

## Interspecific brood parasitism in galliform birds

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Mode of development in birds helps determine the form of brood parasitism a species exhibits. Most knowledge of precocial brood parasites comes from a single avian family, the waterfowl (Anatidae: Anseriformes). Here we review cases of interspecific brood parasitism (IBP) in a second group of precocial birds, the order Galliformes. IBP is uncommon but taxonomically widespread, occurring in at least 11 species and in four of five galliform families. By far the most common brood parasite is the Ring-necked Pheasant *Phasianus colchicus*. Hosts were generally other ground-nesting precocial species. It is unclear whether the absence of IBP in the Cracidae (Guans, Curassows, and Chachalacas) is due to the paucity of research on tropical gamebirds or because tropical birds such as the Cracidae may be less likely to practise IBP. Galliform birds mirror the trend found in ducks in which virtually all species that parasitize heterospecifics are also conspecific brood parasites (CBP). This association supports the hypothesis that IBP as an adaptive tactic or strategy may evolve from CBP. Alternatively, or additionally, egg-dumping may represent reproductive error on the part of females, such that concordance between CBP and IBP could be a byproduct of having sufficient knowledge of breeding biology only for a subset of galliform species.

**Keywords:** Anseriformes, egg-dumping, facultative strategies, Galliformes, nest parasitism, *Phasianus colchicus*, precocial development.

Maternal (including biparental) care of offspring is the norm in birds. Because females assume a partial or full role in raising young in more than 95% of avian species (Lack 1968), the evolution of alternative parental strategies has generated considerable interest. In particular, brood parasitism, in which a female lays her egg in another nest to be cared for by another individual, has long fascinated biologists. There is speculation that brood parasitism can evolve first as a facultative strategy in which females target conspecifics (conspecific brood parasitism, CBP), and then may further develop into either facultative or obligate parasitism of other species (interspecific brood parasitism, IBP) (Hamilton & Orians 1965, Payne 1977, Yamauchi 1995). However, in altricial birds, tests of this hypothesis have revealed that obligate

brood parasitism may arise directly from non-parasitic behaviour rather than from facultative intermediates (Sorenson & Payne 2001, 2002, Yom-Tov & Geffen 2006). The evolutionary development of IBP in precocial birds has yet to be studied in a comparative context, although CBP has been investigated in select clades (Beauchamp 1999, Geffen & Yom-Tov 2001).

Mode of development is a strong predictor of the degree to which brood parasites retain their ability to provide parental care (Lyon & Eadie 1991). The higher prevalence of facultative brood parasitism in precocial groups makes them ideal for investigating the proposed relationship between CBP and IBP (Rohwer & Freeman 1989). Ninety-four percent (33 of 35) of reported facultative interspecific brood parasites, along with 53% (124 of 232) of conspecific brood parasites (which are by definition facultative) have precocial young (Lyon & Eadie 1991, Yom-Tov 2001). In contrast,

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only 1% (1 of 100, the Black-headed Duck *Heteronetta atricapilla*) of obligate brood parasites develop precocially.

Although it is clear that facultative brood parasitism is more prevalent in precocially developing species, there is a lack of consensus on the causal factors behind this pattern. Rohwer and Freeman (1989, 1992) argued that the cost to the host of raising parasitic offspring may differ between altricial and precocial species, with altricial species more likely to evolve defensive strategies against parasitism (e.g. territoriality) to avoid the relatively more costly additions to their brood. Alternatively, the relative benefit for a potential parasite in pursuing a parasitic strategy may differ depending on developmental mode. In precocial species, host nests may be accessed more easily prior to incubation and dumped eggs may be less likely to cause nest failure; these factors make a facultative parasitic strategy more likely to augment parasite fitness (Sorenson 1992). Variation exists in the presence of CBP even within precocial clades. For example, in a comparative analysis of life-history characteristics of both gamebirds and waterfowl, Geffen and Yom-Tov (2001) found CBP was associated with higher clutch sizes and cavity nesting.

Various life history parameters have contributed to the particularly high prevalence of facultative brood parasitism in the family Anatidae (Rohwer & Freeman 1989, 1992, Lyon & Eadie 1991, Sorenson 1992, Geffen & Yom-Tov 2001). Twenty-seven percent (64 of 232 species) of all conspecific brood parasites are waterfowl, as are the vast majority (31 of 35) of birds that facultatively parasitize other species. Thus far, the association between IBP and CBP has emerged from this single family; a broader taxonomic review of IBP is required to determine whether this relationship is unique to waterfowl or represents a more general pattern in birds with reduced post-hatch parental care. The order Galliformes is another logical group in which to examine facultative parasitic strategies (Geffen & Yom-Tov 2001); it is second only to Anatidae in terms of the number of precocial species that practise CBP (32 species, Yom-Tov 2001). Until now, this group has been overlooked when considering IBP, although Lyon and Eadie (1991) list two species of interspecific brood parasites, Ring-necked Pheasants *Phasianus colchicus* and Northern Bobwhite *Colinus virginianus*. Two reviews of avian brood parasitism fail to mention galliform birds (Rothstein & Robinson 1998, Davies 2000).

The purpose of this study was to undertake a review of IBP by galliform birds. The taxonomic distributions of both the parasitic Galliformes and their hosts are summarized and used to examine the co-occurrence of CBP and IBP in this clade. Anatids that parasitize other species typically also parasitize conspecifics (Lyon & Eadie 1991); this relationship supports the hypothesis that CBP could be a precursor to adaptive IBP in precocial birds (Hamilton & Orians 1965, Payne 1977). Alternatively, or additionally, egg-dumping could reflect reproductive errors on the part of females, and associations between CBP and IBP could stem from biases in reporting, or IBP existing as a by-product of CBP in some species. Although our study is not designed to distinguish between these possibilities, our hope is that it will facilitate future research on brood parasitism in precocial birds.

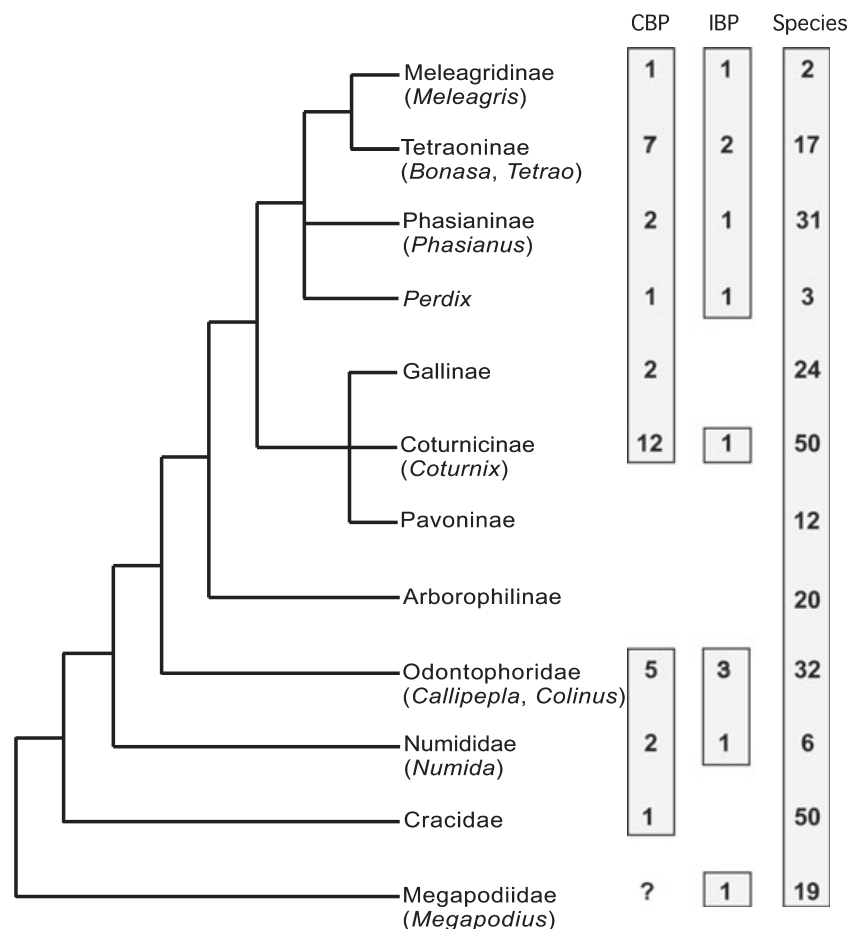
## METHODS

Observations of brood parasitism were included only from reports identifying both host and brood parasite to species. Reports were excluded when the author expressed doubt regarding the nature of the interspecific interaction, for example instances in which the observer suggested the possibility of two species simultaneously incubating at a nest, two species laying in a nest in which it was unclear which species incubated, or cases in which either the host or the brood parasite was not identified to species. Additionally, observations were excluded in which either the host or the brood parasite was described as feral or domestic, or a species was clearly feral; we were concerned that human-imprinted or mis-imprinted birds might exhibit unusual nesting behaviour not found in wild individuals. Introduced or re-introduced species were included, as several species (e.g. Ring-necked Pheasant, Wild Turkey *Meleagris gallopavo*, Grey Partridge *Perdix perdix*) are now considered widely established outside of their historic range. Published accounts of brood parasitism were collected by searching a variety of English language sources including periodical databases (Biosis, Wildlife Worldwide and Web of Science) as well as print resources in the University of California Berkeley library specifically dealing either with the natural history of galliform birds or the natural history of birds from specific geographic regions. A list of more than 50 print resources examined that did not document IBP is available from the authors.

To illustrate the taxonomic distribution of CBP and IBP within Galliformes, a composite phylogeny was constructed based upon several sources (Fig. 1; Crowe *et al.* 2006, Kaiser *et al.* 2006, Kimball *et al.* 2006, Cox *et al.* 2007, Kimball & Braun 2008). The precise relationships between families and sub-families are unimportant for the non-phylogenetically controlled test we conduct (see below). A more rigorous phylogenetic test was not possible due both to the absence of a phylogeny with all species that exhibit brood parasitism and the difficulty in determining whether the absence of brood parasitism in a species might represent a failure to detect the behaviour rather than a true

lack of brood parasitism. Although the family of megapodes and brush-turkeys (Galliformes: Megapodiidae) contains at least one interspecific brood parasite (Table 1), they will be excluded from comparisons involving rates of CBP (following Yom-Tov 2001, Yom-Tov pers. comm.). Given their unique nesting biology (Jones *et al.* 1995), it is impossible to apply current definitions of brood parasitism to this group.

To test the hypothesis that IBP is associated with CBP in both Galliformes and Anseriformes, G-tests for independence (Sokal & Rohlf 1995) were used to test whether IBP occurs significantly more often in species that are known to engage in



**Figure 1.** Cladogram showing major galliform lineages. Within the Phasianidae, subfamily designations match those recently proposed by Crowe *et al.* (2006), with genera exhibiting interspecific brood parasitism noted in parentheses. Relationships are a composite of several recent sources (Crowe *et al.* 2006, Kaiser *et al.* 2006, Kimball *et al.* 2006, Cox *et al.* 2007, Kimball & Braun 2008); minor differences among these sources occur in the relationship among the Meleagridinae, Tetraoninae, and *Perdix* as well as among the Gallinae, Coturnicinae, and Pavoninae, though none of these differences affects the conclusions of this study. Columns *CBP* and *IBP* indicate the number of reports of brood parasitism describing a conspecific or interspecific host. The *Species* column indicates the number of species included in that clade (some species of unknown phylogenetic position are not included in the species counts).

**Table 1.** List of galliform birds reported to practise interspecific brood parasitism.

Brood parasitic species		Host species		
Scientific name	Common name	Scientific name	Common name	References
Family Cracidae				
No reported instances of interspecific brood parasitism				
Family Megapodidae				
<i>Megapodius freycinet</i>	Dusky Megapode	<i>Aepyodopus arfakianus</i>	Wattled Brushturkey	Dwyer 1980
Family Numididae				
<i>Numida meleagris</i>	Helmeted Guineafowl	<i>Plectropterus gambensis</i>	Spur-winged Goose	Wolff 1976
Family Odonotophoridae				
<i>Callipepla californica</i>	California Quail	<i>Meleagris gallopavo</i>	Wild Turkey	Krakauer 2003
		<i>Oreortyx pictus</i>	Mountain Quail	Grinnell <i>et al.</i> 1918
		<i>Pipilo maculatus</i>	Spotted Towhee	Bleitzi 1956
		<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	Bent 1932
<i>Callipepla gambelii</i>	Gambel's Quail	<i>Toxostoma curvirostra</i>	Curve-billed Thrasher	Bent 1932
<i>Colinus virginianus</i>	Northern Bobwhite	<i>Phasianus colchicus</i>	Ring-necked Pheasant	Hamerstrom 1936 Eklund 1942 Blain 1954 McHenry 1966 Holcomb 1968 Platt 1968
Family Phasianidae				
<i>Bonasa umbellus</i>	Ruffed Grouse	<i>Dendragapus fuliginosus</i>	Sooty Grouse	Finley 1896
<i>Coturnix pectoralis</i>	Stubble Quail	<i>Coturnix ypsilophora</i>	Brown Quail	Serventy & Whittell 1962
<i>Meleagris gallopavo</i> <sup>a</sup>	Wild Turkey	<i>Bonasa umbella</i>	Ruffed Grouse	Kenamer 1989 Stoll 1992 <sup>a</sup> Hewitt 1993
<i>Perdix perdix</i> <sup>a</sup>	Grey Partridge	<i>Phasianus colchicus</i>	Ring-necked Pheasant	Millais 1909 Tegetmeier 1911 <sup>a</sup> Hamerstrom 1936
<i>Phasianus colchicus</i>	Ring-necked Pheasant	<i>Tetrao tetrix</i>	Black Grouse	Sargent 1886
		<i>Anas acuta</i>	Northern Pintail	Sharp & McClure 1945
		<i>Anas clypeata</i>	Northern Shoveler	Bennett 1936 Sharp & McClure 1945 Miller & Collins 1954 Evans & Wolfe 1967
		<i>Anas cyanoptera</i>	Cinnamon Teal	Miller & Collins 1954
		<i>Anas discors</i>	Blue-winged Teal	Bennett 1936 <sup>a</sup> , Bennett 1938, Carlson 1943 <sup>a</sup> , Nickell 1966 <sup>a</sup> , Evans & Wolfe 1967
		<i>Anas platyrhynchos</i>	Mallard	Bennett 1936, Carlson 1943 Sharp & McClure 1945 Miller & Collins 1954 Evans & Wolfe 1967
		<i>Anas strepera</i>	Gadwall	Miller & Collins 1954
		<i>Bonasa umbellus</i>	Ruffed Grouse	Finley 1896 Leffingwell 1928 Clark 1939 Bump <i>et al.</i> 1947 <sup>a</sup> Kenaga <i>et al.</i> 1955 <sup>a</sup>
		<i>Colinus virginianus</i>	Northern Bobwhite	Carlson 1943 Leedy & Hicks 1945 Westemeier <i>et al.</i> 1989 <sup>a</sup>

Table 1. Continued.

Brood parasitic species		Host species		
Scientific name	Common name	Scientific name	Common name	References
		<i>Crex crex</i>	Corncrake	Millais 1909
		<i>Crossoptilon mantchuricum</i>	Brown-eared Pheasant	Tegetmeier 1911
		<i>Dendrogapus fuliginosus</i>	Sooty Grouse	Zheng-wang 1995 <sup>a</sup>
		<i>Meleagris gallopavo</i>	Wild Turkey	Leffingwell 1928
		<i>Perdix perdix</i>	Grey Partridge	Schmutz 1988 <sup>a</sup>
				Tegetmeier 1911 <sup>a</sup>
				Bennett 1936 <sup>a</sup>
				Hamerstrom 1936
				Errington & Hamerstrom 1938
				Carlson 1943
				Knott <i>et al.</i> 1943
				Yocum 1943
				Leedy & Hicks 1945
		<i>Rallus elegans</i>	King Rail	Bennett 1936
				Hamerstrom 1936
		<i>Rallus limicola</i>	Virginia Rail	Bennett 1936
		<i>Scolopax rusticola</i>	Eurasian Woodcock	Tegetmeier 1911
		<i>Tetrao tetrrix</i>	Black Grouse	Millais 1909
		<i>Tetrao urogallus</i>	Capercaillie	Millais 1909
		<i>Tympanuchus cupido</i>	Greater Prairie-chicken	Carlson 1943
				Westemeier <i>et al.</i> 1998 <sup>a</sup>
		<i>Tympanuchus pallidicinctus</i>	Lesser Prairie-chicken	Hagen <i>et al.</i> 2002 <sup>a</sup>
<i>Tetrao tetrrix</i>	Black Grouse	<i>Lagopus lagopus</i>	Red Grouse	Millais 1909
		<i>Tetrao urogallus</i>	Capercaillie	Millais 1909

<sup>a</sup>Denotes an interaction resulting in hatching of parasitic egg.

CBP than in species for which CBP has not been documented. Separate tests were conducted for each order, and included Williams' corrections for small sample size (Sokal & Rohlf 1995). The occurrences of CBP for both orders were obtained from a recent review (Yom-Tov 2001) and included two additional galliform species not listed in this review (see Results). Data on IBP in Anseriformes were obtained from Lyon and Eadie (1991). Analyses were conducted using EXCEL (Microsoft Corp., Redlands, WA, USA).

## RESULTS

### Taxonomic distribution of parasites and hosts

Eleven species (4% of 281 species) in the order Galliformes have been reported to deposit eggs into 29 species of hosts in a total of 35 parasite/host interactions (Table 1). Interspecific brood parasites were found broadly distributed across the Galliformes, with occurrences in most families and

many lineages within the speciose Phasianidae (Fig. 1). The only family in which IBP was not reported was the neotropical Cracidae (Guans and Chachalacas). Ring-necked Pheasants were implicated as the brood parasite in the majority (19 of 35) of interactions, and all but two of the 13 interactions that were known to result in parasitic eggs hatching.

Rates of parasitism were difficult to assess in many of the published reports; however, it is clear that brood parasitism by galliform birds is typically an uncommon occurrence. Five of the 11 parasitic species were only observed in a single event with a single host (Table 1). The remaining six parasitic species could be assigned to some combination of (1) parasitizing multiple host species, (2) multiple observers reporting the same parasite–host interaction, or (3) a single report documenting multiple parasitized nests. In studies that mentioned the total number of nests surveyed, the number of parasitized nests rarely exceeded 10%. Exceptions to this trend included Holcomb's (1968) report of a 23% parasitism rate (seven of 31 host nests) by

Northern Bobwhite, as well as Errington and Hamerstrom's (1938) description of a 27% parasitism rate (seven of 26 nests) by Ring-necked Pheasants. In a long-term study, Westemeier *et al.* (1998) monitored parasitism rates while measuring the growth of a Ring-necked Pheasant population. Parasitism rates increased from zero prior to the presence of Pheasants to 29% of host nests during years of peak Pheasant density. In some study areas within the larger population, annual IBP rates exceeded 50% (Westemeier *et al.* 1998).

Of the host species, 15 were other Galliformes, seven were Anseriformes, three were Gruiformes, three were Passeriformes and one belonged to the Charadriiformes. All 'waterbird' hosts were parasitized by Ring-necked Pheasants with one exception, a Helmeted Guineafowl, which was reported to lay in the nest of a Spur-winged Goose *Plectropterus gambensis* (Wolff 1976). All three instances of parasitism of passerine nests involved New World Quail of the genus *Callipepla*.

### Conspecific and interspecific brood parasitism

IBP was strongly associated with CBP (Table 2, Fig. 1). In the order Galliformes, at least nine of the 10 interspecific brood parasites (excluding a single megapode for which CBP status could not be defined) also parasitized members of their own species. Seven of 10 interspecific brood parasites were listed in Yom-Tov's (2001) review of CBP. For two of the three species not included, Gambel's Quail and Ruffed Grouse, Bent (1932)

**Table 2.** Associations between interspecific brood parasitism (IBP) and conspecific brood parasitism (CBP) in Galliformes and Anseriformes.

	Galliformes <sup>a,b</sup> ( <i>n</i> = 256)		Anseriformes <sup>b</sup> ( <i>n</i> = 150)	
	CBP present <sup>c</sup>	CBP absent	CBP present	CBP absent
IBP present	9	1	28	3 <sup>d</sup>
IBP absent	25	221	36	83

<sup>a</sup>Excludes Megapodiidae, as CBP status cannot be assessed.

<sup>b</sup>Fisher's exact test, *P* < 0.0001.

<sup>c</sup>Includes 32 species from Yom-Tov (2001), plus two species from Bent (1932).

<sup>d</sup>Facultative brood parasites only, does not include *Heteronetta atricapilla*.

describes one or more nests containing a clutch more than twice the mean clutch size for the species, thereby meeting one of Yom-Tov's criteria. We found no report of CBP in the poorly studied Stubble Quail. In a phylogenetically uncontrolled comparison, the proportion of interspecific brood parasites was significantly higher in species that also engage in CBP (G-test:  $\chi^2_1 = 28.7$ , *P* < 0.0001). This association was also significant for the order Anseriformes (G-test:  $\chi^2_1 = 38.4$ , *P* < 0.0001).

## DISCUSSION

### Distribution of brood parasites and limitations of the dataset

IBP has been documented in all but one major group of galliform birds. Although published reports frequently described single incidents of parasitism, six of the 11 parasitic species were found to engage in parasitism more than once. When parasitism rates could be estimated, they were typically low, although occasionally exceeded 20% of host nests. Hosts were frequently other species of Galliformes or other ground-nesting precocial species such as waterfowl. From this we conclude that IBP in this order is generally uncommon but taxonomically widespread typically with hosts and parasites having similar nesting biology.

The only galliform family not represented in this survey was the Cracidae. One possible explanation for the apparent absence of IBP in this group involves the relatively small clutch size of cracids (typically two to four eggs, del Hoyo *et al.* 1994). Moreover, clutch size increases with latitude in Galliformes (Lack 1968), suggesting that latitudinal patterns of clutch size could contribute to the apparent over-representation of north-temperate species among observed brood parasites. Geffen and Yom-Tov (2001) found that larger clutch size relative to body size was positively associated with the presence of CBP in both the Anatidae and Galliformes. Increased clutch size is thought to promote CBP by extending the period during which host nests are vulnerable to parasitism prior to incubation (Yom-Tov 1980). This reasoning would fail to explain a clutch-size effect on IBP unless IBP was a non-adaptive byproduct of CBP.

Biases in the likelihood of detecting and reporting brood parasitism in the literature available to

the authors almost certainly contribute to the observed patterns of IBP and CBP (e.g. the under-representation of tropical taxa such as the family Cracidae). Many observations of IBP arose from intensively managed populations or studies that carefully monitored a host species, populations that may be more common in north-temperate regions. Additionally, geography might influence the likelihood that a given observation makes it into print. A chance observation of brood parasitism by an amateur ornithologist seems more likely to be published if local birding newsletters or magazines devoted to management of that species are available. Thus it is possible that biases such as these could also account for the apparent concordance of IBP and CBP, as the species found to exhibit both are some of the most intensively studied in the order.

### Evolution of brood parasitism in precocial birds

Given the limitations of the dataset described above, it may be unwise to compare parasitism rates across avian orders. However, the strong relationship between CBP and IBP warrants closer attention. Excluding the megapodes, for which CBP was not assessed (Y. Yom-Tov pers. comm.), all but one species identified as interspecific brood parasites also parasitize conspecifics. This trend mirrors that seen in the waterfowl, in which 28 of 31 species of interspecific parasites are also documented conspecific parasites (Lyon & Eadie 1991). Thus, for two orders of precocial birds, the two types of nest parasitism appear to be associated. This relationship may support the hypothesis that for facultative brood parasites, IBP may arise only after CBP has evolved (Hamilton & Orians 1965, Payne 1977, Yamauchi 1995, Cichón 1996). Researchers should search for interspecific brood parasites in other likely groups of precocial birds that may live at high density and are known to practise CBP (e.g. Rallidae: Gibbons 1986, Lyon 1993, Lyon & Eadie 2004). Comparative studies of altricial birds suggest that obligate brood parasitism did not arise through facultative intermediates (Yom-Tov & Geffen 2006); more complete knowledge of facultative brood parasitism will help determine the evolutionary sequence of brood parasitic strategies in precocial birds.

Unfortunately, nothing is known about the adaptive context of IBP in galliform birds. Given

the typical rarity of the behaviour, it might be tempting to consider this reproductive error or aberrant egg-laying, or possibly making 'the best of a bad job' (Weller 1959, Eadie *et al.* 1988, Sorenson 1992). Thus, brood parasitism may be akin to the laying of eggs away from a nest. This 'egg-dropping' is known from several galliform species (Stoddard 1931, Glading 1938, Labisky 1968, Wolff 1976, Williams & Austin 1988). However, there is some potential for a fitness benefit for parasitic mothers. At least 16 authors have reported chicks hatching from parasitic eggs in the nests of heterospecifics (Table 1). It is not known whether these young survived to reproductive age. It should be noted that we were unable to find documentation of adult recruitment of parasitic young of any species of facultative interspecific brood parasites, altricial or precocial; this is not surprising given the rarity of these observations. Even if IBP in galliform birds does represent reproductive error on the part of the parasitic female, the factors determining the presence and prevalence of this behaviour among different species and environments are worthy of further investigation.

### Implications

Interspecific brood parasitism may have important fitness consequences for individuals in both host and parasite populations. Parasitic young could become imprinted on the host species rather than on their own species (Slagsvold *et al.* 2002). This incorrect imprinting could result in unnatural behaviour at adulthood, as has been hypothesized to occur in one host-parasite system (Vance & Westemeier 1979). Mis-imprinting might also lead to improper mate choice, which could facilitate hybridization between hosts and parasites. In certain circumstances, facultative parasitism can have substantial negative impacts on host fitness, often through increased nest abandonment or decreased incubation efficiency (Kimmel 1988, Zheng-wang 1995, Westemeier *et al.* 1998). Further progress on facultative IBP requires continued collection and compilation of data on the presence and circumstances of this behaviour.

We would like to thank M. Hauber, E. Lacey, E. DuVal, W. Koenig, the University of California Berkeley Bird Group, and three anonymous reviewers for comments

on drafts of this manuscript, and Y. Yom-Tov for early advice. During portions of this research A.H.K. was supported by a National Science Foundation Graduate Research Fellowship and a Maillard Fellowship from the Museum of Vertebrate Zoology at the University of California Berkeley.

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Received 5 June 2008;  
revision accepted 21 January 2009.