

Prevalence of different modes of parental care in birds

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Estimates of the incidence of major classes of parental care by birds are drawn from classical studies that preceded both the publication of a massive secondary literature and the revolution driven by molecular approaches to avian phylogeny. Here, I review this literature in the light of new phylogenetic hypotheses and estimate the prevalence of six distinct modes of care: use of geothermal heat to incubate eggs, brood parasitism, male only care, female only care, biparental care and cooperative breeding. Female only care and cooperative breeding are more common than has previously been recognized, occurring in 8 and 9% of species, respectively. Biparental care by a pair bonded male and female is the most common pattern of care but at 81% of species, the pattern is less common than once believed. I identify several problems with existing hypotheses for the evolution of parental care and highlight a number of poorly understood contrasts which, once resolved, should help elucidate avian social evolution.

Keywords: cooperative breeding; uniparental care; biparental care; brood parasitism; polyandry; avian phylogeny

1. INTRODUCTION

Two of the most widely cited statistics concerning sociality and parental care in birds are the estimates by Lack (1968) that 92% of birds of all birds form pair bonds and Brown (1987) that 2.5% of all birds breed cooperatively. Although these classic sources remain the basis for much comparative analysis, they suffer from two problems. First, while Lack's observation concerned the frequency of pair bonding, it is often misquoted as indicating an estimate of biparental care. For example, Quillfeldt *et al.* (2004, p. 613) open with: 'More than 90% of bird species have biparental care, with both sexes contributing to feeding the offspring (Lack 1968)'. However, Lack explicitly emphasized that pair bonds and biparental care are not synonymous. For example, pair bonds are found among species with male only care (Coddington & Cockburn 1995), female only care (McKinney 1986), no parental care (Martinez *et al.* 1998; Göth & Vogel 2004) and cooperative breeding (Cockburn 2004).

Second, the original estimates were based on a limited literature and preceded the recent publication of large-scale reviews of regional avifaunas and taxa. Incomplete data pose the question of how to interpret the large number of species in which nesting behaviour is unknown. With respect to analyses of cooperative breeding, the usual approach has been to assume that any species not listed in early compilations is a pair breeder (Edwards & Naem 1993). Detailed reviews of some avian taxa discredit this method. For example, an excellent recent review increased the number of Falconiformes known to breed cooperatively from the 2% of species reported by Brown to 14% (Kimball *et al.* 2003). However, interpretation of this

increase remains difficult until comparable care is applied to data from other taxa. This lack of a comprehensive approach to data plagues all recent attempts to compare the prevalence of cooperative breeding across birds, which are invariably based on detailed analyses of some taxa but outdated views of other clades (Arnold & Owens 1998; Ligon & Burt 2004). Indeed, recent data have changed the appropriate hypothesis for the predominant mode of care for whole genera (e.g. Lammertink 2004) and even families of birds (e.g. Tobias *et al.* 2002; Tobias & Seddon 2003). In addition, the original estimates were developed before the revolution in avian phylogeny prompted by DNA methods. As an example of how phylogenetic information can help understand parental care, improved phylogenies have reduced estimates of the number of origins of brood parasitism. For example, all brood parasitic ploceid finches belong to just one clade, the viduines (Sorenson & Payne 2001) and all members of the cowbird genus *Molothrus* are brood parasitic (Lanyon 1992). These rearrangements change the systematic level at which contrasts between modes of parental care occur and at which comparative analysis should be focused. In other taxa, new phylogenetic data have thrown into question the direction of evolution of patterns of parental care (Cockburn 1998, 2003).

In an attempt to remedy these difficulties, I here review what is known about the mode of parental care exhibited by each bird species. Where there are no data, I provide an estimate by extrapolating from the behaviour of the nearest relatives of the species. My primary aim is to revise our understanding of the incidence of the rare forms of parental care (no care, male only care, female only care, cooperative breeding). I also highlight areas in which natural history data and phylogenies require refinement and point to neglected evolutionary transitions that are likely to illuminate the evolution of patterns of care in comparative analyses.

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2. MATERIAL AND METHODS

(a) *Data sources*

This manuscript improves my earlier data compilation for the oscine passerines (Cockburn 2003) and has been extended to include all birds. My primary source was the secondary literature (reviews and regional and taxon-level monographs). I also conducted detailed literature searches for species not covered by secondary sources, using the electronic version of the *Zoological Record* for the period 1975 until Early 2005. Despite the increasingly comprehensive availability of data, for many species parental care remains undescribed and for many the nest has never been seen. These species and any in which data sources were contradictory, were initially classified as *unknown*.

(b) *Modes of parental care*

Where data were available, I recognized the following modes of parental care. A small number of birds have escaped the need to incubate their eggs and provision their offspring. This is achieved via *brood parasitism* and in the case of some megapodes, via the use of *geothermal* heat to rear young. Where care is provided to the young, it can be provided by just one sex and either males (*male only*) or females (*female only*) may be the primary carers. However, in many cases the brood is provisioned and/or defended by two adults (*biparental* or *pair*). Finally, the brood can be cared for by more than two individuals (*cooperative breeding*). Cooperative breeding is difficult to determine without colour-ringing or phenotypic differences among group members, so I have classified many cases as *suspected*. In addition, I also identified cases in which birds live in groups founded by natal philopatry (*group*), but in which cooperative breeding does not occur, as these have provoked considerable recent interest (Ekman *et al.* 2004).

The habits of many species vary across their range and within populations, hindering the process of classification. While acknowledging this variation, here I adopt a typological approach. For example, in some species of polygynous bird, the male feeds the young of his first mate but not those of subsequently acquired mates. I call such cases biparental care because there are predictable contexts that lead to male provisioning. By contrast, in other species males usually do not feed at any nest but are occasionally observed to deliver a small amount of food late in the period of parental care when no other mating opportunities are available. I call this case female only care. Cooperative breeding also varies within and between populations. Some authors have used the terms obligate and facultative to indicate this distinction, but I follow Ligon & Burt (2004) in arguing that these terms are misleading and that obligate cooperative breeding should be restricted to the rare cases in which an unassisted pair is incapable of rearing young (Boland *et al.* 1997). Instead, I use the term cooperative breeding to characterize the case in which there is some evidence that more than 10% of nests in one or more populations are attended by more than two birds. In cases in which few nests have been observed (e.g. Ragusa-Netto 2001), this criterion was deemed to be satisfied. My classification focuses primarily on care of the eggs and nestlings. This is unfortunate, as post-fledging care is of great interest and of particular importance in understanding the evolution of cooperative breeding (Russell 2000; Öst *et al.* 2005). However, data are currently too few for a broad-scale analysis of the sort attempted here.

Our understanding of patterns of parental care varies with biogeographical region and taxon. For example, Holarctic species have generally been studied much more comprehensively than Neotropical species and conspicuous species like ducks that are harvested by hunters are better known than small denizens of the rainforest canopy. In order to test possible effects of these biases, I used phylogenetic information to erect a hypothetical state for each of the unknown species. First, if all members of a genus whose habits are known exhibit a particular pattern of care, I inferred that habit in the remaining members of the genus. Where the habits of a genus were unknown, I first considered whether natural history habits gave strong reason to infer the likelihood of a particular habit (e.g. birds that displayed in leks but whose nesting habits were unknown were inferred to have female only care and some genera that lived year round in groups were presumed likely to be cooperative breeders). If there were no natural history data supporting such inference, I assumed that species had the habits of their closest relatives using molecular phylogenies if possible or the adjacent species in the conventional systematic sequence in which phylogenies were unavailable. Extrapolation was not possible in some cases. For example, some monospecific genera fell between cooperative breeders and pair breeders in the systematic sequence. In this case, I conservatively assigned the birds as pair breeders. In genera in which more than one type of care was known to occur and in which data were missing for only a few species, I interpolated using the same approach, filling species with missing values with the habits of their closest relatives. The primary difficulty arises in genera in which more than one type of care occurs but data for the majority of species are missing (e.g. *Tangara*). In this case, I assigned the remaining species in proportion to the habits of known species, unless there were natural history data that suggested such extrapolation was inappropriate. The most likely problems in adopting this approach work in opposite directions. First, rare exceptions will not be identified, which is likely to lead to an underestimate of the rarer forms of care. By contrast, there may be a tendency to study the strange and unusual and to ignore the usual (in this case, biparental care). I know of no simple way to correct these problems and hope that my attributions, while likely to contain errors, will still be more accurate than previous compilations and that identification of problems will prompt the necessary field work to remedy the deficiencies.

I used Sibley & Monroe (1990) as the primary source for species boundaries. I excluded from their compilation 81 species that are extinct so that confirmation of behaviour is impossible, three species that were probably hybrids and 181 that were treated as subspecies in the sources I used to determine patterns of care. In several cases, my primary source on behaviour used new species boundaries and if these altered estimates of the number of evolutionary transitions in care I included those changes. I augmented the phylogenetic hypotheses of Sibley & Ahlqvist (1990) with insights from new molecular phylogenetic analysis, which has particularly marked effects on the relationships of the passerines (Barker *et al.* 2002, 2004; Ericson *et al.* 2002, 2003). A number of taxa of uncertain affinity have not been sampled using molecular approaches or have been recognized as of uncertain affinity, yet clearly misplaced in the Sibley & Monroe sequence. Rather than force these into taxa without biological justification, I have treated these species as of uncertain affinity (*incertae sedis*). My phylogenetic hypotheses are

Table 1. The number of bird species known and inferred to exhibit different modes of parental care.

no. of carers	mode of care	subcategory	known pattern of care	%	unknown	total inferred	%
0	geothermal heat		5	0.1	0	5	0.1
	brood parasitic		87	1.7	12	99	1.0
1	male only care		52	1.0	38	90	1.0
	female only care	conventional	533				
		group	1				
		total	534	10.4	238	772	8.2
2	pair	conventional	3676				
		occasional cooperation	150				
		cooperation in captivity	7				
		group	20				
		total	3853	74.9	3785	7638	80.8
3+	cooperative	conventional	462				
		strongly suspected	148				
		cooperation in captivity	2				
		total	612	11.9	240	852	9.0
	grand total		5143	4313	9456		

summarized in the electronic supplementary material part A. Relationships are presented in a form suitable for comparative methods incorporating phylogenetic information.

3. RESULTS

(a) Data

My analysis recognizes 9456 species and 188 families (electronic supplementary material, part A). I have conservatively not assigned 96 passerine species to a Family. I found enough data to draw preliminary conclusions about the pattern of parental care for 5143 of the 9456 species considered (54%; table 1). The pattern of uncertainty is not random, with data being particularly poor for the Neotropical and Indomalayan regions, a problem exacerbated by the absence of monographic summaries of data and because many birds nest in the rainforest canopy. Unsurprisingly, data for this habit are universally poor. Data are worse for passerines than for non-passerines.

(b) Prevalence of care

My compilation confirms that the majority of birds have biparental care but suggests the frequency is much lower than has been assumed. Biparental care occurs in 75% of the known species but is inferred for 81% of all species, supporting the hypothesis that birds with rare patterns of social organization and parental care are more likely to be studied or written about. Hereafter, I therefore use the inferred data unless I state otherwise. Summaries of the inferred patterns of care for each family are presented in the electronic supplementary material, part B.

A small number of species (1%) escape parental care through brood parasitism or the use of geothermal heat and my compilation does not add to conventional wisdom concerning the prevalence or phylogenetic distribution of these habits (Davies 1992; Jones *et al.* 1995).

Male only care occurs in 90 species (1%) from 12 families. My summary differs from recent comparative analyses (Owens 2002) only in the removal of the mesites (Seddon *et al.* 2003) and the addition of some megapodes (Birks 1997). Male care predominates in five clades of birds (which differ sharply in taxonomic rank): these are

ratites and four clades within the Charadrii (the monospecific Pedionomidae, the clade including Jacanidae and Rostratulidae, Phalaropodinae and Turnicidae, which have recently been shown to be nested within the waders rather than representing a distinct Order). Within the Charadrii, exclusive male care also occurs in species in the genera *Actitis* (Scolopacidae) and *Charadrius* (Charadriidae). Male only care also occurs in some megapodes (Birks 1997) and in at least one species of coucal (Andersson 1995; Goymann *et al.* 2004).

Female only care is inferred for 772 species (8%) in 40 families (21%). This is a much wider distribution than has been acknowledged in recent comparative analysis (Owens 2002). While part of this difference stems from refinement of phylogenies, new natural history is also important. Prevalence of a particular trait can arrive in two ways. First, there may be speciation within a clade. Such speciation may be unrelated to the trait of interest, but the trait can also contribute to its prevalence. For example, it has been frequently suggested that intersexual selection facilitates speciation (see Barraclough *et al.* 1995; Price 1998; Edwards *et al.* 2005), so clades in which lek promiscuity is prevalent may diversify rapidly. Second, a trait may arise repeatedly within a clade. Such convergent origins provide strong evidence of selection. Families with high prevalence or a high number of transitions are represented in table 2.

Cooperative breeding is inferred to occur in 852 species (9%). This represents almost a fourfold increase on recent reports and comparative analyses (Arnold & Owens 1998; Ligon & Burt 2004). This increase is made more dramatic because I have treated 150 species that only occasionally exhibit cooperative breeding as pair breeders, though some of these were included as full cooperative breeders in Brown's (1987) review and have been treated as such by some comparative analysis (Arnold & Owens 1998). Cooperative breeding occurs in 84 families (45%; table 3) and I have conservatively not assigned 32 cooperative species to a family, which is a substantial proportion of the passerines I have treated as *incertae sedis* (33%).

As for female only care, it is possible to distinguish groups with very high incidence of cooperation and those

Table 2. Taxa with a high incidence of female only care (greater than 25%) or that contain at least three transitions to or from female only care.

		species	female only	p (female only, %)	transitions	possible correlates
<i>taxa with a high incidence of female only care</i>						
Trochilidae	hummingbirds	314	314	100	1	nectarivory
Pipridae	manakins	51	51	100	1	frugivory
Menuridae	lyrebirds and scrubbirds	4	4	100	1	slow growth
Thinocoridae	seedsnipe	4	4	100	1	precocial chicks
Cnemophilidae	cnemophilids	3	3	100	1	frugivory
Orthonychidae	logrunners	2	2	100	1	predation?
Oxyruncidae	sharpbill	1	1	100	1	frugivory
Paradisaeidae	birds-of-paradise	38	32	84	1	frugivory
Ptilonorhynchidae	bowerbirds	19	16	84	1	frugivory
Otitidae	bustards	25	20	80	1	precocial chicks
Cotingidae	cotingas	67	34	51	≥4	frugivory
Philepittidae	asities	4	2	50	1	nectarivory
Anatidae	ducks	151	69	46	≥5	precocial chicks
Phasianidae	pheasants and allies	173	59	34	≥4	precocial chicks
Dendrocolaptidae	woodcreepers	47	13	28	2	predation?
<i>taxa with numerous transitions to and from female only care</i>						
Cracidae	curassows, etc.	50	8	16	?3	frugivory, precocial chicks
Ploceidae	weavers	268	42	16	≥3	reduced insectivory
Icteridae	new world blackbirds	96	15	16	3	rich habitats
Nectariniidae	sunbirds	123	16	13	≥5	nectarivory
Scolopacidae	sandpipers	86	7	8	≥4	precocial chicks
Tyrannidae	tyrant-flycatchers	337	18	5	≥5	frugivory, rich habitats
Emberizidae	buntings and tanagers	603	4	<1	3	(?), unknown rich habitats (?), unknown

in which transitions have occurred frequently (table 3). It has long been known that there are substantial differences between clades of birds and avifaunal regions in the frequency of cooperative breeding. However, the differences revealed in my analysis do not necessarily reflect accepted wisdom. Most notably, cooperative breeding is most common in the Afrotropical region (277 or 15% of species). In part this is because the prevalence in the Australo-Pacific (174; 12%) is diluted by a low incidence of cooperative species among the diverse avifauna endemic to islands (Cockburn 2003), which have not been included in compilations of the Australian avifauna alone. However, an increased frequency among African species also results from new natural history data. Similarly, Arnold & Owens (1998) devoted discussion to why cooperative breeding was virtually absent in parrots, despite a life history amenable to this form of care. My compilation reveals that cooperation may have evolved repeatedly among parrots (see electronic supplementary material, part A).

4. DISCUSSION

Classical estimates of the frequency of different modes of parental care underestimate the frequency of cooperative breeding and female only care, even though these rare systems appear more likely to attract study and reporting than species with biparental care. I contend that the classical estimates are unreliable and should not be used as descriptive statistics or as a basis for comparative analysis.

While the primary aim of this paper is to erect a hypothesis of prevalence that can be used in comparative

analyses, it is clear that traditional views will require re-evaluation because of changes to phylogenies and our understanding of prevalence. Here, I briefly review some of the novel insights from the new dataset.

(a) *Male only care*

It has proved extremely difficult to identify a common pattern between the groups in which males are the predominant carers (Oring 1986; Clutton-Brock 1991; Andersson 1995, 2005; Ligon 1999; Bennett & Owens 2002). Even the best-known correlate, with precocial young (Lack 1968), is now known to have at least one exception (Andersson 1995). Much of the focus of empirical study and comparative analysis has been on waders migrating to high latitudes in the Holarctic (Szekely & Reynolds 1995; Reynolds & Szekely 1997). This emphasis is understandable, because in many waders parental care is dynamic and either the male or female can abandon care to the other at various stages of the nesting cycle. Hence, this group provides rich insights into the evolution of uniparental care. Some analyses have focused on behaviour peculiar to these taxa, such as the extent of the migration undertaken by the birds (Reynolds & Szekely 1997). However, male only care is primarily found in resident Gondwanan taxa that lack female only care. Transitions are from male only care to biparental care and have occurred twice in ratites, once in jacanas and once in painted snipe. Three of the transitions involve a decline in the incidence of male care with increasing distance from the Equator. Although some kiwis have male only incubation, biparental incubation becomes

Table 3. Taxa with a high incidence of cooperative breeding (more than 25%) or that contain at least three transitions to or from cooperative breeding. Some exclusively cooperative taxa may have evolved from a cooperative ancestor.

	species	cooperative	<i>p</i> (cooperative, %)	transitions	
<i>taxa with a high incidence of cooperative breeding</i>					
Maluridae	fairy-wrens	28	28	100	ancestral
Galbulidae	jacamars	18	18	100	1
Prunellidae	accentors	13	13	100	1
Coliidae	mousebirds	6	6	100	1
Phoeniculidae	woodhoopoes	5	5	100	ancestral
Pomatostomidae	Australian babblers	5	5	100	ancestral
Todidae	todies	5	5	100	1
Psophiidae	trumpeters	3	3	100	1
Bucorvidae	ground hornbills	2	2	100	ancestral
Corcoracidae	mudnest builders	2	2	100	1
Falcunculidae	shriketits	2	2	100	1
Neosittidae	sitellas	2	2	100	1
Upupidae	hoopoes	2	2	100	1
Anseranatidae	magpie goose	1	1	100	1
Opisthocomidae	hoatzin	1	1	100	1
Rhynchocetidae	kagu	1	1	100	1
Scopidae	hamerkop	1	1	100	1
Meropidae	bee-eaters	25	20	80	2
Climacteridae	treecreepers	7	5	71	1
Artamidae	cracticids and woodswallows	24	17	71	2
Mesitornithidae	mesites	3	2	67	1
Lybiidae	barbets	41	26	63	4
Acanthisittidae	New Zealand wrens	2	1	50	1
Corvoidea <i>incertae sedis</i>		24	12	50	unknown
Rheidae	rheas	2	1	50	1
Pardalotidae	pardalotes, scrubwrens, etc.	67	29	43	≥ 8
Corvidae	crows and jays	116	47	41	> 10
Aegithalidae	long-tailed tits	10	4	40	≥ 2
Malagasy warblers	tetrakas	10	4	40	1
Bucerotidae	hornbills	51	20	39	≥ 6
Picathartidae	rockfowl and rockjumpers	3	1	33	1
Paridae	tits	62	20	32	2
Passerida <i>incertae sedis</i>		72	20	28	unknown
Petroicidae	Australian robins	43	12	28	3
<i>taxa with numerous transitions to and from cooperation</i>					
Falconidae	falcons	62	15	24	≥ 4
Dacelonidae	kookaburras and kingfishers	59	14	24	≥ 4
Ramphastidae	toucans	48	11	23	≥ 3
Malaconotidae	bush-shrikes and vangas	101	23	23	≥ 3
Timaliidae	old world babblers	385	84	22	> 10
Mimidae	mockingbirds and thrashers	34	6	18	≥ 3
Pycnonotidae	bulbuls	121	20	17	≥ 7
Sturnidae	starlings	112	18	16	≥ 5
Rallidae	rails	132	18	14	> 10
Apodidae	swifts	91	12	13	4
Meliphagidae	honeyeaters	174	22	13	9
Icteridae	new world blackbirds	96	12	13	≥ 6
Cisticolidae	cisticolas	116	12	10	≥ 7
Acrocephalidae	acrocephalids	42	4	10	4
Emberizidae	buntings and tanagers	603	53	9	> 10
Picidae	woodpeckers	214	18	8	8
Muscicapidae	old world flycatchers	291	23	8	≥ 9
Ploceidae	weavers	268	19	7	≥ 3
Accipitridae	hawks and eagles	235	14	6	> 10
Campephagidae	cuckooshrikes	80	5	6	≥ 3
Psittacidae	parrots	347	19	5	10
Furnariidae	horneros, spinetails, etc.	213	7	3	≥ 4
Fringillidae	seedeaters and honeycreepers	159	5	3	≥ 3
Turdidae	thrushes	143	4	3	4
Nectariniidae	sunbirds	123	3	2	≥ 3
Tyrannidae	tyrant-flycatchers	337	6	2	≥ 3

more prevalent in populations from colder, southern sites and the extreme southerly populations are cooperative breeders, to the point that the dominant male may not incubate at all (Colbourne 2002). In both jacanas and rostratulids, it is also the species furthest from the Equator in which biparental care occurs. Attempts to link male only care to migration to extreme latitudes may therefore be misleading.

Owens (2002) has argued that contrasts between families exhibiting male and female only care support a *low-density* hypothesis, which proposes that males should care if density is sufficiently low to prevent them gaining any benefit by desertion, as they are unlikely to find alternative mates. The basis for this contrast is again motivated by the dynamic desertion strategy of Holarctic waders. However, there are problems with this analysis. First, the evolutionary transition in the majority of taxa is between biparental and male only care and it is unclear why the low-density hypothesis favours female desertion relative to biparental care. Second, it is clear that in at least two groups (ratites and megapodes), male only care is combined with polygyny and facilitates access to additional mates, rather than being a response to the low likelihood of obtaining another mate. Indeed, it appears that the evolution of biparental care in ostriches from an ancestral state involving male only care may reflect the advantage that the incubating female gains from pushing the eggs of supernumerary females away from the main clutch, so the eggs of supernumeraries are not incubated and vulnerable to predators (Bertram 1992; Kimwele & Graves 2003). I therefore concur strongly with Andersson's (2005) assertion that a single hypothesis is unlikely to encompass all cases of male only care.

(b) *Female only care*

By contrast with male care, there is abundant evidence that common selection pressures have driven convergent evolution of female only care. As has long been recognized (Lack 1968) and as for male only care, female only care occurs in a number of clades with precocial nidifugous young, which do not require provisioning so the benefits of additional care are restricted. 257 of 1052 precocial species (24%) have uniparental care, compared to 605 of 8401 altricial species (7%; three species could not be assigned as precocial or altricial). However, by contrast with male only care, there are numerous origins of female only care among taxa with nidicolous, altricial young. It has been previously suggested that in such taxa, female only care has evolved in birds that feed largely on tropical fruit and nectar (Snow 1963). My compilation strongly supports this assertion. Many transitions in many families are associated with frugivory and nectarivory (table 2), including several not included in table 2 because they represent rare events within their families (e.g. two transitions within the broadbills, one within the bulbuls and possibly one or two within pigeons, electronic supplementary material, part A). The correlation has been explained in complementary ways from female and male perspectives. Because tropical fruit and flowers can be massively abundant, yet availability can be patchy on short-term spatial and temporal scales, males may gain advantage from the defence of fruiting trees or geographical locations that females frequently traverse in order to find fruiting or flowering trees (the hotspot hypothesis,

Bradbury 1981). From the female perspective, the limitation on reproduction is likely to be associated with the ability of the young to extract nutrition from abundant but low quality food. Hence male care is of limited value, allowing females to choose freely among males for good genes rather than for direct benefits from the male such as a high quality territory or paternal provisioning (the constrained female hypothesis, Mulder *et al.* 1994; Gowaty 1996).

Given the strength of this association between frugivory and female only care, it is profitable to examine the exceptional cases in which female only care has evolved in primarily insectivorous taxa, in which male care should be at a premium. There are two ways that insectivorous species could conform to the constrained female hypothesis. It has previously been pointed out that slow growth of chicks in the family Menuridae could reduce the cost of female provisioning and hence increase the value of good genes relative to paternal care (Lill 1986). A comparable argument can be made for low metabolic rates in Caprimulgiformes (Lane *et al.* 2004). More commonly, many of the insectivorous taxa with female only care occur in dense nesting aggregations in rich marshlands in which high abundance of food occurs because of seasonal irruptions of aquatic insects. This reduces the need for females to obtain care and together with high female densities, facilitates the evolution of polygyny (e.g. Verner 1964; Orians 1969; Wittenberger 1976).

However, a variety of taxa cannot be explained via this approach, particularly some insectivorous denizens of rainforests (e.g. Willis & Oniki 1995, 1998; Frith *et al.* 1997). It has been suggested variously that predation might be important in these species, because as originally suggested for frugivores (Willis *et al.* 1978), males might enhance detection of the nest by predators (Frith *et al.* 1997), because any attempt by males to guard a single female against extra-pair mating would impose impossible costs from the sit-and-wait predators that predominate in rainforest interiors (Willis & Oniki 1995, 1998) and because the intrinsic mortality schedules of long-lived tropical species may make parents reluctant to take risk during reproduction (Martin 2002). Further investigations of these cases will be extremely valuable.

(c) *Cooperative breeding*

Cooperative breeding is sufficiently pervasive that a useful first stage of comparative analysis may be to identify those taxa in which cooperative breeding is extremely rare, as the factors that determine the presence or absence of cooperative breeding may not be the same as those that lead to variation in the number of cooperative species within cooperative clades (Cockburn 1996, 2003). Cooperative breeding is rare in clades with precocial young (4% of 789 species, excluding those with zero or uniparental care), in contrast to taxa with altricial young (11% of 7698 species). The only clades in which there is a high frequency of cooperative breeding combined with precocial young are Rallidae, the small families Psophiidae and Mesitornithidae and the monospecific Rhynchocetidae and Anseranatidae. Complex cooperative systems have developed among rails, but many of the species contributing to prevalence show a simple level of cooperation, characterized by chicks of the first brood provisioning later broods in the same season.

Low levels of cooperation among precocial taxa are unsurprising, for the same factors that often allow one sex to provide exclusive care probably reduce the benefits that both dominants and supernumeraries obtain from care of offspring.

Despite these arguments, it is clear that cooperative breeding does not always reflect dependency on care. Some of the cases in which care by more than one parent are most important are not associated with cooperative breeding. For example, almost all species foraging at sea yet breeding on land form strong pair bonds and exhibit exclusive biparental care (307/308, 99.7%). Lack (1968) argued that such species face distinctive selective forces and should be analysed separately from other birds. The nine families involved, while coming from a number of distinct clades (Charadrii, Ciconiida, Sulida, Phaethontidae), share the habit of feeding on marine prey but often breed in dense colonies on offshore islands or cliffs. The reasons underlying obligate monogamy are several-fold. First, species feeding in marine environments must return to the land to breed, yet still obtain food from the sea, in which resources are often distributed patchily, necessitating prolonged departures to forage. Second, the greatest concentrations of food occur in areas of oceanic upwelling, including the polar regions, where eggs and/or young would freeze if left unattended. Third, there are extreme risks to reproduction posed by intraspecific interference and both intra and interspecific predation, to the extent that some species specialize on preying on the nests of others. Collectively, these forces conspire to enforce constant nest attendance. Although additional birds might be able to provide assistance, failure to coordinate such care may pose unacceptable risks to the parents and promote exclusive pair bonds. Some evidence for the evolution of help occurs in Adelie penguins, in which non-breeders (or failed breeders) improve survival of chicks, by huddling, herding into shelter and defending chicks against skuas (Tamiya & Aoyanagi 1982). Additional attendants have been observed in a number of species of tern (Cullen 1957; Gochfeld & Burger 1996; Nisbet 2002), but the adaptive significance of this 'help' is uncertain. For example, in white terns *Gygis alba*, when parents are absent, other adults and juveniles may approach, preen and brood other chicks. However, these supernumeraries are driven off by the parents and eventually by the chick itself (Niethammer & Patrick 1998), which is consistent with misplaced or redirected parenting. The exception among these marine taxa tends to prove the rule. Brown skuas (*Catharacta lonnbergi*) are true cooperative breeders (Young 1999). Males live the early part of their lives in 'clubs' in the low quality centres of the islands where breeding occurs. Eventually, these males form coalitions to take over breeding and feeding territories that are situated on the periphery of the island. Coalitions of males are necessary to drive off territory owners. Although there is a single chick, mating is egalitarian and all coalition males probably contribute paternity over many years. Classical biparental care only arises when all but one of the coalition partners has died, leaving a single male to monopolize the territory and mating options.

Cooperation is well known to be more common among residents than migrants. Elsewhere, I have argued that migratory and island faunas are more likely to be

comprised of pair breeders because colonization is facilitated by dispersal of both sexes (Cockburn 2003). While these approaches are promising, most of the stark differences in prevalence remain unexplained. Perhaps the most striking dichotomy is that between the two great radiations of passerines. In the 1097 species of New World suboscines, cooperative breeding is consistently rare, inferred in just 16 species from eight or nine transitions (1%). By contrast, a very large proportion of all oscines are cooperative breeders (577 of 4456 species; 13%) and there has been repeated evolution of cooperative breeding from pair breeding and vice versa. It is unlikely that there is a simple ecological or life history explanation for this difference. Both clades have diversified into an enormous range of niches and show overlapping variation in life history (Martin *et al.* 2000). The low prevalence in suboscines is unlikely to be a result of the environment they occupy. Several oscine taxa have primarily radiated in the Neotropics and hence overlap the range of the New World suboscines. Many of these have a high incidence of cooperation (e.g. New World jays, mimids, emberizids, icterids and wrens). Indeed, among the New World oscine clades containing more than just a few species, only the vireos, polioptilids and parulids are poor in cooperative breeders. The difference between oscines and suboscines is doubly remarkable because any ecological separation between the two clades is associated with oscine colonization of the canopy, while suboscines are most diverse at lower levels of the vegetation strata (Ricklefs 2002). Some authors have argued that foraging on the ground is particularly conducive to the evolution of cooperative breeding (Ford *et al.* 1988), which runs counter to the empirical pattern in this case.

The foregoing examples are a small subset of the unexplained evolutionary contrasts in avian parental care. Hopefully, this new data compilation will help focus on these and other problems and allow us to proceed to the development of predictive models.

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REFERENCES

- Andersson, M. 1995 Evolution of reversed sex roles, sexual size dimorphism, and mating system in coucals (Centropodidae, Aves). *Biol. J. Linn. Soc. Lond.* **54**, 173–181. (doi:10.1006/bjil.1995.0010)
- Andersson, M. 2005 Evolution of classical polyandry: three steps to female emancipation. *Ethology* **111**, 1–23. (doi:10.1111/j.1439-0310.2004.01057.x)

- Arnold, K. E. & Owens, I. P. F. 1998 Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proc. R. Soc. B* **265**, 739–745. (doi:10.1098/rspb.1998.0355)
- Barker, F. K., Barrowclough, G. F. & Groth, J. G. 2002 A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc. R. Soc. B* **269**, 295–308. (doi:10.1098/rspb.2001.1883)
- Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004 Phylogeny and diversification of the largest avian radiation. *Proc. Natl Acad. Sci. USA* **101**, 11 040–11 045. (doi:10.1073/pnas.0401892101)
- Barracough, T. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. B* **259**, 211–215.
- Bennett, P. M. & Owens, I. P. F. 2002 *Evolutionary ecology of birds: life histories, mating systems and extinction*. Oxford, UK: Oxford University Press.
- Bertram, B. C. R. 1992 *The ostrich communal nesting system*. Princeton, NJ: Princeton University Press.
- Birks, S. M. 1997 Paternity in the Australian brush-turkey, *Alectura lathami*, a megapode bird with uniparental male care. *Behav. Ecol.* **8**, 560–568.
- Boland, C. R. J., Heinsohn, R. & Cockburn, A. 1997 Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *J. Anim. Ecol.* **66**, 683–691.
- Bradbury, J. W. 1981 The evolution of leks. In *Natural selection and social behaviour: recent research and new theory* (ed. R. D. Alexander & D. W. Tinkle), pp. 138–169. New York, NY: Chiron Press.
- Brown, J. L. 1987 *Helping and communal breeding in birds: ecology and evolution*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Cockburn, A. 1996 Why do so many Australian birds cooperate: social evolution in the Corvidae? In *Frontiers of population ecology* (ed. R. B. Floyd, A. W. Sheppard & P. J. De Barro), pp. 451–472. East Melbourne, Australia: CSIRO.
- Cockburn, A. 1998 Evolution of helping behaviour in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* **29**, 141–177. (doi:10.1146/annurev.ecolsys.29.1.141)
- Cockburn, A. 2003 Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proc. R. Soc. B* **270**, 2207–2214. (doi:10.1098/rspb.2003.2503)
- Cockburn, A. 2004 Mating Systems and Sexual conflict. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 81–101. Cambridge, UK: Cambridge University Press.
- Coddington, C. L. & Cockburn, A. 1995 The mating system of free-living emus. *Aust. J. Zool.* **43**, 365–372. (doi:10.1071/ZO9950365)
- Colbourne, R. 2002 Incubation behaviour and egg physiology of kiwi (*Apteryx* spp.) in natural habitats. *NZ J. Ecol.* **26**, 129–138.
- Cullen, J. M. 1957 Plumage, age and mortality in the Arctic tern. *Bird Study* **4**, 197–207.
- Davies, N. B. 1992 *Dunnock behaviour and social evolution*. Oxford, UK: Oxford University Press.
- Edwards, S. V. & Naeem, S. 1993 The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* **141**, 754–789. (doi:10.1086/285504)
- Edwards, S. V., Kingan, S. B., Calkins, J. D., Balakrishnan, C. N., Jennings, W. B., Swanson, W. J. & Sorenson, M. D. 2005 Speciation in birds: genes, geography, and sexual selection. *Proc. Natl Acad. Sci. USA* **102**, 6550–6557. (doi:10.1073/pnas.0501846102)
- Ekman, J., Dickinson, J. L., Hatchwell, B. J. & Griesser, M. 2004 Delayed dispersal. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 35–47. Cambridge, UK: Cambridge University Press.
- Ericson, P. G. P., Christidis, L., Cooper, A., Irestedt, M., Jackson, J. A., Johansson, U. S. & Norman, J. A. 2002 A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. R. Soc. B* **269**, 235–241. (doi:10.1098/rspb.2001.1877)
- Ericson, P. G. B., Irestedt, M. & Johansson, U. S. 2003 Evolution, biogeography, and patterns of diversification in passerine birds. *J. Avian Biol.* **34**, 3–15. (doi:10.1034/j.1600-048X.2003.03121.x)
- Ford, H. A., Bell, H., Nias, R. & Noske, R. 1988 The relationship between ecology and the incidence of cooperative breeding in Australian birds. *Behav. Ecol. Sociobiol.* **22**, 239–249. (doi:10.1007/BF00299838)
- Frith, C. B., Frith, D. W. & Jansen, A. 1997 Nesting biology of the chowchilla *Orthonyx spaldingii*. *Emu* **97**, 18–30. (doi:10.1071/MU97002)
- Gochfeld, M. & Burger, J. 1996 Family Sternidae (terns). In *Handbook of the birds of the world* (ed. J. del Hoyo, A. Elliott & J. Saragatal) *hoatzin to auks*, vol. 3, pp. 624–667. Barcelona, Spain: Lynx edicions.
- Gowaty, P. A. 1996 Field studies of parental care in birds: new data focus questions on variation among females. *Adv. Stud. Behav.* **25**, 477–531.
- Goymann, W., Wittenzeller, A. & Wingfield, J. C. 2004 Competing females and caring males, polyandry and sex-role reversal in African black coucals, *Centropus grillii*. *Ethology* **110**, 807–823. (doi:10.1111/j.1439-0310.2004.01015.x)
- Göth, A. & Vogel, U. 2004 Is monogamy in the Polynesian megapode (*Megapodius pritchardii*) related to its high relative egg-weight. *Auk* **121**, 308–317.
- Jones, D. N., Dekker, R. W. R. J. & Roselaar, C. S. 1995 *The Megapodes: Megapodiidae*. Oxford, UK: Oxford University Press.
- Kimball, R. T., Parker, P. G. & Bednarz, J. C. 2003 Occurrence and evolution of cooperative breeding among the diurnal raptors (Accipitridae and Falconidae). *Auk* **120**, 717–729.
- Kimwele, C. N. & Graves, J. A. 2003 A molecular genetic analysis of the communal nesting of the ostrich (*Struthio camelus*). *Mol. Ecol.* **12**, 229–236. (doi:10.1046/j.1365-294X.2003.01727.x)
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London, UK: Chapman & Hall.
- Lammertink, M. 2004 Grouping and cooperative breeding in the great slaty woodpecker. *Condor* **106**, 309–319.
- Lane, J. E., Swanson, D. L., Brigham, R. M. & McKechnie, A. E. 2004 Physiological responses to temperature by whip-poor-wills: more evidence for the evolution of low metabolic rates in Caprimulgiformes. *Condor* **106**, 921–925.
- Lanyon, S. M. 1992 Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. *Science* **255**, 77–79.
- Ligon, J. D. 1999 *The evolution of avian breeding systems*. Oxford, UK: Oxford University Press.
- Ligon, J. D. & Burt, D. B. 2004 Evolutionary origins. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 5–34. Cambridge, UK: Cambridge University Press.
- Lill, A. 1986 Time-energy budgets during reproduction and the evolution of single parenting in the superb lyrebird. *Aust. J. Zool.* **34**, 351–371. (doi:10.1071/ZO9860351)

- Martin, T. E. 2002 A new view of avian life-history evolution tested on an incubation paradox. *Proc. R. Soc. B* **269**, 309–316. (doi:10.1098/rspb.2001.1879)
- Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000 Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482–1485. (doi:10.1126/science.287.5457.1482)
- Martinez, J. G., Burke, T., Dawson, D., Soler, J. J., Soler, M. & Møller, A. P. 1998 Microsatellite typing reveals mating patterns in the brood parasitic great spotted cuckoo (*Clamator glandarius*). *Mol. Ecol.* **7**, 289–297. (doi:10.1046/j.1365-294X.1998.00348.x)
- McKinney, F. 1986 Ecological factors influencing the social systems of migratory dabbling ducks. In *Ecological aspects of social evolution: birds and mammals* (ed. D. I. Rubenstein & R. W. Wrangham), pp. 153–171. Princeton, NJ: Princeton University Press.
- Mulder, R. A., Dunn, P. O., Cockburn, A., Lazenby-Cohen, K. A. & Howell, M. J. 1994 Helpers liberate female fairywrens from constraints on extra-pair mate choice. *Proc. R. Soc. B* **255**, 223–229.
- Niethammer, K. R. & Patrick, L. B. 1998 White tern. In *Birds of North America: life histories for the twenty-first century* (ed. A. Poole, P. Stettenheim & F. Gill), 371, pp. 1–20. Washington, DC: American Ornithologist's Union and Academy of Natural Sciences.
- Nisbet, I. C. T. 2002 Common tern. In *Birds of North America: life histories for the twenty-first century* (ed. A. Poole, P. Stettenheim & F. Gill), 618, pp. 1–40. Washington, DC: American Ornithologist's Union and Academy of Natural Sciences, Philadelphia.
- Orians, G. H. 1969 On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**, 589–603. (doi:10.1086/282628)
- Oring, L. W. 1986 Avian polyandry. *Curr. Ornithol.* **3**, 309–351.
- Owens, I. P. F. 2002 Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in mating opportunities. *Phil. Trans. R. Soc.* **357**, 283–293. (doi:10.1098/rstb.2001.0929)
- Öst, M., Vitikainen, E., Waldeck, P., Sundstrom, L., Lindstrom, K., Hollmen, T., Franson, J. C. & Kilpi, M. 2005 Eider females form non-kin brood-rearing coalitions. *Mol. Ecol.* **14**, 3903–3908. (doi:10.1111/j.1365-294X.2005.02694.x)
- Price, T. 1998 Sexual selection and natural selection in bird speciation. *Phil. Trans. R. Soc.* **353**, 251–260. (doi:10.1098/rstb.1998.0207)
- Quillfeldt, P., Masello, J. F. & Hamer, K. C. 2004 Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. *Anim. Behav.* **68**, 613–620. (doi:10.1016/j.anbehav.2003.12.002)
- Ragusa-Netto, J. 2001 Sentinels in *Saltator atricollis* (Passeriformes: Emberizidae). *Rev. Bras. Biol.* **61**, 317–322. (doi:10.1590/S0034-71082001000200015)
- Reynolds, J. D. & Szekely, T. 1997 The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behav. Ecol.* **8**, 126–134.
- Ricklefs, R. E. 2002 Splendid isolation: historical ecology of the South American passerine fauna. *J. Avian Biol.* **33**, 207–211. (doi:10.1034/j.1600-048X.2002.330301.x)
- Russell, E. M. 2000 Avian life histories: is extended parental care the southern secret? *Emu* **100**, 377–399. (doi:10.1071/MU0005S)
- Seddon, N., Tobias, J. A. & Butchart, S. H. M. 2003 Group living, breeding behaviour and territoriality in the subdesert mesite. *Ibis* **145**, 277–294. (doi:10.1046/j.1474-919X.2003.00150.x)
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT and London, UK: Yale University Press.
- Sibley, C. G. & Monroe, B. L. 1990 *Distribution and taxonomy of birds of the world*. New Haven, CT and London, UK: Yale University Press.
- Snow, D. W. 1963 The evolution of manakin displays. In *Proc. XIII Int. Ornithological Congress Ithaca, NY 17–24 June 1962* (ed. C. G. Sibley, J. J. Hickey & M. B. Hickey), pp. 553–561. Baton Rouge, LA: American Ornithologists union.
- Sorenson, M. D. & Payne, R. B. 2001 A single ancient origin of brood parasitism in African finches: implications for host–parasite coevolution. *Evolution* **55**, 2550–2567.
- Szekely, T. & Reynolds, J. D. 1995 Evolutionary transitions in parental care in shorebirds. *Proc. R. Soc. B* **262**, 57–64.
- Tamiya, Y. & Aoyanagi, M. 1982 The significance of reoccupation by non-breeding birds in the Adelie penguin *Pygoscelis adeliae* during their incubation, guard and creche periods. *J. Yamashina Inst. Ornithol.* **14**, 35–44.
- Tobias, J. A. & Seddon, N. 2003 Breeding, foraging, and vocal behavior of the white-throated jacamar (*Brachygalba albogularis*). *Wilson Bull.* **115**, 237–240.
- Tobias, J. A., Züchner, T. & de Melo-Júnior, T. A. 2002 Family Galbulidae (Jacamars). In *Handbook of the birds of the world*, vol. 7 (ed. J. del Hoyo, A. Elliott & J. Saragatal), pp. 74–101. Barcelona, Spain: Lynx edicions.
- Verner, J. 1964 Evolution of polygamy in the long-billed grasswren. *Evolution* **18**, 400–413.
- Willis, E. O. & Oniki, Y. 1995 On *Dendrocincla tyrannina*: morphology, behavior and conservation of a shy lek-type insectivore. *Caldasia* **18**, 131–140.
- Willis, E. O. & Oniki, Y. 1998 One-parent nesting in cinnamon-vented pihas (*Lipaugus lanioides*, Cotinginae, Tyrannidae). *Ornithol. Neotrop.* **9**, 129–159.
- Willis, E. O., Wechsler, D. & Oniki, Y. 1978 On the behaviour and nesting of McConnell's flycatcher (*Pipromorpha macconnelli*): does female rejection lead to male promiscuity? *Auk* **95**, 1–8.
- Wittenberger, J. F. 1976 The factors favouring the evolution of polygyny in altricial birds. *Am. Nat.* **110**, 779–799. (doi:10.1086/283102)
- Young, E. C. 1999 *The millennium bird: cooperative breeding in Chatham Island skuas* (#EB00004269). Auckland: www.fatbrain.com.