

Prolonged offspring dependence and cooperative breeding in birds

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It has been suggested that the evolution of cooperative breeding in birds is associated with unusually long periods of offspring dependence; this appears paradoxical because cooperative breeders often produce more broods than their noncooperatively breeding relatives. I compared the duration of parental care between cooperatively and noncooperatively breeding species using phylogenetically independent contrasts and matched pairs. The incubation and nestling periods did not differ between the two parental care systems, but the duration of postfledging offspring care was significantly longer in species that regularly breed cooperatively. This relationship remained when other factors that are thought to affect the duration of fledgling care (breeding habitat, body size, latitude of breeding, diet) were controlled statistically. Cooperative breeders appear to provide more prolonged postfledging care because additional care providers reduce the costs of parenting, offspring have less incentive to become independent, and a division of labor can develop during reproduction—helpers continue to feed fledglings while breeders initiate the next nesting attempt. *Key words:* avian reproduction, cooperative breeding, life-history trade-offs, parental care. [*Behav Ecol* 11:367–377 (2000)]

Parents may provide several forms of care for their offspring: warmth, access to resources, protection from predators, and food (Clutton-Brock, 1991). In cooperatively breeding birds, other individuals contribute to the care of the young in addition to the genetic parents. For some of these species, cooperative breeding results in a greater number of offspring or more viable offspring in each brood because of a decreased risk of starvation or predation (reviewed in Brown, 1987; Cockburn, 1998; Emlen, 1991). It has been suggested that offspring of cooperatively breeding birds receive more prolonged care than noncooperative breeders (Heinsohn, 1991; McGowan and Woolfenden, 1990), but there has been little comparative evidence published to support this conjecture.

A few life-history traits have been shown to be associated with cooperative breeding, including higher adult survivorship, smaller clutch sizes, and more broods per breeding season than noncooperative breeders (Arnold and Owens, 1998; Brown, 1987; Poiani and Jermini, 1994). In most species of birds, parental care of a brood is terminated soon after the production of the next brood begins (e.g., Verhulst and Hut, 1996; Weatherhead and McRae, 1990; With and Balda, 1990; Zaias and Breitwisch, 1989). By prolonging brood care, parents may increase the survivorship of offspring, at the costs of deferred production of the next brood or a reduction in their own survivorship (Davies, 1976; Verhulst et al., 1997; Weathers and Sullivan, 1989). It seems paradoxical that cooperatively breeding birds can both produce more broods and provide more extensive care than noncooperative breeders.

Unfortunately, the main causes of variation in the duration of offspring care remain uncertain. For example, there is continuing controversy over which factors have the greatest effect on the duration of incubation and nestling care: diet, predation, or sibling competition (Lack, 1968; Martin, 1995; Rick-

lefs, 1993). Even less is known about the duration of care once offspring have left the nest (Nice, 1943; Skutch, 1976), yet for many species the longest period of offspring care and the peak rate of offspring provisioning occurs after fledging (e.g., Langen and Vehrencamp, 1999; McGowan and Woolfenden, 1990; With and Balda, 1990). The duration of postfledging offspring care may be influenced by (1) body size, as are the length of incubation, postnatal metabolic rate, and many other life-history traits (Daan and Tinbergen, 1997; Lack, 1968; Weathers and Siegal, 1995); (2) latitude of breeding, with tropical and southern hemisphere temperate species providing more extensive care than northern hemisphere temperate species (Ricklefs, 1969; Rowley and Russell, 1991); (3) diet, with birds that exploit food that is difficult to locate, capture, or process having prolonged offspring care (Ashmole and Tovar, 1968; Fogden, 1972; Heinsohn, 1991; Higuchi and Momose, 1981); and (4) the conflicting interests of offspring and parents (Mock and Forbes, 1992; Trivers, 1974).

Many resemblances among cooperatively breeding species can be attributed to shared ancestry (Cockburn, 1996; Edwards and Naeem, 1993; Ligon, 1993). I compared the duration of parental care between cooperative and noncooperative breeders after controlling for statistical non-independence due to phylogenetic relatedness and for ecological variables that may also affect this duration. Here I discuss why these parental care systems might differ in the duration of parental care and speculate on the evolutionary consequences of such a difference.

METHODS

Estimating the duration of offspring dependence

Measuring the duration of incubation and nestling care is straightforward, but there is no standard way to estimate the duration of parental care once offspring have left the nest. In this study, I compared the lengths of time that offspring are fed by parents or others after fledging, called the duration of postfledging nutritional dependence. This duration includes both the period that offspring are completely dependent on parents for food and the additional period in which offspring can potentially self-feed but benefit from parental provision-

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ing during shortfalls that occur while young acquire foraging skills (Langen, 1996; Sullivan, 1988). The duration of post-fledging nutritional dependence should reflect the duration of offspring care but is not necessarily related to the peak magnitude or total magnitude of parental effort (e.g., the peak rate of provisioning or the cumulative amount of food provided to offspring).

The age at which offspring become completely self-feeding is undoubtedly less accurately estimated than dates of hatching or fledging (Skutch, 1976). This is due in part to the inherent difficulties associated with observing young birds after they leave the nest. Moreover, there can be considerable intraspecific variation in the duration of nutritional dependence depending on whether parents have an opportunity to renest (last broods are provisioned longer than others; Nice, 1943; Skutch, 1976), the abundance of food (offspring have longer periods of dependence when food is scarce; Byle, 1990; Seki and Takano, 1998; Yoerg, 1998), and brood size (individuals from large broods become independent earlier; Heinsohn, 1991). Imprecise estimates of the mean duration of nutritional dependence due to these factors may obscure correlations with other life-history variables but are unlikely to create spurious associations.

However, there are at least three reasons that there might be a directional measurement bias in estimates of the duration of postfledging nutritional dependence associated with a parental care system. First, some observers may confound food exchanges that function as a form of social bonding with parental care. Such allofeeding occurs in cooperatively breeding Arabian babblers *Turdoides squamiceps*, Florida scrub-jays *Aphelocoma coerulescens*, and other species (McGowan and Woolfenden, 1990; Zahavi, 1990). Second, scrounging or stealing food by juveniles, which occurs commonly in many species of birds (Wunderle, 1991), may sometimes be classified erroneously as parental provisioning within groups of cooperative breeders. Finally, family groups of cooperative breeders may have greater territorial fidelity than others and hence are easier to locate and monitor than noncooperative breeders that provide equally prolonged care.

I evaluated these possibilities by comparing the results from the entire data set (see below) with those derived from a subset of studies in which the duration of nutritional dependence appeared to have been estimated with the most precision. This subset was composed of those studies in which parental food provisioning behavior was repeatedly quantified at regular, short intervals until offspring were entirely self-feeding, for more than one brood. Bias would be indicated if there were a trend in the residuals toward positive or negative deviations from zero. Systematic negative residuals among the cooperative breeders suggest that other, less careful studies tend to overestimate the duration of nutritional dependence in this group, whereas positive residuals for the noncooperative breeders indicate that most other studies underestimate the duration for this group.

Sources of comparative data

Members of the large monophyletic avian order Passeriformes are ecologically diverse, but the young of all species are altricial and require feeding by adults. Searching three encyclopedic collections of avian life histories (Brown et al., 1982–1997; Cramp and Perrins, 1977–1994; Poole et al., 1990–1997), all issues between 1970 and 1998 of several major ornithological journals (*Auk*, *Condor*, *Emu*, *Ibis*, *Notornis*, *Ornis Scandinavica*, *Ostrich*, *Wilson Bulletin*) and other sources, I found 261 species of Passerine birds for which an estimate of the duration of nutritional dependence in the wild has been made. I also noted the duration of nutritional dependence

among species in nonpasserine clades that include cooperative breeders and that feed their young, including semi-pre-social and altricial species. I included all sources that contained an estimate of the duration of nutritional dependence, regardless of whether the authors provided explicit details on how such estimates were made (data available by request). I recorded the mean duration of nutritional dependence (in days) for each species, or the midpoint of the range of ages if no mean was reported.

For each species in the data set, I also recorded the mean (or mid) incubation period and age at fledging (in days), mean adult female body mass (in grams, unsexed adult mass used if female mass unknown), and annual survivorship if measured. For asynchronously hatching species, the mean incubation period for the total brood was recorded (i.e., from the initiation of sustained incubation until half the clutch had hatched). The duration of care of the first brood of a breeding season was used when specified. Body masses were recorded primarily from Dunning (1993) or from the cited source.

I also noted the latitude of breeding, breeding habitat, and adult diet of each species. Breeding latitude was categorized as (1) northern hemisphere temperate, (2) southern hemisphere temperate, or (3) tropical. If a species breeds at more than one of these latitudes, I used the latitude at which the duration of nutritional dependence was estimated. Habitat was categorized as (1) forest (closed canopy of trees), (2) mixed (noncontinuous tree cover including savannah, gardens, and agricultural areas), or (3) open (desert, grassland, and marsh). Adult diet was categorized by the proportion of animal food (arthropods, vertebrates, etc.) and vegetable food (fruit, seeds, and nectar) as: (1) primarily animal, (2) mostly animal, some vegetable, (3) mostly vegetable, some animal, or (4) primarily vegetable. Migratory status was also recorded, but because virtually all migratory species were northern hemisphere temperate in my data set and none was cooperatively breeding, this factor was not included in the analyses.

Finally, each species was categorized into three groups according to the size of the breeding unit: frequently cooperatively breeding species (rank = 3) are those in which the mean number of birds that regularly feed offspring averages 2.5 or more per breeding unit in at least one studied population (these include both species with nonbreeding helpers and species with more than 2 genetic parents per brood); noncooperatively breeding species (rank = 1) are those with a mean of ≤ 2.0 adults that feed offspring in all studied populations; and occasionally cooperatively breeding species (rank = 2) are those species for which the mean is intermediate (2.1–2.4).

Treatment of comparative data

I used the computer application Comparative Analysis by Independent Contrasts (CAIC) 2.0 (Purvis and Rambaut, 1995) to calculate standardized phylogenetically independent contrasts for statistical analysis (for justifications and underlying evolutionary and statistical assumptions, see Felsenstein, 1985; Martins and Hansen, 1996; Pagel, 1992). The duration measures and body mass were natural-log transformed, and survivorship was arcsine transformed before calculating the contrasts. Branch topology of the phylogeny was based on Sibley and Ahlquist (1990) at deeper nodes and other recent phylogenies if available at terminal nodes (phylogenies: Badyaev, 1997; Bledsoe, 1988; Espinosa de los Monteros and Cracraft, 1997; Freeman and Zink, 1995; Johnson et al., 1988; Lanyon, 1994; Leisler et al., 1997; Patten and Fugate, 1998; Peterson and Burt, 1992; Price et al., 1997; Rowley and Russell, 1997; Sheldon and Winkler, 1993; Sheldon et al., 1992; Zink and

Blackwell, 1996). Species that did not appear on any phylogeny were placed adjacent to relatives that did, relatedness inferred from the standard taxonomy in Sibley and Monroe (1990). If no other information was available, I assumed that species in the same genus were more closely related than species in sister genera. Branch lengths were estimated using Sibley and Ahlquist (1990) data at 1.0 delta $T_{50}H$ units or greater and equal branch lengths below (= 1.0 delta $T_{50}H$ units) because branch lengths from other phylogenies were not comparable. I used Garland et al.'s (1992) method to appropriately scale the branch lengths; those used in the reported analyses were natural-log transformed. However, using untransformed branch lengths or setting all branch lengths equal did not qualitatively change the results.

For bivariate comparisons of truly continuous variables, I calculated standardized phylogenetically independent contrasts using the CAIC 2.0 option CRUNCH [this option calculates contrasts using the method of Felsenstein (1985) as modified by Pagel (1992) for non-bifurcating nodes on a phylogeny]. The option BRUNCH was used for comparisons that included one ranked categorical variable (BRUNCH uses parsimony to estimate the evolutionary pattern of the categorical variable, then calculates contrasts of a continuous variable at nodes where there is a transition from one categorical state to another). In the BRUNCH analyses, the association between the dependent variable and the independent variable was tested via sign tests, since the contrasts of the ranked variable were scaled relative to the lowest such that the null expectation (no difference between ranks) equaled zero. To produce a general linear model using multiple ranked and continuous variables, I used the CRUNCH option to calculate contrasts [for a justification of this approach, see Grafen (1989) and a brief discussion in Purvis and Rambaut (1995)]. The distribution of the residuals was inspected to verify the assumption of normality (Grafen, 1989). Regressions were fit through the origin (Garland et al., 1992).

Depending on how traits have evolved and the magnitude of estimate errors, there is evidence that analyses based on raw species data provide different information, and are sometimes more appropriate, than phylogenetically independent contrasts (Price, 1997; Ricklefs and Stark, 1996). Therefore, throughout this paper I report duplicate statistical analyses using both the independent contrasts and the raw species data. In each case, durations were natural-log transformed before analysis.

Finally, I also used a matched-pairs comparative method (Felsenstein, 1985; Møller and Birkhead, 1992), limiting comparisons of offspring care duration to closely related taxa that differ primarily in the parental care system. The chief weakness of using matched pairs over independent contrasts or other methods is that many potential comparisons are excluded and hence statistical power is lowered. This results in conservative statistical tests, but fewer assumptions are made about how the traits have evolved than when using other comparative methods (Harvey and Nee, 1997; Ridley and Grafen, 1996).

I compared frequently cooperatively breeding taxa with sister taxa of noncooperative breeders, using data from some of the passerine species included in the independent contrasts analyses and additional nonpasserine taxa. Occasional cooperative breeders were not used in the matched-pairs analyses but are mentioned in the results if they lie within a clade used in the comparisons. To identify the appropriate pairings, I primarily relied on the phylogenies used in the independent contrasts analyses (above), but alternative pairings were also used when other sources disagreed with these. The most distantly related pairings used in the analyses were at the subfamily level [maximum distance from Sibley and Ahlquist (1990)

data = 7.5 delta $T_{50}H$ units, mean \pm SE = 2.9 \pm 0.56]. No taxon was included in more than one matched pair.

When I had data from multiple species within a clade, I used the mean species value in the comparisons. In a few instances, more than one species with each parental care system shared a node on the phylogeny; for these the mean value of all cooperative breeders was compared to the mean of the noncooperative breeders. Substituting medians for means in the analyses did not alter the results. Sign tests were used as statistical tests of whether general patterns exist in the direction of differences between matched pairs, uninfluenced by the magnitude of the differences.

For a subset of matched pairs, published phylogenetic reconstructions of the evolution of parental care systems exist (such reconstructions assume parsimony and use many more species than are included in the matched pairs; e.g., Edwards and Naem, 1993; Peterson and Burt, 1992). These studies allowed me to infer whether cooperative breeding was ancestral or derived within the matched pair. For some other matched pairs, I could infer that the ancestral state of the parental care system was noncooperative breeding because, with the exception of the cooperative breeding species of the matched pair, other species within the genus and closely related genera are noncooperative breeders. I used these reconstructions to ask whether directional changes in the duration of care were equally frequent when the parental care system changed in either direction.

RESULTS

Independent contrasts and raw species data

Among the 261 species of passerine birds in my data set, the average duration of offspring care after leaving the nest (as measured by the duration of food provisioning) is nearly equal in duration to the total period of care within the nest (mean \pm SE days: incubation period = 14.1 \pm 0.15, nestling period = 15.7 \pm 0.36, fledgling period = 27.3 \pm 1.50). The period of care after fledging is much more variable among species than the incubation and nestling periods (coefficient of variation \pm SE: incubation = 17.2 \pm 0.79%, nestling = 37.2 \pm 1.85%, fledgling = 89.1 \pm 6.27%).

Frequently cooperatively-breeding passerine birds do not differ from noncooperative breeders in incubation duration per brood judging from the independent contrasts (11 of 18 contrasts $>$ 0, sign test $p = .5$), although the raw species data suggest that cooperative breeders incubate longer ($t_{240} = 3.2$, $p = .002$; frequent cooperative, mean \pm SE = 15.3 \pm 0.50 days, $n = 33$, noncooperative breeders = 13.9 \pm 0.16, $n = 209$). Time in the nest after hatching does not differ between the two parental care categories in passerine birds (9 of 19 contrasts $>$ 0, sign test $p = 1.0$; raw species $t_{245} = 1.6$, $p = .12$; frequent cooperative breeders = 17.0 \pm 1.00 days, $n = 34$, noncooperative breeders = 15.4 \pm 0.40, $n = 213$). However, the contrasts for the duration of fledgling feeding are significantly higher for frequent cooperative breeders than for occasional cooperative breeders and noncooperative breeders (frequent cooperative breeders: 20 of 20 contrasts $>$ 0, sign test $p < .0001$; occasional cooperative breeders: 5 of 9 contrasts $>$ 0, sign test $p = 1.0$). This supports the pattern indicated by the raw species data (Figure 1; $F_{2, 258} = 30.6$, $p < .0001$).

Using either contrasts or raw species data, the parental care system is a significant predictor of the duration of fledgling feeding in a multiple regression that also includes diet, habitat, latitude, and mass as predictors (Table 1; contrasts full regression model, $F_{5, 185} = 18.2$, $p < .0001$, $r^2 = .31$; raw species full regression model, $F_{5, 255} = 44.6$, $p < .0001$, $r^2 = .46$).

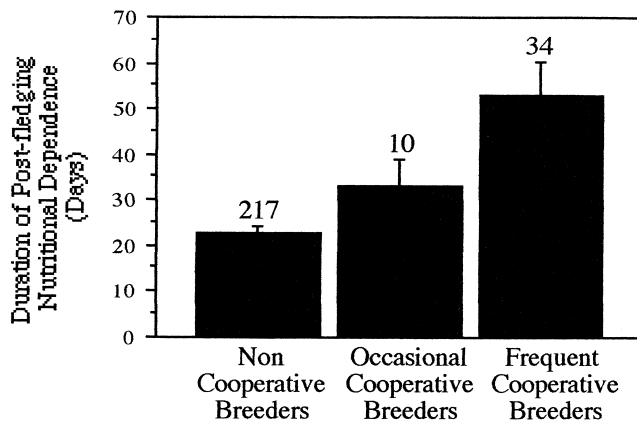


Figure 1

The mean and SEM duration of fledgling feeding in passerine birds of each parental care category. The number of species is shown above each bar.

This regression also indicates that offspring dependence is longer when the diet consists of animal food, the habitat occupied is woodland, breeding latitude is tropical, and body size is large (Table 1). Incubation or nestling care duration is not significantly associated with the breeding system when these other factors are included in a multiple regression model.

To test whether there is a directional bias in the estimates of the age of nutritional independence associated with the parental care system, I calculated the residuals of the multiple regression of raw species data presented in Table 1. I then inspected the standardized residuals of the subset of studies that estimated the age of nutritional independence with greatest precision (Table 2; data include 4% of the noncooperative breeders and 12% of the frequent cooperative breeders). Neither the standardized residuals for the frequent cooperative breeders nor those of the noncooperative breeders differ significantly from zero (frequent cooperative breeders: $t_3 = 0.9$, $p = .5$; noncooperative breeders: $t_7 = 0.1$, $p = .9$).

Finally, among the subset of species for which there are data on annual survivorship, the duration of fledgling feeding is significantly correlated with adult survivorship (contrast, $r = .30$, $p = .007$, $n = 80$; raw species, $r = .38$, $p = .0002$, $n = 92$). This correlation remains if the shared association with body mass is partialled out. The parental care system remains a significant predictor of the duration of fledgling dependence when survivorship is included in a regression model (parental care: contrast $F_{1,76} = 2.0$, $p = .04$, standardized regression coefficient = .202; survivorship: contrast $F_{1,76} = 1.8$, $p = .08$, coefficient = .198).

Matched pairs

The matched pairs of passerines (16 pairings) and nonpasserines (7 pairings) are described in the Appendix. Duration of incubation does not differ significantly between the matched pairs (frequent cooperative breeders longer in 13 of 20 non-tied comparisons, sign test, $p = .3$), nor does the length of time between hatching and fledging (frequent cooperative breeders longer in 8 of 16 non-tied comparisons, sign test, $p = 1.0$). However, cooperatively breeding species do feed offspring significantly longer after fledging (frequent cooperative breeders longer in 21 of 23 comparisons, sign test, $p < .0001$). On average, they feed offspring twice as long as their noncooperative relatives [median ratio (cooperative/

Table 1

Significance of predictors of the natural log-transformed duration of postfledging nutritional dependence in general linear models using species values and independent contrasts

Predictor	Standardized coefficient	
	Species	Contrasts
Breeding system	0.27***	0.26***
Habitat	-0.27***	-0.15*
Latitude	0.27***	0.26***
Diet	-0.18**	-0.23**
ln(Mass)	0.38***	0.11†

*** $p < .0001$; ** $p < .01$; * $p < .05$; † $p < .1$.

noncooperative) = 2.05]. As a consequence, the postfledging period accounts for a relatively higher proportion of the total duration of offspring investment between the initiation of incubation and the age of nutritional independence [frequent cooperative breeders higher in 21 of 22 non-tied comparisons, sign test, $p < .0001$; median ratio (duration of postfledging feeding/duration of nest care): frequent cooperative breeders = 1.27, noncooperative breeders = 0.73].

Using alternative phylogenies to create matched pairs does not qualitatively change the results, nor does limiting pairings to very closely related taxa (subtribe and below) based on the Sibley and Ahlquist (1990) DNA-DNA hybridization criterion, nor does restricting matched pairs to those consisting of species in the same genus. Limiting comparisons to species-pairs that are similar in body size, that breed in the same habitat or at the same latitude, or that share diets does not qualitatively change the results either.

Noncooperative breeding is likely to have been the ancestral state in eight of the matched pairs, and cooperative breeding is likely to have been the ancestral state in six pairs (ancestral state of other pairs uncertain; see Appendix). Among these pairs, it is as likely for the evolution of cooperative breeding to be associated with an increase in duration of fledgling care (seven of eight pairs) as it is for the loss of cooperative breeding to be associated with a reduction (five of six pairs; Fisher's Exact test, $p = 1.0$).

DISCUSSION

General conclusions

The results can be summarized by four main points. (1) The total duration of parental care at the nest (incubation and nestling periods) does not differ between cooperatively and noncooperatively breeding taxa. (2) Cooperatively breeding taxa do feed fledged offspring significantly longer than noncooperative breeders, and this association is not merely the result of other factors such as diet or latitude of breeding that covary with both the parental care system and the duration of postfledging care. (3) Changes in the parental care system in either direction (cooperative to noncooperative or the reverse) are both associated with directional changes in the length of postfledging offspring care. (4) Adult survivorship and the duration of fledgling feeding are positively associated. Cooperative breeders generally have higher adult survivorship than other birds (Arnold and Owens, 1998; Brown, 1987). However, the duration of postfledging offspring dependence remains directly associated with the parental care system when adult survivorship is statistically controlled.

The first point may appear surprising; one might expect that the duration of care at the nest would be shorter in

cooperative breeders because a larger workforce could permit more sustained incubation and a higher rate of nestling provisioning, resulting in a faster rate of offspring growth and therefore earlier fledging to escape the risky nest environment. This would be advantageous because the rate of predation does not differ between cooperatively and noncooperatively breeding species (Poiani and Pagel, 1997). Nevertheless, provisioning rate does not increase substantially with additional members in the workforce in many cooperatively breeding species (Brown, 1987; Crick, 1992; Hatchwell, 1999).

The second and third points confirm a modified form of the generalization that cooperatively breeding birds provide more extensive care for their offspring. There is a strong association between the length of postfledging feeding and the parental care system such that transitions in either direction are almost invariably associated with a predictable change in the duration of care. It is not possible to conclude definitively with these correlative data whether cooperative breeding causes a lengthening of parental care or whether taxa that provide extensive care are predisposed to evolve cooperative breeding, but the former is more probable. When closely related species differ in both the parental care system and the duration of parental care, there are no obvious differences in their reproductive biology or life history that explain why the offspring of the cooperatively breeding species intrinsically require more prolonged feeding by adults. Other ecological and social factors seem to provide better general explanations for the evolution of cooperative breeding in birds than inherently long offspring dependence (reviewed in Brown, 1987; Emlen, 1991; Koenig et al., 1992). However, the benefits to breeders and offspring from helper contributions that result in extended brood care may help explain the maintenance of helping behavior (see below).

It could be informative to examine how the duration of offspring dependence varies within a species depending on the number of care providers. I am aware of only two such studies: in white-winged crows (*Corcorax melanorhamphos*) the average duration of postfledging nutritional dependence increases with the number of helpers (Heinsohn, 1991), but in dunnocks (*Prunella modularis*), offspring in breeding units of three adults are not nutritionally dependent significantly longer than those with two adults (Byle, 1990).

Potential causes and evolutionary consequences of prolonged offspring care

In noncooperatively breeding birds, there is typically little overlap between care of one brood and the production of the next, although a male may continue to feed fledglings for a brief period on his own while his mate begins to reneest (e.g., Verhulst and Hut, 1996; Weatherhead and McRae, 1990; With and Balda, 1990; Zaias and Breitwisch, 1989). The duration of fledgling care is thought to be a compromise between the length of time that most improves the viability of the offspring and the length of time that allows the most nesting attempts during the breeding season or least affects the parents' survival. Parental provisioning is terminated when the costs to each parent are no longer compensated by sufficient improvement in the condition of the offspring (Davies, 1976, 1978; Verhulst et al., 1997; Weathers and Sullivan, 1989). Offspring often appear to conflict with parents over the termination of offspring care and may force parents to provide care for a somewhat longer period than is optimal for them, but there is currently little empirical evidence to support this conjecture (Mock and Forbes, 1992; Trivers, 1974).

In cooperatively breeding species, helpers lighten the load on the breeders by sharing in offspring care. Brood size is

often unaffected by helper contributions (Brown, 1987; Crick, 1992; Hatchwell, 1999). Instead, the reduced burden on breeders results in higher survivorship for them or more rapid reneesting (Brown, 1987; Poiani and Jermiin, 1994). In some species, rapid reneesting is facilitated by a division of labor within cooperatively breeding groups: helpers continue to feed fledged young while breeders begin the next nesting attempt (Brown and Brown, 1981; Carlisle and Zahavi, 1986; Langen and Vehrencamp, 1999; Rowley and Russell, 1990). For example, in white-throated magpie-jays (*Calocitta formosa*), reneesting can coincide with the peak period of offspring provisioning, which occurs soon after the first brood has fledged. Helpers do virtually all subsequent provisioning of the first brood while a breeding pair begins production of the second. If the second nest is successful, helpers terminate feeding of the first brood when the second fledges, and begin contributing to the care of the latter (Langen and Vehrencamp, 1999). Unfortunately, for the other species of cooperative breeders there are only anecdotal descriptions of division of labor during multiple brooding.

The principal reason, I suggest, that cooperatively breeding species of birds have more extensive postfledging offspring care than noncooperative breeders is precisely because of helper assistance, which lowers the per capita costs of parenting and sometimes results in more efficient breeding through division of labor. Breeders can recuperate and reneest, while other group members continue to care for the fledglings until the next brood requires significant investment, after the eggs have hatched (Drent and Daan, 1980; Weathers, 1996). Even for the few cooperatively breeding species that breed only once per season, the duration of care may be more prolonged than similar noncooperative breeders if the burden-lightening contributions of helpers allow care providers to maintain better condition. The period of prolonged offspring provisioning may result in a reduction of the considerable risks associated with the acquisition of foraging skills in young birds at negligible costs to the breeders' fitness.

In addition, offspring may benefit more from prolonged care in cooperative than in noncooperative breeders for two reasons. First, the cost of extended parental care to a recipient offspring in terms of any reduced residual reproductive value of related care providers may be lower on average in cooperative than in noncooperative breeders. This is because from the perspective of a recipient offspring in a noncooperatively breeding species, this cost is in terms of lost full or half siblings ($r \geq .25$), whereas from the same perspective in a cooperatively breeding species, some of the care providers (the helpers) are at best full siblings of the recipient and so this cost via the helpers is in terms of lost nieces and nephews or less closely related kin ($r \leq .25$). Second, the offspring in many noncooperative breeders disperse as soon as they become independent to gain an advantage at competing for feeding or breeding territories nearby home or, for migratory species, in the wintering range (e.g., Nilsson, 1990; Yoerg, 1998). It appears to be less advantageous to disperse at an early age in most cooperative breeders (hence the presence of helpers, which are typically philopatric offspring of previous broods), so offspring gain nothing by becoming independent sooner.

Prolonged offspring care in cooperative breeders may not be caused by inherent differences in the rate of development between them and their noncooperative relatives, but this does not preclude a subsequent evolutionary slowing of development in lineages with a long history of cooperative breeding as a consequence of the availability of extended care. For example, development may slow to lower the peak power demand of growing offspring, which in turn lowers the risk of starvation (Ricklefs, 1984). Prolonged care by

Table 2

Species for which the age of nutritional independence has been estimated with the greatest precision in passerine birds, compared with the expected age of independence of each

Species	Parental care ^a	Age of independence		No. of broods	Observed-predicted (days)	Reference
		Mean \pm SD	Range			
<i>Acrocephalus sechellensis</i>	F	69.3 \pm 19.71	52–220	(189 individuals)	12.0	Komdeur (1996)
<i>Aphelocoma coerulescens</i>	F	66.4 \pm 12.91	58–92	9	25.9	McGowan and Woollenden (1990)
<i>Calocitta formosa</i>	F	70.9 \pm 4.00	48–110	(17 individuals)	–8.5	Langen (1996)
<i>Cinclus cinclus</i>	N	12.4 \pm 1.89	8–16	8	–12.8	Yoerg (1998)
<i>Erethacus rubecula</i>	N		17–23	(22 individuals?)	4.1	Harper (1985)
<i>Junco phaeotus</i>	N		22–28	(218 individuals)	6.8	Sullivan (1988)
<i>Muscicapa striata</i>	N		17–18	3	0.4	Davies (1976)
<i>Oenanthe oenanthe</i>	N		15–16	4	2.5	Moreno (1984)
<i>Parus atricapillus</i>	N		17–22	8	0.8	Leonard et al. (1991)
<i>Parus major major</i>	N	19.1 \pm 5.10	7–33	16	3.1	Verhulst and Hut (1996)
<i>Parus major minor</i>	N	16.8 \pm 6.78	9–26	17		Seki and Tokano (1996)
<i>Prunella modularis</i>	F	24.6 \pm 2.20	22–30	18	–2.2	Byle (1990)
<i>Turdus merula</i>	N	18.3		32	–7.3	Edwards (1985)
Mean \pm SE, frequent cooperative breeder		57.8 \pm 10.97			6.9 \pm 7.68	
Mean \pm SE, noncooperative breeder		18.3 \pm 1.15			–0.3 \pm 2.30	

See Methods for criteria of inclusion. To calculate the overall mean age of independence for each parental care class, species mid-values of the range were used for those species lacking mean estimates. The predicted values were calculated using the multiple regression model of raw species data reported in Table 1. Only one subspecies of *Parus major* (ssp. *major*) was included in the multiple regression. *Turdus merula* calculated from the weighted mean of seven time periods for first broods in Figure 6 of Edwards (1985).

^a F, frequent cooperatively breeding species; N, noncooperative breeder.

adults may also facilitate evolutionary specialization toward foraging behavior that requires a long period of development to master, with a consequence that cooperative breeding becomes obligatory, as may be the case in some New World jays (Langen, 1996) and the white-winged chough (Heinsohn, 1991). Finally and most speculatively, slowing of development may be associated with increased life span in birds (Ricklefs, 1993). Because attainment of breeding status occurs substantially later than sexual maturity in most cooperative breeders and mortality is associated with senescence in some (Brown, 1987; Holmes and Austad, 1995; Lawton and Lawton, 1986; McDonald et al., 1996), a potential evolutionary consequence of the availability of extended postfledging care may be a slowing of the maturation rate from selection to increase the life span.

Cooperative breeding and the duration of offspring care in other taxa

As in birds, prolonged offspring care is associated with cooperative breeding in insects (Alexander et al., 1991). The potential for helpers to extend the period of offspring care is thought to be an important factor in the evolution of cooperative breeding in these animals. For example, the advantages provided by a division of labor in which older immature offspring continue to care for their younger siblings while their parents undertake production of the next brood may have facilitated the transition toward eusociality in termites and their relatives, the cooperatively breeding roaches (Nalepa, 1994). Cooperative breeding permits extended offspring dependence even when breeders are at significant risk of dying because helpers can continue to provide care after loss of a breeder. The frequent evolution of cooperative breeding in some groups of social insects may in part have been facilitated by the ability of such insects to provide prolonged offspring care despite relatively low adult survivor-

ship (Alexander et al., 1991; Gadagkar, 1990; Nonacs, 1991; Queller, 1989, 1994).

In mammals, cooperative breeding appears to be associated with species for which offspring production is inherently costly (Creel and Creel, 1991; Creel and MacDonald, 1995; Geffen et al., 1996; Moehlman and Hofer, 1997). Most nourishment to offspring in cooperatively breeding mammals is provided by the mother in the form of milk; other group members can only provision offspring indirectly by providing food to the nursing mother. Unlike insects and birds, it appears that the contributions of helpers result in shorter periods of offspring dependence in mammals, at least for those in the order Carnivora (Creel and Creel, 1991). The period of dependence appears to be shorter because the lactating mother of the offspring provides more milk to them as a consequence of the provisioning she receives from the helpers. More milk results in faster growth of the offspring and therefore earlier independence (Oftedal and Gittleman, 1989). There may be fundamental differences in how cooperative breeding affects offspring care between those animals in which an important form of care such as food provisioning can only be performed by a parent, and those animals in which all members of the breeding group can contribute. For mammals that provide food to weaned young (e.g., canids), it may be worthwhile to examine how offspring provisioning differs after weaning between cooperatively breeding species and their noncooperative relatives.

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APPENDIX

Duration of parental care and other characteristics of the species used to form the 23 matched-pair comparisons

Species ^a	Female mass (g)	Breeding system ^b	Duration of parental care			Latitude ^c	Reference ^d
			Incubation	Nestling	Fledgling		
1. <i>Porphyrio p. melanotus</i>	885	F	24	1	70	S	1
<i>P. mantelli</i>	2268	O	30	1	120	S	2
<i>Porphyryula martinica</i>	235	F	23	1	60	T	3
<i>Porzana pusilla</i>	33	N	19	1	4	N	4
<i>P. parva</i>	49	N	22	1	4	N	4
<i>P. porzana</i>	78	N	21	1	4	N	4
2. <i>Gallinula mortierii</i>	1251	F	22	2	56	S	5
<i>G. tenebrosa</i>	493	F	22	4	63	S	6, 7
<i>G. chloropus</i>	265	O	22	1	44	N, S	4, 8
<i>Fulica atra</i>	750	N	23	1	30	N	4
<i>F. americana</i>	432	N	24	5	25	N	9
3. <i>Merops bullocki</i>	23	F	20	26	35	T	10, 11
<i>M. bullockoides</i>	35	F	20	28	42	T	11, 12
<i>M. apiaster</i>	54	O	20	31	21	N	11
<i>M. superciliosus</i>	48	N	?	?	19	T	4
4. <i>Dacelo novaeguineae</i>	305	F	23	36	74	S	13
<i>Halcyon senegalensis</i>	59	N	14	22	35	T	11
5. <i>Ceryle rudis</i>	86	F	18	25	18	T	4, 14
<i>C. alcyon</i>	148	N	24	28	21	N	15
6. <i>Picoides borealis</i>	48	F	13	27	150	N	16, 17
<i>P. pubescens</i>	28	N	12	21	41	N	18
7. <i>Melanerpes formicivorus</i>	78	F	14	31	60	N	19
<i>M. portoricensis</i>	53	N	?	?	14	T	19
<i>M. chrysauchen</i>	47	N	12	36	51	T	19
<i>M. rubricapillus</i>	49	N	10	32	36	T	19
<i>M. carolinus</i>	56	N	12	25	56	N	19
8. <i>Conopias inornata</i>	30	F	18	18	72	T	20
<i>Myiarchus crinitus</i>	34	N	15	14	21	N	15
9. <i>Climacteris picumnus</i>	37	F	16	24	32	S	21
<i>C. erythropis</i>	23	F	18	25	66	S	21
<i>Cormobates leucopaea</i>	23	N	23	26	35	S	21
10. <i>Manorina melanophrys</i>	32	F	15	12	61	S	22
<i>M. melanocephala</i>	68	F	16	16	43	S	23
<i>Ephthianura albifrons</i>	12	N	14	14	10	S	24
11. <i>Acanthiza reguloides</i>	8	F	15	18	42	S	25
<i>Gerygone igata</i>	6	N	22	17	32	S	26
12. <i>Lanius excubitorius</i>	52	F	14	19	73	T	27
<i>L. senator</i>	29	N	15	18	25	N	4
<i>L. excubitor</i>	66	N	15	20	16	N	28
<i>L. collaris</i>	36	N	14	18	32	T	29
13. <i>Mohoua albicilla</i>	17	F	18	17	35	S	30
<i>M. ochrocephala</i>	?	O	21	18	55	S	31, 32
<i>Pachycephala rufiventris</i>	25	N	16	12	60	S	33
14. <i>Aphelocoma coerulescens</i>	75	F	18	18	66	N	15
<i>A. insularis</i>	109	N	?	?	60	N	34
<i>A. californica</i>	74	N	22	23	34	N	35, 36
15. <i>Buphagus erythrorhynchus</i>	49	F	13	30	90	T	37
<i>Onychognathus tristramii</i>	120	N	16	30	10	N	4
<i>Sturnus unicolor</i>	86	N	11	22	5	N	4
<i>S. vulgaris</i>	79	N	12	21	11	N	15
16. <i>Nesomimus parvulus</i>	51	F	13	15	33	T	38
<i>Mimus polyglottos</i>	47	N	13	12	21	N	15
17. <i>Campylorhynchus griseus</i>	42	F	21	17	30	T	39
<i>C. nuchalis</i>	23	F	17	17	30	T	40
<i>C. brunneicapillus</i>	39	N	16	21	29	N	41
18. <i>Parus (Melaniparus) niger</i>	18	F	15	24	49	S	42, 43
<i>P. (Poecile) palustris</i>	12	N	14	19	11	N	4
<i>P. (Poecile) cinctus</i>	11	N	11	20	10	N	4
<i>P. (Poecile) atricapillus</i>	12	N	13	16	25	N	15
<i>P. (Lophophanes) cristatus</i>	11	N	18	20	23	N	4
<i>P. (Parus) major</i>	18	N	14	19	19	N	4, 44
<i>P. (Baeolophus) bicolor</i>	22	N	13	16	21	N	15
19. <i>Sitta pygmaea</i>	11	F	21	21	27	N	45, 46
<i>S. pusilla</i>	10	O	14	19	26	N	45
<i>S. europea</i>	24	N	15	24	9	N	4
20. <i>Acrocephalus sechellensis</i>	15	F	18	19	69	T	47
<i>A. arundinaceus</i>	28	N	14	13	13	N	4

APPENDIX, continued

Species ^a	Female mass (g)	Breeding system ^b	Duration of parental care			Latitude ^c	Reference ^d
			Incubation	Nestling	Fledgling		
21. <i>Turdoides altirostris</i>	33	F	13	10	49	T	4
<i>T. caudatus</i>	32	F	13	12	180	T	4
<i>T. squamiceps</i>	73	F	14	12	45	N	4
<i>Panurus biarmicus</i>	15	N	12	13	14	N	4
<i>Chamaea fasciata</i>	14	N	15	16	31	N	48
<i>Sylvia undata</i>	9	N	13	12	13	N	4
<i>S. conspicillata</i>	10	N	13	12	21	N	4
<i>S. melanocephala</i>	13	N	13	13	18	N	4
<i>S. leucomelaena</i>	15	N	16	16	40	N	29
<i>S. hortensis</i>	22	N	13	13	6	N	4
<i>S. communis</i>	15	N	12	11	18	N	4
<i>S. borin</i>	19	N	12	10	12	N	4
22. <i>Plocepasser mahali</i>	42	F	14	18	28/90	T	49, 50
<i>Pseudonigrita arnaudi</i>	20	F	14	20	25	T	51
<i>Ploceus cucullatus</i>	37	N	13	20	21	T	52
23. <i>Calcaricus pictus</i>	26	F	12	8	21	N	15
<i>C. lapponicus</i>	23	N	12	9	15	N	53
<i>C. ornatus</i>	20	N	12	10	14	N	15

^a Matched-pairs for which the direction of the transition in parental care system has been inferred include the following (the number refers to the number of the pairing; see Methods for how the polarity of change was determined for pairings lacking a citation): Cooperative Ancestral—9 (Cockburn 1996), 10 (Cockburn 1996), 11 (Cockburn 1996), 12 (Zack 1995), 13 (Cockburn 1996), 14 (Peterson and Burt 1992); Non-Cooperative Ancestral—5, 6, 16, 17 (Edwards and Naeem 1993), 18, 19, 20, 23.

^b F = frequent cooperative breeder, O = occasional cooperative breeder, N = non-cooperative breeder.

^c N = north temperate, S = south temperate, T = tropical.

^d 1. Craig 1980 2. Marchant and Higgins 1990 3. Hunter 1987 4. Cramp and Perrins 1977–1994 5. Ridpath 1972 6. Garnett 1978 7. Garnett 1980 8. Siegfried and Frost 1975 9. Gullion 1954 10. Fry 1972 11. Brown et al. 1982–1997 12. Emlen 1990 13. Parry 1973 14. Reyer 1990 15. Poole et al. 1990–1997 16. Ligon 1970 17. Walters 1990 18. Lawrence 1966 19. Short 1982 20. Thomas 1979 21. Noske 1991 22. Clarke 1988 23. Dow 1978 24. Major 1991 25. Bell and Ford 1985 26. Gill 1982 27. Zack 1986a 28. Paz 1987 29. Zack 1986b 30. McLean and Gill 1988 31. Read 1987 32. Falla et al. 1967 33. Bridges 1994 34. Atwood 1990 35. Ritter 1983 36. Carmen 1988 37. Stutterheim 1982 38. Grant and Grant 1979 39. Rabenold 1985 40. Austad and Rabenold 1985 41. Anderson and Anderson 1973 42. Tarboton 1981 43. McLachlan and Liverside 1970 44. Verhulst and Hut 45. Norris 1958 46. Sydeman et al. 1988. 47. Komdeur 1996 48. Guepal and DeSante 1990 49. Collias and Collias 1978 50. Lewis 1982 51. Collias and Collias 1980 52. Collias and Collias 1970 53. McLoughlin and Montgomerie 1985.

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