



Mating Patterns in Avian Hybrid Zones — A Meta-Analysis and Review

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Mating patterns in avian hybrid zones – a meta-analysis and review

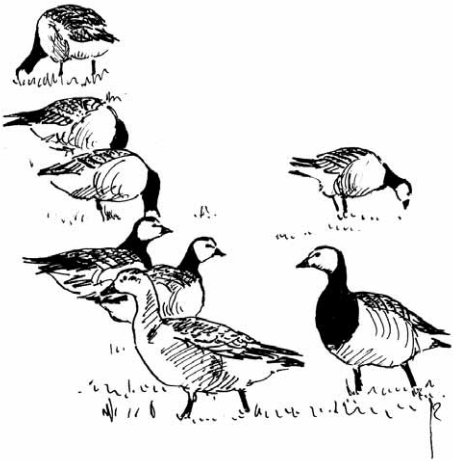
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Hybrid zones provide a unique opportunity to study the dynamics of isolation barriers. Pre-zygotic isolation through assortative or conspecific mating is thought to be an important aspect of reinforcement and speciation. Although assortative mating has received much attention and nearly a hundred theoretical models have been published, there is a large gap between theory on the one hand and empirical data on the other. To fill this gap, I carried out a meta-analysis on 58 studies which were identified as suitable for the analysis. Most studies had been carried out in the field ($n = 52$), and six were based on mate choice experiments. Fifty-three studies used plumage scores and five used genetic evidence to assess parental types. I found no correlation between the magnitude of effect sizes and date of publishing ($r = 0.181$, $P = 0.174$, $n = 58$). A fixed effects model without any underlying model structure showed a heterogeneity of $Q_{\text{total}} = 5454.6$ ($df = 57$; $P < 0.001$) and a significant mean effect size of 0.47 (95% CI 0.46–0.48). The results of the meta-analysis indicate that there is a significant effect of medium strength of assortative mating in avian hybrid zones. By partitioning the data, I found that effect sizes were very large in mate choice trials, and medium in observations in nature. Based on the inspections of the CIs of the mean effect sizes, assortative mating appeared strongest in Passeriformes and Charadriiformes hybrid zones. Further, assortative mating was stronger in narrow hybrid zones compared to wider ones but I found no difference between stable and moving zones.

Key words: assortative mating, hybridisation, hybrid zones, mate choice, meta-analysis, speciation

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INTRODUCTION

Hybrid zones provide a unique opportunity to study the process of speciation (e.g. Randler 2004, 2006a, 2006b, den Hartog *et al.* 2007). In keeping with Barton & Hewitt (1985), hybrid zones are “narrow regions in which two genetically distinct

populations meet, mate and produce hybrids” (p. 497). Such hybrid zones vary in width, although most hybrid zones studied in detail are rather narrow compared to both species ranges. Further, hybrid zones may be stable over time or moving. Different theoretical models have been developed to characterise hybrid zones. First, the ephemeral

zone hypothesis suggests that – after secondary contact – hybridisation either leads to complete reproductive isolation (speciation) or to merger (swamping) of the population (Moore 1977). Second, the dynamic equilibrium hypothesis (the ‘standard hypothesis’; Johnson & Johnson 1985) explains the nature of hybrid zones by a balance between gene flow into the hybrid zone from areas of allopatry and a selection against hybrids (Moore 1977, Johnson & Johnson 1985, Barton & Hewitt 1985). Third, the bounded hybrid superiority model is based on hybrid superiority in a narrow range (the hybrid zone) – which is often an ecotone between two different habitats – where hybrids are superior over their parental forms (Moore 1977). The dynamic equilibrium model was refined by Barton & Hewitt (1985) who claim that most hybrid zones are a shifting balance between dispersal and selection against hybrids. In their view, hybrid zones are ‘tension zones’ that can move, while the bounded-hybrid-superiority model suggest stable hybrid zones.

Different isolation barriers may act to enforce speciation and to prevent hybridisation. Mechanisms constituting such barriers to gene flow may be either pre-zygotic, such as positive assortative mating among parental phenotypes, or post-zygotic, for example reduced fitness in one or both sexes of these hybrids (Saino & Villa 1992, Helbig *et al.* 2001, Randler 2007a), full or partial genetic incompatibility (Helbig *et al.* 2001) or differences in susceptibility to predation (Randler 2007b). Grant & Grant (1992) argue that pre-zygotic isolation mechanisms are more important in birds. However, avian hybrid zones are maintained by pre-zygotic and post-zygotic isolation mechanisms (Helbig *et al.* 2001), although post-zygotic mechanisms have rarely been under investigation (Randler 2007b).

An important pre-zygotic isolation mechanism is assortative or conspecific mating. Here, I present the results of a meta-analysis investigating patterns of assortative mating in avian hybrid zones. In the context of this analysis, I define like-with-like mating as assortative mating irrespective of whether it is based on different species (con-

specific versus heterospecific mating) or subspecies or different plumage morphs (as measured on a hybrid index of plumage scoring) to overcome the problem of defining species status. Assortative mating has also been found with regard to traits that are polymorphic throughout a species’ range, such as age (Coulson 1966), plumage polymorphism (O’Donald 1959) or cultural background (Freeberg *et al.* 1999), but these studies will not be considered here because polymorphism does not form a hybrid zone.

The influence of assortative mating on speciation has received much attention and some hundred or so theoretical models have been published (see discussion in Brodin & Haas 2006). Assortative mating may lead to speciation – even in sympatry – (Kondrashov & Shpak 1998) but these models of speciation are rather strict. While mathematical models on the influence of assortative mating on speciation are widespread, empirical data are scarce (Servedio & Noor 2003). One recent overview contains only three avian species pairs (Howard 1993). Therefore, more empirical studies are required to allow assessment of the relative importance of the various models. Nevertheless, the study of pair composition in hybrid zones dates back at least to the 1950s, during which time pre-zygotic isolation was widely neglected in the scientific literature. For example, Dixon (1955) was one of the first authors who sampled mated pairs of titmice (*Parus bicolor* and *P. atricristatus*), but unfortunately he did not recognise the potential of his own work when writing “...such information tells us little beyond the fact that some mixed matings do occur” (Dixon 1955; p. 163).

Here, I present the results of a meta-analysis on assortative mating in avian hybrid zones to identify general patterns in a comparative manner and to provide an overview of the literature. In particular, I investigate whether the results of experimental and observational studies are in agreement, whether avian orders differ in their degree of assortative mating and whether the degree of assortative mating differs between various types of hybrid zones (stable/moving, narrow/wide).

METHODS

Data collection

Initially, I searched the Scopus and ISI (Web of Science) databases using the following combinations of terms: hybrid and (bird OR avian) and (Sexual selection OR Speciation OR Assortative mating OR Random pairing OR Random mating OR Mate choice OR Pair* OR Mate preference). Second, I used the combination 'hybrid zone' and (Sexual selection OR Assortative mating OR Random pairing OR Random mating OR Mate choice OR Pair composition OR Mate preference OR Heterospecific mat* OR Heterospecific pair* OR Interspecific mat* OR Interspecific pair*). Third, I searched the two databases SORA (<http://elibrary.unm.edu/sora/>) and OWL (<http://egizosrv.zoo.ox.ac.uk/OWL/>); both free of charge) to gain additional data. The search was closed at 20 March 2007. Initially, the abstracts were screened to assess whether the papers contained useful data. This yielded 49 studies. These publications then were obtained and the references were searched for additional relevant papers (snowball system), which yielded an additional number of 103 studies. Additionally, 38 studies from my own database were screened. Although this added to an impressive number of 190 papers, only a minority of these contained useful information for inclusion in the meta-analysis.

Selection criteria

I applied the following selection criteria to extract studies for this analysis:

(1) Data about mate selection/mate choice must have been reported, e.g. as a contingency table (e.g. when based on discrete types such as species or subspecies), as a correlation (e.g. when based on plumage indices / hybrid indices) or as means (e.g. when reporting time spent by females in front of either male type in a mate choice trial). Studies reporting 'verbally' that the pairing is at random or assortative were excluded. (2) Studies reporting data about at least one parental species and mixed pairings with the other parental species were included, while studies focusing on one parental

species and mixed pairing consisting of a parental species and hybrids were excluded (e.g. Picozzi 1976, Risch & Andersen 1998). (3) Studies were excluded when no hybrids, hybrid populations or hybrid zones were reported from the wild. (4) Experimental studies were included in the analysis when based on mate choice trials (i.e. when females were tested in a two-chamber experiment). (5) A bulk of experimental studies in nature was excluded because mount or playback presentations of conspecific or heterospecifics were used to test male reactions. These studies are very valuable and highly appreciated in research on speciation but they do not provide data on assortative mating because they do not quantify female reactions. (6) In some studies different species or subspecies pairs were presented. Each pair was treated as single study.

After applying these selection criteria, 58 studies remained. The data for these studies can be obtained from the author upon request.

Variables

I obtained data from the original research papers if possible, and sometimes these original data were re-calculated. I further extracted data on the width of the hybrid zone (more than a few hundred km were considered 'wide') and on its stability. Zones on islands were excluded from the analyses as were zones that could not be estimated precisely. Data on the movement or stability of hybrid zones were based on historical data and extracted from the original sources. However, these data were not presented in all studies. Data about the age of the hybrid zone could not be reliably estimated from literature because secondary contact after the end of the glaciation was often used as an explanation by the authors rather than based on 'observation' or other direct (e.g. archaeological) evidence. Therefore, I did not control for age of the zone to avoid circular reasoning.

Effect size calculations

I obtained different values from the studies, e.g. correlation coefficients, data from contingency tables, and means. To compare effect sizes, I trans-

formed all contingency tables to a standardised format that contained the number of observed and expected conspecific and observed and expected heterospecific pairings. I used data on expected frequencies when they were published in the original publications, otherwise I recalculated them following the method outlined in Rolando (1993). The chi-square values obtained based on this standardisation were subsequently transformed to a correlation coefficient using the tool MetaWin-Calculator. Effect sizes (expressed as z-scores) and variances were calculated using Meta-Win (Rosenberg *et al.* 2000). The conventional interpretation of the magnitude of effect sizes was used: effect sizes of 0.2 were small, of 0.5 medium, of 0.8 large, and effects greater than 1.0 were considered very large (Gurevitch & Hedges 1999). First, I started with a fixed effects model to look for a general effect and then turned to random effects models to make the results generalisable beyond the set of studies (see results).

RESULTS

I identified 58 studies suitable for the meta-analysis (Table 1). Most studies were carried out using field observations ($n = 52$), and only six were based on mate choice experiments in which females were given a choice between two alternative males. Further, 53 studies used plumage scores and five used genetic evidence to assess parental types.

Considering publication bias, I found no significant relationship between the magnitude of effect sizes and year of the study (date of publishing; $r = 0.18$, $P = 0.17$, $n = 58$).

As a first step, I calculated a fixed effects model without any underlying model structure. The model showed a heterogeneity of $Q_{\text{total}} = 5454.6$ ($df = 57$; $P < 0.001$) and a significant mean effect size of 0.47. The 95% confidence interval (CI) ranged from 0.46 to 0.48, indicating a medium and significant trend towards positive assortative mating in these zones and sub/species across all studies. The heterogeneity is also a measure of the extent to which the results of the stud-

ies are in agreement. That is, significant heterogeneity justifies a search for further effects. Therefore it is possible to partition the effect sizes into within- and between-group components (Verdolin 2006). I divided studies into observational studies ($n = 52$) and experimental evidence (mate choice trials; $n = 6$). I found significant between-study variation ($Q_b = 16.82$, $df = 1$, $P < 0.01$), but no significant variation within studies ($Q_w = 52.47$, $df = 56$, $P = 0.60$). Mean effect size for the observational studies was 0.41 with a CI from 0.26 to 0.57, and for the experimental studies it was 1.49 (CI 0.84 to 2.13), based on a random model. As both CIs excluded zero, the results can be considered significant. Mean effect sizes for the total set of studies under a random model was 0.51 (CI 0.36–0.66).

When looking at the different orders no significant between- ($Q_{\text{between}} = 3.07$, $df = 4$, $P = 0.54$)

Table 1. Studies used for the meta-analysis of assortative mating in avian hybrid zones.

Abraham <i>et al.</i> (1983)	Howell (1952)
Anderson & Daugherty (1974)	Ingolfsson (1970)
Baker (1996)	Johnson & Johnson (1985)
Baker & Boylan (1999)	Lloyd <i>et al.</i> (1997)
Becker (2007)	Moore (1987)
Bell (1997)	Panov <i>et al.</i> (1994)
Bock (1971)	Patten <i>et al.</i> (2004)
Brodsky <i>et al.</i> (1988)	Pearson (2000)
Brodsky <i>et al.</i> (1989)	Randler (2007a)
Bronson <i>et al.</i> (2003)	Rasmussen (1991)
Bronson <i>et al.</i> (2005)	Reudink <i>et al.</i> (2006)
Connors <i>et al.</i> (1993)	Rising (1996)
Delpont <i>et al.</i> (2004)	Ritz <i>et al.</i> (2006)
Dixon (1955)	Robbins (1986)
Emlen <i>et al.</i> (1975)	Rolando (1993)
Faivre <i>et al.</i> (1999)	Saetre <i>et al.</i> (1997)
Fefelov (2001)	Saino & Villa (1992)
Gee (2003)	Short (1965)
Good <i>et al.</i> (2000)	Stein & Uy (2006)
Grant & Grant (1997)	Veen <i>et al.</i> (2001)
Helbig <i>et al.</i> (2001)	Wiebe (2000)
Hofmann <i>et al.</i> (1978)	

and within-study variation ($Q_{\text{within}} = 60.71$, $df = 50$, $P = 0.14$) was found (Table 2). The CI included zero for Anseriformes and Piciformes hybrid zones, suggesting that assortative mating is less pronounced or absent in these orders.

Concerning the width of the hybrid zones, the random model produced a significant heterogeneity of $Q_{\text{total}} = 81.76$ ($df = 41$, $P < 0.001$). Between-study variation was not significant ($Q_{\text{between}} = 0.08$, $df = 1$, $P = 0.77$) in contrast to within-study variation ($Q_{\text{within}} = 81.68$, $df = 40$, $P < 0.001$). The effect sizes were higher in narrow hybrid zones compared to wider ones and the CI included zero in the wider hybrid zones, suggesting that assortative mating is less pronounced (or even absent) in wide hybrid zones.

With regard to the stability of the hybrid zones, there was no significant overall effect $Q_{\text{total}} = 43.20$ ($df = 37$, $P = 0.22$). Neither between- ($Q_{\text{between}} = 0.04$, $df = 1$, $P = 0.82$) nor within-study variation ($Q_{\text{within}} = 43.15$, $df = 36$, $P = 0.19$) was significant, suggesting no differences between moving and stable hybrid zones in the strength of assortative mating.

Table 2. Meta-analysis of assortative mating in avian hybrid zones. Effect sizes compared between taxonomic orders, and width and stability of the zone based on random effects models.

	Number of studies	df	Effect size	95% CI
Order				
Anseriformes	3	2	0.40	-1.01 to 1.82
Passeriformes	27	26	0.54	0.31 to 0.78
Charadriiformes	12	11	0.63	0.27 to 0.99
Piciformes	11	10	0.30	-0.11 to 0.72
Galliformes	2	1	0.97	-4.46 to 6.40
Width				
Narrow	39	38	0.51	0.37 to 0.66
Wide	3	2	0.44	-0.62 to 1.51
Stability				
Stable	27	26	0.43	0.25 to 0.61
Moving	11	10	0.40	0.11 to 0.68

DISCUSSION

The results of the meta-analysis indicate that there is significant assortative mating in avian hybrid zones. By partitioning the data, I found that effect sizes were very large in mate choice trials and medium in nature. This difference in effect sizes suggests that – given a choice between two alternative males – females usually are able to recognise conspecifics and mate assortatively, while in the field a lack of conspecific males may lead to hybridisation. Assortative mating was stronger in narrow hybrid zones compared to wider ones but there was no difference between stable and moving zones. The first result fits with the theoretical models (see below) because assortative mating should narrow a hybrid zone and should act against hybridisation. Thus, like-with-like pairings will reduce the width of a hybrid zone and enhance prezygotic isolation. Therefore, assortative mating should be higher in narrow zones.

Concerning stable and moving hybrid zones most studies report the presence and absence of assortative mating, and only a few studies provide evidence that in some hybrid zones one type is preferred over the other by females of both species (e.g. Bronson *et al.* 2003, Stein & Uy 2006). These two hybrid zones are moving as a result of this biased mate choice. Moving hybrid zones deserve further attention to answer the question of which factors may cause a hybrid zone to move.

In an overview, Howard (1993) identified 16 animal hybrid zones in which the random mating expectation was fulfilled, and 19 in which it was not. In these zones, the pattern of interaction was positively assortative and evidence for negative assortative mating was not found. The present study provides evidence for positive assortative mating in avian hybrid zones across studies. Further, it supports theoretical and mathematical models that predict parapatric speciation by assortative mating patterns (Kondrashov & Shpak 1998, Kirkpatrick 2000, Servedio & Noor 2003, Brodin & Haas 2006). From a theoretical point of view, assortative mating should lead to reinforcement and speciation and should narrow any hybrid zone

(Barton & Hewitt 1985). However, this meta-analysis shows that most hybrid zones are narrow and stable over time, suggesting that assortative mating is counteracted by other factors. Here, the models proposed by Barton & Hewitt (1985) provide some explanation: one contributing factor may be that inexperienced individuals from outside the hybrid zone regularly immigrate into the zone and subsequently mate heterospecifically.

How should assortative mating arise and what are the proximate cues? If we assume that hybridization is a result of 'mistakes' in mate recognition, we could find the answer in avian social recognition. Early imprinting on father or mother (ten Cate & Vos 1999) or on social mates (Brodsky *et al.* 1988) starts a process of social preferences (Gill 1998). Such early experience often determines mating preferences (ten Cate & Vos 1999, Randler 2005). Then assortative mating may persist and imprinting may have a considerable effect on the genetic structure of a population (Findlay 1987).

Assortative mating does not necessarily need to be based on social recognition but may also arise passively (Wiebe 2000), e.g. if two groups have different breeding chronologies or timing of migration (prevalence hypothesis, Findlay 1987).

Another aspect may be the role of mate choice copying (Freeberg *et al.* 1999) where one female copies the mate choice tactic of another. If a given female chooses the wrong male (perhaps as a result of imprinting, see above) and her choice is copied by other females, then such a cultural transmission of mate choice may contribute to the ongoing process of hybridisation.

Further, the results of the comparison between experimental and observational studies could be used to distinguish between two competing hypotheses of hybridisation (Randler 2002). Hybridisation may be regarded either as mistake in mate recognition (see above) or it may be an active choice of females 'making the best of a bad job'. In the latter case, females choose heterospecific males because conspecific males are absent or already paired. In hybrid zones, it may be better to produce at least some viable hybrid offspring rather than remain unpaired and abandon repro-

duction (Baker 1996, Veen *et al.* 1999). This latter view is supported by data of the meta-analysis because in the mate choice trials where females had the opportunity to choose between two possible mates most decisions were 'correct' (i.e. choosing a conspecific mate). The analysis detected a large effect size in these trials. For example, quails of the genus *Callipepla* mated assortatively in an aviary test but not in the wild (Gee 2003) and female flycatchers were able to choose the correct male in an aviary test but did hybridise in nature (Saetre *et al.* 1997). Caution is required in the interpretation of these results as the set of species that were investigated in captivity (mate choice trials) was biased towards species that were particularly amenable to being held in captivity (e.g. Passerines, ducks). Nevertheless, the results of the present meta-analysis suggest that females are able to choose the 'correct' mate in mate choice trials but do not always pair assortatively in nature, which could keep hybridisation an ongoing process acting against narrowing of hybrid zones.

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SAMENVATTING

Als tussen twee populaties van een soort lange tijd geen uitwisseling plaatsvindt, zullen die populaties genetisch van elkaar gaan verschillen. Komen dergelijke populaties weer met elkaar in contact, dan kunnen er drie dingen gebeuren: (1) individuen uit beide populaties herkennen elkaar niet meer als soortgenoten (er is soortsvorming opgetreden), (2) ze paren net zoveel met elkaar als met individuen uit hun eigen populatie (er is geen soortsvorming opgetreden), of (3) ze paren wel met elkaar, maar minder vaak dan met individuen uit hun eigen populatie. In het laatste geval is soortsvorming onvolledig en kan er een hybridezone ontstaan. In dit artikel wordt aan de hand van een literatuuronderzoek nagegaan hoe sterk soortspecifieke paring is in hybridezones van vogels. In totaal werden 58 schattingen gevonden in de literatuur. Paarvorming in hybridezones was verre van willekeurig. Verder bleek soortspecifieke paarvorming sterker in experimentele studies dan in veldstudies voor te komen. Dit suggereert dat de vogels wel degelijk onderscheid kunnen maken, maar dat ze in het veld niet altijd de mogelijkheid hebben te paren met het type partner dat hun voorkeur heeft. Hybridisatie kan dan gezien worden als een 'beter-dan-niets' oplossing. (KK)

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