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MALE PARENTAL BEHAVIOR IN BIRDS

Ellen D. Ketterson and Val Nolan, Jr.

Department of Biology and Center for the Integrative Study of Animal Behavior,
Indiana University, Bloomington, Indiana 47405

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Abstract

Male parental care is rare in most groups of animals but common in birds. Among birds considerable variation exists in the form of care provided their young; recent developments in several areas may help to explain this variation. These include (i) improvements in the comparative method, particularly the use of phylogenies to investigate questions about the evolution (origin) of behavior; (ii) field studies designed to determine the fitness benefits of care and the selective factors that maintain it; and (iii) investigations of the mechanisms of care, especially its neural and hormonal bases. The greatest challenge to functional explanations of male care has come from the revelation that males frequently provide care for offspring that are not genetically their own. Resolving this apparent paradox will require more accurate accounting of the costs and the benefits of care, and greater attention to the form of care provided by males. Data support the following working hypothesis: In taxa in which males incubate, as opposed to providing other forms of care, sexual selection may be less intense and males may resemble females more in appearance and physiology. Males may also be more likely to be the genetic sires of the offspring they care for, perhaps because of the greater cost to females of multiple matings or perhaps because male incubation is incompatible with sustained sexual behavior. Ultimately, an integrated consideration of history, function, mechanism, and development should reveal the interplay of factors that have led to male parental care in birds and that account for its maintenance in various forms today.

INTRODUCTION

With the exception of brood-parasitic species, which lay their eggs in the nests of other birds, virtually all birds provide some form of parental care after eggs are laid, and parental care by males is more extensive in birds than in any other vertebrate class (9, 38, 43, 70). Sometimes the care provided by males is indirect, as when they help build nests (65% of avian subfamilies—70) or feed the female during egg-laying or incubation (48% of avian subfamilies—70), but what clearly distinguishes male birds is the extent to which they give direct attention to eggs or young. In most avian subfamilies, according to Silver et al (70), males incubate eggs (68%) and care for young, either by feeding them (71%) or by escorting them to feeding sites (73%). While male care after egg-laying or parturition has been described in fish, amphibians, and mammals, it is decidedly rarer than in birds (9, 23, 25, 63).

Our particular interest in this subject stems from 12 years of study of male parental behavior in the dark-eyed junco (*Junco hyemalis*), a species of songbird in which males feed and protect offspring but leave most other forms of parental behavior to females. As behavioral ecologists, we tested whether male care was essential to reproduction by removing males at the time the eggs hatched and comparing the reproductive success of male-aided and unaided females (100, 101, 102). We next manipulated testosterone in male juncos, a treatment that simultaneously enhances courtship and suppresses parental behavior (38, 41). Our objective was to determine whether females, which had to increase parental effort to compensate for reduced male investment, based their subsequent choice of mates on the level of care previously provided by males.

We review the results of these studies below, but one initial finding of interest concerned the behavior of the males that took over the territories of those we removed. These replacement males courted the females and frequently paired with them for subsequent breeding attempts. Typically, replacement males provided only limited care for their predecessors' young, but a few behaved like fathers and brought food (40, 100). We became curious about the stimuli that elicited care and hence about the nature of the mechanisms governing care and how they might evolve (38). Our findings that testosterone suppressed male feeding (41, 71) while enhancing attractiveness to females (D Enstrom, ED Ketterson, V Nolan, Jr, unpublished data) suggested that this hormone might be pivotal to the physiology underlying variation in patterns of mating and parental care (38).

We concluded that a full understanding of the evolution of male parental care would require all the approaches recommended by Niko Tinbergen (74): historical, functional, mechanistic, and developmental. One of our objectives in this article is to develop the case for a multi-level analysis of parental care.

Another objective is to report particular advances in the study of male parental care in birds as an example of general progress in the area of behavioral ecology. The key questions we address are: (i) How does current understanding of avian parental behavior differ from previous understanding (e.g. 15–20 years ago)? And (ii) what areas of research were not foreseen about two decades ago? We begin with an overview of the changes that have occurred, which we do not attempt to document in detail, then narrow the focus to topics to be addressed in greater detail.

Then and Now

Some 20 years ago, behavioral ecologists interested in reproduction focused on mating systems, parental care, and sexual dimorphism in secondary sex characteristics (size, structures, or coloration). Perhaps the central question was why male parental care tended to co-occur with monogamy and sexual monomorphism, whereas reduced male care, or its absence, was correlated with polygyny and with sexual dimorphism (43, 77). Those most interested in the evolution of polygyny made within-species comparisons of the reproductive success of primary (first-mated) and secondary females of polygynous males (7, 54, 76). The expectation was that secondary females would receive less male help than they would receive if mated monogamously, but that nevertheless they would be as successful as females mated to males that attracted only one mate. Thus, the polygyny threshold model (54, 76) predicted that territories held by polygynists would provide resources sufficient to compensate for diluted male care. Those most interested in monogamy assumed that the parental care provided by males in monogamous species was essential, or at least very important, for successful reproduction (43, 99), and some began field studies to test that hypothesis (28, 62). Also underway were long-term assessments of variance in male lifetime reproductive success; males were marked and counted as were the females they paired with and the offspring produced (10). Variance in reproductive success was expected to be greater among males than among females and to be correlated with mating system; sexual selection, it was thought, would be more intense in polygynous species, accounting for their greater sexual dimorphism (10, 57, 68).

Preconceptions may have inhibited other lines of inquiry. For example, adaptation and mechanism were often studied independently, probably in the belief that “how” and “why” questions represented different levels of analysis. Adaptation was assumed, and the challenge was to identify function; mechanisms would evolve to enable function. Less attention was paid to the origin of parental behavior, as opposed to its current utility, perhaps because any hypothetical reconstruction would remain controversial as long as systematists could not agree on which taxa were primitive and which were advanced.

Rather, attention was focused on seeking ecological correlates of interspecific variation in mating systems, parental care, and dimorphism.

Behavioral ecologists are still interested in these issues, but their approaches to such studies have changed significantly. Methodological breakthroughs permit us to measure genetic relatedness with greater certainty at many levels (e.g. parent-offspring, species complexes). The discoveries that extra-pair paternity (EPP) is frequent in pair-bonded birds and that females of some species lay eggs in the nests of other females (conspecific brood parasitism, CBP) (4, 29, 84) have had enormous impact on the way we think about mating systems, male care, and sexual dimorphism. In fact, the existence of EPP and CBP have called into question our ability even to categorize mating systems and have cast doubt on past efforts to measure reproductive success (24). Terms like *monogamy* and *polygyny*, formerly entrenched in the literature, are now qualified as "apparent monogamy" or "social monogamy" when they are contrasted with alternatives such as "social or overt polygyny."

Extra-pair paternity also raised the unforeseen question of how male parental care evolved if the cared-for individuals frequently are not related to the care giver (4, 50, 57, 85, 88, 106). This has generated new interest in assessing the fitness consequences of male parental care in order to determine just how costly or beneficial it is (3, 16, 49, 81, 100, 102). EPP also raises the possibility that the variance in reproductive success among apparently monogamous male birds is greater than was once thought, but, given the existence of CBP, not necessarily greater than in females. Much research has focused on mate choice by females and the implications of choice for sexual selection and sexual dimorphism (summarized in 4).

Improved techniques for measuring relatedness have also acted synergistically with improvements in the comparative method (33) and in methods for building phylogenies (21), fostering greater confidence in hypotheses about adaptation (5, 53). The better our phylogenies, the greater our ability to reconstruct the order of evolution of behavioral alternatives and thus to ascertain the relative importance of ancestry and ecology in accounting for interspecific variation. In the near future we can expect a spate of studies relating behavior to molecular-based phylogenies.

Understanding of the ultimate causes of parental behavior, mating systems, and sexual dimorphism has also been enhanced by the study of mechanism. The circulating level of testosterone, a hormone long known to orchestrate sexual differentiation and thus to account for sexual dimorphism, has now been shown to correlate with mating systems and parental behavior (92–94). We may be on the verge of identifying the proximate mechanisms (i.e. changes in organismal attributes) that accompany loss or origin of social monogamy, male parental care, and monomorphism. Knowledge of mechanisms, particularly developmental mechanisms, is also important if we are to describe limits to

adaptation, i.e. constraints, and also to account for the plasticity that apparently allows males to adjust their investment in mating and parental effort. Such adjustments are likely to depend on the relative frequency of individuals that behave in alternative ways, emphasizing the importance now attached to frequency dependence. Some such alternative adjustments may be made early in the individual's life, as we are just beginning to appreciate the role of early environment in shaping variation in reproductive tactics (36, 67, 80a, 97).

Clearly, we cannot develop all these points in a brief review. One theme we explore is that further progress in understanding the evolution of male care is likely to require both careful specification of the kind of care under consideration (i.e. the nature of the behavior), particularly whether the care is incubation of eggs, and also study of the mechanisms controlling care. Labeling of any behavior that appears beneficial to offspring simply as parental care may obscure important differences and impede integration of knowledge about history, function, mechanism, and development.

MALE PARENTAL CARE: THE COMPARATIVE APPROACH TO ITS EVOLUTION

Ecological and Life History Approaches to the Evolution of Male Parental Care

Lack (43) is probably most closely associated with the view that the environment as a collection of currently acting selective factors is the overriding determinant of avian life history traits. Although this approach is now seen by most as overly simplistic, Lack (43) was able to document and explain, to an extraordinary degree, the considerable variation in avian mating systems and parental care. An example of this approach is the speculation that in some shorebirds, classical polyandry—in which females have multiple mates and are the brighter sex and males incubate—may have evolved in the high arctic environment because time available for reproduction is so brief (19, 20, 44, 61). If females and males originally shared incubation, and if then, in response to the need for haste, females began to lay one clutch to be incubated by males and another for themselves, such a system would be only one step away from the system in which females lay clutches sequentially for more than one male and cease to incubate eggs themselves (20). This explanation is intuitively very appealing, but how might it be tested?

To render the study of the evolution of parental care more objective, Silver et al (70) used canonical correlation to describe the taxonomic distribution of avian parental behavior among 237 avian subfamilies. Five kinds of male parental care (feeding female, building nest, incubating, feeding young, escorting young) were coded along with 29 life-history traits and ecological attributes

(e.g. mode of development of young, degree of sexual dimorphism, preference in diet, selection of habitat). Four pairs of canonical correlates were identified, the first accounting for 29% of the variation in male care, and several widely held adaptive hypotheses that had not yet been subjected to rigorous testing were supported.

Male parental care was found to be more common when the mating system is apparently monogamous and the habitat terrestrial. It is also more common when young are altricial as opposed to precocial; interestingly, mode of development also affects the kind of care provided. Males with altricial young are likely to feed the female and the young, but not to incubate eggs. Conversely, males with precocial young are more likely to incubate or to escort young to feeding sites, but not to feed the female or young. This seems reasonable from a mechanistic perspective, because the motor patterns of feeding are similar whether the recipient is a male's mate or his offspring, whereas the mechanisms underlying incubation are likely to prove quite different (see below).

Silver et al (70) concluded that biparental care was probably ancestral to altriciality and that, when the latter evolved, the already heavily invested female required help in gathering food for the dependent young. Thus, they reasoned, male feeding of young may have come later and replaced male help with incubation.

Sexual Monomorphism, Speciation, and the Form of Male Parental Care

In a recent study, Pierotti & Annett (60) reported that intra-generic hybrids are more common in taxa with male care than in those without male care. They suggested as a reason that females that rely on care may be more attuned to cues that predict it and correspondingly less attuned to exaggerated traits such as body size or plumage color (e.g. 37, 90, 105). If females whose mates provide care are less particular about male appearance when selecting a mate, speciation may be less likely and hybridization more likely (cf West-Eberhard—83).

To support their thesis, Pierotti & Annett (60) examined avian families or subfamilies (46 nonpasserines, 48 passerines) and classified them as [socially] monogamous and monomorphic (MM, 55 taxa), [socially] monogamous and dimorphic (MD, 24 taxa), or [overtly] polygynous and dimorphic (PD, 9 taxa). The MM group contained fewer species per family than the MD and PD groups, and the percentage of species that hybridized was greatest in the MM group (34%), intermediate in the DM group (17%), and least in the PD group (9%). Because male parental care is characteristic of socially monogamous species, they concluded that speciation is less likely when the sexes are similar and males provide care.

Especially striking was a difference in the kind of parental behavior exhibited: Among passerines, the parental behavior most closely associated with sexual monomorphism was male incubation (60, data from 77). Male nest-building was common in both the monomorphic and dimorphic taxa (94% and 71%), as was feeding of nestlings (100% and 80%); but while males incubated in 79% of the monomorphic taxa, they did so in only 25% of the dimorphic taxa. Recall the finding by Silver et al (70) that male birds tend either to incubate or to feed but not to do both. Pierotti & Annett added that incubation tends to co-occur with monomorphism, while nest-building and feeding of young do not. How might this come about?

One suggestion is that male incubation may be the most confining of male parental behaviors because it consumes time and cannot be postponed. Further, incubation may require physiological changes that interfere with sexual behavior. In either case incubation may come at the cost of lost mating opportunities, reducing variability in reproductive success among males. If true, and if we accept the generalization that sexual dimorphism (including dichromatism) usually reflects the intensity of sexual selection, then collectively these observations suggest that sexual selection may be less intense in taxa in which males incubate, hypothetically because males allocate more effort to parental care and less effort to mating. If we now add that females belonging to taxa with male incubation may base their choice of mate on attributes that correlate with parental behavior rather than appearance (and especially if natural selection independently favors cryptic appearance in incubating males), then the observed co-variation among male incubation, monomorphism, and social monogamy may be better explained. Conversely, dimorphism and polygyny may be more likely to evolve in lineages in which males do not incubate but may feed, especially if feeding does not greatly interfere—in terms of time or underlying physiology—with attracting multiple mates (overt polygyny) or, in socially monogamous species, with extra-pair mating opportunities.

These arguments could be countered by noting the existence of extra-pair paternity in monomorphic species in which males incubate (e.g. 51; L Whittingham, unpublished data on house martins) or by asserting that even in monomorphic species females prefer males of higher “quality” (4). Confirmation or rejection will require more data on the incidence of EPP and on variance in male reproductive success (the only reliable basis for defining mating system) in species in which males do and do not incubate. Also needed are more data comparing variance in success between males and females. However, to repeat, one key to unraveling the linkage among sexual dimorphism, criteria used by females in mate choice, and male parental care is to refine the classification of species according to kind of care males provide.

Advances in the Comparative Approach

The integration of phylogenetic systematics and ecology has led to fundamental improvements in the comparative method (5, 11, 33) and may represent the most important breakthrough in evolutionary biology of the past two decades (53). Critics of comparative method studies carried out prior to this integration argue that statistical analyses like those used by Silver et al (70) and Pierotti & Annett (60) assume independence of data points, whereas because related taxa are inextricably linked by their common ancestry, they cannot be treated as independent. In this view, it is simply not helpful to know how many taxa exhibit a trait; rather we must know how many times a trait has arisen and how many times it has been lost (48). To know these things, we need an accurate determination of each lineage's history (48).

Phylogenetic analysis offers testable hypotheses about sequence of trait evolution, ease of reversal (strength of constraints), and rates of evolution. When applied to parental care, it offers objective criteria for determining whether males exhibit care because care is more adaptive than any alternative route to reproductive success or because ancestry dictates it. A fine example of this approach is that of Winkler & Sheldon (98), who mapped the mode of nest construction of swallows onto a molecular phylogeny and found this trait to be very conservative. Among 17 species exhibiting five diverse modes of nest construction, each mode apparently arose only once. Further, what would seem intuitively to be the simplest form, adoption of a cavity already made by another species, is the most recently evolved (Figure 1).

McKittrick (48) applied phylogenetic techniques to the evolution of male parental care in 60 avian taxa and confronted all the difficulties that currently face cladists: multiple and barely distinguishable trees, trees whose form varies depending upon which taxa are analyzed and upon assumptions regarding the likelihood of reversals of traits, incomplete behavioral data, etc. Nevertheless, her work is very provocative, and, because the methods are rigorous and clearly stated, it will be possible to adjust conclusions as more data become available and methods of analyzing trees progress.

Of the 60 taxa considered by McKittrick (48), 52 exhibited some form of biparental care. Her phylogenies were based on both anatomical (69 characters) and behavioral (15 characters) data, and her outgroup was a reptilian ancestor with no post-hatching care. When she used feeding of young as the index of parental care, her trees showed male care (male-only or biparental) as the ancestral state in birds. Thereafter, male feeding was lost only twice: once in the lineage that led to ducks and grouse and once in the hummingbird genus *Eulampis*, which clusters with birds of prey.

Interestingly, and unlike Silver et al (70), McKittrick (48) found no association between male care and altriciality. Of the two losses of male feeding,

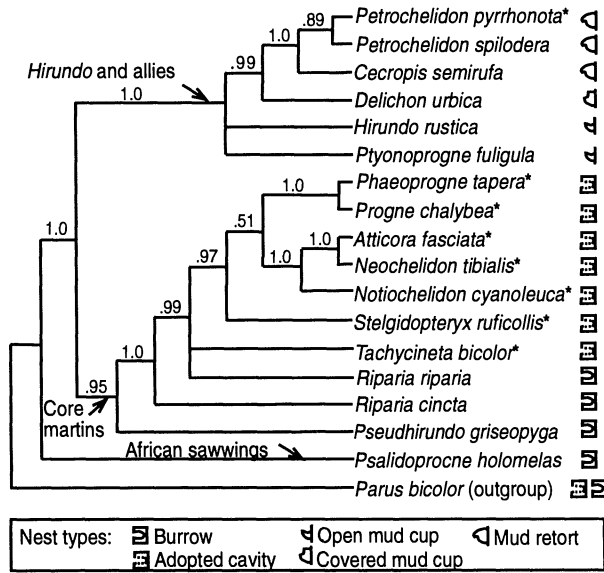


Figure 1 Phylogenetic tree (50% majority rule consensus, based on DNA hybridization) of 17 swallows and a titmouse that maps the origin of different modes of nest construction. English names for the taxa are, from top to bottom, cliff swallow, South African cliff swallow, rufous-chested swallow, house martin, barn swallow, rock martin, brown-chested martin, gray-breasted martin, white-banded swallow, white-thighed swallow, blue-and-white swallow, southern rough-winged swallow, tree swallow, sand martin, banded martin, gray-rumped swallow, black sawwing, and tufted titmouse (from Winkler & Sheldon—98).

one was associated with the evolution of precocial young and one was not. McKittrick’s analysis does support the speculation that male-only incubation tends to be preceded by biparental incubation (19): male-only care originated five times, and ratites (e.g. rheas, kiwis) were the only one of these groups not preceded by an ancestor in which both sexes incubated. The stability of male incubation in the lineages described by McKittrick (48) and the conservatism of nest construction in swallows (98) both suggest that various forms of parental care may exhibit considerable inertia, i.e. be difficult to modify once they have evolved.

Unfortunately, much of the active field work on parental care in birds is done with songbirds (passerines), and McKittrick’s anatomical data do not readily distinguish among members of this large group. The blackbirds (Icterinae), for example, should prove a fascinating subfamily for study because mating systems vary greatly and care in some species is biparental, in others female-only, and in still others (brood parasites) absent. Finally, some

icterines are sexually dimorphic in size but not color, while others are similar in size but are dichromatic (43; D Enstrom, unpublished data). Even greater diversity among shorebirds (which are not passerines) would make them another fascinating group for study (20, 43, 44, 61).

In sum, biparental care is probably ancestral in birds. Mode of development may or may not have a determining effect on the kind of parental behavior expressed by males, although it seems likely that it does. Groups in which males incubate may be more likely to be socially monogamous and monomorphic, and they may also be less likely to speciate. They may also be less variable in their reproductive success and under less intense sexual selection. The degree of lability of all these traits and their order of evolution are not yet known, but there is reason to be optimistic that questions like these will be answered.

MALE PARENTAL CARE: THE FUNCTIONAL APPROACH

Turning to a cost-benefit approach, we ask whether male care, in the species in which it exists, has been shown to be the option most beneficial to males, i.e. is it currently maintained by natural selection? Such questions require a theoretical framework (85, 88, 96), the most enduring treatment of which has been provided by Maynard Smith in his classic paper, "Parental investment: a prospective analysis" (46).

Maynard Smith (46) assessed conditions that should favor the evolution of care and also asked when it should be biparental and when uniparental. The obvious consideration is the extent to which care improves survival of offspring, but other crucial considerations are (i) the relative benefits of providing care instead of deserting one's mate to pursue alternative reproductive options, and (ii) the response the mate might make to its partner's decision to stay or desert. If, for example, parental care improves survival of young but only one parent is sufficient, the sexes are in conflict: Which should stay and which desert? According to Maynard Smith (46), the answer lies in differences between the sexes in the factors that determine fecundity. Males must weigh the benefits of care against the costs of lost opportunities for additional matings. Females must weigh the benefits of care against any increase in fecundity that might come from withholding care, e.g. the ability to produce a larger current clutch or to produce a future clutch more promptly.

Most interesting was Maynard Smith's insight (46) into the evolutionary interdependence of these effects. Whether males gain more from extra matings than they would from parental care, in a population in which care is left to the female, will depend on the extent to which female-only care decreases female fecundity. If female-only care lengthens the time required

to rear young, then males seeking extra matings will find fewer fertile females to mate with. Similarly, if female-only care results in smaller clutches, then the payoff of extra matings to males is reduced. On the other hand, if male care leads to laying of larger clutches by females, then male care may be favored. In short, the optimal solution for one sex depends on the choice made by the other sex.

According to Maynard Smith (46), biparental care in birds should prevail over mate desertion because, in general, reproductive success when two parents attend young is greater and because the male's chances of finding additional mating partners is low. Using his notation, biparental care is maintained because

$$P_2 > P_1 + pP_1,$$

where P_2 is productivity with two parents, P_1 is productivity with one parent, and p is the males' probability of finding an additional mate.

Tests of the Fitness Consequences of Male Parental Care

Can this theory be tested? A value may be placed on male care by measuring any change in reproductive success that occurs when care is eliminated or reduced. Several approaches have been used, including removal of the male leaving the female to rear her young alone (3, 16, 100) as well as manipulations that reduce male care. Care can be reduced by hormonal treatment (35, 38, 41, 71), by psychological means (e.g. decreasing the male's perception of his paternity—13), or by making flight more difficult, thereby increasing the energetic cost of care (72, 103). The other approach is to manipulate the environment, e.g. by varying the operational sex ratio (73), the reproductive value of the brood (106), or the need for male help (87, 105). In the following subsection, we focus on removal of the male.

With or without such manipulations, any accounting of benefits of care must consider the extent to which it facilitates the production of genetic offspring, and thus the accounting must be corrected for the occurrence of extra-pair fertilizations (EPF) both by the focal male and by other males at his expense. Using molecular techniques, workers are rapidly accumulating information on the frequency of extra-pair fertilizations and addressing the question whether certainty of paternity is related to level of paternal care (4, 51, 85, 88). The approaches have been theoretical (85, 88, 104), comparative (51), and experimental (13, 89).

Male Removal Studies

Male removal was pioneered by Gowaty (28) and Richmond (62) and summarized by Wolf et al (100), Bart & Tornes (3), Dunn & Hannon (16), and

Clutton-Brock (9). The technique assumes that the benefits of male care can be assessed by measuring any decline in female reproductive success that occurs when females are unaided. Benefits of male care can be direct or indirect and also immediate or delayed. Direct benefits are improved reproductive success, attributable to the male's attentiveness to the offspring themselves. Indirect benefits are derivative, through the female and her well being, which, of course, is relevant to the male only insofar as female condition affects male fitness. An example of a direct benefit would be an increase in numbers of fledglings produced when the male feeds or protects nestlings; an indirect benefit would be a difference in the female's ability to produce more young as a result of the male's contribution to care. Immediate benefits are those associated with the breeding attempt during which the male was removed, again including numbers of fledglings produced. Delayed benefits bear on future reproduction, assuming that the male and female remain paired, and include time elapsed before the female makes her next breeding attempt, the size of the next clutch, or the probability of her surviving to breed again. Delayed effects can be direct, e.g. if caring for young affects male survival, or indirect, e.g. if an unaided female is less likely to survive and females are the limiting sex.

Most male removal studies have reported only the numbers of fledglings produced by aided and unaided females, but a few have followed young to independence (e.g. 100). That is, they have reported only direct, immediate effects. Some have shown a significant decline in success when the male is absent (e.g. 65), but others have not (e.g. 28, 45). When males incubate, they may be essential to successful reproduction (16, 20), but males that merely guard the young or provide food are more likely to have either no detectable effect on success or only an incremental effect (3, 16, 100). Among passerines, only female black-billed magpies failed to produce any young in the absence of male help, and in this species males incubate (16).

In their summary of male removal studies in passerines, Wolf et al (100) speculated that male help was rarely essential to nest success, i.e. to the production of at least one fledgling, and that it appeared to be more beneficial in cavity nesters where broods are often larger, or at high latitudes, where weather may constrain the ability of females to feed when poikilothermic nestlings require brooding. Bart & Tornes's review (3) included both passerine and nonpasserine species, and, as interpreted by Webster (81), reported that unaided females produced 77% as many fledglings as did aided females. Bart & Tornes concluded that male parental behavior may be maintained by selection as long as it is at least occasionally beneficial and of relatively low cost to the male (see 18). Dunn & Hannon (17) showed that the effects of male removal may be apparent only when food is limiting.

Can male removal studies address Maynard Smith's prediction that in order

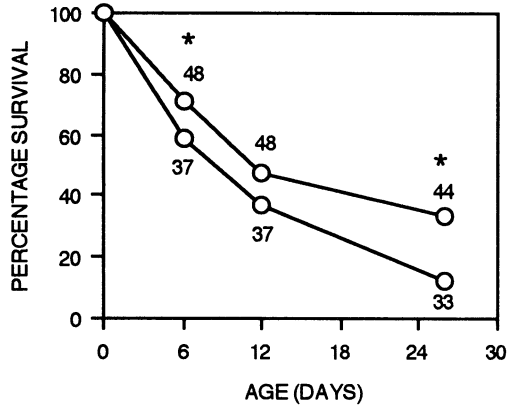


Figure 2 Survivorship of young dark-eyed juncos raised from hatching to independence by one (lower line) or two (upper line) parents. Measurements are mean percentage of broods surviving to three ages: mid-way through the nestling phase (day 6), fledging (day 12), and independence (day 26), from Wolf et al (100, asterisks indicate one-tailed $p < 0.05$, Mann-Whitney U).

for biparental care to evolve, the productivity of two parents should be greater than that of one? In juncos that had broods of four at hatching (the modal size), unaided and aided females did not differ in numbers of young fledged (Figure 2). However, unaided females reared an average 1.0 young to independence (i.e. of parental care), as compared to 2.6 for pairs (100, Figure 2). Thus, two parents do rear more young than one, and if a male were to desert his brood without caring for them, he would need to acquire an average of three females to perform as well as a care-giving male. And what of the other term in Maynard Smith's inequality, the probability of obtaining additional mating opportunities? We return to this subject below but emphasize here that in juncos, male parental care provides immediate and direct benefits.

Birkhead & Moller (4, pp. 241-42) asserted that "evidence from male removal studies conducted so far should not be used at all since the value of male care can be evaluated only if widowed females do not suffer any reduction in survival or future reproduction" and "survival and reproduction costs [of male removal] are experienced [by the female] at some later stage." We disagree with this position for two reasons. First, it cannot be assumed that females experience costs at some later stage; later effects, if any, on females should be measured to determine whether they are important. Second, increased female effort in compensation for the loss of male help is not necessarily detrimental to male fitness.

We looked for delayed and indirect effects in the junco (102) and found

that unaided females lost significantly more mass while tending nestlings alone (10.4% vs 8.6%; here and below, the mean or percentage for unaided females is stated first). However, we found no significant differences in the percentage of females that renested after our manipulation (100% vs 91%), in the interval between broods (19.3 vs 15.9 days; the later brood apparently sired by males that replaced removed males), or in the size of the clutch in the female's next nesting attempt (3.5 vs 3.7 eggs) (all $p > 0.1$) (102). We also found no treatment difference in the proportion of females that returned to breed the following season (58% vs 45%) or in recruitment to the breeding population of young reared by aided and unaided females (15% vs 15%) (100; ED Ketterson, V Nolan, Jr, L Wolf, unpublished data; see also 28, 45).

We grant the low power of these comparisons because the sample sizes were small. Thus the conclusions are tentative. Nevertheless, they suggest that delayed costs of unaided reproduction to female juncos are not large. The reason for this is probably that fledglings cared for by unaided females were more likely to die before independence; after such deaths, the parental effort required of unaided females was reduced. If this is correct, then, contrary to the position of Birkhead & Moller, the cost to the male and female junco of lost male help is immediate and up front; it is the production of fewer independent young from the current brood. One observation (ED Ketterson, V Nolan, Jr, L Wolf, unpublished data), however, does suggest an important potential delayed effect on the fitness of males, if they were to force females to rear young alone. Although unaided females were as likely to survive (i.e. be present next year; see above), they were not as likely as aided females to return to the previous year's breeding territory (48% vs 75%). Because some male juncos fail to obtain females (the adult sex ratio favors males) and surviving pair members usually re-mate in successive years, this tendency of unaided females to switch territories would increase the probability that nonhelping males would remain unmated next year. However, in this situation the agent favoring male parental care could be female mate choice (sexual selection), not the cost of reproduction to unaided females (102).

In sum, we argue that male removal studies, like those in which male care is experimentally reduced (13, 35, 38, 41, 71, 72, 103), can provide a useful approach to quantifying the utility (fitness benefits) of male parental care. Rather than discourage their use, we suggest that they employ standardized methods and be performed on species in which samples can be large enough to allow confidence in the conclusions. Immediate and delayed, as well as direct and indirect, effects need to be quantified. In addition, more studies on nonpasserines are needed. Perhaps most importantly, more emphasis needs to be placed on the kind of care males provide. For example, is male care not only beneficial but essential when males incubate? When males simply guard

their nests, what is the benefit of guarding (45, 105, 107; K Yasukawa, WE Richmond, unpublished data)?

Paternity and Male Parental Care

A critical consideration when quantifying the benefits of male care is the male's relatedness to the young in question (29, reviews in 4, 84). Despite earlier theoretical work to the contrary (57, 82), most students of avian parental behavior assumed that male care could evolve only if the beneficiaries were the genetic offspring of the caregivers. Newer theoretical treatments identify conditions in which relatedness and level of care are expected to co-vary (85, 88, 104) and also those in which they are not (85, 88).

Empirical studies are addressing the question both comparatively and experimentally (13, 50, 51, 89). Moller & Birkhead (51) reported, in interspecific comparisons, that the proportion of feeding trips by males can be used to predict the proportion of young sired with their social mates. Their conclusion has been seriously challenged by Dale (12), and resolution of this question must await more extensive data and data of higher quality. On the intraspecific level, Davies (13) has outlined an experimental approach to determining the effect of perceived level of paternity on paternal care: He systematically removed males for short periods of time during the female's presumed fertile period and then returned the males and documented their subsequent behavior. Male dunnocks are more likely to care for young if they have access to the female at the time she is presumably fertile (15).

One question of particular interest is whether the frequency of extra-pair fertilizations will vary with the form of male care provided, and the prediction made above was that EPP will be lower when males incubate (e.g. in black vultures and oystercatchers, 14, 34). Moller & Birkhead reviewed (51) 50 species in which both percentage of young sired by extra-pair males in focal nests and percentage of incubation contributed by the males associated with those nests were reported. Among the 38 passerines reviewed, males of three species incubated. We calculated that for those males the average percentage of young sired by extra-pair males was 5.2%; this compares to 19.1% extra-pair young among the 35 passerines whose males did not incubate (statistical tests are not appropriate). Among the nonpasserine species, five exhibited no paternal care at all. Of those with male care, six showed male incubation and one did not. For these seven species, the respective percentages of young sired by extra-pair males were 2.3% and 5.4%. Thus, EPP appears low in nonpasserines with male care but, consistently with the prediction, was lowest in species in which males incubate. We tried to compare sister taxa to see whether the percentage of time spent incubating was negatively related to EPP, but for various reasons (e.g. no sister taxon available for comparison) only four comparisons were possible. In all four, EPP was lower in the taxon with the higher

percentage of male incubation. Obviously, a firmer conclusion that EPP is lower when males incubate will require more data.

Many people working in this area are fascinated with the question of why females mate with more than one male. The question is beyond the scope of this review, but one area of overlap between multiple mating by females and male parental care relates to a theme that we have already raised repeatedly: the relationship among kind of male care provided, monomorphism, and the basis for female mate choice. Regardless of the importance of variation among males—in their quality, their genes, or their resources—it seems likely to us that the fundamental reason that females mate multiply is to ensure the acquisition of sufficient sperm to fertilize their ova. This hypothesis has been considered and rejected several times (4, 84, but see 80b) but has not been adequately tested. If incubating males in sexually monomorphic species are less variable in their sperm production than males in more sexually dimorphic species whose males do not incubate, then females in monomorphic species may have less to gain from multiple mating (i.e. less need of fertilization insurance) and possibly more to lose (potential loss of male parental care). Have we any reason to expect less variation in sperm production in monomorphic males that incubate? To our knowledge, no one has looked directly, but we have speculated that one cost of extreme sexual dimorphism may be impaired fertility in some individuals owing to possible inhibitory effects of high testosterone levels on sperm production (ED Ketterson, V Nolan, Jr, in preparation; T Kast, ED Ketterson, V Nolan, Jr, unpublished data). Here again, more data are needed.

Relative Costs and Benefits of Mating Effort and Parental Effort: Phenotypic Engineering

One of our research objectives is to determine whether male parental behavior is currently maintained by natural selection, and for that we need a quantitative accounting of both detrimental and beneficial effects of male care on male fitness. Traditionally, these questions have been explored by comparisons of individuals in various natural categories (e.g. older vs younger males when these differ in amount of care provided), but an obvious drawback with this approach is that it is not experimental. One simple experimental approach is to alter the environment and ask how paternal behavior responds to food enhancement or to a change in brood size. But, as Lack said (43, p. 8), “It is easy to change the number of eggs or young in a nest, but no one has yet found how to make a monogamous species polygynous or a solitary species colonial...” Thus it was a breakthrough when Wingfield (91) reported that treatment with testosterone could induce polygyny in species that were ordinarily monogamous. We followed this lead, in an approach we call “phenotypic engineering,” by using testosterone implants to alter the physiology and behavior of dark-eyed juncos (summarized in 38).

We found that experimental males (T-males) and controls (C-males) differed in a number of traits that would be expected to influence reproductive fitness. T-males sang more (41), were more attractive to females (D Enstrom, ED Ketterson, V Nolan, Jr, unpublished data), and ranged over wider areas (8). Concomitantly they fed young less frequently (41) and were slower to detect, hence to defend against, a model predator placed near the nest (M Cawthorn, D Morris, V Nolan Jr, ED Ketterson, and CR Chandler, unpublished data). The question then was the effects of these differences on the relative fitness of T-males.

We are now attempting to quantify all components of reproductive success for both phenotypes to determine whether individuals that deviate from the norm are at a disadvantage. Starting with the traditional measure of reproductive success, *apparent success*, which is the number of young produced by the female(s) mated (pair-bonded) to the focal male, we have found virtually no difference between T- and C-males (38, 41). *Realized success* consists of apparent success with social mates minus paternity losses to extra-pair fertilizations by other males (cf 24 for a different use of "realized success"), and this requires knowledge of the genetic relationship between male and offspring. On this measure, T-males perform slightly but not significantly less well than controls, and we are now asking whether these losses might be because T-males range more widely and leave their mates unprotected (PG Parker, ED Ketterson, V Nolan, Jr, SA Raouff, C Ziegenfus, T. Peare, and CR Chandler, unpublished data). The greater challenge comes in quantifying *covert success*, which consists of all the focal male's fertilizations of females other than his social mate. On this measure, T-males perform somewhat better than controls to date, perhaps again because of greater time spent off territory (8) or greater attractiveness (D Enstrom, ED Ketterson, Val Nolan, Jr, C. Ziegenfus, unpublished data), but here, too, the differences are not significant (PG Parker, ED Ketterson, V Nolan, Jr, SA Raouff, C Ziegenfus, T Peare, and CR Chandler, unpublished data). *Actual reproductive success* is the sum of realized and covert success, and on this measure, T- males and C-males are virtually identical (PG Parker, ED Ketterson, V Nolan Jr, SA Raouff, C Ziegenfus, T. Peare, and CR Chandler, unpublished data).

Returning to Maynard Smith (46) and his formula predicting patterns of parental behavior, we ask, "Does the model fit the junco?" Male parental care increases the production of independent young (Figure 2, 100). But evidently males could decrease their contribution to feeding nestlings by 50%, as they do when they are treated with testosterone, and suffer no fitness loss in apparent reproductive success (41). However, the physiological changes required to reduce the level of care might have consequences for other components of fitness such as survival or increased losses to EPP (39, 52; PG Parker, ED Ketterson, V Nolan, Jr, SA Raouff, C Ziegenfus, T Peare, and CR Chandler, unpublished data). This study is still in progress.

Some workers might prefer to test Maynard Smith's model by altering the environment, not the animal. One way to vary the availability of fertile females is through simulated nest predation, i.e. destruction of nests on neighboring territories. In many open-nesting passerines, nest predation can be very high, at least in some years (e.g. > 80% in juncos), and until late in the breeding season the effect of predation is usually to cause the female to become fertile again as she begins a new attempt to reproduce. She is then a candidate for EPFs. It would be interesting to know whether high predator densities influence the time males allocate to guarding their nests as opposed to seeking extra mating opportunities. (Note that high nest predation also decreases the likelihood that nests will succeed in producing young, and this lowers the probable value of any EPFs.) We expect more studies that address the responses of males to natural or staged variation in the environmental contingencies that may raise or lower the value of male care. Male red-winged blackbirds, for example, change their contribution to parental care in response to changes in brood size, nestling age, and food abundance (86, 87, 106, see also 73; K Yasukawa, WE Richmond, unpublished data).

If we find that males are effective at adjusting their allocation of effort to parenting and mating, depending upon environmental contingencies, a next step will be to determine the cues and physiological adjustments required to make the necessary behavioral shifts. To answer questions like these, more needs to be known of the mechanisms underlying male parental behavior.

MALE PARENTAL CARE: THE MECHANISTIC APPROACH

Phylogenies may reveal the order of evolution of life-history traits, and studies of function aim to reveal why one or another of a set of alternative behaviors is maintained under natural selection. But neither of these approaches can reveal what happens in organismal terms when paternal care evolves from non-care, or vice-versa. Full understanding of the evolution of a behavior pattern requires that we know what physiological changes in the animal permit or accompany the behavioral change. Such changes might include altered response to the stimuli that elicit care, alterations in the processing and integrating of potentially conflicting sensory input, and altered output in the cascade of neural and neurosecretory events that influence target tissues and affect internal state and behavior. Obviously, evolution of one pattern of male parental care from another necessarily involves modification in this whole system.

As an example, modifications that might be required in the evolution of male incubation (from no-incubation) could include a shift in response to eggs as stimuli to sit on, coordination of male and female bouts of sitting, alteration

of schedule in male appetite so as to facilitate feeding in bouts rather than ad lib, and, in some cases, development of a brood patch for effective transfer of heat to eggs. At least equally important might be suppression of responsiveness to competing stimuli such as other males or fertile females.

Comparisons with Male Parental Care in Mammals

The systems of vertebrate parental behavior that are best understood at the level of mechanisms are mammalian (for review see 64). However, because male parental care is relatively rare in mammals, the focus has been on maternal behavior (e.g. 42, 59). More recently, researchers have addressed mechanisms of male parental care (6, 30–32, 98a, 108).

Despite the obvious differences in avian and mammalian parental behavior, e.g. birds do not lactate and mammals do not incubate, one common element is the formation of parental bonds with young. Moreover, there is reason to think that the mechanisms underlying these attachments in a variety of vertebrate taxa may be related to secretions of the neurohypophysis (59, 69, 98a). Pursuit of other parallels between birds and mammals might also prove profitable. Gubernick et al (32) studied the medial preoptic area (MPOA) of the hypothalamus, a region known to be important to the control of maternal behavior in mammals and one that is usually sexually dimorphic. In the California mouse, males provide parental care and the MPOA is sexually dimorphic only until the first litter is reared, after which the sexes become similar in this nucleus. Application of comparable methods to birds might reveal the neural basis for interspecific sex differences in the expression of parental care (69).

Circulating Hormones and Male Parental Care in Birds

Study of mechanisms of parental care in birds has focused on circulating hormones, by addressing the effects that hormones have on behavior as well as the effects that behavior and the environment have on hormones. Major contributions have been made by studying the inhibitory effect of testosterone on male parental behavior (summarized by Wingfield et al in 94) and investigating the role of prolactin in avian incubation (summarized by Goldsmith—26, 27). The approach has been comparative, as workers have elected to study free-living species believed to be of special interest because of some aspect of their life history. For example, in cooperative breeders, juvenile birds often delay maturation and participate in care of siblings or unrelated young, and researchers have asked whether their hormone profiles suggest delayed reproductive maturation (47, 66, 79, 95). Similarly, Dufty (15) compared the hormone profile of a brood parasite, which provides no care, to those of care-giving species. For role-reversed species, in which females court males and males incubate (22, 56), the question has been this: Are the hormone profiles

of the sexes the reverse of those of the much more numerous species in which only females incubate or in which incubation is biparental (26, 27, 40)?

Testosterone and Male Parental Care

As a rule, the onset of breeding in male birds is associated with a rise in gonadotropins followed by a rise in testosterone (1). Later, when males begin to behave parentally, testosterone levels decline (1). Wingfield and his associates have amassed information on seasonal profiles of testosterone from a variety of birds (93, 94). They have also documented the endocrine response of males to females and to male intruders (actual or simulated) onto their territories (92, 93), and following the lead of Silverin (71), they and we have manipulated testosterone levels in the field and measured the consequences for male parental behavior, mating behavior, and fitness (35, 91, summaries in 38, 78).

Interesting generalizations have emerged from interspecific comparisons of testosterone profiles (92, 94). One is that most species show a peak in testosterone (T) early in the breeding season, but the duration of this peak varies. For some species, it is brief; for others, it lasts nearly the entire breeding season. Another is that species differ in their hormonal responsiveness to intruders or other challenges; some show little response, while others exhibit rapid elevation of plasma T following a territorial intrusion. This variability can be related to mating system and parental care. First, the duration of the seasonal peak is longer in overtly polygynous species than in socially monogamous ones (93). Second, experimental treatment with T suppresses feeding of offspring in species in which males feed young (35, 38, 41, 71) and disrupts incubation in species in which males incubate (55). It can also induce polygyny in normally monogamous sparrows (91). Third, the species that are most responsive to intruders are those that provide the most parental care (92).

To examine the links among hormones, mating system, and parental care in a sample of 20 species, Wingfield et al (94) correlated the height of the breeding season peak of testosterone with an index of aggressiveness and parental care. High values of the ratio represented aggressive species that provide little parental care, low values the opposite. When the height of the seasonal peak was plotted against aggression/parental care (Figure 3), species in which males provide care showed the greatest seasonal variation in hormone levels, suggesting that testosterone secretion is suppressed except for brief periods. Males not providing care appear to live in a state of readiness to behave aggressively, and that state evidently interferes with the tendency to behave parentally. The states are loosely associated with traditional mating systems (Figure 3). Further progress will require better measures of aggressiveness, clearer distinctions regarding the kind of male care, data on variance

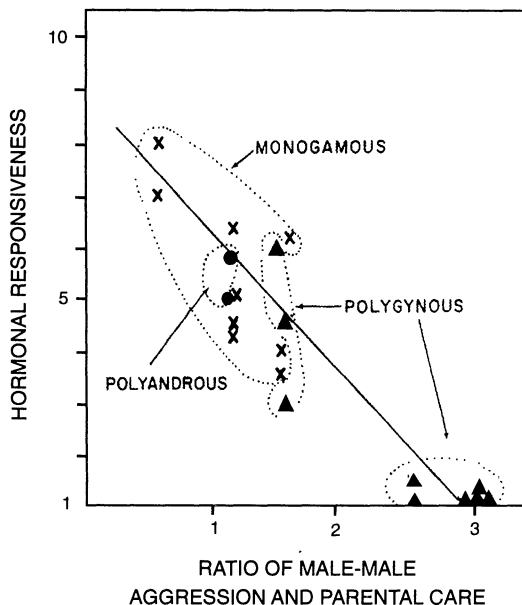


Figure 3 Interspecific variation in hormonal responsiveness of males (i.e. height of breeding season peak of testosterone) in relation to male-male aggression and parental care. High, sharp seasonal peaks in testosterone are associated with low levels of aggression and high parental care and also with social monogamy. In aggressive species with little parental care, the seasonal testosterone peak is less pronounced and the mating system tends toward overt polygyny, from Wingfield et al (94).

in actual male reproductive success, and data from species with different phyletic histories.

Less attention has been paid to the fact that socially monogamous, care-giving males may be less rigid in their allocation to parental and mating effort and accordingly more responsive hormonally to changing environmental cues. If so, the mixed reproductive strategy first delineated by Trivers (75) may have a mechanistic counterpart. We have begun an investigation of the coordinated responses of male juncos to changed opportunities for mating or parenting. We measure their testosterone levels, song rate, sperm density, and feeding of nestlings when they are confronted with enhanced broods or fertile females. We anticipate that other workers ask similar kinds of questions in other species.

The key general point, however, is that testosterone—a compound that we ordinarily associate with male courtship and sexual behavior, aggression, and sexual dimorphism—may lie at the core of the trade-off between mating effort and parental effort. A useful, if simple, analogy may be to think of testosterone

as a compound that can be turned up or down like a dial regulating the volume of sound. When testosterone is blaring, male and female roles diverge; when it is muted, the sexes look and behave more alike.

Prolactin and Male Parental Care

For prolactin, the generalization is that onset of incubation is associated with a decline in gonadal steroids and a rise in circulating levels of prolactin (1). In the few species in which only males incubate, prolactin is higher in males than females (22, 56). When both sexes incubate, both have elevated prolactin, and when only the female incubates, usually only she shows elevated prolactin (review in 27). There are exceptions to these generalizations. In cooperative breeders, helping birds also have elevated prolactin, even though they do not incubate (79; C Vleck, unpublished data on Mexican jays). Similarly, although they do not incubate, male European starlings in North America, and brown-headed cowbirds of both sexes, elevate prolactin during the breeding season (1). These examples serve as reminders that hormones have multiple effects and that evolution of hormonal regulation need not proceed simply by altering secretion (27). Tissue responsiveness to hormones can also show evolutionary change (22). Indeed, Ball et al (2) report that the brain tissue of cowbirds binds less radioactive prolactin than the same tissue in parental species, an indicator of lowered brain tissue response to prolactin.

A longstanding debate has centered on whether prolactin causes incubation or simply supports it once it has been initiated (26, 27, 64). Future developments regarding the role of prolactin are likely to come from experimental field studies involving the administration of vasoactive intestinal peptide (VIP), a releasing hormone for prolactin (C Vleck, personal communication). In particular, we might learn whether the physiology of incubation, if it can be experimentally induced, conflicts with the physiology of mating.

MALE PARENTAL CARE: THE DEVELOPMENTAL APPROACH

We expect important future discoveries in the area of development. Much individual variation in behavior or morphology, once assumed to be genetic, is now thought to reflect age or condition. In lizards, Hews et al (36) have shown that the expression of alternative reproductive strategies in males can be induced by applying testosterone early in life. In mammals (house mice), vom Saal (e.g. 80a) has shown that a female's aggressiveness and sexual attractiveness as an adult are influenced naturally by whether her intra-uterine neighbors are male or female. Until recently, similar effects were not widely known in birds. Schwabl (67) reported that adult female canaries and zebra finches incorporate testosterone into their eggs and that the amount incorpo-

rated varies with order of laying the eggs. Last-laid eggs have higher levels of testosterone, regardless of the sex of the offspring, and young from last-laid eggs achieved higher social status in flocks of juveniles (67; see 97 for a summary of possible research questions raised by these findings). Applying the concept of environmentally induced variability in phenotypic expression to male parental care, we might predict that males hatched in years when food is abundant would develop to focus on achieving fitness via extra-pair fertilizations, whereas those hatched when food is scarce and the value of male parental care greater might behave more parentally as adults. This assumes, of course, some environmental carry-over from year to year and is meant merely to illustrate the kinds of effects that may be discovered.

SUMMARY

In sum, males of most avian taxa that help care for offspring tend to be what we now call socially monogamous and, in contrast to overtly polygynous males, to be more likely to resemble females in external appearance and morphology. That these traits often present themselves as a complex presumably reflects their common evolutionary history. It may also indicate common causation, for example, by hormonal mechanisms, some of which act early in development. Improvements in the comparative method, including the phylogenetic approach, may reveal not only the conditions that are ancestral and the lineages that have proved to be more plastic but also the ecological correlates of male parental care. Using a functional approach and molecular techniques for determining relatedness, the effort to discover which components of fitness are most affected by male care can be expected to continue. Future studies focusing on proximate causation and development will illuminate the links between genes and behavior through which evolution proceeds.

What may have emerged from our attempt at a unifying consideration of history, function, and causation, beyond confirmation of the traditional view that male birds that do care-giving also tend to be sexually monomorphic and socially monogamous, is the view that incubation is the form of care most closely linked to monomorphism and that extra-pair paternity may be less common in groups with male incubation. If this proves true, and if variance in male reproductive success in groups in which males incubate proves to be lower than in groups without male care or groups with other forms of care, we will then need to determine why. One cause may be the greater dependence of females on male care when it is in the form of incubation; another might be lower variability among males that incubate in the amount of sperm they offer to ensure fertilization. These effects could increase the costs to females of multiple mating while decreasing the benefits. As a result, when selecting a mate, females in species in which males incubate may be more attentive to

cues that predict paternal behavior and less attuned to exaggerated traits. A predicted outcome, beyond monomorphism, is less highly developed species-isolating mechanisms and more local adaptation (60). At the level of mechanism, ontogenetic, seasonal, and short-term variation in testosterone may lie at the core of this complex of traits, including male allocation to mating and various forms of parental care. We think of this as the integrative approach to male parental care in birds and hope that it will prove fruitful.

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Literature Cited

1. Ball GF. 1992. Endocrine mechanisms and the evolution of avian parental care. *Proc. XXth Int. Ornithol. Congr.*, pp. 984–91. Christchurch, New Zealand
2. Ball GF, Dufty AM, Goldsmith AR, Buntin JP. 1988. Autoradiographic localization of brain prolactin receptors in parental and non-parental songbird species. *Soc. Neurosci. Abstr.* 14:88
3. Bart J, Tornes A. 1989. Importance of monogamous male birds in determining reproductive success. *Behav. Ecol. Sociobiol.* 24:109–16
4. Birkhead TR, Moller AP. 1992. *Sperm Competition in Birds*. London: Academic. 282 pp.
5. Brooks DR, McLennen DA. 1991. *Phylogeny, Ecology and Behavior*. Chicago, IL: Univ. Chicago Press. 434 pp.
6. Brown E. 1993. Hormonal and experiential factors influencing parental behaviour in male rodents: an integrative approach. *Behav. Processes* 30:1–28
7. Carey MD, Nolan V Jr. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. *Evolution* 33:1180–92
8. Chandler CR, Ketterson ED, Nolan V Jr, Ziegenfus C. 1994. Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.* In press
9. Clutton-Brock TH. 1991. *The Evolution of Parental Care*. Princeton: Princeton Univ. Press. 331 pp.
10. Clutton-Brock TH, ed. 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago, IL: Univ. Chicago Press
11. Clutton-Brock TH, Harvey PH. 1979. Comparison and adaptation. *Proc. R. Soc. Lond. B* 205:547–65
12. Dale J. 1994. Comment on Moller and Birkhead (1993): Does certainty of paternity covary with paternal care? *Anim. Behav.* In press
13. Davies NB. 1992. *Dunnock Behaviour and Social Evolution*. Oxford: Oxford Univ. Press. 272 pp.
14. Decker MD, Parker PG, Minchela DJ, Rabenold KN. 1993. Monogamy in black vultures: genetic evidence from DNA fingerprinting. *Behav. Ecol.* 4:29–35
15. Dufty, AM Jr., Goldsmith AR, Wingfield JC. 1987. Prolactin secretion in a brood parasite, the brown-headed cow-

- bird, *Molothrus ater*. *J. Zool. Lond.* 212: 669–75
16. Dunn PO, Hannon SJ. 1989. Evidence of obligate male parental care in black-billed magpies. *Auk* 106:635–44
 17. Dunn PO, Hannon SJ. 1992. Effects of food abundance and male parental care on reproductive success and monogamy in tree swallows. *Auk* 109:488–99
 18. Dykstra CR, Karasov WH. 1993. Nesting energetics of house wrens (*Troglodytes aedon*) in relation to maximal rates of energy flow. *Auk* 110:481–91
 19. Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–23
 20. Erckmann WJ. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In *Social Behavior of Female Vertebrates*, ed. SK Wasser, pp. 113–68. New York: Academic
 21. Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15
 22. Fivizzani AJ, Oring LW, El Halwani ME, Schlinger BA. 1990. Hormonal basis of male parental care and female intersexual competition in sex-role reversed birds. In *Endocrinology of Birds: Molecular to Behavioural*, ed. M Wada et al, pp. 273–86. Tokyo: Japan Sci. Press/Berlin: Springer-Verlag
 23. Francis, CM, Anthony, EL, Brunton JA, Kunz, TH. 1994. Lactation in male fruit bats. *Nature* 367:691–92
 24. Gibbs HL, Weatherhead PJ, Boag PT, White BN, Tabak LM, Hoysak DJ. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science* 250: 1394–97
 25. Gittleman JL. 1981. The phylogeny of parental care in fishes. *Anim. Behav.* 29:936–41
 26. Goldsmith AR. 1983. Prolactin in avian reproductive cycles. In *Hormones and Behaviour in Higher Vertebrates*, ed. J. Balthazart, E Prove, R Gilles, pp. 375–87. Berlin: Springer-Verlag
 27. Goldsmith AR. 1992. Prolactin and avian reproductive strategies. *Proc. XXth Int. Ornithol. Congr.*, pp. 2063–71. Christchurch, New Zealand
 28. Gowaty PA. 1983. Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). *Am. Nat.* 112: 144–57
 29. Gowaty PA, Karlin AA. 1984. Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* 15:91–95
 30. Gubernick DJ, Nelson RJ. 1989. Prolactin and paternal behavior in the biparental california mouse, *Peromyscus californicus*. *Horm. & Behav.* 23:203–10
 31. Gubernick DJ, Schneider KA, Jeanotte LA. 1994. Individual differences in the mechanisms underlying the onset and maintenance of paternal behavior and the inhibition of infanticide in the monogamous biparental California mouse, *Peromyscus californicus*. *Behav. Ecol. Sociobiol.* 34:225–31
 32. Gubernick DJ, Sengelaub DR, Kurz EM. 1993. A neuroanatomical correlate of paternal and maternal behavior in the biparental california mouse (*Peromyscus californicus*). *Behav. Neurosci.* 107: 194–201
 33. Harvey PH, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford Univ. Press. 239 pp.
 34. Heg D, Ens BJ, Burke T, Jenkins L, Kruijt JP. 1993. Why does the typically monogamous oystercatcher (*Haematopus ostralegus*) engage in extra-pair copulations? *Behaviour* 126:257–89
 35. Hegner RE, Wingfield JC. 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* 104:462–69
 36. Hews DK, Knapp R, Moore, MC. 1994. Early exposure to androgens affects adult expression of alternative male types in tree lizards. *Horm. & Behav.* 28:96–115
 37. Hoi-Leitner M, Nechtelberger H, Dittami J. 1993. The relationship between individual differences in male song frequency and parental care in blackcaps. *Behaviour* 126:1–12
 38. Ketterson ED, Nolan V Jr. 1992. Hormones and life histories: an integrative approach. *Am. Nat.* 140: S33–62
 39. Ketterson ED, Nolan V Jr., Wolf L, Dufty AM Jr., Ball GF, Johnsen TS. 1991. Testosterone and avian life histories: effect of experimentally elevated testosterone on corticosterone, body mass, and annual survivorship of male dark-eyed juncos (*Junco hyemalis*). *Horm. & Behav.* 25:489–503
 40. Ketterson ED, Nolan V Jr., Wolf L, Goldsmith A. 1990. Effect of sex, stage of reproduction, season, and mate removal on prolactin in dark-eyed juncos. *Condor* 92:922–30
 41. Ketterson ED, Nolan V Jr., Wolf L, Ziegenfus C. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). *Am. Nat.* 140:980–99

42. Krasnagor NA, Bridges RS, eds. 1990. *Mammalian Parenting: Biochemical, Neurobiological, and Behavioral Determinants*. New York: Oxford Univ. Press
43. Lack D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen. 409 pp.
44. Ligon JD. 1994. The role of phylogenetic history in the evolution of contemporary avian mating systems and parental care systems. *Curr. Ornithol.* 10:1-46
45. Martin K, Cooke F. 1987. Bi-parental care in willow ptarmigan: a luxury? *Anim. Behav.* 35:369-79
46. Maynard Smith J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1-9
47. Mays N, Vleck CM, Dawson J. 1991. Plasma luteinizing hormone, steroid hormones, behavioral role, and nest stage in cooperatively breeding Harris' Hawks (*Parabuteo unicinctus*). *Auk* 108: 619-37
48. McKittrick MC. 1993. Phylogenetic analysis of avian parental care. *Auk* 109: 828-46
49. Mock DW, Fujioka M. 1990. Monogamy and long-term pair bonding in vertebrates. *Trends Ecol. Evol.* 5:39-43
50. Moller AP. 1988. Paternity and paternal care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36:996-1005
51. Moller AP, Birkhead TR. 1993. Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* 33:261-68
52. Nolan, V Jr., Ketterson ED, Ziegenfuss C, Cullen DP, Chandler CR. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on prebasic molt and survival in male dark-eyed juncos. *Condor* 94:364-70
53. Nylin S. 1991. The phylogenetic approach to ecology [book review]. *Evolution* 45:1731-33.
54. Orians GH. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589-603
55. Oring LW, Fivizzani AJ, El Halawani ME. 1989. Testosterone-induced inhibition of incubation in the spotted sandpiper (*Actitis macularia [sic]*). *Horm. & Behav.* 23:412-13
56. Oring LW, Fivizzani AJ, El Halawani ME, Goldsmith A. 1986. Seasonal changes in prolactin and luteinizing hormone in the polyandrous spotted sandpiper, *Actitis macularia*. *Gen. Comp. Endocrin.* 62:394-403
57. Parker GA. 1984. Sperm competition and the evolution of animal mating strategies. In *Sperm Competition and the Evolution of Animal Mating Systems*, ed. RL Smith, pp. 1-60. Orlando, FL: Academic
58. Payne RB. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* 33:1-52
59. Pedersen CA, Caldwell JD, Jirikowski GF, Insel TR, eds. 1992. *Oxytocin in Maternal, Sexual, and Social Behaviors*. New York: Ann. NY Acad. Sci. Vol. 652. 492 pp.
60. Pierotti R, Annett CA. 1993. Hybridization and male parental investment in birds. *Condor* 95:670-79
61. Pitelka FA, Holmes RT, MacLean SF. 1974. Ecology and evolution of social organization in Arctic sandpipers. *Am. Zool.* 14:185-204
62. Richmond A. 1978. *An experimental study of advantages of monogamy in the cardinal*. PhD thesis, Indiana Univ., Bloomington, IN
63. Ridley M. 1978. Paternal care. *Anim. Behav.* 26:904-32
64. Rosenblatt JS. 1992. Hormone-behavior relations in the regulation of parental behavior. In *Behavioral Endocrinology*, ed. JB Becker, MS Breedlove, D Crews, pp. 219-59. Cambridge MA: MIT Press
65. Sasvari L. 1986. Reproductive effort of widowed birds. *J. Anim. Ecol.* 55:553-64
66. Schoech SJ, Mumme RL, Moore MC. 1991. Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida scrub jays (*Aphelocoma c. coerulescens*). *Condor* 93:354-64
67. Schwabl H. 1993. Yolk is a source of maternal testosterone for developing birds. *Proc. Natl. Acad. Sci. USA* 90: 11446-50
68. Selander RK. 1972. Sexual selection and dimorphism in birds. In *Sexual Selection and the Descent of Man*, ed. B Campbell, Ch. 8. London: Heinemann
69. Silver R. 1990. Avian behavioral endocrinology: status and prospects. In *Endocrinology of Birds, Molecular to Behavioral*, ed. M Wada, S Ishii, CG Scanes, pp. 261-72. Berlin:Springer-Verlag
70. Silver R, Andrews H, Ball GF. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am. Zool.* 25:823-40
71. Silverin B. 1980. Effects of long acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Anim. Behav.* 28:906-12

72. Slagsvold T, Liffeld JT. 1989. Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology* 69:1918–22
73. Smith HG, Montgomerie R. 1992. Male incubation in barn swallows: the influence of nest temperature and sexual selection. *Condor* 94:750–59
74. Tinbergen N. 1963. On aims and methods of ethology. *Z. Tierpsychology* 20: 410–33
75. Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, ed. B. Campbell, pp. 136–79. London: Heinemann
76. Vehrencamp SL, Bradbury JW. 1984. Mating systems and ecology. In *Behavioural Ecology*, ed. JR Krebs, NB Davies, pp. 251–78. Oxford: Blackwell Sci. 2nd ed.
77. Verner J, Willson MF. 1969. Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.* 9:1–76
78. Vleck CM, Dobrott SJ. 1993. Testosterone, antiandrogen, and alloparental behavior in bobwhite quail foster fathers. *Horm. & Behav.* 27:92–107
79. Vleck CM, Mays NA, Dawson JW, Goldsmith A. 1991. Hormonal correlates of parental and helping behavior in the cooperatively breeding Harris' Hawk, *Parabuteo unicinctus*. *Auk* 108:638–48
- 80a. Vom Saal FS. 1983. Models of early hormonal effects on intrasex aggression in mice. In *Hormones and Aggressive Behavior*, ed. Svare, BB, pp. 197–222. New York: Plenum
- 80b. Wagner RH. 1992. The pursuit of extra-pair copulations by monogamous female razorbills: how do females benefit. *Behav. Ecol. Sociobiol.* 29:455–64.
81. Webster MS. 1991. Male parental care and polygyny in birds. *Am. Nat.* 137: 274–80
82. Werren JH, Gross MR, Shine R. 1980. Paternity and the evolution of male parental care. *J. Theoret. Biol.* 82:619–31
83. West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58:155–83
84. Westneat DF, Sherman PW, Morton ML. 1989. The ecology and evolution of extra-pair copulations in birds. In *Current Ornithology*, ed. DM Power, 7:331–69. New York: Plenum
85. Westneat DF, Sherman PW. 1993. Parentage and the evolution of parental behavior. *Behav. Ecol.* 4:66–77
86. Whittingham LA, Robertson RJ. 1993. Nestling hunger and parental care in red-winged blackbirds. *Auk* 110:240–46
87. Whittingham LA, Robertson RJ. 1994. Food availability, parental care and male mating success in red-winged blackbirds (*Agelaius phoeniceus*). *J. Anim. Ecol.* 63:139–50
88. Whittingham LA, Taylor PD, Robertson RJ. 1992. Confidence of paternity and male parental care. *Am. Nat.* 139:1115–25
89. Whittingham LA, Dunn PO, Robertson RJ. 1993. Confidence of paternity and male parental care: an experimental study in tree swallows. *Anim. Behav.* 46:139–39
90. Wiggins DA, Morris RD. 1986. Criteria for female choice of mates: courtship feeding and paternal care in the common tern. *Am. Nat.* 128:126–29
91. Wingfield JC. 1984. Androgens and mating systems: testosterone-induced polygyny in normally monogamous birds. *Auk* 101:665–71
92. Wingfield JC. 1992. Mating systems and hormone-behavior interactions. *Proc. XXth Int. Ornithol. Congr.*, pp. 2055–62. Christchurch, New Zealand
93. Wingfield JC, Ball GF, Dufty AM Jr., Hegner RE, Ramenofsky M. 1987. Testosterone and aggression in birds. *Am. Sci.* 75:602–08
94. Wingfield JC, Hegner RE, Dufty AM Jr., Ball GF. 1990. The "challenge" hypothesis: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136:829–46
95. Wingfield JC, Hegner RE, Lewis DM. 1991. Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow weaver, *Ploceopasser mahali*. *J. Zool. Lond.* 225:43–58
96. Winkler DW. 1987. A general model for parental care. *Am. Nat.* 130:526–43
97. Winkler DW. 1993. Commentary: Testosterone in egg yolks: an ornithologist's perspective. *Proc. Natl. Acad. Sci. USA* 90:1139–41
98. Winkler DW, Sheldon FH. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. *Proc. Natl. Acad. Sci. USA* 90:5705–07
- 98a. Winslow JT, Hastings N, Carter SC, Harbaugh CR. 1993. A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature* 365:545–48
99. Wittenberger JF. 1979. The evolution of mating systems in birds and mammals. In *Handbook of Behavioral Neurobiology*, Vol. 3, *Social Behavior and Communication*, ed. P Marler, J. Van-

- denbergh, pp. 271–349. New York: Plenum
100. Wolf L, Ketterson ED, Nolan V Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Anim. Behav.* 36: 1601–18
 101. Wolf L, Ketterson ED, Nolan V Jr. 1990. Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Anim. Behav.* 39:125–34
 102. Wolf L, Ketterson ED, Nolan V Jr. 1991. Female condition and delayed benefits to males that provide parental care: a removal study. *Auk* 108:371–80
 103. Wright J, Cuthill I. 1989. Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* 25:171–81
 104. Xia X. 1992. Uncertainty of paternity can select against paternal care. *Am. Nat.* 139:1126–29
 105. Yasukawa K, Knight RL, Skagen SK. 1987. Is courtship intensity a signal of male parental care in red-winged blackbirds (*Agelaius phoeniceus*)? *Auk* 104: 628–34
 106. Yasukawa K, Leanza F, King CD. 1993. An observational and brood-exchange study of paternal provisioning in the red-winged blackbird, *Agelaius phoeniceus*. *Behav. Ecol.* 4:78–82
 107. Yasukawa K, Whittenberger LK, Nielsen TA. 1992. Anti-predator vigilance in the red-winged blackbird, *Agelaius phoeniceus*: do males act as sentinels? *Anim. Behav.* 43:961–69
 108. Yogman MW. 1990. Male parental behavior in humans and nonhuman primates. In *Mammalian Parenting*, ed. NA Krasnegor, RS Bridges, pp 461–481. New York: Oxford Univ. Press