

# Mode of development and interspecific avian brood parasitism

Avian interspecific brood parasites differ considerably in their commitment to parasitism; 87 species are obligate brood parasites, whereas 35 species are known to be facultative brood parasites. This variation is strongly related to mode of development. Obligate parasitism is found almost exclusively in altricial species, whereas facultative interspecific parasitism is predominant in precocial birds. We propose that the association between mode of development and form of parasitism reflects a fundamental difference between altricial and precocial birds in the relative benefits of emancipation from parental care after laying. We argue that altricial brood parasites obtain such a large increase in realized fecundity by avoiding the costs of parental care that obligate parasitism is favored over facultative parasitism. In contrast, precocial brood parasites gain relatively little in terms of increased fecundity via obligate parasitism, and much of this increase could potentially be gained by facultative parasitism. Thus, obligate interspecific brood parasitism will not be favored in precocial birds. Three factors influence this difference between altricial and precocial species: (1) altricial birds have relatively more energy and nutrients with which to lay additional eggs, (2) altricial birds can produce more eggs for the same amount of energy and nutrients, and (3) altricial birds realize a greater relative gain in fecundity for each additional egg laid. We suggest further that facultative interspecific parasitism in birds may originate simply through a carry over of intraspecific parasitism; 29 of 33 facultative interspecific parasites also parasitize conspecifics. Facultative parasitism of other species would provide a greater range of potential host nests and could be maintained as an evolutionarily stable end point by the same mechanisms that maintain intraspecific brood parasitism. [*Behav Ecol* 1991;2:309–318]

Parental care can be costly, and it is therefore not surprising that individuals in a variety of organisms parasitize the parental care of other individuals (e.g., birds: Hamilton and Orians, 1965; Payne, 1977b; insects: Talamy, 1986; Wilson, 1975; fish: McKaye, 1985). One of the most common forms of reproductive parasitism is egg dumping or brood parasitism, whereby females lay their eggs in the nests of others and the hosts provide all subsequent care for the parasitic eggs and offspring. Although brood parasitism occurs both within and among species, parasitism of interspecific hosts is particularly intriguing because it often involves situations in which individuals of one species depend entirely on hosts of another species to rear their offspring. Such obligate brood parasitism occurs in a few insect taxa (Wilson, 1975), but is best known in birds, where it occurs in about 1% of all species (Lack, 1968; Payne, 1977b).

One obvious prerequisite for the evolution of obligate brood parasitism is the ability to

successfully parasitize another species (Hamilton and Orians, 1965). This may not be the only requirement, however, because several species of birds are facultative interspecific parasites. In these species, successful parasitism of interspecific hosts occurs, yet parental care has not been replaced by obligate parasitism. Why is there such variation among species in the degree of commitment to parasitism? Weller (1959) and Lack (1968) proposed one possibility. They argued that facultative parasitism is an intermediate step in the evolution of obligate brood parasitism and suggested that extant facultative parasites may be in evolutionary transition from a population with parental care to one that reproduces solely through interspecific parasitism. If this is correct, then the variation in commitment to parasitism simply reflects different stages in the evolution of obligate parasitism.

Here, we propose an alternative hypothesis; namely, that facultative and obligate brood parasitism represent different evolutionary

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end points and that these end points are influenced by a fundamental life history trait, mode of development. We first show that the frequency of facultative and obligate interspecific brood parasites differs across development modes. We then illustrate how mode of development will determine which form of brood parasitism is evolutionarily stable. Note that we are not concerned with the factors that initially give rise to parasitic behavior (see Hamilton and Orians, 1965), but rather with the factors that influence whether a species will become an obligate brood parasite once it is able to successfully parasitize another species.

### Mode of development and commitment to parasitism

We surveyed data from the literature to determine the relationship between mode of development and commitment to parasitism in birds (Payne, 1977b, for obligate parasites; Table 1 for facultative parasites). This analysis revealed that the relative abundance of obligate versus facultative interspecific brood parasites differs significantly according to developmental mode (Table 2). In altricial birds, 86 of 88 parasitic species are obligate brood parasites, whereas in precocial birds, only 1 of 34 parasitic species is an obligate brood parasite ( $G$  test with William's correction,  $G_{\text{adj}} = 111.2$ ,  $p < .001$ ). Most of the world's birds are altricial species (90% altricial, 10% precocial; Lack, 1968), and the relative abundance of altricial and precocial species within either type of parasitism may simply reflect the relative abundance of altricial and precocial birds in general (see Payne, 1977b). However, this does not appear to be the case. Considering first obligate brood parasites, precocial species are rarer than expected based on the relative abundance of precocial birds ( $G_{\text{adj}} = 11.7$ ,  $p < .001$ ). Among facultative interspecific brood parasites, fewer altricial species are observed than predicted by the relative abundance of altricial species ( $G_{\text{adj}} = 135.1$ ,  $p < .001$ ). Thus, the association between commitment to parasitism and mode of development appears to be real and results from a rarity of obligate brood parasitism in precocial birds and a rarity of facultative parasitism in altricial birds.

This analysis may be biased by phylogenetic constraints (Pagel and Harvey, 1988): interspecific brood parasitism is concentrated in only four altricial families and two precocial families of birds. Consequently, we may have inflated the sample size by considering each species as an independent observation. To ensure that this did not affect our results, we repeated the analysis by grouping species into

higher taxonomic categories. For altricial obligate brood parasites, we followed Lack (1968), who suggested that obligate interspecific parasitism arose independently six times. In both gallinaceous birds and cuckoos, facultative interspecific parasitism occurs in two species belonging to a single family, and we used family as the upper taxonomic unit. In waterfowl, the occurrence of facultative interspecific parasitism is variable within all tribes and most genera. An analysis of the phylogenetic distribution of parasitism in the Anseriformes indicates that the expression of parasitism reflects ecology, rather than phylogeny (Eadie, 1991). Although using genera, and possibly even species, in our comparison is probably justified for waterfowl, we used the more conservative level of tribes for this group. When we repeat our analysis using these more stringent criteria, the association between mode of development and the form of brood parasitism remains (Table 2;  $G$  test with Yates correction,  $G_{\text{adj}} = 6.6$ ,  $p < .02$ ).

### Mode of development and fecundity trade-offs of parasitism

Why should mode of development be associated with commitment to parasitism? We argue that this pattern is a result of differences in the relative benefits of brood parasitism to altricial and precocial birds. Specifically, we propose that altricial brood parasites obtain such a large increase in relative fecundity through emancipation from parental care after laying that obligate parasitism is favored over facultative parasitism. In contrast, we argue that precocial brood parasites gain little in terms of relative fecundity and that much of this additional fecundity can be gained through facultative parasitism. Thus, we would not expect obligate interspecific brood parasitism to evolve in precocial birds. To illustrate our logic, we develop a simple cost-benefit model and then use this model to consider how the costs and benefits of obligate and facultative brood parasitism differ for altricial and precocial birds.

#### *Cost-benefit model of brood parasitism*

Consider the trade-off involved in the evolution of obligate interspecific brood parasitism. Reproductive success can be partitioned into two components that could differ between a parasitic and a parental individual: fecundity ( $F$ ; the number of eggs that an individual lays) and egg success ( $S$ ; here defined as the proportion of eggs that result in fledged young). The product of these two components ( $F \times S$ ) yields the number of young fledged for an individual. For simplicity, we assume that the

Table 1  
Species of facultative interspecific brood parasites

Species	Reference
Altricial birds	
Family Cuculidae	
Yellow-billed cuckoo ( <i>Coccyzus americanus</i> ) <sup>a</sup>	Nolan and Thompson (1975); Weller (1959)
Black-billed cuckoo ( <i>C. erythrophthalmus</i> ) <sup>a</sup>	Nolan and Thompson (1975); Weller (1959)
Precocial birds	
Family Anatidae	
Tribe Dendrocygnini	
Fulvous whistling duck ( <i>Dendrocygna bicolor</i> ) <sup>a</sup>	Palmer (1976); Weller (1959)
Black-bellied whistling duck ( <i>D. autumnalis</i> ) <sup>a</sup>	Palmer (1976)
Tribe Anserini	
Snow goose ( <i>Anser caerulescens</i> ) <sup>a</sup>	Prevett et al. (1972)
Canada goose ( <i>Branta canadensis</i> ) <sup>a</sup>	Palmer (1976)
Tribe Cairini	
Wood duck ( <i>Aix sponsa</i> ) <sup>a</sup>	Bellrose (1976); Bouvier (1974); Palmer (1976)
Tribe Anatini	
Mallard ( <i>Anas platyrhynchos</i> ) <sup>a</sup>	Bellrose (1976); Weller (1959)
Gadwall ( <i>A. strepera</i> ) <sup>a</sup>	Weller (1959)
Pintail ( <i>A. acuta</i> )	Weller (1959)
Cinnamon Teal ( <i>A. cyanoptera</i> )	Palmer (1976); Weller (1959)
Blue-winged teal ( <i>A. discors</i> )	Palmer (1976); Weller (1959)
Shoveller ( <i>A. clypeata</i> )	Weller (1959)
Tribe Aythyini	
Redhead ( <i>Aythya americana</i> ) <sup>a</sup>	Bellrose (1976); Johnsgard (1978); Joyner (1976); Palmer (1976); Weller (1959)
Lesser scaup ( <i>A. affinis</i> ) <sup>a</sup>	Bellrose (1976); Johnsgard (1978); Palmer (1976); Weller (1959)
Greater scaup ( <i>A. marilla</i> ) <sup>a</sup>	Weller (1959)
Canvasback ( <i>A. valisineria</i> ) <sup>a</sup>	Bellrose (1976); Johnsgard (1978); Palmer (1976); Weller (1959)
Common White-eye ( <i>A. nyroca</i> ) <sup>a</sup>	Johnsgard (1978)
Red-crested pochard ( <i>Netta rufina</i> ) <sup>a</sup>	Johnsgard (1978)
Rosybill ( <i>N. peposaca</i> ) <sup>a</sup>	Johnsgard (1978)
Tribe Mergini	
Common goldeneye ( <i>Bucephala clangula</i> ) <sup>a</sup>	Bellrose (1976); Bouvier (1974); Eadie (1989); Palmer (1976)
Barrow's goldeneye ( <i>B. islandica</i> ) <sup>a</sup>	Eadie (1989); Erskine (1972); Palmer (1976); Weller (1959)
Bufflehead ( <i>B. albeola</i> ) <sup>a</sup>	Bellrose (1976); Erskine (1972); Palmer (1976)
Hooded merganser ( <i>Lophodytes cucullatus</i> ) <sup>a</sup>	Bellrose (1976); Bouvier (1974); Palmer (1976); Weller (1959)
Common merganser ( <i>Mergus merganser</i> ) <sup>a</sup>	Palmer (1976)
Red-breasted merganser ( <i>M. serrator</i> ) <sup>a</sup>	Palmer (1976); Weller (1959)
Smew ( <i>Mergellus albellus</i> ) <sup>a</sup>	Johnsgard (1978)
White-winged scoter ( <i>Melanitta fusca</i> ) <sup>a</sup>	Bellrose (1976); Palmer (1976)
Common eider ( <i>Somateria mollissima</i> ) <sup>a</sup>	Prevett et al. (1972)
Spectacled eider ( <i>S. fischeri</i> ) <sup>a</sup>	Bellrose (1976); Palmer (1976)
Tribe Oxyurini	
Ruddy duck ( <i>Oxyura jamaicensis</i> ) <sup>a</sup>	Bellrose (1976); Johnsgard (1978); Joyner (1976); Palmer (1976)
White-headed duck ( <i>O. leucocephala</i> ) <sup>a</sup>	Johnsgard (1978)
Maccoa duck ( <i>O. maccoa</i> ) <sup>a</sup>	Johnsgard (1978)
Family Phasianidae	
Ring-necked pheasant ( <i>Phasianus colchicus</i> ) <sup>a</sup>	Weller (1959)
Bobwhite quail ( <i>Colinus virginianus</i> ) <sup>a</sup>	Weller (1959)

<sup>a</sup> Species also known to exhibit intraspecific parasitism. Sources for intraspecific brood parasitism were Nolan and Thompson (1975) for Cuculidae; Eadie et al. (1988) and Johnsgard (1978) for Anatidae; Yom-Tov (1980) for Phasianidae.

number of chicks fledged is a reasonable index of fitness and that adult survivorship does not differ between parasitic and parental individuals (we consider the validity of this assumption below). Thus, an individual that reproduces via obligate brood parasitism will have

higher fitness than an individual that cares for its own eggs and offspring when

$$F_o \cdot S_o > F_p \cdot S_p \tag{1}$$

where the subscripts *o* and *p* refer to obligate

**Table 2**  
The number of obligate and facultative interspecific brood parasites according to developmental mode

Mode of development	Type of parasitism	
	Obligate	Facultative
Species		
Altricial	86	2
Precocial	1	33
Higher taxonomic groups		
Altricial	6	1
Precocial	1	8

Data for facultative brood parasites are given in Table 1. Data for obligate brood parasites are from Payne (1977b).

parasite and parental egg-laying strategies, respectively. Rearranging, we get:

$$F_o/F_p > S_p/S_o \quad (2)$$

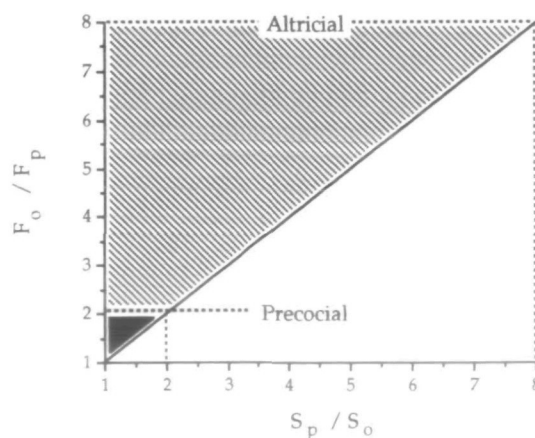
Equation 2 illustrates the basic trade-off involved in the evolution of obligate brood parasitism: increased fecundity versus reduced egg success. Because the time and energy invested in parental care after laying might otherwise be invested in increased egg production, parental care constrains realized fecundity. Emancipation from care, through brood parasitism, removes this constraint and so permits a potentially large increase in fecundity (i.e.,  $F_o/F_p > 1$ ). However, eggs laid parasitically could produce proportionally fewer offspring if parental care provided by the host species is inferior (i.e.,  $S_p/S_o > 1$ ). Obligate interspecific brood parasitism should evolve only when the relative gains in fecundity exceed the relative reduction in egg success (Figure 1).

**Figure 1**

A cost-benefit threshold for obligate brood parasitism. Obligate parasitism is favored above the solid diagonal line, where fecundity gains of a brood parasite ( $F_o/F_p$ ) exceed the reduction in egg success ( $S_p/S_o$ ). Horizontal dotted lines indicate the proposed upper limit on the fecundity gains for altricial and precocial brood parasites, respectively. Vertical dotted lines indicate the maximum reduction in relative egg success that could be sustained by altricial and precocial brood parasites, respectively, while still yielding a net benefit to obligate parasitism. Shaded areas indicate the possible regions where benefits exceed costs for hypothetical altricial (hatched) and precocial (solid) brood parasites.

#### Benefits of obligate parasitism for altricial and precocial birds

We propose that the cost-benefit ratio derived above differs markedly for altricial and



precocial birds because the relative gain in increased fecundity through brood parasitism ( $F_o/F_p$ ) is much higher for altricial birds than for precocial birds (Figure 1). There are at least three factors that could contribute to this difference:

**Factor 1: energy and/or nutrients available for egg production.** Clutch size in many altricial birds appears to be limited by factors other than the energy and/or nutrients available for egg production [e.g., the time and energy required for parental care after laying (Klomp, 1970; Lack, 1947), nest size (Slagsvold, 1982), or adult predation risk (Lima, 1987)]. Consequently, realized parental clutch sizes of altricial birds appear to be well below the maximum clutch size that would be possible if energy for egg production were limiting. Emancipation from parental care through obligate parasitism should permit a large increase in the total number of eggs that can be laid.

In contrast, the young of precocial species require little care after laying relative to altricial birds, and clutch sizes may be much closer to their potential maximum determined by the energy and/or nutrients available for egg production. There is now considerable evidence for some species of waterfowl that clutch size is limited by the availability of energy and nutrients, rather than by the demands of care after laying (Ankney and MacInnes, 1978; Ar and Yom-Tov, 1978; Drobney, 1980; Krapu, 1981; Ryder, 1970). Accordingly, emancipation from parental care would yield a smaller increase in egg production in precocial birds.

**Factor 2: egg size and the cost of egg production.** The eggs of altricial species are generally smaller and contain fewer nutrients and energy reserves than the eggs of most precocial species after controlling for differences in body size (Ar and Yom-Tov, 1978; Rahn et al., 1975; Ricklefs, 1977). For example, the eggs of Passeriformes and Cuculiformes are approximately one-half the size of eggs of Anseriformes when the influence of body size is controlled (Rahn et al., 1975). Moreover, even when the effects of egg size are removed, yolks of precocial eggs are nearly twice the size of yolks of altricial eggs (Carey et al., 1980). Thus, the eggs of altricial birds are cheaper to produce, and altricial birds should be able to produce more eggs for the same amount of available energy and nutrients than precocial species, once the constraints of providing parental care are removed.

We note that factors 1 and 2 are not mutually exclusive. For example, clutch sizes of precocial birds may be limited by energy and/or nutrients constraints (factor 1) because precocial birds make relatively large, energy-

rich eggs (factor 2). However, species that make large eggs are not necessarily energy limited, or vice versa. Hence, we consider these factors separately.

**Factor 3: clutch size and the relative value of each additional egg.** The fitness of a parasite relative to a parental individual depends on parental clutch size. Clutch sizes of altricial birds are generally smaller than those of precocial species, at least in taxa that contain brood parasites (Lack, 1968). Most waterfowl have clutch sizes of 6–12 eggs, and clutch sizes of grouse and quail range from 8 to 20 eggs. In contrast, clutch sizes of passerines are usually 4–6 eggs. Each additional egg laid by an altricial parasite therefore represents a greater relative increase in realized fecundity ( $F_o/F_p$ ) than it does for a precocial parasite. For example, if an altricial bird with a clutch of five eggs were able to lay five additional eggs by becoming a parasite, then the relative gain in fecundity ( $F_o/F_p$ ) of the altricial parasite would be  $10/5 = 2.0$ . Conversely, a precocial bird with a clutch of 10 eggs that laid 5 extra eggs by becoming parasitic would realize a relative gain in fecundity of only  $15/10 = 1.5$ .

We argue, then, that altricial birds (1) have relatively more energy and nutrients with which to lay additional eggs, (2) can produce more eggs for the same amount of energy and nutrients, and (3) realize a greater relative gain in fecundity for each additional egg laid. Together, these three factors should result in a high value of  $F_o/F_p$  for altricial birds, but a much lower value for precocial birds. This claim is supported by empirical data in the literature. Parasitic cowbirds, cuckoos, and weavers all lay five to eight times the number of eggs reared by closely related nonparasitic species (Payne, 1973, 1976, 1977a; Scott and Ankney, 1980). Moreover, egg-removal experiments show that nonparasitic altricial birds, such as flickers (*Colaptes auratus*) or wrynecks (*Jynx torquilla*), can lay up to 60–70 eggs in a single breeding season; i.e., 8–10 times the number of eggs laid in a normal clutch (Welty, 1975). The relative fecundity gain for an altricial parasite ( $F_o/F_p$ ) will therefore be five to eight times that of a nonparasitic bird.

In contrast, there is little empirical evidence that precocial brood parasites experience much of a fecundity gain via brood parasitism. Parasitic redheads (*Aythya americana*) laid approximately 10.8 eggs, which is identical to the average clutch size found in nests of parental females (Weller, 1959). Parasitic wood ducks (*Aix sponsa*; Clawson et al., 1979) and goldeneyes (*Bucephala* spp.; Eadie, 1989) laid a few more eggs than nonparasitic females, but the difference was small. Experimental egg removals with willow ptarmigan (*Lagopus lagopus*) resulted in doubling the normal clutch

size ( $F_o/F_p \approx 2$ ; Host, 1942). Similarly, Buss et al. (1951) found that ring-necked pheasants (*Phasianus colchicus*) laid, on average, twice the number of eggs found in a normal clutch. However, both Host (1942) and Buss et al.'s (1951) studies were of captive birds, presumably with access to unlimited food. Such increments in fecundity may not be possible under field conditions (see Rohwer, 1986). In several species of dabbling ducks, experimental egg removals did not result in any increase in the number of eggs laid, and clutch size was increased only slightly in captive mallards (*Anas platyrhynchos*; Rohwer, 1984). These results suggest that precocial birds gain only a slight increase in fecundity by laying parasitically, and the advantage is considerably less than that for altricial birds (i.e.,  $F_o/F_p$  is generally  $<2$ ).

#### *Costs of parasitism for precocial and altricial birds*

**Egg success.** Although parasitism offers potentially large increases in fecundity, the value of these additional eggs will depend on the success of those eggs once laid in the nest of another species. We expect the egg success of an interspecific brood parasite to be lower than that of a parental bird for a variety of reasons: (1) the host species may differ in diet, habitat, or parental care patterns such that parasitic offspring receive inadequate or inappropriate care; (2) hatch success of eggs in parasitized nests may be lower as a result of mismatched timing, reduced incubation efficiency, or inadvertent displacement from host nests; or (3) young in enlarged parasitized broods may suffer inadequate brooding, increased competition for food, or greater predation risk (e.g., Eadie and Lumsden, 1985; Hamilton and Orians, 1965; Payne, 1977b). This is not an exhaustive list of the factors that might reduce the success of parasitic eggs, and we have ignored the influence of host defenses such as egg ejection, egg burial, or nest desertion (see Payne, 1977b). Our point is simply that egg success of parasites is lower than that of parental birds, and this difference must be more than compensated for by the increase in fecundity in order for obligate brood parasitism to evolve (Figure 1).

How will this influence the relative frequency of obligate parasitism in altricial and precocial birds? We cannot envision any means by which differences in egg success of altricial versus precocial birds would directly give rise to the observed association between mode of development and type of parasitism. If anything, differences between altricial and precocial birds in the success of parasitic eggs could produce a pattern opposite to the one

we found. Eggs laid by precocial parasites should be more successful than those of altricial parasites, simply because precocial young feed themselves and are therefore less dependent on receiving appropriate parental care. However, even in precocial birds, egg success of parasites is likely to be lower than that of parental birds. Although data are scant, studies of facultative interspecific brood parasites indicate that the success of parasite eggs may be less than half that of eggs laid parentally (Joyner, 1976; Sorenson, 1990). Comparable data are not available for altricial species because most extant parasites are already specialized for a parasitic lifestyle, and egg success rates may not reflect those of an incipient obligate brood parasite. Nonetheless, it seems reasonable to suppose that egg success would be reduced for an interspecific parasite when parasitic behavior first arises.

Egg success therefore indirectly influences the association between mode of development and type of parasitism by limiting obligate parasitism to only those species that obtain sufficient increases in fecundity to exceed reductions in egg success. We propose that the fecundities of altricial parasites will frequently be high enough that an altricial parasite could sustain a considerable reduction in egg success before parasitism becomes less successful than parenting (Figure 1). If our estimates of the potential fecundity gains of an altricial parasite are correct (see above), then altricial parasites could sustain reductions in egg success of up to  $\frac{1}{2}$  to  $\frac{1}{3}$  that of a parental nesting female. In contrast, reductions in the success of parasitic eggs of a precocial parasite could quickly reduce the net benefit of parasitism below the cost-benefit threshold, simply because the fecundity gains for a precocial parasite are much lower. For example, if the egg success of a parasite were only half that of a parental female (e.g., Sorenson, 1990), precocial birds would fall below the threshold for the evolution of obligate brood parasitism (Figure 1).

**Host availability.** A second factor that will limit the success of an interspecific brood parasite is host availability. Host availability is a function of the abundance of nests of suitable host species as well as the time and energy costs of locating those nests. Although we have not explicitly included this factor in our model, the effect of host limitation will be to reduce realized parasite fecundity below the maximum potential, if host limitation actually prevents females from laying eggs, or to reduce egg success if host limitation forces females to lay in unsuitable nests. Either of these situations will reduce the relative benefit of parasitism. There are probably few consistent differences in host availability between altri-

cial or precocial birds and thus the effect of host limitation will simply be to offset the relative benefit of obligate parasitism for altricial and precocial species alike. As discussed earlier, we propose that the potential fecundity gains of an altricial parasite are often sufficient to offset these costs, whereas the gains of a precocial parasite are not.

#### *Obligate versus facultative parasitism*

We have so far considered the costs and benefits of obligate brood parasitism for altricial and precocial birds. However, we also need to contrast obligate with facultative interspecific brood parasitism because a facultative parasite may obtain many of the benefits of an obligate brood parasite without sacrificing the advantages of parental care. A simple modification of our cost-benefit model allows us to address this issue. For this comparison, a facultative parasite is an individual that raises the normal number of offspring through parental care, but also gains some extra fitness through parasitism. Fitness of a facultative parasite is therefore

$$F_p \cdot S_p + F_f \cdot S_o \quad (3)$$

where  $F_f$  is the number of parasite eggs that can be laid by a facultative parasite. For simplicity we assume that facultative parasites do not reduce their parental clutch size and that the eggs they lay parasitically have the same success as eggs laid by obligate parasites ( $=S_o$ ). By laying parasitically in this manner, a facultative parasite can increase her total production of offspring over what she would obtain as pure parent. Regardless of how poorly parasitic eggs fare, facultative parasitism will be favored as long as the benefits from parasitic eggs exceed the fitness costs of producing the eggs and getting them into host nests. However, when the fecundity benefits of complete emancipation from parental care are high enough and are coupled with a reasonable success of parasitic eggs, facultative parasitism may be less profitable than obligate parasitism. Thus, obligate parasitism is favored over facultative parasitism when

$$F_o \cdot S_o > F_p \cdot S_p + F_f \cdot S_o \quad (4)$$

or

$$(F_o - F_f)/F_p > S_p/S_o \quad (5)$$

Equation 5 shows that obligate parasitism will be favored over facultative parasitism only when the fecundity of an obligate parasite greatly exceeds the fecundity that a parent can achieve through facultative parasitism (i.e.,  $F_o - F_f$  is large). This difference depends on the extent to which parental care constrains a female's ability to achieve her maximum po-

tential fecundity as a facultative parasite. Thus, potential fecundity gains as a facultative parasite can act as an additional constraint on the evolution of obligate parasitism, just as lower egg success and host availability act as constraints.

In altricial birds, a facultative parasite would achieve only a fraction of the fecundity of an obligate parasite. Parasitism must generally occur outside the period of parental care because birds seem to be unable to lay eggs during the period that they are caring for their own eggs and young (e.g., see Gibbons, 1986; Lyon, 1991; Sorenson, 1990). Caring for young requires a large time investment; most altricial species require 4 weeks to produce a brood of four to six young (Harrison, 1984). Given that altricial birds are not energy limited and are capable of laying almost one egg per day, a facultative parasite would suffer a large loss in potential fecundity during the period it raises its own young relative to an obligate parasite. As soon as an altricial parasite includes a period of brood rearing in its overall reproductive strategy, its fecundity gain as a parasite is drastically reduced. The difference between  $F_o$  and  $F_f$  will therefore be large, and obligate parasitism should be favored.

In precocial birds, however, emancipation from parental care via obligate parasitism will not yield a large increase in fecundity relative to a facultative parasite because fecundity is limited more by energy than by time. Even if a precocial parasite is released from the time constraints of parental care, nutrient and energy limitations still constrain the number of additional eggs that can be laid (see above). As a result, a facultative parasite should be able to achieve almost the same fecundity as an obligate parasite by laying some eggs parasitically and, after sufficient time to recoup resources, laying a second clutch to raise parentally—a pattern observed in some species (Sorenson, 1990; Weller, 1959). For this reason, the difference between  $F_o$  and  $F_f$  is likely to be small for precocial birds, and, when combined with the effects of host limitation and lower parasite egg success, facultative parasitism should be the prevalent form of parasitism (Table 2).

## DISCUSSION

Our analyses demonstrate a clear association between mode of development and the form of interspecific brood parasitism in birds. Although other authors have hinted at this pattern previously, there have been few attempts either to assess its validity or to propose an explanation for its occurrence. In the one attempt that we are aware of, Payne (1977b)

suggested that the higher frequency of obligate brood parasitism in altricial birds was due simply to the fact that there are far more altricial than precocial species. We tested and firmly rejected this hypothesis. Moreover, the higher frequency of facultative interspecific brood parasites in precocial birds directly contradicts Payne's (1977b) hypothesis. Thus, the association between mode of development and type of parasitism appears to be real and requires explanation.

We have proposed that the explanation for this pattern lies primarily in the difference in the potential fecundity gains of an altricial versus precocial brood parasite. We suggest that altricial birds realize such large increases in fecundity through complete emancipation from parental care that obligate parasitism will frequently be a profitable tactic even when reductions in egg success and the effects of host limitation are considered. Facultative interspecific parasitism, on the other hand, will not be a stable end point for most altricial parasites because much of the increase in fecundity gained through parasitism will be lost once any period of parental care is included in the reproductive repertoire. Thus, once an altricial bird is able to successfully parasitize another species, parasitism should proceed to the obligate state. In contrast, precocial birds will realize only a slight increment in fecundity via complete emancipation from parental care, and reductions in egg success and host availability will rapidly reduce the benefits of parasitism below the threshold for the evolution of obligate parasitism. Moreover, facultative parasitism may yield much of the increment in fecundity provided by obligate parasitism, without complete abandonment of parental care. Thus, we expect obligate parasitism to be uncommon in precocial birds, as observed.

We recognize that our hypothesis is based on several untested assumptions. For example, few data are available on the relative fecundities or egg success of facultative versus obligate brood parasites, yet this information is critical to assess the proposed trade-offs identified in Equations 2 and 5. Similarly, we identified three factors that would cause the fecundity gain of an altricial interspecific brood parasite to greatly exceed that of a precocial interspecific brood parasite, yet we do not know the relative importance of each factor. It has long been accepted that clutch size in altricial birds is limited by parental care after laying, whereas clutch size in precocial birds is limited by energy or nutrients for egg formation (Lack, 1968). However, there are several exceptions to this pattern (e.g., Jones and Ward, 1976; Safriel, 1975), and there is currently some debate over its generality (Winkler and Walters, 1983). Nonetheless, we



do know that egg sizes and clutch sizes of altricial birds are smaller, on average, than those of precocial birds, and these two differences alone may be sufficient to give rise to large fecundity gains for an altricial brood parasite but not for a precocial parasite.

We also assumed that survival of parasitic females is similar to that of parental females, although this is probably unrealistic given that obligate parasites avoid the risks of incubation and parental care. Accordingly, we underestimated the potential benefits of obligate parasitism. However, this does not markedly affect our general conclusions if altricial and precocial species experience similar changes in survivorship via a switch from parental to parasitic egg laying. We have no evidence to suggest otherwise.

If our hypothesis is correct, then extant facultative parasites are not simply in evolutionary transition to the obligate state as Weller (1959) and Lack (1968) proposed. Rather, facultative and obligate brood parasitism differ fundamentally in their ecological basis. In our discussion above, we concentrated on factors promoting the transition from facultative to obligate interspecific brood parasitism. The question that remains, however, is what factors favor the origin of facultative interspecific brood parasitism in the first place? One possibility is that facultative parasitism between species is simply a carry-over from parasitism within species. In support of this notion, we found that, among precocial birds, 29 of the 33 facultative interspecific brood parasites also exhibit intraspecific parasitism (Table 1). This carry-over from intraspecific parasitism could be due simply to misidentification of host nests by the parasite species, although this seems unlikely given the large number of facultative interspecific brood parasites (Table 1). Alternatively, facultative interspecific parasitism could be an adaptive extension of intraspecific parasitism and could be maintained by the same factors that favor parasitism within species. For example, intraspecific parasitism has been suggested to occur as a conditional tactic, in response to constraints or restraints on parental breeding or as a side-payment tactic, whereby females lay some parasitic eggs in addition to rearing a brood of their own as a means of enhancing total reproductive output (see reviews in Andersson, 1984; Eadie et al., 1988; Sorenson, 1990; Yom-Tov, 1980). Similar factors might promote facultative parasitism between species. Moreover, a parasite that uses both conspecific and heterospecific hosts could benefit through an increase in the availability of potential host nests and a longer period over which suitable hosts can be found, providing that host species differ in nesting phenologies.

This link between intraspecific and interspecific facultative parasitism also suggests a possible evolutionary route to obligate parasitism (see also Payne, 1977b). There is growing evidence that intraspecific brood parasitism is a common reproductive behavior in several species of birds (Andersson, 1984; Rohwer and Freeman, 1989; Yom-Tov, 1980). Under certain ecological conditions, parasitic females may expand their repertoire to include interspecific hosts. A female that parasitizes other species gains initially through increased host availability. However, in an altricial bird, once successful interspecific parasitism becomes established, the rapid extinction of parental care should follow due to the huge fecundity gain for specialist parasites. Thus, intraspecific brood parasitism may have served as an initial stepping-stone to the evolution of obligate interspecific brood parasitism in altricial birds.

The association between mode of development and type of parasitism is important because it reveals a general ecological prerequisite for the evolution of obligate brood parasitism; namely, sufficient increases in realized fecundity to offset reductions in egg success (Figure 1). However, this prerequisite appears to be necessary, but not sufficient; most altricial taxa have not given rise to obligate brood parasitism, and it is not clear why obligate parasitism has evolved in only some altricial taxa. Hamilton and Orians (1965) identified specific ecological factors associated with each parasitic taxon that might explain why these groups were "preadapted" for the evolution of obligate parasitism, but as Payne (1977b) pointed out, some nonparasitic taxa also share these features. Moreover, if intraspecific parasitism does act as a stepping stone to obligate parasitism, as we suggest, then the fact that obligate parasitism has arisen independently only six times in altricial birds (Lack, 1968) is even more surprising given the apparent frequency of intraspecific parasitism in some altricial birds (e.g., Brown, 1984; Evans, 1988; Yom-Tov, 1980). All of this evidence suggests that the primary obstacle to the evolution of obligate brood parasitism in altricial birds is the ability to successfully parasitize other species (see also Hamilton and Orians, 1965). Understanding the factors that allow parasitic species to make the switch from conspecific to heterospecific hosts may therefore provide the key to understanding the evolution of obligate brood parasitism.

If our reasoning is correct, then two groups of birds are of particular interest: the two species of altricial facultative interspecific parasites and the one precocial obligate parasite (Table 1). Why do these species oppose the trend? In the case of the two North American



cuckoos, Nolan and Thompson (1975) showed that parasitic egg laying in the yellow-billed cuckoo occurred only rarely under average conditions, but occurred frequently in a year when the abundance of prey was exceptionally high. The fecundity potential of this cuckoo may be unusually limited for an altricial bird, given that its relative egg size is among the largest for an altricial bird (Lack, 1968). Thus, clutch size in yellow-billed cuckoos may be limited more by energy than time constraints. Periodic flushes of prey could remove this constraint and permit large gains in fecundity through parasitic egg laying.

Alternatively, the correlation between food abundance and the frequency of parasitism may reflect the influence of host availability; densities of both black-billed and yellow-billed cuckoos were much higher during the year of abundant food, and most interspecific parasitism involved one cuckoo species parasitizing the other (Nolan and Thompson, 1975). Host limitation is known to affect the reproductive output of at least one species of obligate brood parasite. European cuckoos (*Cuculus canorus*) normally lay 8 eggs, but when Chance (1922) experimentally increased the total availability of host nests, he found that cuckoos are capable of laying up to 25 eggs.

A similar argument may hold for the one precocial obligate brood parasite. Weller (1968) emphasized the availability of highly suitable hosts and the extreme independence of young as important factors favoring the evolution of obligate brood parasitism in the black-headed duck (*Heteronetta atricapilla*). In terms of our model, this equates to a high value of  $S_0$ . Consequently, only slight increases in fecundity ( $F_0$ ) would be necessary to tip the balance in favor of obligate brood parasitism. It is also possible that the clutch size of black-headed ducks is not limited by energy or nutrients such that female black-headed ducks have more to gain from emancipation of parental care than females of other species of ducks. Information on the energetics of egg production in black-headed ducks would be particularly informative.

Finally, we note that the framework we have provided may prove useful for understanding the pattern of reproductive parasitism in other groups of organisms. Aside from birds, obligate interspecific parasitism is common in only one other taxonomic group, the Hymenopteran insects, in which obligate parasitism has arisen independently several times (Wilson, 1975). Interestingly, Hymenopteran young are effectively altricial, requiring a considerable period of feeding and maintenance before independence. This suggests that mode of development, and altriciality in particular, may play an important role in the evolution

of obligate reproductive parasitism in insects as well as in birds.

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