Evolutionary routes to joint-female nesting in birds

Sandra L. Vehrencamp

Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

Cooperative breeding systems in birds vary widely in terms of group composition and degree of reproductive skew among male and female group members. A new classification scheme based on different combinations of male and female skew is proposed. A review of cooperative species reveals a fundamental dichotomy between low-skew joint-female species on the one hand, and joint-male and high-skew helper species on the other. All cooperative joint-female systems are characterized by male-biased incubation, whereas either gender (but usually females) may perform the majority of incubation in non–joint-female systems. Male incubation is thus a necessary, but not a sufficient, precursor for the evolution of communal laying. Other characteristics of joint-female systems, such as mating system, group composition, and nestling developmental mode, differ greatly. Three evolutionary scenarios for the evolution of male incubation and joint laying are outlined: (1) large body size relative to egg size, which enables the successful incubation of more eggs than a single female can lay (e.g., ratites and magpie goose); (2) energetically costly egg laying, incubation, and nestling care, coupled with adaptations permitting incubation of very large clutches (e.g., anis); and (3) cooperative polyandry in lineages with male-biased incubation (e.g., woodpeckers and gallinules). All three scenarios presume that an incubating male resource increases the selective pressure on females to lay joint clutches. Available evidence for the origin and maintenance of the critical precursors, constraints, and adaptations are summarized and shown to be absent in non–joint-laying species. These factors and conditions affect the critical parameters of the skew models in ways that are predicted to result in low reproductive skew. *Key words:* bird breeding systems, communal laying, cooperative nesting, male incubation, reproductive skew. *[Behav Ecol 11:334–344 (2000)]*

A diversity of avian cooperative (also called communal) breeding strategies exists (Brown, 1987; Cockburn, 1998; Skutch, 1987). Cooperative breeding has been defined as social systems in which conspecific individuals in addition to a single male–female pair aid in the care of young at a single nest, excluding cases of brood parasitism, brood mixing, and extrapair fertilization. This definition unfortunately eliminates some forms of cooperative reproduction, such as the ratite communal laying system, in which a single male raises the joint clutch of several females. A more inclusive definition might be: temporary or permanent breeding units composed of two or more adults of the same gender that engage in some form of mutual reproductive activity at a single nest. Reproductive activity includes direct genetic contributions to a clutch and all forms of parental care, and the term "mutual" implies that the joint activity is sanctioned by same-gender individuals.

The feature that most distinguishes the different forms of cooperative breeding is the relative direct contribution of genes by same-gender individuals in the breeding unit, or the reproductive skew. When primarily one individual contributes genes while the others provide care (high skew), it is called a helper-at-the-nest system. When most or all fully adult unit members of the same gender contribute at least some genes to the clutch (low skew), it is called a joint-nesting system. Joint nesting traditionally refers to multiple-female clutches. However, with the development of DNA techniques for assigning paternity, growing numbers of cooperative species with shared-paternity clutches have been discovered. It is therefore important to distinguish between joint-female (or communally laying) systems and joint-male (or cooperatively polyan-

drous) systems. Dispersal and helping strategies, relatedness, and degree of skew often differ for males and females within breeding units (Cockburn, 1998). Allowing for the additional possibility that only one male or one female exists in a typical breeding unit, there are nine possible combinations of male and female skew within cooperative groups. Table 1 illustrates the factorial nature of these combinations and gives some avian species examples for each one.

In theory, the degree of reproductive skew among the same-gender members of a cooperative breeding unit can vary over a continuous range (Sherman et al., 1995). A variety of quantitative skew measures have recently been developed, the most useful having a range from 0 (no skew or equal contributions) to 1.0 (high skew, only one individual reproduces) (Pamilo and Crozier, 1996; Reeve et al., 1996; Sherman et al., 1995; Tsuji and Tsuji, 1998). Figure 1 shows the distribution of reproductive skew for avian species for which data are available. It is clearly bimodal, with a few intermediate exceptions. Thus, dichotomizing the skew for males and/or females into high versus low is a reasonable and useful simplification for avian cooperative breeders. Such bimodal distributions do not seem to arise in other social taxa such as termites, ants, and wasps (Reeve, 1991; Reeve et al., 1998; Shellman-Reeve, 1997).

This review examines the factors that lead to the evolution of low-skew versus high-skew cooperative systems. Reproductive skew models shed some light on the possible causes of these alternative social systems. The classic models are based on the assumption that selfish competitive interests among cobreeding group members favor suppression or reduction of the direct reproductive contributions of weaker group members by stronger or dominant members (Emlen, 1982; Keller and Reeve, 1994; Reeve and Ratnieks, 1993; Vehrencamp, 1979, 1983). If dominant individuals can control subordinate reproduction, then the only counterstrategy of subordinates against fitness biasing is to leave the group. Subordinates will leave if their fitness in the group is reduced below what their fitness would be if they dispersed and attempted to breed on their own. The maximum degree of skew dominants can at-

Table 1

Examples of different cooperative breeding systems, categorized on the basis of solitary breeding, low skew, or high skew among males and among females

		Females		
		Solitary	Low skew	High skew
Males	Solitary	Noncooperative monogamous pair (most passerines)	Rhea, tinamous, magpie goose	Ostrich
	Low skew	Galapagos hawk	Anis, pukeko	Tasmanian hen, trumpeter
	High skew	Florida scrub-jay, red-cockaded woodpecker	Acorn woodpecker	Magpie-jay, bicolored and stripe-backed wrens

Sources: Bertram (1992), Gibbs et al. (1994), Goldizen et al. (1998), Haig et al. (1994), Handford and Mares (1985), Haydock et al. (1996), Koenig and Stacey (1990), Langen (1996), Marchant and Higgins (1990), Rabenold et al. (1990), Sherman (1995), Whittingham et al. (1997).

tain is therefore determined by the options available to subordinates for leaving and the benefits they obtain by staying.

The three primary factors that affect the degree of skew are the probability of successfully dispersing, d, the per capita reproductive success of group breeding, $\overline{W}(k)$, versus solitary breeding $\overline{W}(1)$, and the coefficient of relatedness between potential cobreeders, r (analogous to x, k, and r in the more recent models). Figure 1 also portrays the proposed skew model parameters that determine low, medium, and high degrees of skew in animal societies. Low skew results from the combination of low relatedness, high probability of successfully dispersing, and higher per capita reproductive output in cooperative groups. The highest skew arises when dispersal costs are very high, which leads to retention of close relatives on a natal territory and thus high degrees of relatedness. Intermediate skew can occur when there are intermediate values for group reproductive benefit, dispersal success, and/or relatedness. Two parameters, the shape of the per capita fitness versus group-size curve ($\overline{W}$), and the level of habitat saturation (which determines dispersal success d), seem to be most important for birds and mammals (Emlen, 1997; Jennions and Macdonald, 1994; Koenig et al., 1992). In Hymenoptera, on the other hand, variation in degree of relatedness, r, due to queen mating strategies may be responsible for the more continuous distribution of skew (Bourke and Heinze, 1994; Heinze, 1995; Ross and Carpenter, 1991; Strassmann, 1989; but see Field et al., 1998; Hughes et al., 1993, for alternative views).

Some of the variance in skew illustrated in Figure 1 may be explained by alternative models. Incomplete control (or lack of control) by dominants over the reproduction of subordinates could cause lower skew than the maximum predicted by the dominant-control models (Cant, 1998; Clutton-Brock, 1998; Johnstone and Cant, 1999; Reeve et al., 1998). Potential causes of incomplete control could include condition-dependent effects on reproduction, high costs of ejecting subordinates, and conflicting interests of males and females. It is still too early to know whether the conditions proposed in these models are met in real animal societies, but all low-skew systems should be scrutinized for such effects. Incest avoidance between close relatives has been proposed as an alternative explanation for the right-hand cluster of high-skew species (Emlen, 1996; Koenig et al., 1998). However, there are several examples of high skew among females that can avoid inbreeding by mating outside the group, as well as examples of frequent inbreeding within low-skew systems (Craig and Jamieson, 1988; Heinsohn et al., 1999; Langen, 1996). Incest avoidance thus does not generate unique predictions and may be

better incorporated into existing skew models as an additional cost–benefit effect (Emlen, 1999; Reeve and Keller, 1996).

What, then, are the key adaptations and/or conditions that determine whether a low-skew joint-nesting system, as opposed to a high-skew helper system, will evolve? I first show that all systems with frequent joint nesting by females are associated with a strong or sole role of the male in incubation, whereas in most joint-male and helper species the female performs a majority of the incubation. The question can therefore be rephrased as, Why is male incubation associated with low skew among females? I then explore the possible mechanisms by which parental care strategies might affect reproductive skew. Several features of the reproductive biology of birds are unique to the taxon, such as obligatory incubation of eggs in a nest and the provisioning of nestlings with small food items. These activities can be costly in terms of energetic expenditure, time, and predation risk. Cooperation may sometimes ameliorate these costs, and parental care adaptations can constrain future evolutionary trajectories (Ligon, 1993). My goal is to identify the ways in which reproductive constraints and social strategies can affect the critical parameters of the skew model.

The distribution of male incubation and joint-female nesting

Joint-female nesting is characterized by the routine laying of eggs by two or more females in a single nest, followed by simultaneous incubation of the joint clutch. My criterion for joint laying was 20% or more of all nests must consist of joint clutches. Table 2 lists these joint-laying species and the major species and/or families of birds with cooperative breeding systems in which joint clutches are absent or rare, which I have called helper species. A complete list of cooperatively-breeding species is given by Brown (1987). Most helper species are characterized by the retention of offspring on the natal territory, although helpers in some species are unrelated to the birds they assist. Male offspring are often preferentially retained or retained for longer, but females are the primary helping gender in a few species. The helpers assist with the guarding and provisioning of their parent's subsequent broods and later may attain breeding status by inheriting the parental territory or by dispersing to a vacancy in a nearby territory. Male helpers essentially never copulate with the primary female when she is their mother, but they do occasionally contribute genetically to the clutch with a stepmother (leading to S values of 0.45–0.85 in Figure 1) (Haydock et al., 1996; Rabenold et al., 1990; Whittingham et al., 1997). Older
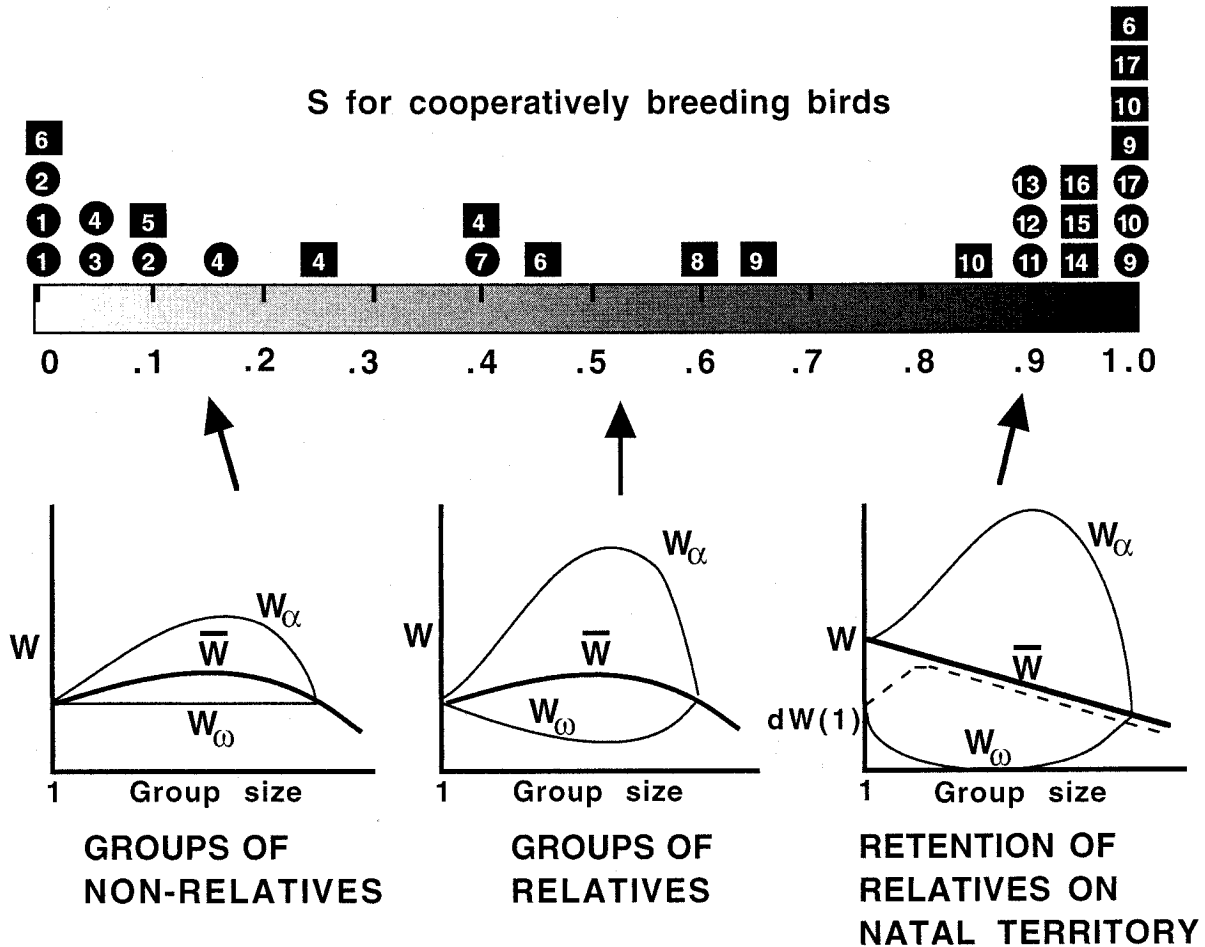
Figure 1

Range of reproductive skew in birds. Top: the skew index, *S*, of Pamilo and Crozier (1996) has been computed for females (circles) based on relative egg contributions to communal clutches in breeding units with two or more potential adult female breeders, and for males (squares) based on paternity analyses of nestlings in breeding units with two or more adult males present. Species and sources: 1, groove-billed ani *Crotophaga sulcirostris* (two- and three-pair groups), Koford et al. (1990); 2, moorhen *Gallinula chloropus* (related and unrelated females), McRae (1996b); 3, acorn woodpecker *Melanerpes formicivorus* (omitting incest-avoiding helpers), Jamieson (1999); 4, pukeko *Porphyrio porphyrio* (saturated and unsaturated habitats, omitting helpers), Jamieson (1997); 5, Galapagos hawk *Buteo galapagoensis,* Faaborg et al. (1995); 6, scrub wren *Sericornus frontalis* (low, medium, and high relatedness), Whittingham et al. (1997); 7, ostrich *Struthio camelus,* Bertram (1992); 8, Tasmanian hen *Gallinula mortierii,* Gibbs et al. (1994); 9, stripe-backed wren *Campylorhynchus griseus* (medium and high relatedness), Haydock et al. (1996); 10, bicolored wren *Campylorhynchus nuchalis* (medium and high relatedness), Rabenold et al. (1990); 11, magpie jay *Calocitta formosa,* T. A. Langen (unpublished data); 12, Seychelles' warbler *Acrocephalus sechellensis,* Komdeur (1994); 13, Arabian babbler *Turdoides squamiceps,* Zahavi (1974); 14, red-cockaded woodpecker *Picoides borealis,* Haig et al. (1994); 15, European bee-eater *Merops apiaster,* Jones et al. (1991); 16, Harris' hawk *Parabuteo unicinctus,* Faaborg and Bednarz (1990); 17, Florida scrub jay *Aphelocoma coerulescens,* Quinn et al. (1999). Bottom: graphical representation of hypothetical conditions for low, medium, and high skew (based on Vehrencamp, 1983). Heavy lines are the per capita $\overline{W}$ fitness curves as a function of group size; light lines are the fitness of dominant (W_α) and subordinate (W_ω) breeders. The dashed line shows the effect of a low dispersal probability d on the $\overline{W}$ curve when family members must disperse to breed solitarily.

female helpers occasionally dump eggs into the primary breeder's nest (sometimes 10–15% of nests, leading to *S* values of ~0.9 in Figure 1) (Komdeur, 1994; Langen, 1996; Rowley, 1978; Zahavi, 1974).

The cooperative species in Table 2 are further subdivided into those in which male incubation effort is greater than female effort, and those in which female incubation effort is greater. Relative incubation effort is evaluated on a 24-h basis over the entire incubation period. For species in which male and female share diurnal incubation, the critical determinant of relative effort is therefore whether nocturnal incubation is performed exclusively by one gender. The pattern is clear: males do the majority of incubation in all joint-laying species, whereas either gender can do the majority of incubation in helper species.

Joint-paternity species are not shown in a separate column of Table 2 because some are included in the joint-laying category and others are included in the helper category. Well-documented cooperative species with joint-paternity clutches include the acorn woodpecker, pukeko, Tasmanian hen, dunnock, Galapagos hawk, trumpeter, and stepmother breeding units of the scrubwren (Faaborg et al., 1995; Gibbs et al., 1994; Koenig et al., 1998; Lambert et al., 1994; Sherman, 1995; Whittingham et al., 1997). The first three species have male nocturnal incubation; the remaining four have female incubation. Thus, joint-paternity systems, like helper species, can be associated with either male- or female-biased incubation.

A quantitative comparison of the association between male incubation and joint nesting requires a phylogenetic correction because all joint-laying species are nonpasserines with a

Table 2

Joint-nesting versus helper species split according to whether males or females perform the majority of incubation

Incubation	Joint-nesting	Helper
Male > female	Rhea, ostrich, tinamous, magpie goose, megapodes, acorn woodpecker,[a] anis,[a] guira,[a] pukeko,[a] moorhens (8)	Barbets, red-cockaded woodpecker, purple gallinule (3)
Female > male	(0)	Kingfishers, bee-eaters, green wood hoopoe, swifts, hawks, trumpeter, jays, babblers, starlings, fairy wrens, warblers, honey-eaters, wrens, shrikes (84)

[a] Indicates joint-nesting species that also have helpers. Test of association between gender of primary incubator and female skew strategy (Ridley, 1983; Ridley and Grafen, 1996) was based on conservative estimates of the independent cooperative breeding evolutionary events shown in parentheses. One evolutionary transition to cooperative breding per genus was assumed, except where more detailed phylogenies indicated several events or where two sister taxa containing large fractions of cooperatively breeding species indicated a common cooperative ancestor. Sources: Brown (1987), Edwards and Naeem (1993), Kendeigh (1952), Restrepo and Mondragón (1998), Ridley (1978), Skutch (1976), Stacey and Koenig (1990).
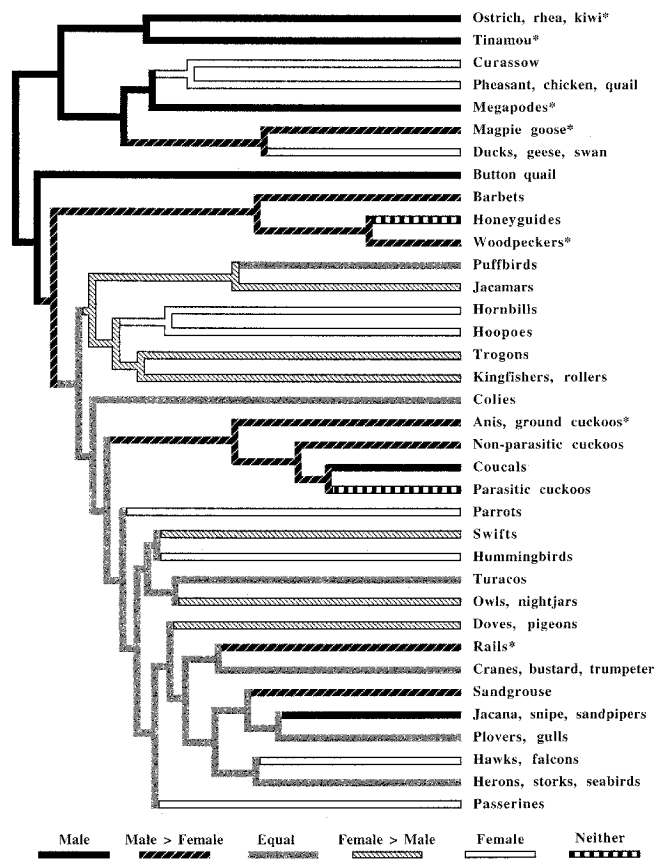

Figure 2

Phylogeny of male and female incubation patterns. Sibley and Ahlquist's (1990) phylogenic tree of avian orders, with the predominant state of relative male and female incubation shown for each order. Ancestral states were determined by parsimony using MacClade (Maddison and Maddison, 1992). The ancestral state for birds is pure male incubation, and from this state several forms of shared incubation and female only care have arisen. There are several reversions to male incubation from a shared incubation ancestor. General sources of incubation patterns: Kendeigh (1952) and Skutch (1976).

variable ancestral history of gender-biased incubation, and many helper species are passerines with a conserved history of predominantly female incubation. Figure 2 shows the phylogenetic tree of the orders of birds based largely on Sibley and Ahlquist (1990), with slight modifications from the re-analysis by Harshman (1994). Buttonquail (Turnicidae) are placed in the position tentatively suggested by Sibley and Ahlquist (1990). The orders with joint-laying species have been expanded to lower taxon levels to elucidate within-order patterns. Each taxon was classified into one of the following six incubation states: male only, male > female, male = female, female > male, female only, and neither (brood parasitic). In taxa with some variation in incubation effort, the most commonly occurring pattern was assigned. The ancestral states were reconstructed by parsimony using MacClade (Maddison and Maddison, 1992). I examined the reconstruction using incubation states coded as both ordered and unordered. Sometimes one method resolved the ancestral state in a clade while the other method gave an equivocal result; the figure shows the results from the resolving method in ambiguous cases.

Visual inspection of this tree shows that all joint-laying species occur sporadically in taxa with an ancestral history of male-biased incubation. For example, ratites and tinamous have sole male incubation, but communal laying apparently occurs in only a few of these species (Handford and Mares, 1985). Similarly, all woodpeckers and nonparasitic cuckoos have male nocturnal incubation, but only a few species have evolved joint laying (Andersson, 1995; Calder, 1967; Kendeigh, 1952; Ralph, 1975; Skutch, 1959, 1966; Vernon, 1971). Megapodes and magpie geese are also characterized by sole or primary male care derived from the basal avian pattern (Horn et al., 1996; Marchant and Higgins, 1990). Gender-biased incubation patterns in the rails and gallinules are poorly known, but male nocturnal incubation has been documented in several species, including at least one (coot) that is not considered a joint layer (Craig and Jamieson, 1990; Garnett, 1980; Gullion, 1954; Siegfried and Frost, 1975).

I used Ridley's (1983; Ridley and Grafen, 1996) independent contrasts method to test the hypothesis that joint laying is more likely to evolve from a male-incubating ancestor and helping from a female-incubating ancestor. The number of independent evolutionary transitions to the two forms of cooperative breeding was tallied for male- and female-incubating species. One evolutionary transition to cooperative breeding

per genus was assumed, except where more detailed phylogenies indicated several events or where two sister taxa containing large fractions of cooperatively breeding species indicated a common cooperative ancestor. There are eight transitions to joint laying, all in male-incubating taxa. There are 87 transitions to other forms of cooperative breeding, 69 in passerines alone (Edwards and Naeem, 1993). Among non-passerines with helper systems, 3 have male-biased incubation, and 15 have female-biased incubation. The association between incubation gender and form of cooperative breeding is highly significant ($\chi^2 = 56.4$, $p < .0001$). The association is not perfect: a few helper species show greater male incubation effort, and some joint-laying species also have helpers. In addition, there are other male-incubating species such as buttonquail, mesites, sandgrouse, and shorebirds that have neither helpers nor communal cooperation (Ridley, 1978). Thus male-biased incubation is a necessary, but not a sufficient, condition for joint-female nesting.

Additional factors or conditions must also exist before joint laying is favored; these factors must be sufficiently unusual or specific to account for the rare occurrence of joint-female nesting. It is also unlikely that the same set of conditions applies to all of the joint nesters, given that they differ greatly in mating systems and critical aspects of their breeding biology. For example, ratite, megapode, and magpie goose breeding units are composed of single-male polygynous groups, ani breeding units are composed of monogamously mated pairs, and woodpecker and gallinule units usually contain more males than females and mate promiscuously within the group. I suggest that these mating system differences reflect at least three different causes for the evolution of male incubation and joint laying: (1) large body size relative to egg size, (2) high cost of egg-laying, incubation, and nestling care, and (3) cooperative polyandry. In all three scenarios incubating males are a critical resource for females; females will be selected to exploit or parasitize parental males, and males will be selected to attract multiple females if they can manage to care for their eggs. The scenarios differ in the factors initially favoring male incubation and in the conditions affecting the shape of the fitness versus group-size curves for each gender. The current utility of cooperative nesting is relatively easy to demonstrate in a cooperative species by comparing the success of groups with and without auxiliary individuals. Understanding why a noncooperative species would not benefit from group breeding is more difficult because birds cannot be forced to breed communally. However, comparative studies can be used to show that noncooperative species lack the critical condition or feature purported to cause the benefit in related cooperative species.

Scenario 1: large body size relative to egg size

If body size is large relative to egg size, a single individual can successfully incubate a large number of eggs. Furthermore, if the number of eggs that can be incubated is larger than the number of eggs a single female can lay in a reasonable period of time, then joint-female clutches can be accommodated. Among birds, this condition is most likely to be met in species with large absolute body size because of the allometric relationship between body size and egg size: larger birds produce proportionally smaller eggs (Rahn et al., 1975). This argument has been invoked to explain joint-female nesting in the ratites (Bertram, 1992; Handford and Mares, 1985).

Maximum clutch size among 19 ratite species is significantly positively correlated with male body mass (independent contrasts analysis, $r = .668$, $p = .0013$), as shown in Figure 3. A species-based correlation between clutch size and body mass in tinamous also shows a significant relationship ($r_s = .491$, N
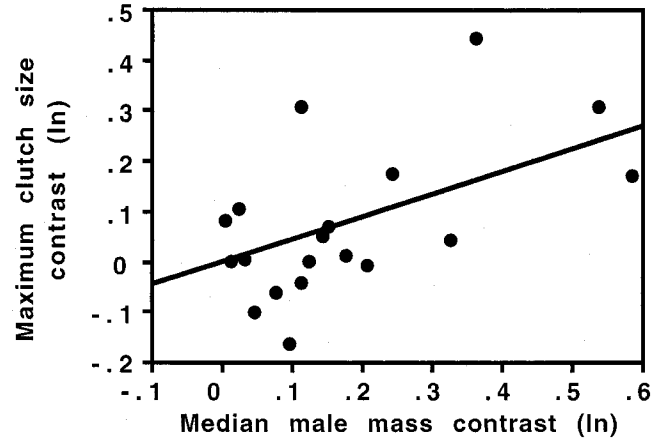

Figure 3
Maximum clutch size versus body mass in ratites. Independent contrasts analysis using CAIC 2.0 with an equal branch lengths model (Purvis and Rambaut 1995). Regression analysis with no intercept: $F = 14.54$, $N = 19$, $p = .0013$ (Langen TA, personal communication). Phylogeny based on Sibley and Ahlquist (1990); clutch sizes and body mass from Hoya et al. (1992).

$= 28$, $p = .0128$; both analyses courtesy of T. A. Langen). Ostriches, with an egg mass representing 1.5% of female body mass, can successfully hatch up to 20 eggs (Bertram, 1992). Rheas have high hatchability up to clutches of 24, after which hatchability starts to decline (Fernández and Reboreda, 1998). Large clutches are more likely to be produced by several females than by one because of constraints on the ability of a single female to lay so many eggs in a moderate period of time. The maximum egg-laying rate for female ratites is one egg per 2 days. It would therefore take a single female 40–50 days to lay the maximum clutch that could be incubated. This is too long a preincubation period for eggs to sit in a ground nest, where they are vulnerable to predation and to embryo death from exposure to high temperatures. If several females contribute eggs simultaneously, a full clutch can accumulate during the optimal 15-day laying period (Bertram, 1992).

Joint clutches are not only more feasible in these large-bodied ratites, but they are also more successful than small, single-female clutches for several reasons. Ratite young are precocial and self-feeding, so the parental brood provisioning and nestling food competition that severely constrain the upper limit on brood size in altricial species are not limiting factors. Fledgling survival is often higher in larger broods because of dilution effects on predators and has led to the amalgamation of adjacent groups of offspring in ostriches, several other precocial avian species, and some cichlid fishes (Beauchamp, 1997; Hurxthal, 1979; McKaye and McKaye, 1977). In rheas, very small and very large clutches are more likely to be abandoned during incubation compared to intermediate-sized clutches (Bruning, 1974). Thus the female $\overline{W}$ curve is often humped for large-bodied ratites. The reproductive skew among rhea and tinamou females is low because the male performs all incubation and completely controls the nest, not because a dominant female must offer concessions to obtain the assistance of subordinate females. Skew in ostriches is relatively high (0.41) because one female does remain with the male to assist with incubation and fledgling care. Ostrich females are the only joint nesters that can distinguish their own eggs (Bertram, 1992). The egg-tossing behavior of the major hen maximizes her own relative contribution to the joint clutch and optimizes brood survival without regard for the incidental costs and benefits to the secondary non-cooperative and polyandrous females.

The ratite male $\overline{W}^*$ curve decreases with increasing number of males because a male does not benefit from sharing the females he has attracted with other males. Fitness declines sharply if a male splits the females with another male (Fernández and Reboreda, 1995). Males also do not appear to benefit from sharing incubation with another male to permit feeding, nor do they need assistance in defending a territory. However, a few cases of helping behavior have been described in the greater rhea, in which an adult male recruited a sub-adult male to incubate a clutch of eggs while he established a second clutch (Codenotti and Alvarez, 1997).

The mechanism for the linkage between male incubation and joint-female laying in this scenario is not clear. If large body size relative to egg size is the key factor facilitating communal laying, we would expect to find a few large-bodied species with joint clutches in female-incubating lineages as well; however, there do not appear to be any. All of the examples of joint clutches in female-incubating lineages are either anomalous instances of female–female pairs in monogamous populations with a shortage of males (gulls: Kovacs and Ryder, 1983) or cases of intraspecific brood parasitism (Yom-Tov, 1980). An alternative explanation is that male incubation evolved from a nonparental ancestor in the first birds in a monogamous context, perhaps to optimize offspring survival and maximize female egg investment, as argued by Maynard Smith (1977) and Wesolowski (1994). Selective pressure on parental males to attract more females and the facilitating condition of large body size may then have favored the subsequent evolution of communal laying. A third possibility is that male incubation evolved in conjunction with joint laying. A modified version of Maynard Smith's (1977) parental care game shows that if parental males can attract more females than nonparental males, there is a stronger evolutionarily stable strategy for sole male care coupled with joint clutches, sequential polyandry by females, and a polygynandrous mating system (Vehrencamp and Bradbury, 1984). This scenario has been proposed for fish, where parental males collect and guard the clutches of several females (Gittleman, 1981; Ridley, 1978). To resolve whether the ancestral bird was monogamous or polygynandrous, we need to examine the evolutionary trends in body size among the ratites and determine whether communal laying is perhaps more widespread among emu, cassowaries, tinamous, and buttonquail than indicated in early accounts (Handford and Mares, 1985; Ligon, 1999).

Scenario 2: high cost of egg laying and incubation

In a monogamous species with a significant egg-production cost, energetically expensive incubation, and some type of posthatch expenditure by the female that affects male fitness, males should be selected to take over the expensive portion of incubation so that their mates can recuperate from the energy losses of laying. Under these circumstances, a male will benefit if his incubation effort permits the female to produce a larger clutch, lay replacement clutches, or contribute her half of nestling care. Egg-laying cost is high when clutch size or egg size is large or critical nutrients are rare in the environment. The energetic cost of incubation can be as low as 19% above nonincubator resting metabolic rate, but can range up to 50% above resting rate in some species (Williams, 1996). Factors that increase incubation cost include large clutch size, low ambient temperature, ground nesting, and facultative hypothermia by nonincubators (Biebach, 1984; Drent, 1970; Haftorn and Reinertsen, 1985; Mertens, 1977; Moreno and Sanz, 1994; Reinertsen, 1996; Tatner and Bryant, 1993). Parental care costs are higher in species with altricial and/or provisioned young compared to precocial self-feeding young. A similar argument has been proposed for the evolu-

tion of male incubation in shorebirds, where the laying of replacement clutches is the key postincubation cost for females (Erckmann, 1983; Székely and Reynolds, 1995).

Costly egg laying, incubation, and nestling care favor only the first step toward joint laying, the evolution of male-biased care from a monogamous, biparental ancestor. The second step must be the lack of severe constraints against the simultaneous incubation of two or more females' clutches. Many species with male-biased incubation appear to be limited by the number of eggs they can incubate, and therefore have not evolved joint laying. For example, the shorebird brood patch can only contact four of the typically large eggs, and experimental enlargement of clutch size leads to a significant reduction in hatchability (Hills, 1980). Temperate-zone species with large single-female clutches and cool ambient temperatures are already constrained by the energetic cost of incubation and cannot incubate joint clutches. However, if male incubation has evolved to enable females to conserve energy by lowering their body temperature, then the incubation of enlarged clutches may be less constrained.

Facultative hypothermia will make incubation energetically expensive if incubators must maintain higher body temperatures than nonincubators. Some facultatively hypothermic species (colies, several coraciiforms) alleviate this cost by group roosting on the nest, but this adaptation has not led to the evolution of joint laying (Deucoux, 1978; Ligon et al., 1988; White et al., 1978). The facultatively hypothermic nonparasitic cuckoos have opted to alleviate this cost by shifting the expensive nocturnal incubation entirely to the male. The nocturnally incubating male roadrunner maintains a very high body temperature at night (40°–41°C) compared to that of females and nonincubating males (33°–39°C) (Vehrencamp, 1982). The estimated daily energy savings from hypothermia are equivalent to approximately 30% of the caloric value of a roadrunner egg (Ohmart and Lasiewski, 1971). Summed over the entire incubation period, this savings equals the value of a female's whole clutch. Despite the benefits of male incubation in this and other nonparasitic cuckoos, most species incubate single-female clutches.

Joint laying has evolved in the anis and guira, and their special adaptations for this unusual breeding system demonstrate the large incubation constraints that must be overcome. Groove-billed anis can hatch up to 14 eggs in a communal nest, more than three times the normal clutch size (four) of a solitary-nesting pair (Figure 4). Hatchability rates are also extremely high (93%) for all but abnormally large clutches. This feat is particularly noteworthy given the fact that crotophagine eggs are very large (16–25% of body weight), well above that predicted for a 70-g bird (~10%; Rahn et al., 1975). The key factors responsible for the high hatching success appear to be (1) the high body temperature of the nocturnally-incubating male (39°–42°C) compared to nonincubators (35°–39 °C) (Warren, 1960; Vehrencamp SL, unpublished data on radio-telemetered body temperatures); (2) a bulky, open-cup nest structure that can accommodate variable clutch sizes; (3) a green-leaf nest lining, which may simultaneously insulate, reflect body heat, generate composting heat, and inoculate nestlings against parasites (Gwinner, 1997; Seymour et al., 1986); (4) thick eggshells, which allow eggs to be layered in the nest and moved around without breaking; and (5) the warm ambient temperatures of the lowland tropical habitat to which anis are restricted, which reduces the temperature gradient between eggs and external air.

As predicted, ani females benefit from the male-biased incubation. They gain weight during the second half of the incubation period after reabsorption of the oviduct (Vehrencamp SL, unpublished data on daily weights from a nest rigged to a scale). Their egg-laying costs are high, not only
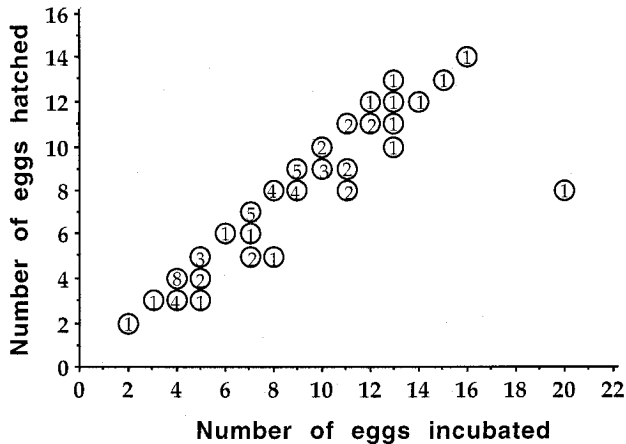
Figure 4
Hatchability as a function of clutch size for groove-billed anis.
Numbers in circles show number of data points.

because of the large egg size, but also because of the large numbers of eggs they must lay (clutches are often more than 100% of body weight). Both of these factors are undoubtedly a consequence of the female–female conflict (e.g., egg tossing and nestling competition) generated in communal groups. Renesting also occurs frequently as a result of high predation rates, sabotage by conspecific nest parasites, and multiple broods.

An ani male with the ability to incubate the clutches of several females would clearly benefit by attracting additional females to his nest, and females incur lower reproductive costs by exploiting such a parental care resource. Because anis have altricial nestlings, the provisioning help of all breeding adults is essential. Most groups consist of an equal number of males and females, divided into monogamous pairs (Vehrencamp, 1978). Occasional groups with extra females do occur, but their reproductive success is reduced compared with equal sex-ratio groups. Figure 5 shows that females benefit from breeding in an optimal group size of four (two pairs) compared to both larger and smaller groups. The equivalent male curve is flatter but also peaks at a group size of four (Vehren-camp et al., 1988). Thus both genders have a humped $\overline{W}$ curve. The egg-tossing behavior of late-laying females reduces the egg skew among females below what it would be without the tossing (Vehrencamp, 1977), and there is no evidence for discrimination or selective treatment of individual eggs or nestlings. Dispersal probabilities are relatively high in anis because they can breed successfully as single pairs in marginal habitat areas, and guiras appear to experience no habitat saturation, so relatedness and reproductive skew are low for both genders, as predicted by the classic skew model (Bowen et al., 1989; Koford et al., 1986; Macedo, 1992; Macedo and Bianchi, 1997; Quinn et al., 1994).

Scenario 3: cooperative polyandry

Cooperative polyandry is a mating system in which two or more males cobreed with a single female (Faaborg and Patterson, 1981). In such a system, a position for an additional female exists. The males may benefit from having a second female join the cooperative group, but the original female may not benefit, creating a conflict of interest between the genders. Cobreeding females only occur in those cooperatively polyandrous species with male-biased incubation (acorn woodpecker, pukeko, Tasmanian hen; Craig and Jamieson, 1990; Gibbs et al., 1994; Goldizen et al., 1998; Koenig et al.,
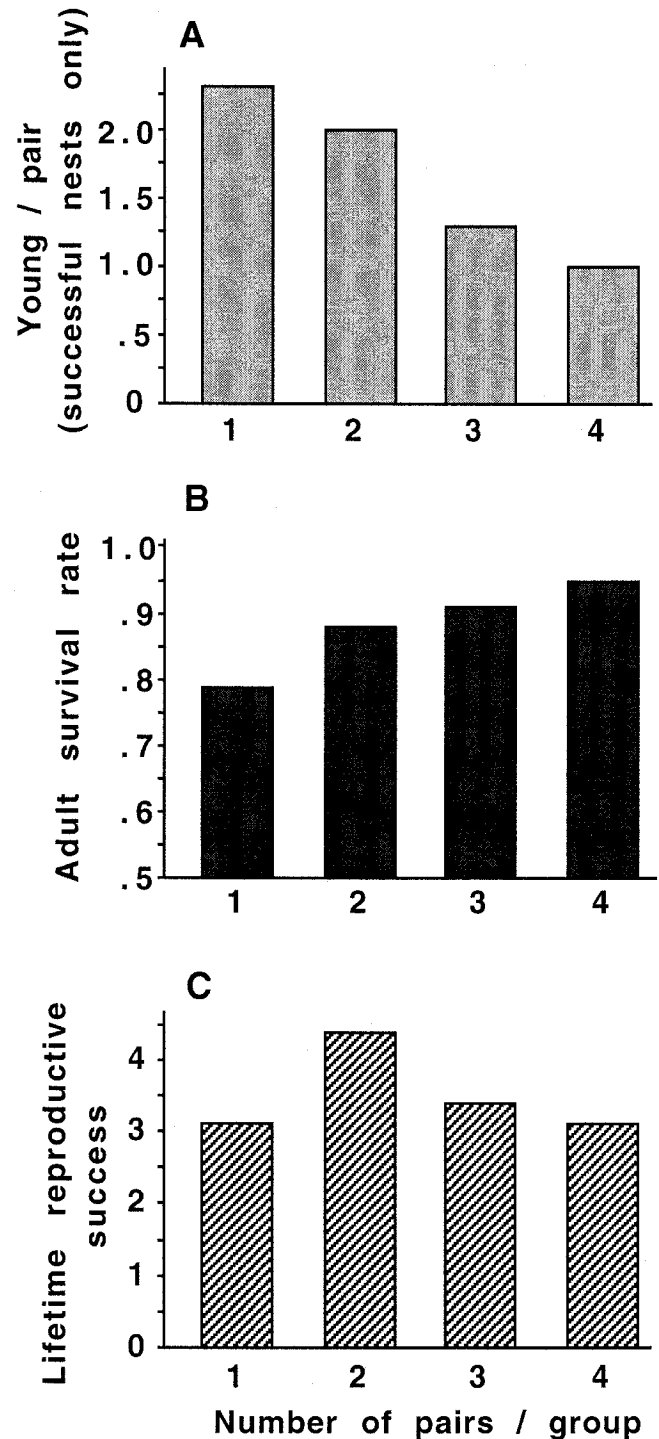

Figure 5
Components of reproductive success as a function of group size (number of pairs) for groove-billed anis. (A) Number of young raised per pair from successful nests only. (B) Annual female survival. (C) Female lifetime reproductive success (based on Koford et al., 1990; Vehrencamp et al., 1988). Male lifetime reproductive success shows a similar relationship to group size. Proportion of successful (versus predated) nests is not correlated with group size.

1983), but not in species with female-biased incubation (Galapagos hawk, dunnock, trumpeter; Faaborg and Bednarz, 1990; Hartley and Davies, 1994; Sherman, 1995). This relationship could arise because males can achieve their optimal

Table 3

Hatchability, computed as percentage of incubated eggs that hatched, for different clutch sizes in five cooperative species

Species	Clutch size			ANOVA or χ^2		Source
	Small	Medium	Large	F	p	
Greater rhea ($n = 40$ nests)	70.9 (9–16)	77.1 (17–24)	59.5 (25–30)	4.018	.026	Fernandez and Reboreda (1998)
Groove-billed ani ($n = 65$ nests)	91.0 (2–5)	93.9 (6–10)	87.9 (11–15)	1.616	.207	Vehrencamp SL unpublished data)
Acorn woodpecker ($n = 377$ eggs)	88.2	78.9	—	$\chi2 = 4.131$	.042	Koenig (1982)
Pukeko ($n = 45$ nests)	88.5 (5–7)	76.5 (8–10)	56.8 (11–15)	8.364	.0009	Jamieson IG (unpublished data)
Magpie-jay ($n = 22$ nests)	64.1 (3–6)	32.1 (7–8)	—	4.369	.049	Langen TA (unpublished data)

Small, medium, and large clutch sizes correspond approximately to clutches laid by one, two, and three females, respectively, except for the rhea where number of laying females is probably about twice as large. The range of clutch sizes for each clutch size category is shown in parentheses.

strategy better when they control access to the nest, or because secondary females gain more from intraspecific brood parasitism when males are the primary incubators. Therefore, the conditions favoring cooperative polyandry must be preceded by (or accompany) selection for male incubation for joint laying to evolve via this scenario.

What conditions favor cooperative polyandry? Koenig et al. (1992) first suggested that adding a cooperative male cobreeder to a monogamous pair may be easier than adding a female cobreeder. Chao (1997) developed the idea further in a quantitative model which showed that two simultaneous criteria must be met. One condition is that three parents must be able to raise more than twice the number of offspring as two parents ($P_3/2 > P_2$). The second condition is that there must be a strongly optimal clutch size, above which reproductive success drops off rapidly, and a single female must be able to produce this optimal clutch. Given these two conditions, it is clearly better to add a male to the pair unit as the third bird rather than a female, who would raise the clutch size far above the optimum. Note that this cooperative polyandry model does not require male incubation.

How can there be a limited optimal clutch size, while at the same time reproductive output increases with additional group members? These conditions can be met if the optimal clutch size is determined by incubation limits on hatchability, whereas fledging success depends on provisioning rates, group antipredation tactics, or group-size–dependent effects on territory size or quality. Chao (1997) presents data on acorn woodpeckers showing that males do indeed benefit on average from polyandry compared to monogamy ($10.5/2 > 4.21$), but males and especially females suffer reduced fitness from polygyny compared to monogamy ($8.21/2 < 4.21$). A pair female, of course, benefits greatly when a male is added to the group, whereas a pair male's benefit from an extra female is not as high.

Similar fitness effects have been found in pukeko, where breeding units may be monogamous, polyandrous, polygynous, or polygynandrous (Jamieson, 1999). Males increase their fitness with a male cobreeder whether there is one or two females in the group because they can defend higher quality territories. The male $\overline{W}$ curve is humped, and reproductive skew is low to medium depending on habitat saturation and relatedness (Jamieson, 1997). Female fitness is reduced when a second female is added to the group because of egg breakage and low hatchability in joint clutches (Table 3). As in the woodpecker, two females produce fewer young per capita than a single female (Craig and Jamieson, 1990; Koenig and Mumme, 1987). The female $\overline{W}$ curve therefore decreases. One female appears to be acting like a brood parasite on the other, but they do appear to be sensitive to the clutch size constraint and reduce total eggs laid to less than

twice what a solitary female would lay (Jamieson, 1999). Primary females seem to be unable to oust a second female or her eggs and subsequently permit the parasite to help provision the young. Although intraspecific brood parasitism is known to occur in some female-incubating birds such as ducks, parasitism appears to be a common phenomenon in several of the rails, where females lay eggs at night during the male's incubation period (Lyon, 1993; McRae, 1996a; Sorenson, 1995).

Habitat saturation appears to be playing a role in both the acorn woodpecker and pukeko systems (Craig and Jamieson, 1990; Koenig and Stacey, 1990). Limited good habitat may be the source of the male reproductive benefit of cooperating because multiple males can defend a higher quality territory than a single male (Ligon, 1999). Low dispersal success leads to retention of offspring as helpers, codefenders, and cobreeders, and the higher relatedness permits greater reproductive skew. Females facing the options of dispersing versus parasitizing a relative may prefer the latter. This option may be far easier when there are multiple breeding males in the group, who benefit if an additional female is added.

Summary and conclusions

Within-gender strategies of group size and reproductive skew often differ for the two genders. Cooperatively breeding species exhibit all possible combinations of solitary, group with low skew, and group with high skew strategies for males versus females. Much of this variation can be explained by different dispersal options, group benefit curves, and/or relatedness values for the two genders, as predicted by skew theory. For example, reproductive skew among scrub wren males varies from 0 to 1.0 with increasing relatedness of the beta male to the birds he is helping (Whittingham et al., 1997). Skew in pukeko is higher in more saturated habitats, where dispersal constraints, relatedness, and group size are higher (Jamieson, 1997). A key conclusion from this review is that male-biased incubation is often associated with a hump-shaped group benefit curve, which favors low-skew joint nesting by females. Thus the reproductive strategies of one gender can significantly affect the group size and skew strategies of the opposite gender.

Figure 6 summarizes the alternate routes from male incubation to the different forms of joint nesting and highlights the factors affecting the shape of the group benefit curve for the two genders. When males incubate, they become a valuable resource for females. Males also benefit from the time and energy they invest in incubation by increasing their mating rate or their single mate's laying rate. Females are therefore attracted to male-tended nests, and primary females may not be able to limit access to such mates by secondary females.
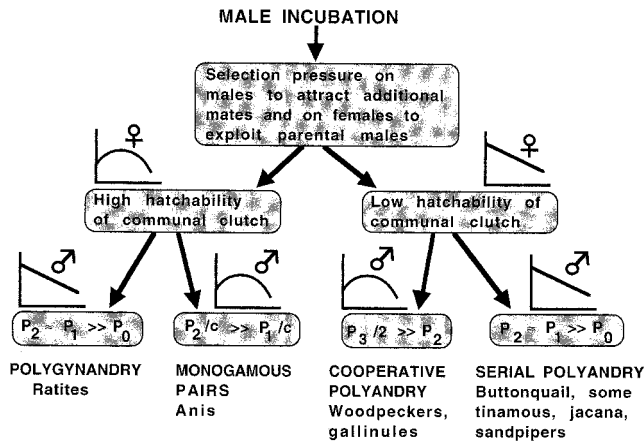
Figure 6
Flow diagram of the conditions leading to different breeding and mating systems in birds with sole or strong male incubation effort. The graphs show the relationship between per capita fitness and group size for males or females and the text in shaded areas identifies the conditions responsible for the fitness curves. The ability to hatch the eggs of a joint clutch of several females' eggs determines whether females have a humped or declining $\overline{W}$ curve. The effect of extra male breeders on the number of young raised determines whether males have a humped or declining $\overline{W}$ curve. $P_2 \approx P_1 \gg P_0$ means that offspring survival is about as high with two parents as with one parent and much better than no parent; $P_2/c \gg P_1/c$ means that two parents per female clutch is much better than one parent per clutch; $P_3/2 \gg P_2$ means that three parents are more than twice as good as two.

If hatchability of joint clutches is high, females benefit from joint clutching and this form of communal nesting can evolve. If an additional male would significantly improve territory defense or offspring provisioning, breeding males will recruit additional males or helpers to form cooperative monogamous pairs; otherwise males will be solitary and polygynous. When males incubate but hatchability is low for joint clutches, joint nesting will only evolve if additional caregivers increase the number of nestlings that can be successfully raised. Additional males will be recruited to form cooperatively polyandrous breeding units. Unattached females may attempt to gain access to the incubating male resource, resulting in a loss of fitness for the average joint-nesting female. Finally, when both hatchability of large clutches and benefits of cooperative nestling care are low, a noncooperative serial polyandrous breeding system is predicted.

The conditions leading to the evolution of joint-male nesting are clearly different from those leading to joint-female nesting. Gender-biased incubation roles are not associated with cooperative polyandry as they are with communal laying. Relatedness values are a more important determinant of male skew than of female skew. For example, in potentially outbred groups of acorn woodpeckers, related males still exhibit high levels of reproductive suppression and skew, whereas related females almost always cobreed with low skew. Degree of skew among male scrub wrens and stripe-backed wrens is also correlated with relatedness. In contrast, mother–daughter cobreeding moorhens show slightly higher skew than unrelated cobreeders, but this is largely due to younger age, smaller clutch size, and inbreeding depression effects on the daughter (McRae, 1996b). Cobreeding female magpie geese and acorn woodpeckers are related, whereas ani females are not. Some of these differences in male and female helper strategies may be due to the simple fact that a male must copulate with a female group member to contribute genetically to the clutch, whereas females can easily avoid inbreeding by seeking extra-

group copulations. However, females must obtain access to the nest to lay an egg. Furthermore, male skews may be more strongly affected by dominance interactions, whereas female skews may be affected by relative laying condition.

Conflicts of interest over the optimal skew between genders also play a role in determining skew and the mating system. Females have greater control over choice of mating partner, potentially causing high skew among males. Males, on the other hand, will prefer low skews among the females with whom they are mating. When males perform the majority of incubation, they have greater control over female access to the nest and can entice secondary females to lay and prevent egg tossing. Females, however, can guard their nests against egg-dumping helpers and intraspecific brood parasites. Future studies will undoubtedly reveal other mechanisms by which male–female conflict affects skew in cooperative breeders.

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