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Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities

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It has been argued recently that the combination of male-only parental care and classical polyandry in birds is the most interesting and yet the least understood of all avian breeding systems. Despite a huge number of hypotheses, careful comparative analyses have repeatedly failed to identify consistent ecological differences between species showing male-only care and closely related species showing other patterns of care. This has led to the suggestion that such analyses fail because the crucial differences are between ancient lineages rather than between closely related species. Here, therefore, I use comparisons between families to test three well-known hypotheses: that male-only care is associated with: (i) a low rate of fecundity; (ii) large egg size relative to female size; or (iii) female-biased opportunities for remating. Families showing male-only care do not differ from families showing female-only care with respect to rate of fecundity or relative egg size. There is, however, a significant difference between these two groups of families with respect to an index of remating opportunities, nesting density. Families showing female-only care nest at high density, while those showing male-only care nest at very low density. This is one of the first times a consistent ecological correlate has been identified for male-only care in birds. It suggests that female-only care arises (or persists) in families where remating opportunities are abundant for both sexes, whereas male-only care arises (or persists) in families where remating opportunities are rare for both sexes and particularly scarce for males. This in turn suggests that sex differences in remating opportunities are the key ecological factor in determining male-only care and classical polyandry in birds.

Keywords: parental care; male-only care; mating systems; polyandry; birds

1. INTRODUCTION

> Polyandry [in birds] has probably been evolved five times.... There seems nothing peculiar in their ecology to suggest why they should have evolved polyandry. (Lack 1968, p. 153)
>
> the evolution and distribution of polyandry and uniparental male care [in birds] remains a puzzle (Clutton-Brock 1991, p. 149)
>
> classical polyandry [in birds] is probably the most interesting, and certainly is the least well understood, of the recognised avian mating systems (Ligon 1999, p. 401).

Although most species of birds show biparental care and social monogamy, many of the best-studied species regularly exhibit uniparental care, where one parent deserts the clutch and their mate is left to provide care alone (Lack 1968; Oring 1982; Davies 1991). In the majority of these cases, it is the male that does the deserting and the female that provides the care. In such species the males are often socially polygynous. However, in a small number of species—such as the emu (*Dromaius novaehollandiae*), the greater rhea (*Rhea americana*), the brown kiwi (*Apteryx australis*), the spotted sandpiper (*Tringa macularia*), the red-necked phalarope (*Phalaropus lobatus*), the Kentish plover (*Charadrius alexandrinus*) and Eurasian dotterel (*Charadrius morinellus*)—the sex roles are 'reversed' and it is the female that deserts, leaving the male to care for the offspring. Where this occurs females are typically socially polyandrous.

Species showing male-only care and sex-role reversal, while few in number, have played an important role in the development of evolutionary theories on mating systems, parental care and sexual selection because they provide the proverbial exception by which to test new hypotheses (Darwin 1871; Williams 1966; Lack 1968; Trivers 1972; Emlen & Oring 1977; Maynard Smith 1977; Oring 1986; Clutton-Brock & Vincent 1991; Ligon 1993, 1999; Owens *et al.* 1994, 1995; Owens & Thompson 1994; Székely *et al.* 1996; Bennett & Owens 2002). It is remarkable, therefore, that we still know so little about why this handful of species exhibit such an extraordinary pattern of parental care (Oring 1986; Clutton-Brock 1991; Ligon 1999). Is there a common ecological factor that predisposes these species to male-only care? And if there is, what is it?

The traditional approach to these questions is to compare species with male-only care (and often social polyandry) with closely related species showing female-only care (and often social polygyny) or biparental care (and often social monogamy) (see reviews in Oring (1986); Clutton-Brock (1991) and Ligon (1999)). The

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classic example is waders, or shorebirds (infraorder Charadriides), which show an enormous range of forms of parental care and mating system including biparental care (e.g. Eurasian oystercatcher, *Haematopus ostralegus*, Eurasian golden plover, *Pluvialis apricaria*, stone curlew, *Burhinus oedicnemus*), female-only care (e.g. Eurasian woodcock, *Scolpax rusticola*, ruff, *Philomachus pugnax*, buff-breasted sandpiper, *Tryngites subruficollis*, least seedsnipe, *Thinocorus rumicivorus*) and male-only care (e.g. painted-snipe (*Rostratula bengalensis*), spotted sandpiper, phalaropes (*Phalaropus* spp.), jacanas (Jacanidae), Kentish plover, Eurasian dotterel). What factor unites the Eurasian dotterel, phalaropes, spotted sandpiper, painted-snipe and Kentish plover, but sets them apart from the other waders?

Despite a plethora of hypotheses (Nethersole-Thompson 1973; Jenni 1974; Pitelka *et al.* 1974; Graul *et al.* 1977; Maynard Smith 1977; Ridley 1978; Myers 1981; Wittenberger 1981; Knowlton 1982; Walters 1984; Trivers 1985; Jehl & Murray 1986; Hamilton 1990), careful comparative tests, using both simple comparisons between species (Erckmann 1983) and evolutionary independent contrasts (Reynolds & Székely 1997), have succeeded in identifying only one ecological correlate of the extent of paternal care in shorebirds; species' typical migration distance. Specifically, Reynolds & Szekely (1997) demonstrated that increases in migration distance are associated with decreases in the extent of paternal care, suggesting in turn that extensive paternal care is associated with short migration distances (see also Myers (1981)). The biological interpretation of this intriguing result is, however, not straightforward, particularly with respect to the direction of causality. Indeed, Reynolds & Székely (1997) explain the association by suggesting that variation in the extent of paternal care has led to changes in migration behaviour, rather than vice versa.

> Cause and effect are difficult to disentangle, but in the case of migration, most parental care patterns must have evolved first, since most of the bifurcations in care in our phylogeny are far older than contemporary migration routes…. Thus, changes in male…care may have affected future options for migration, with species where males provide little care being able to afford to migrate farther due to their energetic savings (Reynolds & Székely 1997, p. 132).

It seems unlikely, therefore, that variation in migration behaviour is a plausible ecological explanation for male-only care in birds (although the negative relationship between the two variables may be important for other questions). Thus, in terms of causal aspects of ecology and life history we still do not know why some lineages have adopted, or maintained, this unusual breeding system.

The great difficulty in identifying consistent ecological correlates of male-only care in birds is worrying, because it undermines the generality of our understanding of parental care and mating systems (Oring 1986; Clutton-Brock 1991). Indeed, the difficulty in identifying consistent ecological correlates of male-only care and polyandry in birds has led Ligon (1993, 1999) to suggest that such approaches are doomed to fail because they do not pay sufficient attention to a critical factor, phylogenetic history. Ligon (1999) suggests that male-only care is, in fact, the ancestral state in birds in general, and many of the polyandrous groups in particular (see also Van Rhijn (1984, 1985, 1990)). As evidence for this position Ligon (1999) cites Hanford & Mares (1985), who suggested that male-only care is the ancestral state for the ratites and tinamous, Székely & Reynolds (1995), who suggested that the same may be true for some shorebird families (e.g. jacanas, painted-snipe, plains-wanderer (*Pedionomus torquatus*) and Feduccia (1995), who suggested that 'transitional shorebirds' were the basal group for modern birds (Ligon 1999, fig. 10.3, pp. 241–246, pp. 411–412). Using this line of argument Ligon contends that 'phylogenetic history', although often ignored in traditional ecological analyses, is a vital component of the evolution of male-only care and classical polyandry (Ligon 1993, 1999). This general point has been made by other authors, but never so specifically applied to male-only care and classical polyandry (see Van Rhijn 1984, 1985, 1990; McKitrick 1992; Sillen-Tullberg & Temrin 1994; Temrin & Sillen-Tullberg 1994, 1995; Wesolowski 1994; Székely & Reynolds 1995; Owens & Bennett 1997; Arnold & Owens 1998, 1999).

The overall aim of this paper is to integrate the traditional view that there must be a consistent ecological basis for male-only care and classical polyandry, with the notion of Ligon (1993, 1999) that phylogeny is the key missing component. Hence, I examine whether the recently proposed 'hierarchical view' of mating systems, i.e. an integration of phylogenetic and ecological factors, can throw any new light on this old problem. Specifically, I test the idea that, if there are no consistent ecological differences between closely related species showing different forms of parental care, perhaps there are consistent ecological differences at higher taxonomic levels.

The hierarchical view of mating systems, alluded to by Emlen & Oring (Emlen & Oring 1977; Oring 1982), Van Rhijn (1984, 1985, 1990) and Ligon (1993, 1999) and recently incorporated into the modern comparative framework (Owens & Bennett 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002), suggests that variation between species in a mating system is not simply due to contemporary differences in ecology. Differences between species are due to a combination of historical and contemporary factors. For instance, in the case of birds, differences between species in the frequency of mate desertion are best explained by an interaction between ancient changes in life history and contemporary variation in ecological factors such as resource distribution (Owens & Bennett 1995, 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002). Hence, in the case of mating systems in birds, the hierarchical view can potentially explain two, otherwise puzzling, observations. First, that species with different mating systems are often very similar in terms of ecology, and second, that species with similar mating systems sometimes have different ecologies. In either case, the lack of association between mating system and ecology is due to the influence of constraints that evolved in the ancient evolutionary history of the lineages concerned (Owens & Bennett 1995, 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002).

The first step in applying the hierarchical method to male-only versus female-only care in birds is to identify which lineages are to be compared. In the case of parental care in birds, we already have good ecological explanations of why some groups show uniparental care rather than

Table 1. Families reported to show male-only or female-only uniparental care, respectively.

male-only care	female-only care
rheas (Rheidae)	pheasants, grouse and turkeys (Phasianidae)
cassowaries and emu (Cassuariidae)	ducks (Anatidae)
kiwis (Apterygidae)	parrots (Psittacidae)
tinamous (Tinamidae)	hummingbirds (Trochilidae)
button quail (Turnicidae)	bustards (Otidae)
coucals (Centropodidae)	herons and bitterns (Ardeidae)
mesites (Mesitornithidae)[a]	seed-snipe (Thinocorus)
plains-wanderer (Pedionomidae)	sandpipers (Scolopacidae)
sandpipers (Scolopacidae)	cotingas and manakins (Tyrannidae)
painted-snipe (Rostratulidae)	lyrebirds (Menuridae)
jacanas (Jacanidae)	bowerbirds (Ptilonorhynchidae)
plovers (Charadriidae)	birds-of-paradise (Corvidae)
	old-world flycatchers (Muscicapidae)
	wrens (Certhiidae)
	African warblers (Cisticolidae)
	old-world warblers (Sylviidae)
	widowbirds (Passeridae)
	new-world blackbirds and allies (Fringillidae)

[a] The form of parental care in mesites is controversial, see § 1 for details.

biparental care (see Sillen-Tullberg & Temrin 1994; Temrin & Sillen-Tullberg 1994, 1995; Owens & Bennett 1997; Bennett & Owens 2002): uniparental care arises, or persists, in lineages predisposed to single-parent care by fast offspring development and in which the opportunities for remating are relatively high. Hence, the crucial comparison for the topic of this paper is between those groups that show male-only care and those that show female-only care. Contrary to the impression given in some reviews, male-only care is not restricted to the shorebirds. In fact, according to the taxonomy of Sibley & Monroe (1990), regular male-only care has been recorded regularly in 11 families (see table 1). It has also been reported in the mesites (Mesitornthidae) (Rand 1936), although more recent evidence has cast some doubt on this suggestion (see Rand 1951; Del Hoyo *et al.* 1996; Ligon 1999) and we must wait for the results of ongoing fieldwork for a definitive answer (N. Seddon and F. Hawkins, personal communication). Regular female-only care, on the other hand, has been recorded in at least 18 families (see table 1). Only one family, the true sandpipers (Scolopacidae) contains species showing regular male-only care and species showing regular female-only care (table 1). For the analyses presented here, I use data on all of these families, performing all analysis both with the mesites included and excluded.

Although most of these families are well studied with respect to the often extravagant sexual ornaments and behaviour of the non-caring sex (Johnsgard 1991*a*,*b*), there is far less information on nesting biology (see Veronon 1971; Bruning 1974; Crome 1976; Hanford & Mares 1985; Johnsgard 1991*a*,*b*; Andersson 1995; Coddington & Cockburn 1995). For many species showing uniparental care only a handful of nests have ever been described and basic data, such as egg mass, have not been recorded. A full review of the differences between these two groups of families is, therefore, beyond the scope of the available data. Instead, I will concentrate on testing three specific hypotheses as follows.

(i) That male-only care occurs in families limited to small clutches or low annual fecundity because, in such families, female emancipation is the only way in which fecundity can be increased—hence, it is suggested, male-only care should be found in families with unusually small clutch sizes (Maclean 1969; Erckmann 1983).

(ii) Male-only care occurs as a result of female exhaustion—hence, male-only care should occur in families with unusually heavy eggs or unusually heavy clutches (Graul *et al.* 1977; Ashkenazie & Safriel 1979).

(iii) Male-only care occurs when the benefits a male would receive from deserting the clutch, in terms of additional mates, are very limited—hence, male-only care should be associated with low nesting density, where a deserting male would be unlikely be able to find an additional mate in breeding condition (Wittenberger 1981; Székely 1996; Székely *et al.* 1999).

A second major problem faced when performing this type of higher-level comparative analysis is that of evolutionary non-independence between families, i.e. where a single evolutionary event is represented by more than one descendant lineage. As Ligon (1993, 1999) and Owens & Bennett (1997; Bennett & Owens 2002) have emphasized, closely related families will probably have more similar patterns of parental care because of phylogenetic niche conservatism and evolutionary lag (see Harvey & Pagel 1991). For instance, Hanford & Mares (1985), Ligon (1993, 1999), McKitrick (1992) and Wesolowski (1994) have all suggested that male-only care is probably the ancestral state for the ratites and tinamous. Similarly, Székely & Reynolds (1995) have suggested that male-only care may be the common ancestral state for several families of waders, including the jacanas, plains-wanderer and painted-snipe (see also Van Rhijn (1985)). Finally, female-only care may, of course, be the ancestral state for the bowerbirds and lyrebirds sister groups and the old-world and African warbler sister groups. It would be unwise, therefore, to treat all such families as statistically independent data points. One solution to this problem would be to identify evolutionary independent contrasts and base all analyses on those contrasts (Felsenstein 1985; Harvey & Pagel 1991). In this case this is not possible because the phylogeny for such closely related groups is insufficiently well resolved. An alternative approach would be to compare sister taxon in a 'matched-pair' type of analysis. Again, however, this is not possible in the case of uniparental care because, with the exception of the true sandpipers, no other groups show variation in the form of uniparental care at an appropriate phylogenetic level. Given these difficulties, I have adopted the next best option of simply collapsing all non-independent families to a single datum point, where non-independent means closely related families representing a single evolutionary event. This minimizes the problem of non-independence as far as is possible and is conservative with respect to sample size (see Harvey & Pagel 1991).

2. MATERIAL AND METHODS

Data were collated from both published and unpublished sources on family typical values for modal clutch size, mean egg weight (g), mean female body weight (g) and modal maximum breeding density for each of the families containing species with male-only care (including the mesites) and each of the families containing species with female-only care (see Appendix A). In the case of families containing less than five species, data on some parameters were only available for a single species and in such cases that value was used as a family typical value. For families containing more than five species, we collected data on as many species as possible and used the average across species as a family typical value. Where data availability allowed, we used species showing uniparental care in preference to species showing biparental care.

Where fresh egg weight, w, was not measured, it was calculated from

$$w = g \times \frac{\pi}{6} \times l \times b^2, \qquad (2.1)$$

where l is the length of the egg in cm, b is the breadth of the egg in cm, and g is the specific gravity of eggs ($1.05\ \mathrm{g\,cm^{-2}}$) (Bergtold 1929; Preston 1974). Relative egg weight was calculated as a percentage by dividing mean egg weight by mean female weight, and relative clutch weight was calculated by multiplying relative egg weight by modal clutch size. Maximum breeding density was measured on a six-point scale based on the estimated maximum number of nests per hectare, where: 6 = more than five nests per hectare (approximately equivalent to nests being regularly less than 20 m apart); 5 = between 0.5 and 4.9 nests per hectare (approximately equivalent to nests being regularly less than 50 m apart); 4 = between 0.05 and 0.49 nests per hectare (approximately equivalent to nests being regularly less than 200 m apart); 3 = between 0.005 and 0.049 nests per hectare (approximately equivalent to nests being regularly less than 500 m apart); 2 = between 0.0005 and 0.0049 nests per hectare (approximately equivalent to nests being regularly less than 2 km apart); 1 = less than 0.00049 nests per hectare (approximately equivalent to nests being regularly more than 2 km apart). When collating species-specific data I used maximum breeding densities (rather than mean or median breeding densities) for two reasons:

(i) maximum breeding density was often the only data available; and
(ii) variation in breeding density estimates for the same species was often highly skewed.

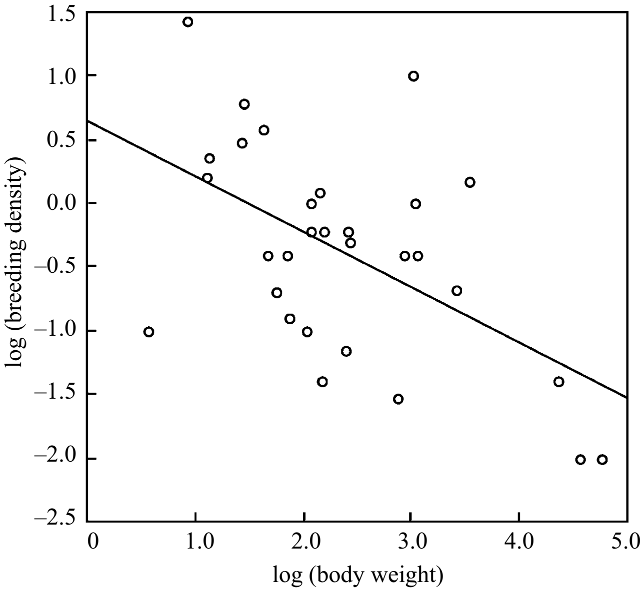

Figure 1. Association between body weight and nesting density across the families analysed in this study (linear regression model on log-transformed data; $r = 0.54$, $n = 30$, $p = 0.002$, slope of line $= -0.44(\pm 0.13)$).

For those families where data on other measures of breeding densities are available, the results remain qualitatively unchanged when either mean or median densities were used instead of maximum density (I. P. F. Owens, unpublished data). I used modal scores when collapsing the database to the family level to minimize the effect of one or a few species having unusually high, or unusually low, estimates of maximum breeding density. Also, because there is a significant negative correlation between body weight and breeding density for the families in this database (figure 1), I performed all analyses involving breeding density both on the breeding density score described above and on 'residual breeding density', controlling for the effects of variation in body weight using regression. When calculating residual breeding density, raw density estimates were used instead of the categories described above, and both body weight data and breeding density data were logged before fitting the regression model.

In order to test the prediction that male-only care is associated with small clutch sizes, low annual fecundity or low breeding density, two-tailed Mann–Whitney tests were used to compare the relative clutch size and fecundity of male-only care families with that of female-only care families. The true sandpipers, the only family in which both of these forms of uniparental care occur regularly, were classified as showing male-only care because this has been predicted to be the ancestral state for this group (Reynolds & Székely 1995); it is also the most common form of parental care in this group (I. P. F. Owens, unpublished data). Subsequently, because several of the families are closely related and may not, therefore, represent statistically independent data points, this analysis was repeated with all the ratite families combined (cassowaries and emu, rheas, kiwis and tinamous), all the sandpipers combined (plains-wanderer, true sandpipers, phalaropes, jacanas and painted-snipe) and both bowerbirds–lyrebirds and old-world–African warblers combined to give mean or modal values as appropriate. I also repeated all analyses with the mesites removed, given that there is uncertainty whether the groups really show either male-only care or classical polyandry.

When testing the predictions that male-only care is associated with relatively heavy clutches, two-tailed Mann–Whitney tests were also used to compare male-only care families and female-only care families. Again, however, there are good *a priori* reasons to suspect that variation between families in relative clutch weight is correlated with differences between species in body weight (Rahn *et al.* 1975). It is possible, therefore, that differences between families in body weight may either mask or magnify differences in relative clutch weight, particularly when considering families at opposite ends of the avian body size spectrum (hummingbirds versus ratites). I therefore used the general exponential equation obtained by Rahn *et al.* (1975) for within-family correlations between family typical body weight (b) and family typical egg size (w) as follows:

$$\log(w) = a\log(b)^{0.675}, \tag{2.2}$$

where the constant a is a family typical value estimated through regression. Using this approach I estimated the weight that the eggs of a family would be if the body weight of the family was 100 g (w) and called this index the 'standardized egg weight'

$$\log(w_{100\,\mathrm{g}}) = \frac{\log(w) \times \log(100)^{0.675}}{\log(b)^{0.675}}. \tag{2.3}$$

I then multiplied this measure by the clutch size to give the 'standardized clutch weight'. Once again, all families were initially used as independent data points, but subsequently the ratite, sandpiper, bowerbird–lyrebird and warbler families were combined. I also again repeated all the analyses with the mesites removed.

3. RESULTS

There was no consistent difference between male-only care families and female-only care families with respect to clutch size (figure 2, table 2). This was also true when the ratite, sandpiper and bowerbird–lyrebird families were combined (table 2) and when mesites were removed from the analysis (table 2).

When all families were treated as independent data points, there was a significant difference between the two groups of families with respect to standardized egg weight (figure 3, table 2). This difference was, however, no longer significant when the phylogenetically non-independent families were pooled (table 2) and when the mesites were removed from the analysis (table 2). There was no consistent difference between male-only and female-only families with respect to relative egg weight (figure 3, table 2). Nor were there any consistent differences between the two groups of families with respect to relative or standardized clutch weight (figure 4, table 2). All of these results remained qualitatively unchanged when the ratite, sandpiper, bowerbird–lyrebird and warbler families were combined (table 2) or when mesites were removed from the analysis (table 2).

There was a consistent difference between male-only care families and female-only care families with respect to breeding density (figure 5, table 2). As predicted, male-only care families have lower nesting densities than female-only care families, even when the ratite, sandpiper and bowerbird–lyrebird families are combined (table 2). This was equally true when mesites were removed from the analysis (table 2), or when 'residual breeding density' (controlling for variation in body size) was used in analyses rather than the raw breeding density score (figure 5, table 2).

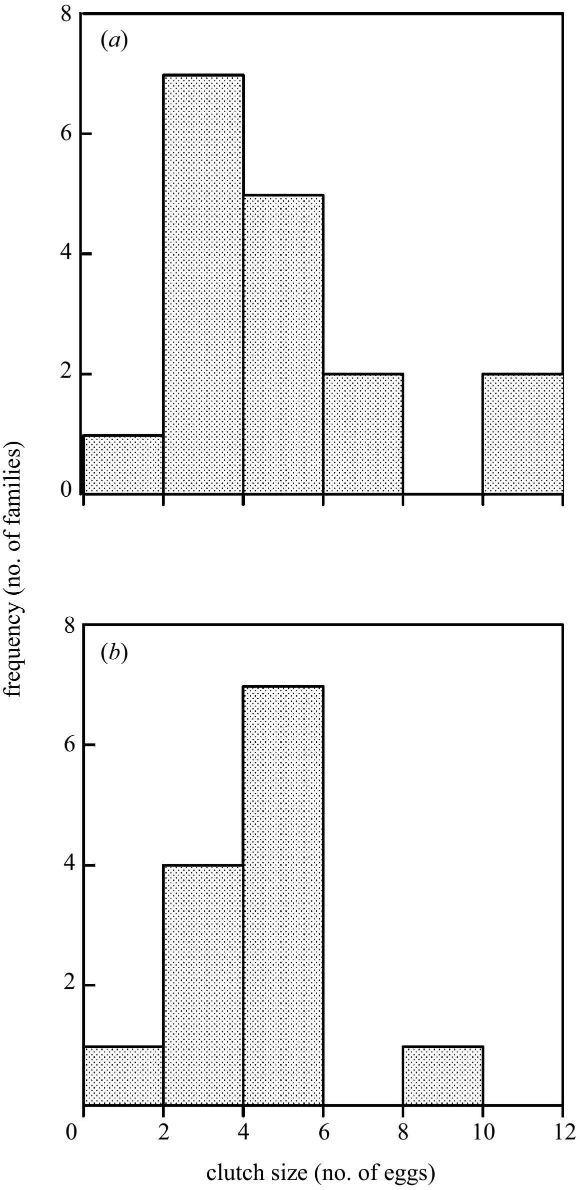

Figure 2. Clutch size in families showing (*a*) female-only care and (*b*) male-only care.

4. DISCUSSION

Using a comparative approach based on differences between independent ancient avian lineages (taxonomic families), I found that there was no consistent difference between male-only care families and female-only care families with respect to fecundity, relative egg weight or relative clutch weight. This was true even when I controlled for differences among families in overall body size. The only indication of a difference between the two groups of families with respect to these parameters emerged when several closely related families were treated

Table 2. Associations between type of uniparental care (male only versus female only) and seven ecological variables.

	type of analysis					
	all families ($N = 30$)		non-independent families pooled ($N = 21$)		non-independent families pooled and mesites removed ($N = 20$)	
explanatory variables	z-value[a]	p-value	z-value	p-value	z-value	p-value
clutch size	0.49	0.63	0.31	0.75	0.27	0.79
relative egg weight	0.08	0.93	0.62	0.53	0.00	1. 00
standardized egg weight	2.45	0.01**	1.25	0.21	0.83	0.41
relative clutch weight	0.90	0.37	0.58	0.56	0.44	0.66
standardized clutch weight	1.19	0.23	0.31	0.76	0.66	0.51
nesting density	3.10	0.001***	2.31	0.02*	2.19	0.03*
residual nesting density	2.78	0.01**	2.64	0.02*	2.33	0.03*

[a] z- and p-values refer to results of Mann–Whitney tests of null hypothesis that there is no difference between families showing male-only care and families showing female-only care. Explanatory variables are described in detail in § 2. Asterisks denote the statistical significance of Mann–Whitney test as follows. $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$.

as independent data points, in which case families showing male-only care had significantly larger eggs than expected once the overall allometry between egg size and body size had been taken into account. However, given that this pattern was non-significant when the evolutionary non-independent families of ratite, shorebird, warbler and bowerbird–lyrebird were combined, it is probably best viewed as a spurious by-product of phylogenetic pseudoreplication. Overall, therefore, there was no phylogenetically robust evidence of a difference in egg size or clutch size between male-only and female-only care families.

In contrast, I found robust evidence of a consistent difference between male-only and female-only care families with respect to my index of the opportunities for remating–breeding density. As predicted by the hypothesis based on the opportunities of remating (Wittenberger 1981; Székely 1996; Székely *et al.* 1999), male-only care families have lower nesting densities than female-only care families, even when ratite, sandpiper, bowerbird–lyrebird and warbler families were combined, or the mesites were removed from the analysis. The relationship between breeding density and male-only care was even robust to controlling for the effects of variation in body size, which is important because there is a strong and potentially confounding negative association between body mass and breeding density (figure 1). Also, the association between density and form of parental care is not an artefact of using maximum breeding density, because for those families where data are available the same pattern is obtained when either mean or median density is used as a measure of clustering (I. P. F. Owens, unpublished results).

The lack of association between pattern of uniparental care and either the rate of fecundity or relative egg size is interesting given the amount of attention that these hypotheses have received (see Oring 1986; Clutton-Brock 1991; Ligon 1999). However, it must be borne in mind that these hypotheses have grown largely from observations on waders alone. It is true that most families of waders do have relatively small clutch sizes and relatively large eggs (see Erckmann 1983; Reynolds & Székely 1997). There are, however, three problems with extrapolating this observation to explain male-only care in birds. First, as demonstrated by Székely & Reynolds (1995), not all of these families of waders can be treated as independent observations with respect to evolution of male-only care. Second, not all families showing male-only care have low fecundity or relatively large eggs. Many species of ratite, for example, have very large clutches, while button-quail and coucals typically have rather small eggs. Finally, small clutches and heavy eggs are not restricted to species showing male-only care. Clutch sizes of four eggs or less are common among families showing female-only care such as the seedsnipe, bustards, hummingbirds, lyrebirds, bowerbirds and birds-of-paradise. Of these families, the lyrebirds, bowerbirds and some of the birds-of-paradise also have unusually large eggs for their size, and yet all three groups show extreme forms of female-only care and male polygyny. Low fecundity and large egg size are not, therefore, consistently associated with male-only, rather than female-only, parental care.

The association between male-only care and low breeding density represents only the second time, to my knowledge, that anyone has found a general and consistent correlation between male-only care and ecology (see Oring 1986; Clutton-Brock 1991; Ligon 1999). The other time that an ecological correlate was found of male-only care was the association of Reynolds & Székely (1997) with migration distance. In that case, however, the original authors indicated that the direction of causality actually ran in the opposite direction to that required here; that is, variation in the extent of paternal care determines migration behaviour rather than vice versa (see § 1 for further details). Hence, breeding density is the first potentially causal ecological correlate. From this angle alone the

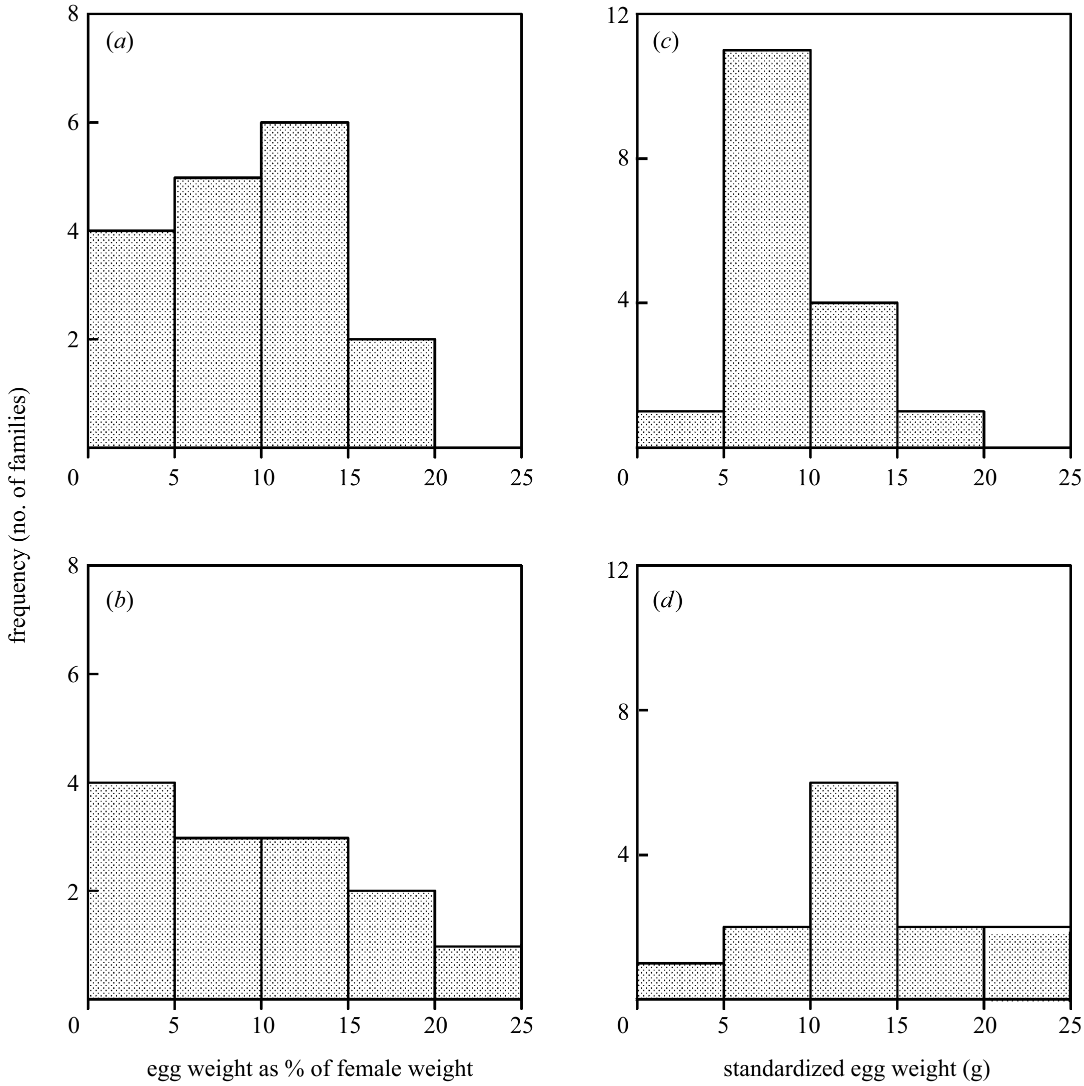

Figure 3. Relative egg weight as a percentage of adult female weight in families showing (*a*) female-only care and (*b*) male-only care. Standardized egg weight controlling for allometric variation in relative egg weight in families showing (*c*) female-only care and (*d*) male-only care.

result is exciting. The result also adds weight to the hierarchical approach to studying the evolution of mating systems (Owens & Bennett 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002) and the argument of Lignon (1993, 1999) that phylogeny is an important part of the overall explanation for classical polyandry in birds. As Ligon (1999, pp. 432–434) suggested, it appears that differences between families, rather than differences between species, may be the crucial ecological factor in determining whether or not a lineage is predisposed to male-only care. This would explain why previous attempts have failed to find consistent ecological differences between closely related species within the male-only care families (Erckmann 1983; Reynolds & Székely 1997). It would also explain why different groups of classically polyandrous bird have such apparently different ecologies, without having to resort to idiosyncratic explanations for each group (cf. Ligon 1999).

But what is the biological interpretation of this pattern? Species that exhibit male-only care tend to come from families that habitually nest at very low densities; usually less than one nest every 10 hectares. Species exhibiting female-only care, on the other hand, tend to come from families that nest at densities of between one and 10 nests in every hectare. This corresponds to a difference of up to three orders of magnitude in terms of the minimum distance between nests. But how is this difference in nesting density linked to sex differences in desertion? I speculate that the answer may be based on what Trivers (1972) called the 'cruel bind'. In species belonging to lineages that are predisposed to offspring desertion and nest at high density, either sex would gain from deserting. It is the male, however, who has the first chance to do so because he can desert immediately after copulation, while the female must wait until she has laid the eggs. In such species the female may experience the cruel bind of having to provide the care because she is the one left holding the eggs. Conversely, in species belonging to lineages that are predisposed the offspring desertion but nest at low density, the male would gain very little from deserting because he is relatively unlikely to find another female in reproductive condition. Females, on the other hand, may experience a larger benefit from desertion because they can mate with any male. Indeed, in some species there is evi-

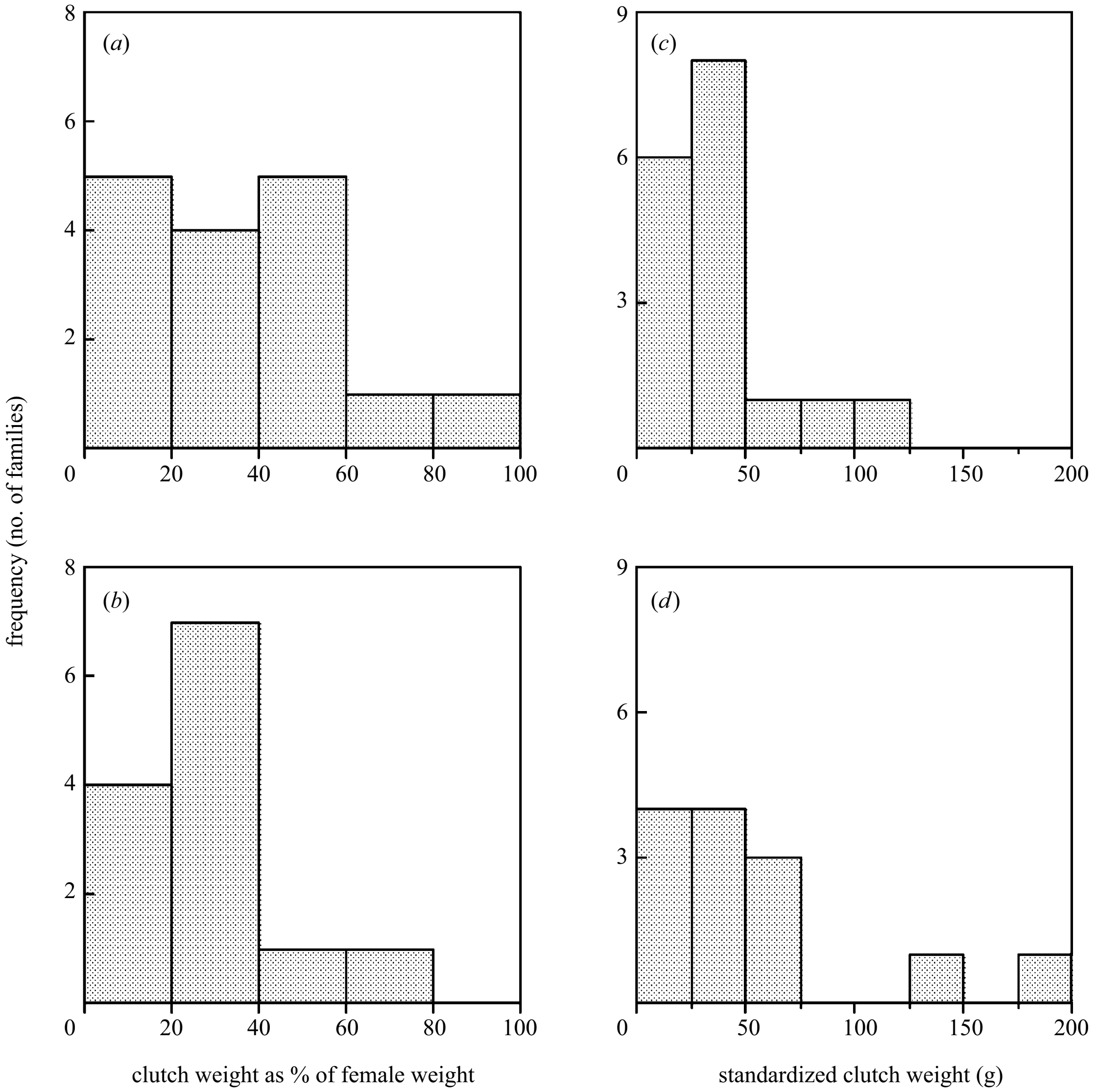

Figure 4. Relative clutch weight as a percentage of adult female weight in families showing (*a*) female-only care and (*b*) male-only care. Standardized clutch weight controlling for allometric variation in relative clutch weight in families showing (*c*) female-only care and (*d*) male-only care.

dence that deserting females store sperm from their first male and use this sperm to lay a second clutch of eggs that are then either incubated by a second male or even by the female herself (i.e. double-clutching). Desertion is, therefore, a safer option for females than males because females can always have at least one more reproductive opportunity, providing the breeding season is sufficiently long.

Under this scenario, the critical ecological difference between lineages that show female-only care and those that show male-only care is with respect to sex differences in the benefits of desertion. In lineages showing female-only care the benefits of desertion are equal between the sexes—the female ends up caring because she is caught by Trivers' cruel bind. In species showing male-only care, the benefits of desertion are greater to females than the males—males end up caring because they have no better option.

This hierarchical explanation of male-only care in birds that I have proposed may be tested empirically as it makes three interrelated predictions. First, it predicts that in species showing male-only care the opportunities for remating should be higher for females than for males. Second, it predicts that this female bias in the opportunities for remating should be smaller, or even reversed, in species showing female-only uniparental care. Finally, it predicts that this pattern should not be restricted to just those species showing uniparental care but should be common to closely related species in the same family (see parallel predictions for uni- versus biparental care in Owens & Bennett (1997)). To my knowledge, only the first of these three predictions has been tested to date and this was by Székely and colleagues working on the Kentish plover (Székely 1996; Székely *et al.* 1999; see also Lessells 1984). The Kentish plover is particularly suitable for this type of work because it is one of the very few species in which either male- or female uniparental care may occur, although male-only care is far more common (Lessells 1984). As predicted by the hypothesis of sex differences in remating opportunities, Székely *et al.* (1999) found that experimentally divorced females remated almost five times as quickly as did comparable males. It would now be interesting to know if the direction of sex difference in the benefits of remating would be reversed if the same experi-

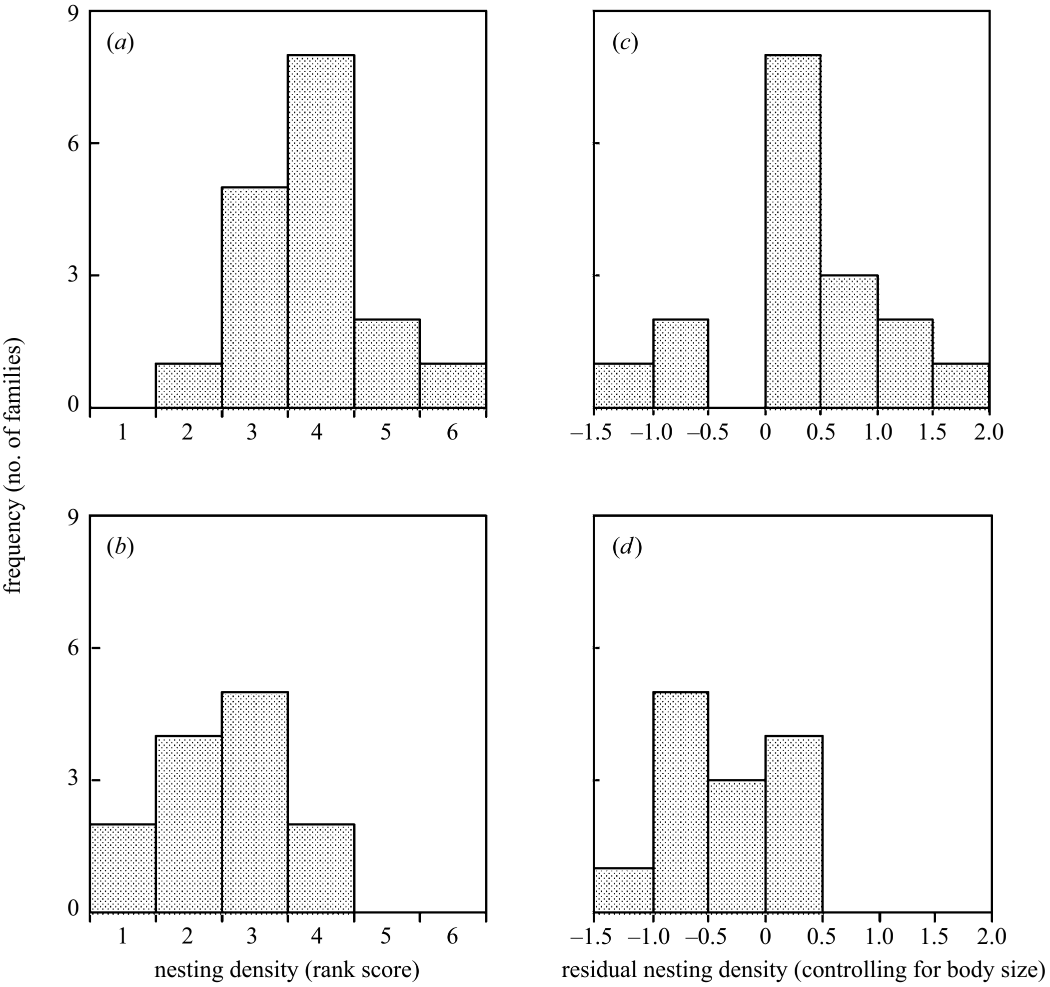

Figure 5. Maximum nesting density in families showing (*a*) female-only care and (*b*) male-only care. Residual nesting density in families showing (*c*) female-only care and (*d*) male-only care. The categorical scale for maximum nesting density and method for calculating residuals are described in § 3.

ments were repeated in a species from a family that showed female-only care.

Alternatively, the effect of breeding density may be mediated through its effect on mate-searching patterns or confidence of paternity. T. Székely (personal communication), for instance, has suggested that at low breeding densities the females may be more willing to visit distant patches than are the males, perhaps because males are more involved in defending territories. Hence, females may have better information about the mating opportunities available over a wide geographical area (see Szekely *et al.* 1999). Similarly, Ligon (1999) has suggested that sex differences in offspring desertion may be due to certainty of paternity, with paternal care being more common in those taxa where extra-pair paternity is relatively rare. Hence, if low-density breeding is indeed associated with low rates of extra-pair paternity, high confidence of paternity may lead to the evolution of paternal care. The applicability of these interpretations to the taxa studied here is, however, unclear because, in the first case, in many of the families showing male-only care the sexes are reversed and it is the females that hold territories. In addition, in the second case, recent phylogeny-based comparative tests have shown no consistent association between breeding density and extra-pair paternity at the level of interest here; i.e. among species and families (Westneat & Sherman 1997). Nevertheless, such hypotheses deserve proper empirical tests, either by studying sex differences in ranging behaviour during the breeding season, or through testing for an association between confidence of paternity and paternal care.

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APPENDIX A

families	common names	body weight (g)	egg weight (g)	standardized egg weight (g)	clutch size	standardized clutch weight (g)	density (nests ha^{-1})	residual density
(*a*) Families showing male-only care								
Rheidae	rhea	22500	600	15.929	9	143.361	0.04	−0.156
Cassuariidae	emu and cassowaries	36900	602	11.473	2	22.947	0.01	−0.664
Apterygidae	kiwis	2620	440	49.339	4	197.356	0.21	0.158
Tinamidae	tinamous	750	60	15.555	3	46.664	0.03	−0.924
Turnicidae	button-quail	70	1.77	2.248	4	8.991	0.4	−0.248
Centropodidae	coucals	150	9	6.859	3	20.577	0.04	−1.104
Mesitornithidae	mesites	107	21.8	20.834	1	20.834	0.1	−0.77
Pedionomidsae	plains-wanderer	72.4	9	11.174	4	44.697	0.125	−0.746
Scolopacidae	sandpipers	47	9	14.926	3	44.777	0.4	−0.323
Rostratulidae	painted-snipe	140	13	10.376	4.9	50.843	1. 2	0.361
Jacanidae	jacanas	261	28	14.723	4	58.894	0.6	0.177
Charadriidae	plovers	115	15	13.659	4	54.637	0.6	0.022
(*b*) Families showing female-only care								
Phasianidae	pheasants and allies	850	33	7.867	12	94.403	0.4	0.224
Anatidae	wildfowl	1096	51	10.254	10	102.541	0.99	0.666
Psittacidae	parrots	250	15.2	8.227	2	16.453	0.07	−0.764
Trochilidae	hummingbirds	3.6	0.56	5.194	2	10.387	0.1	−1.411
Otidae	bustards	3500	41	3.787	3.5	13.253	1.5	1.066
Aredeidae	herons and bitterns	1009	40	8.501	5.3	45.054	10	1.655
Thinocorus	seedsnipe	55	8	11.941	4	47.765	0.2	−0.594
Tyrannidae	cotingas, mannakins and allies	266	23.9	12.409	2	24.817	0.5	0.102
Menuridae	lyrebirds	1142	62	12.127	1	12.127	0.4	0.28
Ptilonorhynchidae	bowerbirds	118	20	17.901	2	35.801	1	0.249
Corvidae	birds-of-paradise and allies	157	9.1	6.726	2	13.453	0.6	0.081
Muscicapidae	old world flycatchers	12.5	1. 7	6.847	7.5	51.355	1.6	0.029
Certhidae	wrens	13.1	1.56	6.089	7	42.624	2.32	0.199
Cisticolidae	African warblers	8.5	1.1	5.737	4.8	27.537	26.7	1. 178
Sylviidae	old-world warblers	28.4	3.1	7.205	5	36.025	6	0.758
Passeridae	widowbirds and allies	27	3	7.213	4.5	32.458	3	0.447
Fringillidae	new-world blackbirds and allies	41.5	3.95	7.12	3.947	28.104	3.8	0.631

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