CHAPTER 8

THE ECOLOGY AND EVOLUTION OF EXTRA-PAIR COPULATIONS IN BIRDS

DAVID F. WESTNEAT, PAUL W. SHERMAN, and
MARTIN L. MORTON

1. INTRODUCTION

Most discussions of the adaptive significance of avian mating systems have focused on the ecological factors that cause various patterns of association between the sexes (Orians, 1969; Emlen and Oring, 1977; Oring, 1982). Males and females that nested together (i.e., formed pair bonds) were assumed to mate exclusively with each other (Kleiman, 1977; Wittenberger and Tilson, 1980). However, recent research has shown that social associations between the sexes do not always reflect exclusive mating relationships. Observations of copulations between individuals not paired to each other have been reported in many species (reviewed by Gladstone, 1979; Ford, 1983; McKinney et *al.*, 1984; Birkhead, 1987*a*), and evidence that these extra-pair copulations (EPC) do often result in fertilizations is increasing (e.g., Alatalo *et al.*, 1984; Westneat, 1987*a*; Evarts and Williams, 1987; Sherman and Morton,

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DAVID F. WESTNEAT • Section of Genetics and Development, Cornell University, Ithaca, New York 14853. PAUL W. SHERMAN • Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853. MARTIN L. MORTON • Department of Biology, Occidental College, Los Angeles, California 90041.

1988). The significance of EPC as a reproductive strategy by both sexes must now be explored.

Preliminary hypotheses about the ecological and social conditions favoring EPC by males have been available for some time (e.g., Trivers, 1972; Beecher and Beecher, 1979). However, the factors affecting female involvement in extra-pair matings have only recently been considered (e.g., Røskaft, 1983; Fitch and Shugart, 1984; Møller, 1985; Smith, 1988), and extra-pair copulations have not yet been integrated into general theory on mating systems. This chapter points out the ramifications of EPC and related behaviors for hypotheses about the adaptive significance of mating systems in birds and specifies the social and ecological factors that determine the costs and benefits of EPC to both sexes.

1.1. Definitions

Definitions of mating systems have always been controversial (e.g., Wickler and Seibt, 1983; Gowaty,1985). This is largely because two different, but related, aspects of mating behavior have been used to categorize mating systems: (1) the patterns of social associations between males and females (Lack, 1968; Selander, 1972; Emlen and Oring, 1977; Wittenberger, 1979); and (2) the patterns of copulations and gene transfer across generations (Wiley, 1974; Gowaty, 1985; Trail, 1985*a*). Each system has its advantages and disadvantages. On the one hand, social associations between the sexes are observable and easily quantified, but they may not reflect the actual flow of genes. On the other hand, categorizations based on mating relationships more closely describe gene flow but may overlook many aspects of observed social behavior.

The present discussion adopts the behavioral categorization rather than the genetic. Thus, a population is termed monogamous if males typically are paired (i.e., form social units) with one female. In a polygynous species, a substantial proportion of breeding males are paired with more than one female, and in a polyandrous species, many breeding females are paired with more than one male. We use this system for three reasons. First, the meanings of the terms are well established in the literature (e.g., Lack, 1968). Second, and more importantly, data on social relationships are available for many species, whereas precise measures of the genetic mating system have not been obtained for any species. Finally, we wish to focus on the factors influencing the patterns of copulations and fertilizations, given observed social bonds.

We define an *extra-pair copulation* as one that occurs when a paired bird copulates with an individual other than its social (pair-bonded) mate. An individual's pair-bonded mate is the one with whom he or she has a consistent social association both before and during egg laying. In most birds, pair formation can be inferred if a female begins building a nest on a male's territory or in association with him. For other species, such as obligate brood parasites, pairing must be defined on the basis of aspects of the species' courtship behavior (e.g., a consistent association coincident with egg laying). The key point is that pair-bonded birds have coordinated social interactions with each other, but not with the extra-pair mate (other than for the copulation itself).

Our definition of EPC excludes copulations that occur during or before the process of forming pair bonds, e.g., considerably before nest building, as in Purple-throated Carib Hummingbirds (*Eulampis jugularis*) (Wolf, 1975) and before pairing as in Herring Gulls (*Larus argentatus*) (Fitch and Shugart, 1984) and Northern Orioles (*Icterus galbula*) (Flood, 1985). Copulations associated with mate switching are also not considered EPC. For example, in Ring Doves (*Streptopelia risoria*), females are associated with, courted, and mated by one male, but may later in the season repeat the pairing process with another male (Erickson and Zenone, 1976). We do not consider these secondary matings to be EPC, even though they might conceivably lead to sperm competition, because of the separate social association between the female dove and each subsequent male. In many communally breeding birds, e.g., Acorn Woodpeckers (*Melanerpes formicivorus*) (Stacey, 1979, 1982; Joste *et al.*, 1985; Mumme *et al.*, 1985) and Noisy Miners (*Manora melanocephala*) (Dow, 1978), females live in social units containing a breeding male and one or more auxiliary males. In our view, matings between females and the auxiliaries are not appropriately viewed as EPC, because each male in the group has a long-term social association with the female, i.e., such copulations would differ from those with males from other groups who have no social association with the female. We do not consider polyandrous copulations to be EPC when the female is normally part of a social unit containing both her primary and secondary mate, as in Dunnocks (*Prunella modularis*) (Davies, 1985). EPC can occur in polyandrous species, however, when a male paired to one female copulates with a different female. For example, Colwell and Oring (1989) witnessed male Spotted Sandpipers (*Actitis macularia*) that were incubating eggs for one female flying some distance and copulating with a second female. In these cases, the second female apparently participated in the EPC as a part of the mate attraction process. Finally, multiple copulations in species that do not form pair bonds obviously cannot be considered EPC, e.g., lek-breeding birds, such as Sage Grouse (*Centrocercus urophasianus*) (Wiley, 1973; Gibson and Bradbury, 1986) and Cock-of-the-rock (*Rupicola rupicola*) (Trail, 1985*b*).

For EPC to be effective, they must occur during the female's fertilizable period (i.e., the interval during which an insemination could result in offspring). Because many birds have sperm storage organs (Hatch, 1983; Birkhead, 1987*b*; Shugart, 1988), this interval may begin well before the initiation of egg-laying. Obviously EPC are of interest primarily because they sometimes result in *extra-pair fertilizations*, defined as the siring of an offspring by an extra-pair male. However, the link between the behavior and the genetic result has been made in only a handful of species and then only indirectly (see below). To move forward, we will use extra-pair copulations (or EPC) as a general term, with the implication that these copulations can result in fertilizations. We assume that a fertilization is the basic currency of fitness resulting from the pursuit of EPC.

Comparisons between territorial and nonterritorial species, and colonial nesting versus dispersed nesting species, are the bases for some hypotheses we will develop about the frequency of EPC. By territorial, we mean any species in which some fixed area is defended, be that an all-purpose territory (Nice, 1937) or simply a nest site (Hinde, 1956). By contrast, nonterritorial species defend no fixed site (e.g., many ducks) (see McKinney, 1986). Following Wittenberger and Hunt (1985), a colonial species is one in which breeding units are aggregated, whereas in a noncolonial nester they are dispersed.

1.2. Extra-Pair Copulations and Fertilizations

Recently there has been a proliferation of studies on EPC under natural conditions. Indeed, extra-pair matings and evidence of mate guarding have been reported from nearly every avian family (Ford, 1983; McKinney *et al.*, 1984). Detailed observations of mating behavior in several species have revealed that attempted EPC can be quite frequent, e.g., in Pied Flycatchers (*Ficedula hypoleuca*) (Alatalo *et al.*, 1987), White Ibises (*Eudocimus albus*) (Frederick, 1987*a*), and Indigo Buntings (*Passerina cyanea*) (Westneat, 1987*b*). Across a range of species, attempted EPC have been observed at each stage in the nesting cycle, but in most species EPC peak during the presumed fertilizable period of the female, e.g., in Rooks (*Corvus frugilegus*) (Røskaft, 1983), Common Guillemots (*Uria aalge*) (Birkhead *et al.*, 1985), Lesser Scaup (*Aythya affinis*) (Afton, 1985), White-fronted Bee-eaters (*Merops bullockoides*) (Emlen and Wrege, 1986), Northern Fulmars (*Fulmarus gla-*

cialis) (Hatch, 1987), Indigo Buntings (Westneat, 1987*b*), Zebra Finches (*Taeniopygia guttata*) (Birkhead *et al.*, 1988*a*), and Rock Ptarmigan (*Lagopus mutus*) (Brodsky, 1988).

Correlations between the frequency of EPC and the frequency of within-pair copulations in several species (Birkhead *et al.*, 1987; Birkhead, 1988) indirectly suggest that EPC lead to sperm competition. Although little is known about the timing of fertilization relative to insemination in most wild species, studies on domesticated birds suggest that the last insemination before fertilization has priority (e.g., Birkhead *et al.*, 1988*b*; Birkhead, 1988), apparently because of layering of sperm in the female's sperm storage glands. Indeed, some male birds behave as if copulating last is advantageous. For example, in Indigo Buntings, intrusions by extra-pair males (which represent potential EPC) are frequently followed by within-pair matings (Westneat 1987*b*).

Five different types of data indicate directly that EPC result in fertilizations. First, vasectomies of male Red-winged Blackbirds (*Agelaius phoeniceus*) did not prevent their mates from laying fertile eggs, suggesting fertilization by another male (Bray *et al.*, 1975). Second, plumage markers were used to infer that some extra-pair fertilizations occurred in captive Mallards (*Anas platyrhynchos*) (Burns *et al.*, 1980) and that 2% of all eggs were fertilized by an extra-pair male in wild Snow Geese (*Chen c. caerulescens*) (Cooke and Mirksy, 1972; Lank *et al.*, 1989). Third, sexual differences in heritabilities of morphological characters, e.g., tarsus or wing length, indicated that about 24% of Pied Flycatcher chicks (Alatalo *et al.*, 1984), 24% of Barn Swallow chicks (*Hirundo rustica*) (Møller, 1987*a*), and 40% of Indigo Bunting chicks (Payne and Payne, 1989) were the result of extra-pair fertilizations. Fourth, electrophoresis of polymorphic proteins and paternity exclusion analyses revealed that 30–40% of Indigo Bunting chicks (Westneat, 1987*a*; Westneat *et al.*, 1987) and 34–38% of White-crowned Sparrow (*Zonotrichia leucophrys*) chicks (Sherman and Morton, 1988) were conceived through EPC. Evarts and Williams (1987) used protein electrophoresis to show that 60% of all Mallard broods at their Minnesota study site had at least one offspring sired through EPC. Electrophoretic analyses have also revealed occasional extra-pair fertilizations in Acorn Woodpeckers (Mumme *et al.*, 1985), Bobolinks (*Dolichonyx oryzivorus*) (Gavin and Bollinger, 1985), White-fronted Bee-eaters (Wrege and Emlen, 1987), and European Starlings (*Sturnus vulgaris*) (Hoffenberg *et al.*, 1988). Fifth, DNA fingerprinting has uncovered occasional extra-pair fertilizations in House Sparrows (*Passer domesticus*) (Burke and Bruford, 1987; Wetton *et al.*, 1987) and in Indigo Buntings (Westneat, unpublished data).

1.3. EPC as a Mixed Reproductive Strategy

The data currently available suggest that among males EPC are part of a mixed reproductive strategy (Trivers, 1972; Beecher and Beecher, 1979; Fitch and Shugart, 1984) rather than a specialized reproductive behavior adopted exclusively by a subset of the population. Indeed in many species, the males involved in EPC are usually resident on neighboring territories and are already paired. For example, in White Ibises, males that pursued EPC defended neighboring nest sites; they were not males from more distant parts of the colony or those without a nest site (Frederick, 1987*a*). Observations of paired neighbors attempting EPC have also been made for Cattle Egrets (*Bubulcus ibis*) (Fujioka and Yamagishi, 1981), Common Guillemots (Birkhead *et al.*, 1985), Northern Fulmars (Hatch, 1987), Pied Flycatchers (Alatalo et *al.*, 1984), White-fronted Bee-eaters (Emlen and Wrege, 1986), Indigo Buntings (Westneat, 1987*a*,*b*), Northern Orioles (Edinger, 1988), Zebra Finches (Birkhead et *al.*, 1988*a*), and Rock Ptarmigan (Brodsky, 1988).

It is less clear whether EPC are part of a mixed mating strategy among females. On the one hand, paired females sometimes do seek and solicit EPC, as in Northern Fulmars (Hatch, 1987) and Black-capped Chickadees (*Parus atricapillus*) (Smith, 1988). On the other hand, many studies have reported that EPC are vigorously resisted by females (McKinney *et al.*, 1984). However, even in these cases, female involvement in EPC could be part of a subtle mixed mating strategy.

1.4. The Ecology of Mating Systems: A Review

Emlen and Oring (1977) and Wittenberger (1979) stressed that ecological factors affecting the ability of males to defend females or resources attractive to females determine the ways breeding units are formed. Specifically, they hypothesized that the temporal and spatial distribution of females influences whether they can be monopolized by males. Patchy distribution of critical resources could lead to clumped distributions of females, and asynchrony in sexual receptivity could allow males to form new pairs after courting and copulating with the first mate. In both situations, the operational sex ratio (OSR), which is the number of unpaired females available to an average male, is skewed >1 such that polygyny is expected. On the other hand, an OSR of <1 favors polyandry, and when the OSR $\cong 1$, monogamy is expected.

Although Emlen and Oring (1977) provided a framework for categorizing the ecological factors that affect the patterns of social associations between the sexes, they did not directly consider the possibility of EPC. The current analysis is predicated on the idea that overlapping but not identical sets of ecological factors influence social associations and mating preferences (see also Gowaty, 1985). We shall first analyze the factors influencing male pursuit of EPC. Then, after reviewing the costs and benefits of EPC to females, we examine in detail how females respond to attempted EPC.

2. MALES

2.1. Tradeoffs in Reproductive Effort

In any sexual species, the reproductive success of males theoretically is limited more by the availability of mates than is female reproductive success (Trivers, 1972). Males typically can increase their fitness through copulating with multiple partners. However, the optimal level of effort a male expends pursuing additional matings must balance (1) the gains from such pursuit against (2) the gains from parental effort (Maynard Smith, 1977; Low, 1978). The conventional wisdom—namely that in most monogamous birds male parental care is required for offspring survival and that in polygynous species males are "emancipated" from providing care—is insufficient to explain why males do or do not behave parentally. For paternal care to be advantageous, males must gain more, on average, from parental efforts than they gain from equal efforts expended on other behaviors—in particular from pursuing additional matings. Understanding how this tradeoff balances out is complicated, because it is the relative gain from each type of effort that matters, rather than the reproductive benefits of either alone. Obviously, substantial gains in offspring survival or condition due to paternal efforts will reduce the net benefits of pursuing additional matings; conversely, easy accessibility of secondary matings will reduce the net gain from behaving parentally.

EPC and polygyny are both forms of mating effort; however, most tests of the tradeoff between mating and parental effort have focused on the effects of polygyny. If we now consider EPC as a form of mating effort, we can refine our explanations of patterns of paternal care in birds. High levels of paternal care correlate with monogamy across avian taxa (Silver *et al*., 1985), but within all mating systems there is considerable variation in the amounts and types of care given by males (Verner and Willson, 1969; Silver *et al*., 1985). Furthermore, the manifestations of paternal care typically change as the nesting cycle progresses. For example, males in most North American passerines con-

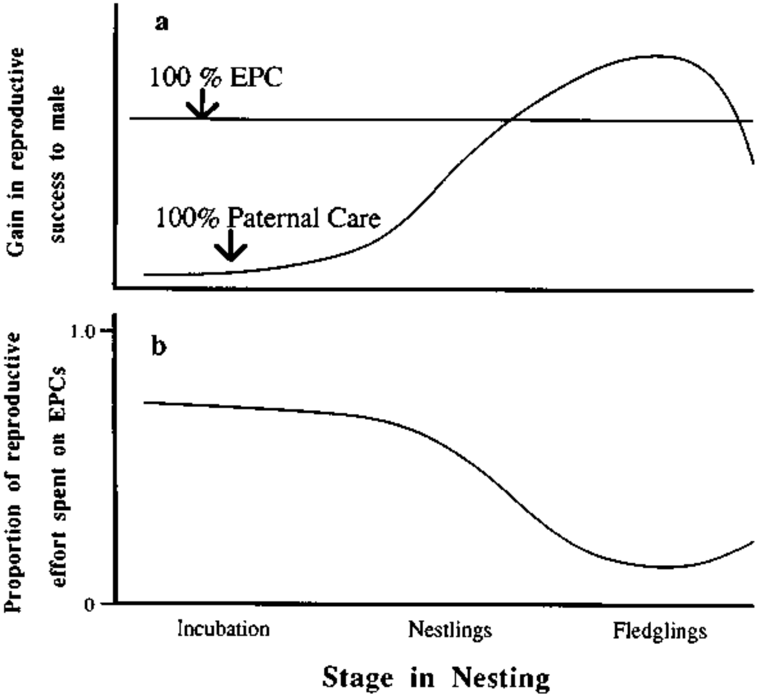

FIGURE 1. Graphical representation of the tradeoff between that component of male mating effort devoted to the pursuit of EPC and parental effort in an asynchronously breeding species. (a) Impact of either pursuit of EPC or parental care on the reproductive success of the male. Each line shows the payoff per unit of time over the course of the nesting cycle for the maximal effort a male could give to each behavior. (b) Proportion of effort spent pursuing EPC that results in the maximum reproductive success for a male with the curves shown in (a). This is an illustration, rather than a quantitative model. To quantify the tradeoff one must know the rate of change in payoff as effort for either pursuit of EPC or parental care changes.

tribute little to nest building or incubation. If males help at all, they do so later on, usually by feeding or protecting nestlings and fledglings (Verner and Willson, 1969). We suggest that a hitherto unappreciated factor contributing to patterns of paternal care is that males may be pursuing EPC as an alternative, especially during early stages of nesting when male help may have relatively little impact on male fitness compared to the benefit of pursuing EPC.

As a hypothetical example, imagine a species in which male care contributes little to the survival of young during incubation, but has a major effect during the nestling and fledgling stages (Fig. 1a). By contrast, assume that a male's gain from the pursuit of EPC is relatively constant throughout the nesting cycle. Because males ought to behave in ways that maximize their net benefit, a male of this hypothetical species should pursue EPC most vigorously during incubation and gradually reduce such mating effort in favor of an increase in parental effort during the nestling and fledgling stages (Fig. 1b). In support of this scenario, Westneat (1988) found that male Indigo Buntings pursue EPC during incubation, when they contribute little to the care of young.

For temperate zone noncolonial passerines, the pattern of behavior in Fig. 1 is reasonable because predation rates are high and through most of the season females will renest quickly if their eggs or chicks are destroyed (e.g., Zimmerman, 1966; Nolan, 1978; Carey and Nolan, 1979; Payne, 1982). Thus, there is a relatively constant pool of fertilizable females available to males. By contrast, in species that breed synchronously and in which predation is low, females in local populations may be fertilizable during only a fraction of each breeding season (see Birkhead and Biggins, 1987). In these species, both the gains from parental care and from EPC will change over the season (Fig. 2a). In these cases, males should decrease effort spent on pursuit of EPC and increase parental effort sooner in the nesting cycle (Fig. 2b).

2.2. Factors Affecting Tradeoffs in Reproductive Effort

Male reproductive behavior should thus be viewed as a tradeoff between mating effort and parental effort. The factors that affect this tradeoff fall into two main categories: (1) those affecting the value of paternal care to the survival of young, and (2) those affecting the opportunity for additional matings. Again, we wish to focus on the factors affecting EPC (as opposed to polygyny) as the route by which additional matings are gained. We shall discuss each factor separately, although it should be remembered that many of these factors will be acting in concert, and univariate tests of the impact of any given factor may fail to reveal its importance.

2.2.1. The Value of Paternal Care

The effect of a male's parental care on the survival of young depends on both the life style of the species (e.g., food preferences) and on the habitat in which any given pair nests (Armstrong, 1955; Crook, 1964, 1965). Differing levels of male care across species may indicate either that over evolutionary time (1) the care differed in its value to the survival of offspring, (2) the species differed in the opportunities

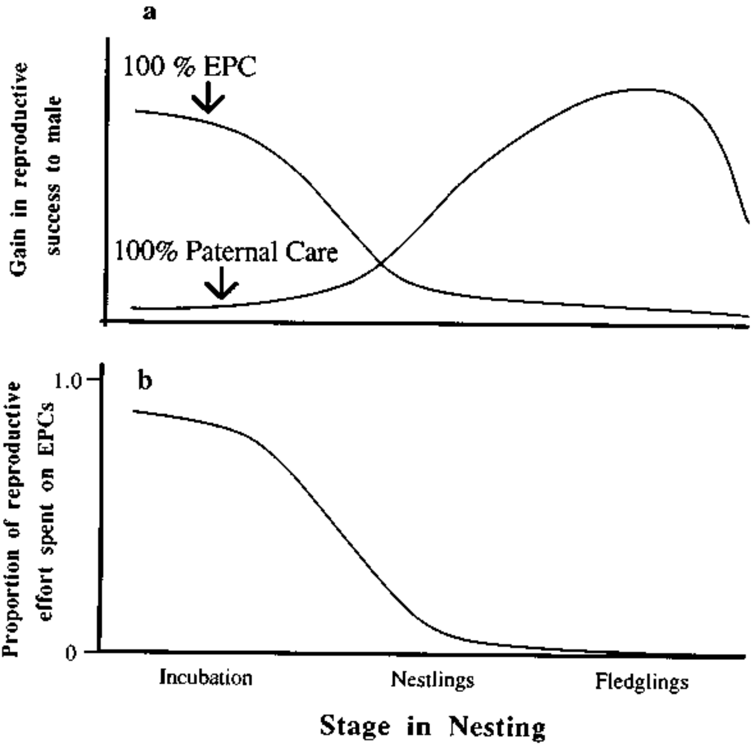

FIGURE 2. Graphical representation of the dynamic between that component of male mating effort devoted to the pursuit of EPC and parental effort in a synchronously breeding species. Sections (a) and (b) are similar to those shown in Fig. 1. In (a), however, the mating effort curve is not a straight line because the number of females that are fertilizable decreases as the nesting cycle progresses.

for males to obtain additional matings, or both (1) and (2). Many male-removal experiments have suggested that the male's presence during the nestling period has little impact on offspring survival, e.g., in Song Sparrows (*Melospiza melodia*) (Smith *et al.*, 1982), Eastern Bluebirds (*Sialia sialis*) (Gowaty, 1983), Seaside Sparrows (*Ammodramus maritimus*) (Greenlaw and Post, 1985), Snow Buntings (*Plectrophenax nivalis*) (Lyon and Montgomerie, 1985), Willow Ptarmigan (*Lagopus lagopus*) (Martin and Cooke, 1987), and Dark-eyed Juncos (*Junco hyemalis*) (Wolf *et al.*, 1988). At first, paternal care in such species may seem puzzling; however, it may be that males in these species provide care because they have few opportunities for additional matings (through polygyny or EPC). In other species, male removal typically results in mortality of eggs or young, e.g., some colonial seabirds (Gladstone, 1979) and Killdeer (*Charadrius vociferus*) (Brunton, 1988). It is inappropriate to conclude that male parental care has evolved in these species because it is more valuable to young. Current value does not always reflect the evolutionary reasons for the development of an observed trait. Although present paternal care would appear to be useful, consistent lack of opportunities for additional matings may have selected males to behave parentally over evolutionary time, resulting in the current dependence of females and chicks on such assistance. In addition, present levels of paternal care exist in the context of current opportunities for additional matings. These considerations lead us to suggest that mate-removal experiments alone should not be used to decide whether (1) or (2) has most strongly affected the patterns of paternal care observed today. Measures of the potential value of male parental care must be independent of the amount of care presently provided by males.

One ecological factor that should affect the ease of raising offspring is the availability of food. For example, if food is abundant near the nest or is easily gathered, the efforts a female expends on each offspring will be less than if food is located far away or is hard to obtain. The time taken to collect a load of food also reflects how long the nest would be left exposed if the female had no male assistance. During the nestling and fledgling stages, foraging trip time affects how often chicks can be fed, and presumably limits both chick growth rate and the number of young reared. Comparisons across species of the mean and variance in the duration of female absences might thus be used to assess the relative potential value of male parental care. We predict that males in species with long or variable foraging trip times ought to expend more effort on paternal care and less on EPC and polygyny than males in species with short foraging trip times.

We realize that foraging trip time alone is a simplistic and incomplete descriptor of the value of male care. Its value for specific comparisons will depend on other aspects of the species' biology, such as average amount of food carried on each trip, body size, and the intensity of predation on nestlings. Nevertheless, some general predictions can be made. For example, foraging trip time is likely to be much less (and the value of male care correspondingly less) in species where nest sites are located on territories containing food resources than in species nesting at sites distant from food resources, e.g., colonial birds such as White Ibises (Frederick, 1987*a*) and Gannets (*Sula bassanus*) (Montevecchi and Porter, 1980) or with unpredictable availability of prey, e.g., Snail Kites (*Rostrhamus sociabilis*) (Beissinger, 1987*a*,*b*). If this dichotomy is correct, males that defend territories containing nest sites and food resources should be more likely to engage in EPC and polygyny than should males in species that nest far from food. Foraging trip time is a much better measure within a species. Males on good territories (short foraging trip times) would be expected to pursue EPC or polygyny more than males on poor territories (long foraging trip times).

The value of male parental care may also vary with predator pressure. Foraging trip time obviously affects the length of exposure of eggs or young to predators; predictions about EPC are the same as above. However, other aspects of predation pressure may have additional effects. Males of many species respond to predators with alarm calls and distraction displays. If a pair can defend better than one, e.g., in Killdeer (Brunton, 1988), or if some males can provide better defense than others, some males may lose more by pursuing EPC than by helping keep watch for and defending against potential predators. EPC should thus be less frequent in species with joint defense of the nest or young. Beyond the addition of an extra defender, the effectiveness of males in directly thwarting predators will also affect the gains to males of being vigilant. Larger birds or those with weapons (e.g., raptors) are likely to be more effective in deterring predators. We also predict that in general males of these species will be less likely to pursue EPC and more likely to assist with nest defense than males of smaller or less dangerous species.

2.2.2. Opportunities for EPC

2.2.2a. Density. Several investigators have suggested that the density of breeding individuals will increase the chances for EPC (Hoogland and Sherman, 1976; Birkhead, 1978; Møller, 1987*b*). Although there is a positive relationship between EPC and breeding density in the Barn Swallow (Møller, 1985, 1988*a*), the impact of density will not necessarily increase linearly, and will depend on the nature of interactions between neighbors. If breeding individuals are widely scattered (i.e., at very low density), there obviously will be few opportunities for EPC. However, in territorial species, once the breeding density reaches the point at which most breeders are surrounded by neighbors, additional increases in density will not necessarily affect the number of neighbors and thus the opportunities for EPC. For example, in the colonial White Ibis, pairs have a similar number of adjacent, territorial neighbors as in the dispersed nesting Indigo Bunting. Because in Ibises and Buntings it is the males living within several nest sites who achieve EPC with a given female (Frederick, 1987*a*), the differences in density between Ibises and Buntings do not appear to have a large impact on the frequency of EPC (Westneat, 1987*a*,*b*). In other species, the nature of social interactions during EPC is different. For example, in some colonial swallows females copulate away from the nest site and thus can potentially interact with any male in the colony (Beecher and Beecher, 1979; Møller, 1985, 1987*a*). Increases in the numbers of individuals within a colony thus might increase the chances of EPC in such species.

2.2.2b. Polygyny and EPC: Environmental Homogeneity. The tradeoff between mating effort and parental effort exists whether males gain additional matings from attracting previously unpaired females to a territory (polygyny) or pursuing EPCs. Even when there are few unpaired females, males may still have opportunities to fertilize other males' mates. Emlen and Oring (1977) suggested that the operational sex ratio (OSR), would reflect the opportunity for males to mate with multiple females. This concept of an OSR must now be divided into two components: (1) the ratio of sexually active males to *unpaired* females (a measure of the potential for polygyny; Emlen and Oring (1977), and (2) the ratio of the number of sexually active males to *fertilizable, but paired*, females (a measure of the potential for EPC). These two separate measures sum to what we term the *inclusive OSR*, a measure of the availability of fertilizable females for any given male.

The mating effort–parental effort tradeoff will depend on both components of the inclusive OSR. For example, in a polygynous species, a high traditional OSR (1) reflects an excess of unpaired females. Whether males will also pursue EPC will depend on the ratio of sexually active males to fertilizable paired females (2). Thus, for any species the likelihood of polygyny on the one hand and EPC on the other can be estimated by using the OSR for polygyny in the former case and the OSR for EPC in the latter.

Although occasional polygyny occurs in many birds, the majority are primarily monogamous (Lack, 1968; Ford, 1983). We interpret this prevalence of monogamy (as did Orians, 1969 and Emlen and Oring, 1977) as a reflection of the ecological conditions affecting the settlement of males and females, limiting the potential for polygyny. Such restrictions on settlement and pairing patterns have minimal effects on the OSR for EPC. Indeed, it is possible for EPC to be common even in species in which polygyny is rare (and vice versa).

Males that pursue polygynous social associations might not be able to gain EPC simultaneously. If obtaining exclusive sexual access to secondary mates requires defense of a territory and self-advertisement, whereas gaining EPC involves leaving a territory unguarded and seeking out receptive females, males will be forced into a tradeoff between these two types of mating effort. If so, the ecological factors that increase the incidence of polygyny will have an inverse effect on the pursuit of EPC.

In birds that defend territories containing resources valuable to females, polygyny occurs when some males control considerably larger or better territories than others. Unpaired females presumably benefit more by settling on the high quality territory of an already paired male instead of the poorer territory of an unpaired male (Verner, 1964; Verner and Willson, 1966; Orians, 1969). Thus, heterogeneity in territorial quality or size is a critical ecological condition for resource defense polygyny (Orians, 1969; Emlen and Oring, 1977; Vehrencamp and Bradbury, 1984; Lightbody and Weatherhead, 1987). In general, then, environmental homogeneity should greatly reduce the opportunities for males to attract unpaired females. Although homogeneity may also reduce the number of females in neighboring territories (by reducing polygyny), some neighboring and potentially fertilizable females are likely to be available to males, even in the most homogeneous habitats. Thus homogeneity will affect the potential for EPC far less than the potential for polygyny.

The relationship among environmental heterogeneity, polygyny, and EPC is obviously complex. If males cannot pursue polygyny and EPC simultaneously, the costs and benefits of polygyny will be balanced directly against the costs and benefits of pursuing EPC. We expect that within a species, some males (those holding the best territories) will gain more by advertising for additional mates than by pursuing EPC or behaving parentally. A male on an average territory relative to others but in an environment with plentiful resources might gain the most from the pursuit of EPC instead of advertising for additional mates or providing parental care. Finally, a male on a poor territory (in both absolute and relative senses) might either pursue EPC if he could not attract a mate, or forego EPC in favor of paternal care if he did attract a mate.

In fact, there are major differences in male mating and parental behaviors among populations of several passerines. Notable among these is the Red-winged Blackbird: in some populations, males are often highly polygynous and provide no parental care (Orians, 1961; Verner and Willson, 1969; Searcy, 1979), whereas in others males are less polygynous and often contribute substantially to the feeding of young (Patterson, 1979; Searcy and Yasukawa, 1983; Muldal et *al.*, 1986). EPC occur in several of these populations (Bray et *al.*, 1975; Monnett et *al.*, 1984), but comparative data on the rates of EPC, the value to chicks of paternal care, and the relative attractiveness of male territories to females are unavailable.

Males do not necessarily face a tradeoff between pursuing polygyny and EPC. For example, if females seek extra-pair matings, then males might both attract unpaired females and achieve copulations with neighboring paired females via territorial advertisement. Obviously when continued advertisement or territory defense does not increase the likelihood of attracting additional mates, mating effort would be better spent on active pursuit of EPC. Thus whether polygynous males engage in EPC will depend on the impact of male advertisement on the attraction of mates and on the costs and benefits for females of seeking EPC.

2.2.2c. Breeding Synchrony. When females are fertilizable simultaneously, males will have opportunities for EPC for only a fraction of the season. Synchrony of breeding by females also reduces both components of the inclusive OSR (cf. Figs. 1 and 2). In general, we expect the frequency of EPC in species that breed relatively synchronously to be less than in species that breed relatively asynchronously. However, the effects of synchrony will depend on the structure of breeding populations and on when males pursue EPC (Birkhead and Biggins, 1987). If males pursue EPC with neighboring females after their own mate has finished laying, then synchronized breeding within local subunits of the population will limit the frequency of EPC, even if separate subunits breed asynchronously.

Information on the frequency of extra-pair fertilizations in synchronously breeding species is sparse. Breeding synchrony has often been reported in colonial nesters (reviewed by Wittenberger and Hunt, 1985). Some comparisons of the rate of EPC in colonial versus solitary nesting birds have suggested that, contrary to our prediction, EPC are more frequent in colonial birds (Birkhead *et al.*, 1987; Birkhead, 1987*a*). However, these comparisons were based on observations of copulations, and EPC may be more difficult to observe in solitary nesting species (e.g., in visually occluded habitats) than in colonial species nesting in the open (Westneat, 1987*a*,*b*; Frederick, 1987*a*). In fact, comparison of the rates of extra-pair fertilizations (detected genetically) suggests that colonial species have lower rates than do solitary nesters (see Table V in Lank *et al.*, 1989).

Although this latter result seems to support our prediction, a word of caution is in order. Many colonial birds nest far from food resources (e.g., seabirds and waders) and paternal care of eggs and nestlings may be so valuable that males gain more from behaving parentally than from pursuing EPC. In addition, the density of breeding individuals is often greater in colonial species, perhaps increasing the chances females are subjected to EPC. To remove the influence of these confounding variables, the value of male care (in terms of survival of young) and the nesting density must be standardized. For example, EPC and extra-pair fertilizations could be quantified in synchronously and asynchronously breeding populations, or in artifically de-synchronized sub-populations, of the same species.

2.2.2d. Mate Guarding. Observations of male behavior during their female's fertilizable period indicate that males often attempt to protect mates from EPC. Mate guarding has been observed in a variety of solitary nesters, including Black-billed Magpies (*Pica pica*) (Birkhead, 1982; Buitron, 1983), Pied Flycatchers (Björklund and Westman, 1983), Wheatears (*Oenanthe oenanthe*) (Carlson et *al*., 1985), Indigo Buntings (Westneat, 1987*b*), and Rock Ptarmigan (Brodsky, 1988) and colonial species, including Bank Swallows (*Riparia riparia*) (Hoogland and Sherman, 1976; Beecher and Beecher, 1979), Common Guillemots (Birkhead et *al*., 1985), Barn Swallows (Møller, 1985, 1987*c*), White-fronted Bee-eaters (Emlen and Wrege, 1986), White Ibises (Frederick, 1987*a*), Purple Martins (*Progne subis*) (Morton, 1987). The ability of males to guard fertilizable mates will reduce the opportunities for EPC by other males and thereby influence the benefits to males of pursuing EPC.

Some recent investigators (e.g., Leffelaar and Robertson, 1984; Birkhead, 1987*a*) have implied that the intensity of mate guarding reflects directly the current likelihood of cuckoldry. However, this is not always the case. Frequent EPC obviously should select for increases in mate guarding, but effective mate guarding may prevent EPC. Conversely, low levels of mate guarding may permit many EPC or may indicate that EPC attempts are infrequent and mate guarding is not needed. Contemporaneous levels of mate guarding thus cannot be used to infer current rates of EPC, just as contemporaneous levels of paternal care cannot be used to infer its value.

Mate guarding must be viewed as a tradeoff between the benefits of protecting paternity versus the benefits of competing actions. For example, males in species that rear two broods in a season may reduce their mate guarding in mid-season due to increased benefits from parental care to young in the first brood. Furthermore, males might sacrifice paternity of some offspring if by reducing mate guarding they increase the chances of attracting additional social mates (i.e., polygyny). Sherman and Morton (1988) have suggested that close mate guarding and territorial defense in general may be difficult for a male to perform simultaneously, especially in visually occluded habitats. For example, in mountain White-crowned Sparrows and Indigo Buntings, EPC are quite common, yet a male will often temporarily leave his female to sing at his territorial boundary. In Buntings, at least, this singing appears to be aimed at potential territorial usurpers rather than intruders pursuing EPC (males sing in response to singing intruders, but not to silent ones). Thus males forego mate guarding, in spite of the danger of EPC, when there are other demands directly competing for their time and energy.

A factor influencing mate guarding in colonial species is access to food and water. When nesting sites are far from such resources, males may be faced with the choice of guarding their mate and nest or leaving the colony to forage (Birkhead et *al.*, 1985). Frederick (1987*a*) found variation in the length of time that male White Ibises were able to remain at the colony (without feeding) during their mates' fertilizable period. Direct observations revealed that females paired to males that left the colony early were most likely to be targets of EPC attempts. Similar tradeoffs for males between obtaining resources and mate guarding apparently occur in Snow Geese (Mineau and Cooke, 1979), Little Blue Herons (*Egretta caerulea*) (Werschkul, 1982), and Rooks (Røskaft, 1983).

In summary, we expect EPC to be more frequent in species in which mate guarding competes for a male's time and energy with some other behavior. Tests of the impact of mate guarding on the frequency of EPC will require comparing levels of mate guarding with the frequency of EPC within a species to control for ecological constraints on mate guarding.

3. FEMALES

A male's opportunities for EPC and the likelihood of their success will be strongly affected by the behavior of females. There are several potential costs and benefits to females of mating with more than one male (e.g., Schwagmeyer, 1984; Crozier and Page, 1985; Halliday and Arnold, 1987; Sherman *et al.*, 1988). Those that are germane to EPC and female birds are listed in Table I. Each of these costs or benefits can be categorized by its effects on either the phenotype of the individual female or the genotype of her offspring (Alexander, 1974). In the next section we discuss the details of these potential costs and benefits, making no assumptions about the nature of female behavior. In the final sections, the ways these costs and benefits act to affect female behavior are examined.

TABLE I
Hypothetical Costs and Benefits of Extra-Pair Copulations for Female Birds[a]

Cost/benefit	Time in copulatory sequence when incurred
Benefits	
Phenotypic	
Courtship feeding	Before copulation
Encourage male care	After fertilization (cue is copulation)
Genotypic	
Obtain good genes	Fertilization
Produce progeny with maximum range of genotypes	Fertilization
Ensure fertilization	Postcopulation, prefertilization
Costs	
Phenotypic	
Predation on pairs	During copulation
Transfer of parasites or diseases	During copulation
Reduction in male care	After fertilization (cue is copulation)
Male punishment of female	After copulation (cue is copulation)
Genotypic	
Offspring fathered by male with poor genes	Fertilization
Increased within-brood competition, due to increased genetic diversity	Fertilization

[a] Each cost or benefit is classified as to whether it has phenotypic or genotypic effects (see text) and at what point in the copulatory sequence it is incurred.

3.1. Benefits of EPC to Females

Females might gain phenotypic benefits from EPC. For example, an extra-pair male might provide food during extra-pair courtship or the sperm itself could provide some direct nourishment, as in many orthopteroid insects (see Gwynne, 1984). Males also might behave nepotistically toward a female's offspring if they copulated with her. However, such potential phenotypic benefits for EPC appear to be rare in birds. In most species studied to date, females do not receive courtship feedings from males attempting EPC, nor do such males subsequently behave parentally toward females' chicks (McKinney et *al.*, 1984: Frederick, 1987*b*; Hatch, 1987: Westneat, 1988). Avian inseminations also seem unlikely to contain many nutrients.

Females could gain any of three types of genotypic benefits from EPC: "good genes," genotypic diversity among their offspring, or insurance of fertilization (Table I). Regarding the first point, females could gain two types of good genes from EPC: genes for traits attractive to other females (allowing them to produce sons with those attractive traits; Weatherhead and Robertson, 1979), and genes for general vigor, longevity, or resistance to pathogens (Wittenberger, 1979). Female choice for good genes has been both criticized (on the basis that there is little evidence of heritable genetic variation for traits important to male fitness: Williams, 1975; Halliday, 1978; Searcy, 1982; but see Hedrick, 1988) and defended (Trivers, 1985; Borgia, 1987). This hypothesis depends on the assumption that females benefit from mating with phenotypically superior males. The following discussion treats this assumption as reasonable.

Females might benefit from an EPC if the male to whom they are paired is not the best one available. There are four general circumstances in which a female might pair with a male who was not of the highest genetic quality in the local population. First, in territorial species females probably choose a mate based on the quality of his territory. Females settle first on large, high-quality territories in Red-winged Blackbirds (Lennington, 1980), Lark Buntings (*Calamospiza melanocorys*) (Pleszczynska,1978), and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Lightbody and Weatherhead, 1987). Second females might choose males based on the likelihood that they will provide parental care (Searcy and Yasukawa, 1981; Muldal *et al.*, 1986). Third, females may settle on familiar territories, presumably because familiarity confers advantages in finding food and escaping from predators (Davies, 1976). In particular, females of many species return to a site where they were successful in raising young the previous year, regardless of whether or not their mate of the previous season also returns (e.g., Gavin and Bollinger, 1988). Fourth, in long-lived species with strong pair bonds, females may gain by remaining paired to their previous, and thus familiar, mate.

Male–male competition for territories with characteristics attractive to females might be thought to ensure a strong correlation between territory quality and male quality (Wittenberger, 1979; Heisler, 1981). However, all females obviously cannot settle on the territory of the one best male. In most species, the territory of the best male might attract one or more females, but later-arriving females benefit more by settling in an unoccupied territory with a relatively poorer quality male (Orians, 1969). Moreover males, like females, typically return to a familiar territory with known food resources and predator escape routes (Hinde, 1956; Greenwood and Harvey, 1976; Best, 1977; Nolan, 1978), even if it is not the best one available (although in some cases males do switch to better territories: Beletsky and Orians, 1987; Petersen and Best, 1987).

The combination of (1) site fidelity by both sexes, (2) a limit to the number of females that can settle on the territory of the best male, and (3) choice by females for factors related to territory quality, together often uncouple females' choices of breeding sites from choices of genetic mates (Wittenberger, 1981; Searcy, 1982). In other words, females of territorial species may often pair with a male other than the one with the most preferred phenotype. In an interesting example, female mountain White-crowned Sparrows around Tioga Pass, California return to the breeding grounds each spring at the same time as or even ahead of the males. Females typically return to the site where they bred successfully the previous year, regardless of the presence of their former mate (Morton *et al.*, 1972; Morton, 1976; Morton, unpublished data). Males also show strong breeding site fidelity from year to year. Thus vacancies due to overwinter mortality are often filled by young birds, so the quality of a territory may not reflect the genetic quality of the male holding it. A recent genetic analysis of parentage in this population revealed that a substantial fraction of chicks were the result of extra-pair fertilizations (Sherman and Morton, 1988).

By contrast, in nonterritorial species females appear to choose mates directly, based on phenotypic attributes. Direct choice among males should make it easier for a female to obtain a mate with good genes (Borgia, 1979, 1987). However, under some circumstances females might obtain even better genes through EPC. For example, if courtship is lengthy and complex, requiring a large investment of time and energy, females might not be able to assess adequately the quality of all the males in a local population before they must lay the first egg (Gladstone, 1979; O'Donald, 1980). Furthermore, if males are not all available simultaneously and females sometimes encounter a better male late in courtship but before laying, they might benefit from an EPC. In monogamous species, only one female will be paired with the best male; other females might pair with the top male from the pool of unpaired males, but copulate as well with the best male overall. Finally, many aspects of courtship may allow females to assess a male's abilities and propensity to care for young, e.g., Common Terns (*Sterna hirundo*) (Nisbet, 1973, 1977). It is conceivable that some females might gain by pairing with good fathers and also copulating with males phenotypically superior for other traits (e.g., Benshoof and Thornhill, 1979).

Females might also benefit from EPC through increases in the genetic diversity of the brood produced (Williams, 1975). Genetic diversity presumably maximizes the gain from sexual reproduction; in an unpredictable environment, especially one with coevolving diseases or parasites, genetic diversity of offspring might increase the chances that at least some young will be successful, thereby reducing the variance in reproductive success (Gillespie, 1977; Rubenstein, 1982). However, we know of no data addressing this hypothesis in birds, and theoretically at least this benefit is opposed by the potential cost of increasing intra-brood competition due to the presence of full- and half-sibs in the same nest (Sherman, 1981; Table I).

A major difficulty with testing the genetic diversity hypothesis as an alternative to the good genes hypothesis is that in some cases the types of genes obtained will be the same. For example, females might choose males in good condition, thereby gaining any genes influencing the male's resistance to pathogens, i.e., the "good genes" hypothesis (Hamilton and Zuk, 1982). If females cannot assess the relative resistances of potential mates, they might increase the chances that at least some young carry genes for resistance to pathogens by mating multiply, i.e., the genetic diversity hypothesis. As Sherman et *al.* (1988) have argued, if a species faces an unpredictable array of pathogens, females might gain by mating with several different males if potential genetic differences in pathogen resistance decrease the chances an entire brood is wiped out.

Lastly, EPC might ensure that all the eggs are fertilized (Table I; Gibson and Jewell, 1982). This hypothesis depends on a high frequency of sterility or at least temporary infertility among males. Theoretically this hypothesis seems weak because male infertility is so detrimental that traits increasing fertility ought to be under strong, positive selection. However, we know of no comparative data bearing on the rates of infertility in wild birds.

3.2. Costs of EPC to Females

Extra-pair copulations also carry potential costs for females (Table 1). First, males conceivably might respond to infidelity by physically punishing their mate (Barash, 1976). However, data on responses to cuckoldry suggest that males generally do not respond to EPC with physical sanctions (Power and Doner, 1980; Gowaty, 1981; Frederick, 1987*b*; Hatch, 1987; Morton, 1987; Westneat, 1987*b*; Smith, 1989).

A second potential cost arises because males may have been selected to respond to their female's involvement in EPC by withholding parental care to young that are not their own (Trivers, 1972). Observations on three species—White Ibises (Frederick, 1987*b*), Purple Martins (Morton, 1987), and Indigo Buntings (Westneat, 1988)—revealed no facultative reduction in paternal care in response to cuckoldry. By contrast, Møller (1988*a*) recently reported that male Barn Swallows whose mates copulated repeatedly with other males provided less care to young than did males whose mates rarely copulated outside the pairbond.

Theoretically, cuckolded males might recognize their own young in a mixed brood (e.g., Sherman and Holmes, 1985) and preferentially care for them; however, such paternal discrimination has never been documented in birds. Males lacking discriminating abilities have three alternatives to parental care. First, they could devote more effort to the pursuit of additional matings (EPC or polygyny). However, preliminary evidence suggests that males that are cuckolded are less likely to achieve EPC (Frederick, 1987*a*; Westneat, 1988). Second, cuckolded males might destroy the eggs and renest with the same female. This seems unlikely unless a male's confidence of his paternity changes dramatically between nestings with the same female (Wittenberger, 1981). Finally, cuckolded males might reduce parental care, thereby increasing their survival to another year. A year later they would be older and perhaps less likely to be cuckolded, as in subadult Indigo Buntings (Westneat, 1987*a*).

Data on the impact of parental care on survival of adult birds are sparse. Frequent visits to the nest to feed nestlings might attract predators (Skutch, 1949). Effort expended in providing care might also affect the physical condition of adults. Nur (1984) manipulated brood size in Blue Tits (*Parus caeruleus*) and found that parents with large broods lost more weight and had a lower probability of returning to breed the following year. Similarly, Ekman and Askenmo (1986) found that nonbreeding territorial male Willow Tits (*Parus montanus*) had higher return rates than did breeding individuals. These results suggest that parental care can indeed adversely affect survival, so reduction of paternal care might be a viable counter-strategy to cuckoldry. However, if assistance to the whole brood is reduced, a male risks the survival of chicks that are in fact his own. Unless males have exact knowledge of the paternity of each offspring or paternal care drastically reduces

TABLE II
Three Categories of Female Behavior during Attempted Extra-Pair Copulations

Category	Behavior before male contact	Behavior of female after male contact	Examples
Actively solicited	Female initiates contact with male	Cooperation	Northern Fulmars (Hatch, 1987)
Apparently resisted	Male initiates contact, female avoids contact	Cooperation or struggling	Indigo Buntings (Westneat, 1987*b*), various waterfowl (McKinney *et al.*, 1983)
Passively accepted	Male initiates contact, female does not avoid contact	Cooperation	White Ibises (Frederick, 1987*a*), Barn Swallows (Møller, 1988*b*)

male survival, a male might often lose more than he gains by reducing paternal care.

Females might also incur costs from EPC if they are more likely to be exposed to predators. However, birds generally copulate quickly, and predators attracted to the activity associated with copulation may be unable to attack before the copulation is over. We know of no study in which the effects of predation on copulating pairs of birds has been documented; nonetheless the impact of predation in this case seems slight.

Lastly, EPC might be costly if females are exposed directly to parasites or diseases carried by males. Although parasites and diseases can be strong selective forces, data on rates of transmission during copulation in wild birds are nonexistent. Diseases and parasites are likely to be more common in colonial species because of the proximity of large numbers of conspecific hosts (Hoogland and Sherman, 1976; Brown and Bomberger Brown, 1986; Møller, 1987*b*). If contact during copulation does substantially increase the risk of infection, then females of colonial species may be more at risk from EPC than females of solitary species.

3.3. Female Behavior

Female birds generally respond to EPC in one of three ways: (1) active solicitation, (2) apparent resistance, or (3) passive acceptance (Table II). These are operational categories based on published descrip-

TABLE III
Influences of Various Conditions Associated with EPC on the Predicted Type of Female Response[a]

Conditions	Solicited	Accepted	Resisted	
			Avoidance	Ploy
Male care valuable	+	+	–	–
Male sanctions possible (physical punishment or withholding of parental care)	–	–	+	+/–
Females gain:				
Sons attractive as mates	+	–	–	–
Vigorous, healthy offspring	+	+	–	+
Diseases and parasites costly	–	–	+	–
Predation costly	–	–	–	–
Genetic diversity beneficial	+	+	–	+/–
Assurance of fertilization beneficial	+	+	–	–
Social mate of high quality	–	–	+	–

[a] Pluses (+) or minuses (–) in a column indicate that conditions are likely to have, respectively, a positive or negative influence on that female response. See text for explanation.

tions of female behavior, and they do not necessarily reveal the functions of the behaviors.

In the first category, females initiate contact visually or vocally with extra-pair males and solicit matings. The critical feature is that females take an active role. By contrast, resistance is any action taken by the female that appears to decrease the likelihood of a given copulation attempt transferring sperm. In the third category, passive acceptance, females respond to the approach of nonmates by cooperating with copulation attempts initiated by the male.

Although quantitative data on female behavior during EPC are scarce, most studies suggest that females either passively accept EPC or resist them. To our knowledge, the only reports of solicited EPC are Hatch's (1987) study of Fulmars and Smith's (1988) study of Black-capped Chickadees. However, female solicitation may be difficult to observe if females pursue EPC surreptitiously.

3.3.1. Solicited EPC

Whether females solicit EPC obviously depends on the gains relative to the costs (Tables I and III). Few data on any of the advantages discussed above are available. However, we wish to emphasize several testable predictions. First, if increased genetic diversity is the reason females pursue EPC, then most females should engage in EPC and most broods should be of mixed paternity. By contrast, if females pursue EPC because of the benefits of acquiring good genes, some females, e.g., those paired with males of poor genetic quality, should engage in EPC more than others. The broods of these females should be sired primarily, or solely by the extra-pair male, whereas the broods of females mated to the best males should be fathered solely by their mates. We also predict that if females gain good genes through EPC, they should solicit EPC when the good genes affect the expression of phenotypic attributes that are helpful in attracting mates (e.g., Weatherhead and Robertson, 1979), and when females can easily assess the quality of neighboring males. For example, females in the nonmigratory Black-capped Chickadee seek EPC with neighboring males higher in winter dominance hierarchies than the female's social mate (Smith, 1988).

Females will also be more likely to solicit EPC when males do not benefit from withholding parental care, either because there are few other behavioral options or because their care is critical for offspring survival. It is of interest in this regard that female Northern Fulmars occasionally solicit EPC. In this monogamous species, the single egg laid cannot survive without male care, breeding is synchronous, and adults are extremely long-lived (Hatch, 1987). Desertion by males is rare, whether or not their female mated with another male. One reason even cuckolded males do not desert may be that the chances of repairing or the increases in survival by deferring parental care are small (i.e., they would not outweigh the cost to survival of the chick which might be theirs).

3.3.2. Resisted EPC

Females resist EPC in a variety of ways. Female waterfowl flee from nonmates attempting to copulate (McKinney *et al.*, 1983), female Bank Swallows perform intricate aerial evasive maneuvers (Beecher and Beecher, 1979), Indigo Bunting females give alarm calls or dive into brush when pursued by nonmates (Westneat, 1987*b*), and female White-fronted Bee-eaters drop to the ground and flatten themselves during attempted EPC (Emlen and Wrege, 1986).

Females might resist EPC to avoid the associated phenotypic or genotypic costs (see Table I), or as a ploy to test the phenotypic and presumably the genotypic quality of extra-pair males. Differentiating between these alternatives is difficult, because females are predicted by both to behave in similar ways. The difference lies in the net effect the mating has on female fitness. If females resist EPC to avoid costs, then on average successful EPC must reduce female fitness (Thornhill, 1980). By contrast, if resistance is a ploy that ensures a mating with a superior male, then EPC should increase female fitness. Evidence that females are fertilized by better than average males is not sufficient to prove the resistance-as-a-ploy hypothesis. Even if female resistance occurs because EPC involve a net cost, resistance might still result in better quality males gaining inseminations. As long as the phenotypic cost of the entire copulatory act remains greater than the genetic benefit of the fertilization, resistance is appropriately seen as an attempt to avoid EPC.

3.3.2a. Resistance as Avoidance of Costs. Fitch and Shugart (1984) suggested that males cannot overcome female resistance and gain fertilizations in species without intromittent organs. Presumably even if a male managed to achieve a copulation, the female could prevent insemination by somehow closing her cloaca. The increasing evidence of extra-pair fertilizations in birds lacking intromittent organs might suggest that females are resisting as a ploy and are not attempting to avoid the costs of EPC.

We maintain, however, that female birds may indeed resist EPC to avoid the costs and yet still be fertilized by extra-pair males. Closer examination of the costs to females of extra-pair matings suggests that there may be few advantages to females in controlling fertilization. This is because most costs of EPC seem to be phenotypic, and accrue as a result of the act of copulation, rather than from the fertilization (see Table I). Females would benefit from mechanisms of sperm control after insemination only if genotypic costs were associated with EPC (e.g., males with poor-quality genes fertilizing some of a female's eggs). However, by resisting EPC, a female reduces these costs, because a male successful at overcoming the female's mate's defense and her own resistance will be a male good at gaining EPC.

Some phenotypic costs may arise evolutionarily due to selection resulting from extra-pair fertilizations, and thus might increase the benefits to females for controlling insemination. For example, extra-pair fertilizations might be costly if they lead to selection on cuckolded males either to withhold some parental care or to physically punish the female (Barash, 1976). However, the most likely cue a male can use to tell that he has been cuckolded is witnessing a copulation attempt. If so, a female that prevents fertilization once a copulation has occurred will have no obvious advantage over a female that does not prevent fertilization, because the male will withhold parental care or punish the female in either case. In sum, we believe that female resistance could be an attempt to avoid the costs of EPC. Because the genotypic costs of successful EPC may be insufficient to select for internal control of fertilization, EPC might result in many fertilizations if males can harass or physically threaten females such that females lose less phenotypically by copulating than by continuing to resist.

If resistance by females serves to avoid the net cost of EPC, we would expect females to avoid EPC when they are most costly: when predation on copulating pairs is likely, the danger of contracting venereal diseases is high, males can punish the female or withhold parental care if a female does not respond to EPC with resistance (Table III), and/or females are already paired to high quality males. Of these factors, the latter seems most likely. For example, in many waterfowl females choose social partners directly. Resistance to EPC in waterfowl is extremely vigorous and seems to represent true avoidance (McKinney *et al.*, 1983; see also Thornhill and Thornhill, 1983).

3.3.2b. *Resistance as a Ploy.* Females might resist extra-pair matings to test the quality of males, or to stimulate male-male competition (Christoleit, 1929, as cited in McKinney *et al.*, 1983; Cox and LeBoeuf, 1977). Males that gain EPC in species in which females resist often succeed by leaving their territories, circumventing the defense of the female's mate, and pursuing a resisting female. Males successful at inseminating a resisting female will presumably sire sons carrying the successful traits. Resistance by females could thus be a ploy for gaining good genes rather than an attempt to avoid potential costs.

Resistance-as-a-ploy could be a viable female strategy in almost any species, and conclusive evidence of its existence will be extremely difficult to obtain. We suggest that in some cases of resistance-as-a-ploy, females may behave as if they are pursuing EPC (e.g., by approaching and soliciting extra-pair males) and then resist attempts to copulate. However, females need not be inciting males to be resisting-as-a-ploy. Finally, resistance does involve costs, such as possible injury to the female (see also Table III). Thus we expect resistance-as-a-ploy to be less likely in species in which females have other means to assess the quality of males (e.g., winter dominance status in Black-capped Chickadees; Smith, 1988).

3.3.3. Accepted EPC

Females in many species appear to accept or cooperate with EPC initiated by males (see Table II). Acceptance of EPC by females is an intermediate between the extremes of resistance and solicitation. Thus females might accept EPC in situations in which the costs and benefits of being inseminated by an extra-pair male lie between those associated with either resistance or solicitation (Table III). On the one hand, females might gain good genes by accepting EPC, e.g., Cattle Egrets (Fujioka and Yamagishi, 1981), Barn Swallows (Møller, 1988*b*), Little Egrets (*Egretta garzetta*) (M. Fujioka, unpublished data) if male–male competition during EPC results in the best males gaining matings. For example, male White Ibises are most successful at EPC if they can win fights over contested females. Females sometimes accept EPC from these males (Frederick 1987*a*). On the other hand, there might be few costs to females accepting EPC attempts. Perhaps few diseases or parasites are transmitted through the brief contact of a copulation. Alternatively, if a female's mate does not withhold parental care even if his likelihood of paternity is low, then females might not suffer any additional costs from acceptance. Female cooperation with EPC attempts has been reported in several colonial wading birds (Gladstone, 1979; Fujioka and Yamagishi, 1981; Werschkul, 1982; Frederick, 1987*a*). Paternal care is critical in these species, and males may have few options other than to provide care.

Acceptance by females cannot be taken as a sign that they gain from EPC. A female may accept an EPC if resisting results in physical harm either to her or to her eggs. For example, some EPC take place on the nest during laying in Rooks (Røskaft, 1983) and in White Ibises (Frederick, 1987*a*). Females do not resist these attempts, perhaps because the eggs would be damaged if they did.

Finally, Halliday and Arnold (1987) proposed that multiple mating by females might be due to genetic coupling between male and female copulatory propensity. Strong sexual selection on males for polygyny is hypothesized to drag females into also copulating frequently. As an explanation of female acceptance of EPC, this "nonadaptive" hypothesis requires the assumption that the genetic factors underlying both copulatory propensity and mate choice are the same in males and females. Homology in mate choice mechanisms seems questionable, however, and there is no evidence that selection on males to copulate frequently relaxes female choice of mates. Indeed, female copulatory frequency rarely correlates positively with high variance in male copulatory frequency (Sherman and Westneat, 1988). Halliday and Arnold's (1987) hypothesis thus is unlikely to explain why females mate with more than one partner or accept EPC.

3.4. Effects of Female Behavior on Males

Female behavior will affect how easily males can capitalize on opportunities for EPC. When females seek EPC, chosen males will not sacrifice other forms of reproductive effort to obtain them. Attracting females to a territory for EPC may require considerable effort, but males can still defend their territory, mate, and provide some forms of parental care (such as nest defense) to the offspring of their social mate. Thus, female pursuit of EPC will shift the tradeoff between mating effort and parental effort toward more gain per unit of mating effort. However, in any local population, only a few highly attractive males will benefit from this shift in the mating effort tradeoff; for most, the tradeoff will shift more toward parental care if females strongly resist matings with lower-quality males.

If females do not solicit EPC, males are forced to leave territories to gain extra-pair matings. Since males cannot effectively guard their own female, defend their territory, or contribute to parental care when they are off their territories pursuing EPC, female resistance or passive acceptance will force males into reproductive effort tradeoffs. Once such males have left their territory and have located and approached a female, passive acceptance of attempts at EPC on the part of females will make gaining inseminations easier for males.

4. SUMMARY AND CONCLUSIONS

In many species, paired birds have been observed to copulate with individuals other than their social mate. Recent research using genetic markers has shown that these extra-pair copulations (EPC) frequently result in fertilizations. Until now, theoretical discussions of the evolution of avian mating systems have focused primarily on the ways males and females choose their social mates and not on the additional choice of genetic mates. Here we have tried to fill the gap by discussing the factors affecting why some male and female birds mate with an individual other than their social partner.

We have highlighted the most important factors affecting the costs and benefits of EPC for both males and females. Males ought to pursue additional matings through EPC whenever they have the opportunity. However, the net benefit to males of pursuing EPC depends on the fitness gains from parental care and such other activities as territorial defense or mate guarding versus the gains from EPC (Figs. 1 and 2). Five factors affect the outcome of this reproductive effort tradeoff:

First, the value of male parental care to offspring survival will reduce the benefits to males of pursuing EPC instead of giving care. Environmental variables such as the ease of finding food should affect how valuable a male's contribution will be to the survival of offspring. Easy access to food will reduce the time eggs and nestlings are exposed to predators when a female leaves them and will permit faster provisioning by the female. In addition, lower risks of predation will reduce the gains to males of remaining vigilant, increasing the net gain for pursuit of EPC. If males are able to thwart predation on eggs or young (e.g., if they are large or have weapons), they may gain more by behaving paternally than by pursuing EPC. Finally, in homogeneous habitats males may be unable to monopolize sufficient resources to attract secondary social mates, and so gain more by pursuing extra-pair matings than by advertising. In heterogeneous habitats, three different behavioral tactics may appear: males on average quality territories should pursue EPC, and males on good and poor territories may instead pursue polygyny or provide parental care, respectively.

Second, density of breeding individuals will affect the opportunities for EPC in some circumstances. Extremely low densities, resulting in few neighbors, will present few opportunities for EPC. Because in many territorial species the males engaging in EPC are the residents on neighboring territories, density will have minimal effects once individuals are surrounded by neighbors. By contrast, in nonterritorial species that copulate away from nest sites, the frequency of EPC may increase directly with increasing density.

Third, breeding synchrony by females will confine opportunities for EPC to a short span of time early in the nesting cycle. Synchrony also forces males into making a reproductive effort tradeoff between mate guarding and the pursuit of EPC. Thus we expect synchronously breeding species and populations to have fewer EPC than those breeding asynchronously.

Fourth, the ability of males to guard their mates will affect the opportunities for EPC by other males, regardless of synchrony. Males may often be faced with choices between guarding their mate and defending a territory, pursuing polygyny or EPC, or foraging for themselves or for young. Visually occluded habitats also make mate guarding more difficult and less efficient at preventing EPC.

Fifth, the behavior of females will affect how easily males can capitalize on opportunities for EPC. Female behavior during EPC can be described in one of three ways: (1) females initiate and solicit EPC, (2) females resist attempted EPC, or (3) females accept attempted EPC (Table II). Solicitation by females will reduce the efforts attractive males must expend to obtain EPC, but may decrease the chances of EPC for other, less attractive, males. Resistance and passive acceptance generally will force males to seek out females. Such pursuit in turn results in tradeoffs between activity on the territory such as territorial defense and paternal care, and gaining EPC. Resistance by females will make gaining fertilizations harder for males than will passive acceptance.

Females may often benefit from participating in EPC. They may choose their social mate on the basis of factors such as the quality of his territory, the quality of anticipated paternal care, or previous breeding success with the partner or on the territory. If males and females return to nest sites where they were previously successful, mortality during the non-breeding season can decouple the best genetic mate from the best place to rear young. When this occurs, females may benefit by pairing with one male and copulating with another (Table I). However, interpreting female behavior during attempted EPC is complicated, because females might obtain the same benefit by behaving in several different ways. For example, females could gain good genes for their offspring by pursuing EPC with high-quality males or by resisting all attempted EPC, thereby testing potential genetic mates. Females also might achieve different ends through the same set of behaviors. For example, females might resist EPC either as an avoidance of the costs or as a ploy to test potential genetic mates (Table III).

We predict that female pursuit of EPC will be most likely when (1) female choice of breeding sites is uncoupled from their choice of the best genetic mate, (2) females gain genes for phenotypic traits that are attractive to females (as opposed to genes for general vigor) by mating with an extra-pair male, (3) females can assess the phenotypic and presumably genotypic quality of available extra-pair males (e.g., neighbors), and (4) males have few reproductive options other than the current breeding attempt and so cannot enforce female fidelity by withholding parental care, destroying eggs, or physically punishing the female (Table III).

Whereas few unequivocal cases of female solicitation of EPC have been observed, resistance is commonly seen. This may be because resistance is more visible to human observers than surreptitious solicitation. Resistance could be a mechanism to avoid the costs of EPC or might be a ploy to test potential genetic mates. Resistance seems most likely either when females choose social mates based on the male's phenotype (not the male's territory) and have obtained a high quality social mate, or when females choose mates by settling on territories containing resources and have no way to assess the genotypic quality of neighboring males. Finally, in certain cases females seem to simply accept EPC. This may occur either when females suffer some immediate, phenotypic cost by not cooperating, or when the costs and benefits of cooperating are a compromise between the costs and benefits of solicitation on the one hand and of resistance on the other (Table III).

These factors lead us to predict that EPC will be most common in territorial, migratory species living in visually occluded and relatively homogeneous habitats. EPC should be less frequent in synchronously breeding species in which females choose social mates directly and male parental care is critical for the survival of eggs and young.

Tests of specific hypotheses about the factors affecting EPCs can best be conducted either as experiments and observations within populations or comparisons between populations of the same species. Only in this way will the relevant ecological or social factor (e.g., distance from food, degree of synchrony, effectiveness of mate guarding) be isolated from other ecological and phylogenetic variables that might contribute to the frequency of EPC and thus confound interspecific comparisons.

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