybrids in a recent contact zone between two large gull species. *Journal of Evolutionary Biology*. https://doi.org/10.1111/jeb.12404

Nwankwo, E. C., Mortega, K. G., Karageorgos, A., Ogolowa, B. O., Papagregoriou, G., Grether, G. F., Monadjem, A., & Kirschel, A. N. G. (2019). Rampant introgressive hybridization in Pogoniulus tinkerbirds (Piciformes: Lybiidae) despite millions of years of divergence. *Biological Journal of the Linnean Society*, 127(1), 125–142. https://doi.org/10.1093/biolinnean/blz018

Okuno, M., Mizushima, S., Kuroiwa, A., & Itoh, T. (2021). Analysis of Sex Chromosome Evolution in the Clade Palaeognathae from Phased Genome Assembly. *Genome Biology*
Orr, H. A. (1997). Haldane’s Rule. Annual Review of Ecology and Systematics, 28(1), 195–218. https://doi.org/10.1146/annurev.ecolsys.28.1.195

Ottenburghs, J. (2020). Ghost Introgression: Spooky Gene Flow in the Distant Past. BioEssays, 42(6), 2000012. https://doi.org/10.1002/bies.202000012

Ottenburghs, J., Honka, J., Müskens, G. J. D. M., & Ellegren, H. (2020). Recent introgression between Taiga Bean Goose and Tundra Bean Goose results in a largely homogeneous landscape of genetic differentiation. Heredity, 125(1–2), 73–84. https://doi.org/10.1038/s41437-020-0322-z

Ottenburghs, J., Kraus, R., van Hooft, P., van Wieren, S., Ydenberg, R., & Prins, H. (2017). Avian introgression in the genomic era. Avian Research, 8(1), 30.

Patten, M. M., Carioscia, S. A., & Linnen, C. R. (2015). Biased introgression of mitochondrial and nuclear genes: a comparison of diploid and haplodiploid systems. Molecular Ecology, 24(20), 5200–5210. https://doi.org/10.1111/MEC.13318

Peona, V., Palacios-Gimenez, O. M., Blommaert, J., Liu, J., Haryoko, T., Jønsson, K. A., Irestedt, M., Zhou, Q., Jern, P., & Suh, A. (2021). The avian W chromosome is a refugium for endogenous retroviruses with likely effects on female-biased mutational load and genetic incompatibilities. Philosophical Transactions of the Royal Society B, 376(1833), 20200186. https://doi.org/10.1098/RSTB.2020.0186

Peters, J. L., McCracken, K. G., Pruett, C. L., Rohwer, S., Drovetski, S. V., Zhuravlev, Y. N., Kulikova, I., Gibson, D. D., & Winker, K. (2012). A parapatric propensity for breeding precludes the completion of speciation in common teal (Anas crecca, sensu lato). Molecular Ecology. https://doi.org/10.1111/j.1365-294X.2012.05711.x

Petit, R. J., &Excoffier, L. (2009). Gene flow and species delimitation. Trends in Ecology and Evolution, 24(7), 386–393.

Presgraves, D. C. (2010). The molecular evolutionary basis of species formation. Nature Reviews Genetics, 11(3), 175–180.

Price, T., & Bouvier, M. (2002). The evolution of F1 postzygotic incompatibilities in birds. Evolution, 56(10), 2083–2089. https://doi.org/10.1111/j.0014-3820.2002.tb00133.x
Pulido- Santacruz, P., Aleixo, A., & Weir, J. T. (2019). Genomic data reveal a protracted window of introgression during the diversification of a Neotropical woodcreeper radiation. *Evolution*, evo.13902. https://doi.org/10.1111/evo.13902

Ravinet, M., Faria, R., Butlin, R. K., Galindo, J., Bierne, N., Rafajlović, M., Noor, M. A. F., Mehlig, B., & Westram, A. M. (2017). Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow. *Journal of Evolutionary Biology*, 30(8), 1450–1477.

Rettelbach, A., Nater, A., & Ellegren, H. (2019). How Linked Selection Shapes the Diversity Landscape in *Ficedula* Flycatchers. *Genetics*, 212(1), 277–285.

Rogers, T. F., Pizzari, T., & Wright, A. E. (2021). Multi-copy gene family evolution on the avian W chromosome. *Journal of Heredity*, 112(3), 250–259. https://doi.org/10.1093/jhered/esab016

Runemark, A., Vallejo-Marín, M., & Meier, J. I. (2019). Eukaryote hybrid genomes. *PLOS Genetics*, 15(11), e1008404. https://doi.org/10.1371/journal.pgen.1008404

Sadanandan, K. R., Low, G. W., Sridharan, S., Gwee, C. Y., Ng, E. Y. X., Yuda, P., Prawiradilaga, D. M., Lee, J. G. H., Tritto, A., & Rheindt, F. E. (2020). The conservation value of admixed phenotypes in a critically endangered species complex. *Scientific Reports*, 10(1), 15549. https://doi.org/10.1038/s41598-020-72428-2

Saetre, G.-P., Borge, T., Lindroos, K., Haavie, J., Sheldon, B. C., Primmer, C., & Syvänen, A.-C. (2003). Sex chromosome evolution and speciation in *Ficedula* flycatchers. *Proceedings. Biological Sciences*, 270(1510), 53–59. https://doi.org/10.1098/rspb.2002.2204

Sattler, G. D., & Braun, M. J. (2000). Morphometric variation as an indicator of genetic interactions between Black-capped and Carolina chickadees at a contact zone in the Appalachian mountains. *The Auk*, 117(2), 427–444. https://doi.org/10.1642/0004-8038(2000)117[0427:MVAAC0]2.0.CO;2

Schield, D. R., Scordato, E. S. C., Smith, C. C. R., Carter, J. K., Cherkaoui, S. I., Gombobaatar, S., Hajib, S., Hanane, S., Hund, A. K., Koyama, K., Liang, W., Liu, Y., Magri, N., Rubtsov, A., Sheta, B., Turbek, S. P., Wilkins, M. R., Yu, L., & Safran, R. J. (2021). Sex- linked genetic diversity and differentiation in a globally distributed avian...
species complex. *Molecular Ecology*, mec.15885. https://doi.org/10.1111/mec.15885

Schilthuizen, M., Giesbers, M. C. W. G., & Beukeboom, L. W. (2011). Haldane’s rule in the 21st century. In *Hereditity* (Vol. 107, Issue 2, pp. 95–102). Nature Publishing Group. https://doi.org/10.1038/hdy.2010.170

Secondi, J., Faivre, B., & Bensch, S. (2006). Spreading introgression in the wake of a moving contact zone. *Molecular Ecology*, 15(9), 2463–2475. https://doi.org/10.1111/j.1365-294X.2006.02948.x

Sendell-Price, A. T., Ruegg, K. C., Robertson, B. C., & Clegg, S. M. (2021). An island-hopping bird reveals how founder events shape genome-wide divergence. *Molecular Ecology*, mec.15898. https://doi.org/10.1111/mec.15898

Setter, D., Mousset, S., Cheng, X., Nielsen, R., DeGiorgio, M., & Hermisson, J. (2020). VolcanoFinder: Genomic scans for adaptive introgression. *PLoS Genetics*, 16(6), e1008867. https://doi.org/10.1371/journal.pgen.1008867

Slatkin, M. (1973). Gene flow and selection in a cline. *Genetics*, 75(4), 733–756.

Slatkin, M. (1985). Gene Flow in Natural Populations. *Annual Review of Ecology and Systematics*, 16(1), 393–430. https://doi.org/10.1146/annurev.es.16.110185.002141

Stadie, C. (1991). Erdsanger I: Nachtigall und Sprosser. *Europaische Vogelwelt*, 3, 130–189.

Storchová, R., Reif, J., & Nachman, M. W. (2010). Female Heterogamety and Speciation: Reduced Introgression of the Z Chromosome between Two Species of Nightingales. *Evolution*, 64(2), 456–471. https://doi.org/10.1111/j.1558-5646.2009.00841.x

Stryjewski, K. F., & Sorenson, M. D. (2017). Mosaic genome evolution in a recent and rapid avian radiation. *Nature Ecology & Evolution*, 1(12), 1912–1922. https://doi.org/10.1038/s41559-017-0364-7

Taylor, S. A., Anderson, D. J., & Friesen, V. L. (2013). Evidence for Asymmetrical Divergence-Gene Flow of Nuclear Loci, but Not Mitochondrial Loci, between Seabird Sister Species: Blue-Footed (Sula nebouxii) and Peruvian (S. variegata) Boobies. *PLoS ONE*, 8(4), e62256. https://doi.org/10.1371/journal.pone.0062256

Taylor, S. A., Anderson, D. J., Zavalaga and, C. B., & Friesen, V. L. (2012). Evidence for
strong assortative mating, limited gene flow, and strong differentiation across the blue-footed/Peruvian booby hybrid zone in northern Peru. Journal of Avian Biology, 43(4), 311–324. https://doi.org/10.1111/j.1600-048X.2012.05660.x

Taylor, S. A., White, T. A., Hochachka, W. M., Ferretti, V., Curry, R. L., & Lovette, I. (2014). Climate-Mediated Movement of an Avian Hybrid Zone. Current Biology, 24(6), 671–676. https://doi.org/10.1016/J.CUB.2014.01.069

Toews, D., & Brelsford, A. (2012). The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology, 21(16), 3907–3930. https://doi.org/10.1111/j.1365-294X.2012.05664.x

Tomaszkiewicz, M., Medvedev, P., & Makova, K. D. (2017). Y and W Chromosome Assemblies: Approaches and Discoveries. Trends in Genetics, 33(4), 266–282. https://doi.org/10.1016/J.TIG.2017.01.008

Tubaro, P. L., & Lijtmaer, D. A. (2002). Hybridization patterns and the evolution of reproductive isolation in ducks. Biological Journal of the Linnean Society, 77(2), 193–200. https://doi.org/10.1046/j.1095-8312.2002.00096.x

Turner, T. L., Hahn, M. W., & Nuzhdin, S. V. (2005). Genomic Islands of Speciation in Anopheles gambiae. PLoS Biology, 3(9), e285.

Van Els, P., Spellman, G. M., Smith, B. T., & Klicka, J. (2014). Extensive gene flow characterizes the phylogeography of a North American migrant bird: Black-headed Grosbeak (Pheucticus melanocephalus). Molecular Phylogenetics and Evolution, 78(1), 148–159. https://doi.org/10.1016/J.YMPEV.2014.04.028

Vázquez-Miranda, H., Griffin, J. A., Sheppard, J. M., Herman, J. M., Rojas-Soto, O., & Zink, R. M. (2017). Morphological and molecular evolution and their consequences for conservation and taxonomy in the Le Conte’s thrasher Toxostoma lecontei. Journal of Avian Biology, 48(7), 941–954. https://doi.org/10.1111/JAV.01057

Walsh, J., Shriver, W. G., Olsen, B. J., & Kovach, A. I. (2016). Differential introgression and the maintenance of species boundaries in an advanced generation avian hybrid zone. BMC Evolutionary Biology, 16(1), 65. https://doi.org/10.1186/s12862-016-0635-y

Wang, B., Ekblom, R., Bunikis, I., Siitari, H., & Höglund, J. (2014). Whole genome
sequencing of the black grouse (Tetrao tetrix): Reference guided assembly suggests faster-Z and MHC evolution. *BMC Genomics, 15*(1), 1–13. https://doi.org/10.1186/1471-2164-15-180

Wang, W., Dai, C., Alström, P., Zhang, C., Qu, Y., Li, S.-H., Yang, X., Zhao, N., Song, G., & Lei, F. (2014). Past hybridization between two East Asian long-tailed tits (Aegithalos bonvaloti and A. fuliginosus). *Frontiers in Zoology, 11*(1), 40. https://doi.org/10.1186/1742-9994-11-40

Wolf, J. B. W., & Ellegren, H. (2017). Making sense of genomic islands of differentiation in light of speciation. *Nature Reviews Genetics, 18*(2), 87–100.

Wright, A. E., Dean, R., Zimmer, F., & Mank, J. E. (2016). How to make a sex chromosome. *Nature Communications 2016 7*:1, 7(1), 1–8. https://doi.org/10.1038/ncomms12087

Wright, A. E., Harrison, P. W., Zimmer, F., Montgomery, S. H., Pointer, M. A., & Mank, J. E. (2015). Variation in promiscuity and sexual selection drives avian rate of Faster-Z evolution. *Molecular Ecology, 24*(6), 1218–1235. https://doi.org/10.1111/mec.13113

Wu, C.-I., & Ting, C.-T. (2004). Genes and speciation. *Nature Reviews Genetics, 5*(2), 114–122. https://doi.org/10.1038/nrg1269

Xu, L., Irestedt, M., & Zhou, Q. (2020). Sequence Transpositions Restore Genes on the Highly Degenerated W Chromosomes of Songbirds. *Genes 2020, Vol. 11, Page 1267*, 11(11), 1267. https://doi.org/10.3390/genes11111267

Zhang, D., Rheindt, F. E., She, H., Cheng, Y., Song, G., Jia, C., Qu, Y., Alström, P., & Lei, F. (2021). Most genomic loci misrepresent the phylogeny of an avian radiation because of ancient gene flow. *Systematic Biology*. https://doi.org/10.1093/sysbio/syab024

Zhang, D., Tang, L., Cheng, Y., Hao, Y., Xiong, Y., Song, G., Qu, Y., Rheindt, F. E., Alström, P., Jia, C., & Lei, F. (2019). ‘Ghost introgression’ as a cause of deep mitochondrial divergence in a bird species complex. *Molecular Biology and Evolution, 36*(11), 2375–2386. https://doi.org/10.1093/molbev/msz170
Figures and Tables

**Figure 1.** Overview of the search strategy and the number of studies in the literature review.

**Figure 2.** The literature review revealed that most studies reported introgression patterns in line with Haldane's Rule, with (a) higher introgression of autosomal loci compared to mtDNA, and (b) higher introgression of autosomal loci compared to Z-linked loci. The studies used a variety of methods to infer patterns of introgression.

**Table 1.** Overview of studies estimating introgression rates for different genomic classes.
Table 1. Overview of studies estimating introgression rates for different genomic classes.

| Species                        | Molecular Markers       | Introgression Pattern | Haldane’s Rule | Hybrid Fitness | Reference               |
|-------------------------------|-------------------------|-----------------------|----------------|---------------|-------------------------|
| *Nm Calculation*              |                         |                       |                |               |                         |
| *Phylloscopus collybita*       | mtDNA, microsatellites  | autosomal > mtDNA     | YES            | NO            | (Bensch et al., 2002)   |
| *Phylloscopus brehmii*         |                         |                       |                |               |                         |
| *Aquila clanga*               | mtDNA, AFLP             | autosomal > mtDNA     | YES            | NO            | (Helbig et al., 2005)   |
| *Aquila pomarina*             |                         |                       |                |               |                         |
| *Anas platyrhynchos*          | Set of loci             | mtDNA > autosomal     | NO             | NO            | (Kulikova et al., 2004) |
| *Anas zonorhyncha*            |                         |                       |                |               |                         |
| *Cline analyses*              |                         |                       |                |               |                         |
| *Manacus vitellinus*          | mtDNA, nDNA             | autosomal > mtDNA     | YES            | NO            | (Brumfield et al., 2001) |
| *Manacus candei*              |                         |                       |                |               |                         |
| *Pipilo maculatus*            | mtDNA, AFLP             | autosomal > mtDNA     | YES            | NO            | (Kingston et al., 2012) |
| *Pipilo ocai*                 |                         |                       |                |               |                         |
| *Poecile atricapillus*        | Set of loci             | autosomal > mtDNA     | YES            | NO            | (Sattler & Braun, 2000) |
| *Poecile atricapillus*        | GBS                     | autosomal > Z-linked   | YES            | NO            | (Taylor et al., 2014)   |
| *Aphelocoma californica*      | mtDNA, microsatellites  | autosomal > mtDNA     | YES            | NO            | (Gowen et al., 2014)    |
| (lineages)                    |                         |                       |                |               |                         |
Table 1. Continued

| Species                        | Type of Loci                  | Location of Loci              | Coalescent Analyses |
|-------------------------------|-------------------------------|-------------------------------|---------------------|
| Jacana spinosa                | Set of loci                   | autosomal > mtDNA             | YES                 |
| Jacana jacana                 |                               |                               | NO                  | (Miller et al., 2014) |
| Passer italiae                | SNPs                          | autosomal > mtDNA             | YES                 |
| Passer domesticus             |                               | autosomal > Z-linked          | NO                  | (Hermansen et al., 2011) |
| Passer hispaniolensis         |                               |                               |                     |                      |
| Ammodramus caudacutus         | Microsatellites, set of loci  | autosomal > mtDNA             | YES                 |
| Ammodramus nelsoni            |                               | autosomal > Z-linked          | YES                 | (Walsh et al., 2016)  |
| Pogoniulus chrysoconus extoni | mtDNA, microsatellites        | autosomal > mtDNA             | YES                 |
| Pogoniulus pusillus pusillus  |                               |                               | NO                  | (Nwankwo et al., 2019) |
| Baeolophus inornatus          | Set of loci                   | autosomal > mtDNA             | YES                 |
| Baeolophus ridgwayi           |                               |                               | NO                  | (Cicero, 2004)        |
| Coalescent analyses           |                               |                               |                     |                      |
| Aquila clanga                 | Set of loci                   | autosomal > Z-linked          | YES                 |
| Aquila pomarina               |                               |                               | NO                  | (Backström & Väli, 2011) |
| Passerina amoena              | Set of loci                   | autosomal > mtDNA             | YES                 |
| Passerina cyanea              |                               |                               | NO                  | (Carling et al., 2010) |
| Luscinia luscinia             | Set of loci                   | autosomal > Z-linked          | YES                 |
| Luscinia megarhynchos         |                               |                               | YES                 | (Storchová et al., 2010) |
| Species               | Set of loci | Locus relationship                  | YES | NO  | Reference                               |
|----------------------|-------------|-------------------------------------|-----|-----|-----------------------------------------|
| *Tympanychus* species | Set of loci | autosomal > Z-linked                 | YES | NO  | (Galla & Johnson, 2015)                |
| Certhia americana    | Set of loci | autosomal > Z-linked                 | YES | NO  | (Manthey & Spellman, 2014)             |
| *Certhia americana*  | Set of loci | autosomal > Z-linked                 | YES | NO  | (Manthey & Spellman, 2014)             |
| Aegithalos bonvaloti  | Set of loci | mtDNA > autosomal                   | NO  | NO  | (Wang et al., 2014)                    |
| Aegithalos fuliginosus| Set of loci | mtDNA > autosomal                   | NO  | NO  | (Wang et al., 2014)                    |
| Pheucticus melanocephalus subspecies | Set of loci | autosomal > mtDNA                   | YES | NO  | (Van Els et al., 2014)                 |
| Toxostoma lecontei subspecies | Set of loci | autosomal > Z-linked                 | YES | NO  | (Vázquez-Miranda et al., 2017)         |
| Aquila adalberti      | mtDNA, microsatellites | autosomal > mtDNA                   | YES | NO  | (Martínez-Cruz & Godoy, 2007)          |
| Aquila heliaca        | Set of loci | autosomal > mtDNA                   | YES | NO  | (Peters et al., 2012)                  |
| Anas crecca           | Set of loci | autosomal > mtDNA                   | YES | NO  | (Peters et al., 2012)                  |
| Anas carolinensis     | Set of loci | autosomal > mtDNA                   | YES | NO  | (Peters et al., 2012)                  |
| Sula nebouxii         | Set of loci | autosomal > mtDNA                   | YES | NO  | (Taylor et al., 2013)                  |
| Sula variegata        | Set of loci | autosomal > mtDNA | YES | NO  | (Cheviron & Brumfield, 2009)           |
| Zonotrichia capensis subspecies | mtDNA, microsatellites | autosomal > mtDNA                   | YES | NO  | (Cheviron & Brumfield, 2009)           |
| Icterus galbula       | Set of loci | autosomal > mtDNA                   | YES | NO  | (Jacobsen & Omland, 2012)              |
| Icterus bullockii     | Set of loci | autosomal > mtDNA                   | YES | NO  | (Jacobsen & Omland, 2012)              |
| Species                     | Method                   | Set of loci                  | Autosomal > mtDNA | Result | Reference               |
|-----------------------------|--------------------------|------------------------------|-------------------|--------|-------------------------|
| *Passerina amoena*          |                          |                              | YES               | NO     | (Carling & Brumfield, 2008) |
| *Passerina cyanea*          |                          |                              | YES               | NO     | (Carling & Brumfield, 2008) |

Table 1. Continued

| Species                     | Method                   | Set of loci                  | Autosomal > mtDNA | Result | Reference               |
|-----------------------------|--------------------------|------------------------------|-------------------|--------|-------------------------|
| *Gallus* species            | Whole Genome Sequencing  | autosomal > Z-linked         | YES               | NO     | (Lawal et al., 2020)    |
| *Hippolais icterina*        | mtDNA, AFLP              | autosomal > mtDNA            | YES               | NO     | (Secondi et al., 2006)  |
| *Hippolais polyglotta*      |                          |                              |                   |        |                         |
| *Poecile atricapillus*      | mtDNA, AFLP              | autosomal > mtDNA            | YES               | NO     | (Davidson et al., 2013) |
| *Poecile carolinensis*      |                          |                              |                   |        |                         |
Literature search in Web of Science™:
Introgress* AND bird* OR introgress* AND avian
(N = 511)

Selection of papers based on title and abstract
(N = 185)

Selection of papers based on methods
(N = 30)
Figure 2

(a) Autosomal loci > mtDNA
- Cline analyses (43%)
- Nm calculation (9%)
- Other methods (9%)
- Coalescent Modelling (31%)

(b) Autosomal loci > Z-linked loci
- Cline analyses (36%)
- Coalescent Modelling (55%)
- Other methods (9%)
- Not following Haldane’s Rule

Following Haldane’s Rule
Not following Haldane’s Rule