

Short notes and reviews

Avian hybrids: incidence and geographic distribution of hybridisation in birds

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Review of: **Handbook of Avian Hybrids of the World**,
by Eugene M. McCarthy. Oxford University Press,
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The identification of hybrids between closely related taxa bears relevance for studies of gene flow and the evolution of mechanisms of genetic isolation. As such it is an important phenomenon when studying speciation. Furthermore, hybridisation, or the interbreeding of species, is of pivotal importance in framing ideas about the nature of taxonomic judgments to be made about particular populations (Veith *et al.*, 2006).

Hybridisation is commonly recorded in birds, and the most recent reviews of hybridisation in birds suggested that about one in ten species of bird is known to have hybridised in nature (Grant and Grant, 1992). In fact, with their often distinct plumages and relative ease to observe, it is probably fair to say that hybridisation is better recorded in birds than in any other major animal group (Randler, 2002, 2004).

In 1958 AP Gray produced a survey of avian crosses as reported in the literature, including both crosses that occurred in nature and in captivity. In fact, the most recent data in her survey date back to a year earlier, making it almost 50 years since any widely available reference book on avian hybridisation was produced [In 1989 EN Panov produced a similar survey focussing on natural hybrids only, but its choice of language -Russian- made it less accessible]. Last year, EM McCarthy came with a much awaited update of Gray's survey. The book provides an exhaustive compilation of all cases of avian hybridisation under both wild and captive conditions. About a quarter of the 600 or so pages are formed by the bibliography, and about half of the pages are dedicated to the cross accounts, providing information on the crosses between two species.

The introduction to the book provides an extensive explanation how to find crosses in the book, and what

the evidence for and rate of hybridisation is between species (for example, Natural Hybridisation Reported or Captive or Extensive Natural Hybridisation Inferred). The background information on how to identify hybrids or what are some of the factors that contribute to under-reporting of hybrids is useful and the (brief) section on future research urges researchers to invest more time and energy on subjects such as hybrid fertility, hybrid zones, and the role hybridisation plays in shaping the evolution of new species.

For selected taxa, mostly those with parapatric distributions, McCarthy provides geographic maps, which indeed serve a purpose. For the other type of illustration in the book -diagrams with arrows connecting different genera that hybridise- is confusing and not very illustrative. The sheer amount of data allows for detailed analysis of patterns of hybridisation, although unfortunately, the data are nowhere presented in a summarised or tabular manner. But with pen en paper one comes a long way.

It is interesting to see that the incidence of occurrence within an order, i.e. the number of species within an order that have hybridised divided by the total number of species in that order, shows marked differences. Top of the list are the Anseriformes (ducks, geese and allies), with in 97/161 species (60.2%) hybridisation having been recorded, whereas in taxa like the Apodiformes (swifts) only three of the 103 species is known to have hybridised in nature. In an earlier study (Roselaar *et al.*, 2005), using data from Grant and Grant (1992), we found a highly significant relationship between the number of species in an order and the incidence of hybridisation (Kendall's $\tau = 0.44$, $n = 23$, $P = 0.005$): the more species the order contained the higher the incidence of hybridisation. From a simple mathematical perspective this relationship seems to make sense, as the more species there are in an order, the more species there are potentially for a single species to hybridise with.

For all species listed in McCarthy (2006) we tallied whether hybridisation had indeed been recorded in nature, and summed this over families and orders, and calculated the incidence of hybridisation. With a few exceptions, McCarthy (2006: pp 4 and 11) indicated that, with a few exceptions, he followed the taxonomic treaty of Sibley and Monroe (1990). However, more than once, subspecies in Sibley and Monroe were treated as full species by McCarthy, thus inflating the incidence of hybridisation. Comparing the data from McCarthy (2006) with that of Grant and Grant (1992), we see an overall increase in the number of natural hybrids recorded, from 9.8% in 1992 to 19.0% in 2006 (Table 1). Accepting that new species have been described since Sibley and Monroe's (1990) treaty, the overall figure is not subject to much changes, since if we take the higher number of species [9721] listed in Dickinson (2003), will give an incidence of hybridisation of 18.9%. Even when the inflation due to the elevation of subspecies to species is taken into account, the

true incidence of hybridisation is still twice figure as reported by Grant and Grant (1992).

With these new data there is no longer a significant relationship between the incidence of hybridisation and number of species in an order (Kendall's $\tau = 0.21$, $n = 23$, $P = 0.16$) (Figure 1). Overall, for almost all orders the number of species known to have hybridised in nature has increased (the exceptions being the Turnificornes - buttonquails and Coliiformes - mousebirds: Table 1), but this number has increased relatively more for orders with fewer species. When we explore the incidence of hybridisation between families within one order, we see an equal absence of a relationship between the propensity of hybridisation and size of the order. For example, for the Ciconiiformes (containing seemingly diverse families as storks, hawks and eagles, stilts, and pelicans) the incidence of hybridisation within a family ranges from 0% to 81.8% (26.1% for the order as a whole), the relationship between number of species in a family and incidence of

Table 1. Incidence of hybridisation (the number of species within an order that have hybridised in nature divided by the total number of species in that order) in 23 orders of birds, comparing data from 1992 (Grant and Grant, 1992) with that of 2006 (McCarthy, 2006).

Orders	Species (N)	Incidence of hybridisation	
		1992	2006
Struthioniformes	10	0	20.0
Tinamiformes	47	0	4.3
Craciformes	69	2.9	31.9
Galliformes	214	21.5	32.2
Anseriformes	161	41.6	60.2
Turniciformes	17	0	0
Piciformes	355	13.5	36.9
Glabuliformes	51	3.9	13.7
Bucerotiformes	56	0	16.1
Upupiformes	10	0	60.0
Trogoniformes	39	0	17.9
Coraciiformes	152	5.3	13.8
Coliiformes	6	33.3	0
Cuculiformes	143	2.8	9.8
Psittaciformes	358	7.5	15.9
Apodiformes	103	0	2.9
Trochiliformes	319	19.1	33.2
Musophagiformes	23	0	8.7
Strigiformes	291	0.7	6.5
Columbiformes	313	3.2	8.0
Gruiformes	196	8.7	9.7
Ciconiiformes	1027	13.5	26.0
Passeriformes	5712	8.1	16.8
Aves	9672	9.3	19.0

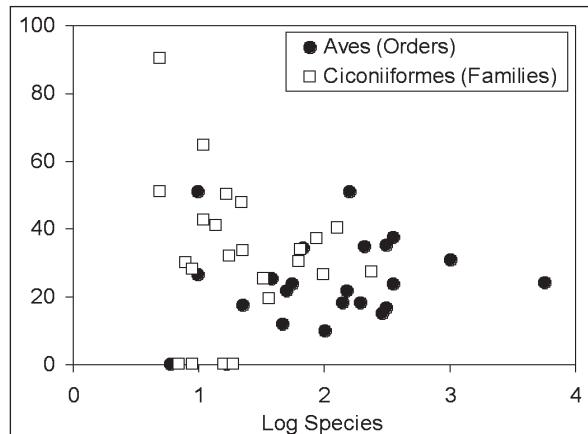


Fig. 1. Relationship between the incidence of hybridisation in an order or family and the number of species in that order or family. Both relationships are not significant.

hybridisation not being significant (Kendall's $\tau = -0.11$, $n = 23$, $P = 0.49$) (Figure 1).

Geographically, hybridisation does not occur randomly in birds (Aliabadian et al. 2005). McCarthy notes that with the exception of rare vagrants, hybridisation occurs where the ranges of the interbreeding populations overlap. For a subset of 717 species (out of 1841 that hybridise in nature) McCarthy provides data on the geographical range overlap. We tallied these and by far the most hybridising species indeed have breeding range overlap (85.8%). A handful of species (6.7%) have a

parapatric contact zone (i.e. the species are largely allopatric but abut along a common geographical boundary), and even less (3.6%) have an altitudinal contact zone (i.e. populations of the two hybridising species are separated by altitude, with contact occurring at a certain intermediate elevation). The remaining hybrids (3.9%) have disjunct breeding ranges.

One of the more striking aspects of the book, and one that has seen an increase with the rise of internet forums in recent years and one that is not restricted to birds only (e.g. Grill et al. 2005), is how poorly hybridisation has often been documented. More often than, the observation of a mere ‘intermediate’ or ‘aberrant’ individual is reason to suggest that hybridisation has occurred. McCarthy has made a to be applauded attempt to clean the record of some of the clear erroneous reports (these crosses are listed throughout, but they are struck through to indicate the error), and in an appendix he lists a further 22 crosses of questionable authenticity. Yet, since rarely (natural) hybrids are thoroughly researched by comparing them with the putative parent species (e.g. morphometrically or genetically) the record remains cluttered with crosses for which there is little supportive data, impeding overall analysis at the macro-taxonomic level. We cannot and will not, however, hold McCarthy accountable for this, and in fact his account is as good as we can expect to be produced at the present day. As such, we should congratulate him with a fine piece of work, one that is a must for all those interested in hybridisation and speciation in birds. We are already eagerly awaiting the update, with yet more crosses and more details. All we can hope for is that we do not have to wait another 50 years.

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