HENPECKED MALES: THE GENERAL PATTERN IN MONOGAMY?[1]

BY SUSAN M. SMITH

Little attention has been given either to patterns of intrapair dominance relations or to their possible adaptive significance. In order to discuss this, one must first attempt to define "dominance." In spite of recent criticisms (e.g., Richards, 1974; Syme, 1974), the concept of social dominance, when carefully defined, continues to be useful. Wolf (1978) defined dominance in terms of the potential ability of an individual to control access to resources such as food or space. In most avian field studies, intrapair dominance data are obtained from supplanting attacks at resources such as food or perches (Woolfenden and Fitzpatrick, 1977; Smith, 1978). For birds in captivity, intersex dominance relations during the breeding season can be meaningful only when the captive birds have had the time and opportunity to form stable pairbonds. For this paper, a dominant is any bird (in the field or in captivity under these conditions) that can forbid access by a second to resources such as food or perches.

Most recent rewiews on social behavior (e.g., Wilson, 1975) claim that year-round male dominance is the general pattern for all vertebrates, regardless of whether they are polygamous or monogamous. (Monogamy may be far more common in vertebrates than is generally realized: besides occurring in more than 90% of bird species studied [Lack, 1968], it is found in at least 9 mammalian orders [Kleiman, 1977], as well as in certain fish [Breder and Rosen, 1966] and reptiles [Kleiman, 1977].) This assumption of year-round male dominance has probably been fostered by two factors in particular. First, in most land vertebrates males outweigh females. Although weight differences of 10% or more probably do reflect dominance (e.g., Brenner et al., 1978), slight differences in weight are not correlated with rank in many birds (Smith, 1976, and included references) or mammals (Ralls, 1976); moreover, in higher vertebrates, monogamous species rarely have large intersex weight differences.

A second, and likely more important factor is that most studies on social dominance have been done with nonbreeding animal groups. Data are more easily obtained during winter food shortages, and flocks may often be more easily studied than breeding pairs. Males in winter clearly dominate females in many birds and mammals, and at first glance there seems no reason to suppose that this would change at other times of year. Yet Hinde (1952) showed that male Great Tits (*Parus major*) are dominant all winter but females become dominant over their mates at the onset of breeding; here data on nonbreeding birds give no indication of intrapair dominance patterns during the breeding season. Similar

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[1] This paper is dedicated with thanks to Margaret Morse Nice.

dominance reversal is now known in many mammals as well (Ralls, 1976).

Females are, in fact, dominant over their mates during the breeding season in a wide variety of monogamous vetebrates. This has been ignored in recent reviews on social behavior, even though the assumption of breeding male dominance as a general phenomenon was challenged as early as 1949 by Nice (1949). The present article explores the adaptive significance of breeding-female dominance in birds, and attempts to explain why it is so strongly correlated with monogamy.

THE PHENOMENON

Table 1 lists 37 monogamous species from 18 families in which females are known to dominate their mates in the breeding season. Only clear-cut examples of dominance appear in Table 1; reports of species having "loss of male dominance" in the early breeding season, e.g., Steller's Jay (*Cyanocitta stelleri*) (Brown, 1963) and Indian Myna (*Acridotheres tristis*) (Counsilman, 1977) have not been included. Although it is sometimes difficult to interpret the reports of others, most, if not all, of the field studies listed in Table 1 indicate that the female is dominant throughout the nesting territory, i.e., female dominance is not restricted to the vicinity of the nest. Approximately two-thirds of the species in Table 1 have dominance reversal twice yearly.

A few of the species in Table 1 have pronounced size dimorphism: in each case the female is markedly heavier than the male. Few, if any, monogamous species exist wherein males significantly outweigh females, but so-called "reverse" dimorphism, with females weighing up to 20% more than males, is the rule in most monogamous predatory birds, the size difference being greatest in species taking the largest prey (Amadon, 1975; Earhart and Johnson, 1970; Reynolds, 1972). In addition to the booby, hawk, and falcons mentioned in Table 1, females weigh 10% more than males in many species of frigatebirds (Fregatidae), skuas and jaegers (Stercorariidae), and both owl families (Tytonidae and Strigidae) (Amadon, 1975). With such marked weight differences, females almost certainly dominate their mates in these four families as well; indeed, most attempts to explain "reverse" dimorphism are based on breeding-female dominance (Cade, 1960; Amadon, 1975). Thus strong evidence exists for breeding-female dominance for more than 40 species of more than 20 families of birds.

Lending weight to this figure is the fact that published reports of intrapair dominance relations are surprisingly scarce. Many monogamous species have little or no plumage dimorphism, making individual marking necessary to get dominance data, yet even studies on color-marked birds often fail to mention intrapair dominance. In some species, aggressive interactions are apparently far rarer in the breeding season than at other times of year (Brown, 1963), but in fact the subject itself is seldom stressed, and even those careful observers who do have relevant data often simply report them in passing (e.g., Davies, 1977).

TABLE 1.

Monogamous birds with breeding-female dominance.

Species	Family	Data[1]	Reversal	Reference
Sula leucogaster	Sulidae	F	no	Simmons, 1970
Accipiter striatus	Accipitridae	F	no	Reynolds, 1972
Falco rusticolus	Falconidae	F	no	Cade, 1960
F. peregrinus	Falconidae	F	no	Cade, 1960
Picoides pubescens	Picidae	F	yes	Kilham, 1974
Dendrocincla fuliginosa	Dendrocolaptidae	F	no	Willis, 1972
Gymnopithys bicolor	Formicariidae	F	yes	Willis, 1967
Garrulus glandarius	Corvidae	L	yes	Goodwind, 1951
Parus major	Paridae	F + L	yes	Hinde, 1952
Sitta carolinensis	Sittidae	F + L	yes	Kilham, 1971
S. canadensis	Sittidae	L	yes	Kilham, 1975
Sialia sialis	Turdidae	F	yes	Krieg, 1971
Muscicapa striata	Muscicapidae	F	?	Davies, 1977
Lanius ludovicianus	Laniidae	F	?	Miller, 1931b
Vireo solitarius	Vireonidae	F	?	James, 1978
V. flavifrons	Vireonidae	F	?	James, 1978
Setophaga ruticilla	Parulidae	F	yes	Ficken, 1963
Icterus galbula	Icteridae	F	yes	Miller, 1931a
Emberiza calandra	Emberizidae	F	yes	Andrew, 1957
E. citrinella	Emberizidae	F + L	yes	Andrew, 1957
E. schoeniclus	Emberizidae	F + L	yes	Andrew, 1957
Melospiza melodia	Emberizidae	F	yes	Nice, 1943
Zonotrichia capensis	Emberizidae	F	no	Smith, 1978
Carduelis carduelis	Carduelidae	F + L	yes	Hinde, 1956
C. tristis	Carduelidae	F	yes	Coutlee, 1967
C. lawrencei	Carduelidae	F	yes	Linsdale, 1957
C. psaltria	Carduelidae	F	yes	Linsdale, 1957
Acanthis flammea	Carduelidae	L	yes	Dilger, 1960
Carpodacus purpureus	Carduelidae	F + L	no	Thompson, 1960
C. cassinii	Carduelidae	F + L	no	Samson, 1977
C. mexicanus	Carduelidae	F + L	no	Thompson, 1960
Loxia curvirostra	Carduelidae	F + L	yes	Tordoff, 1954
Pyrrhula pyrrhula	Carduelidae	F + L	yes	Hinde, 1956
Chloris chloris	Carduelidae	F + L	yes	Hinde, 1956
Coccothraustes coccothraustes	Carduelidae	F + L	yes	Hinde, 1956
Fringilla montifringilla	Fringillidae	F + L	yes	Hinde, 1956
F. coelebs	Fringillidae	F + L	yes	Marler, 1956

[1] F = field data; L = data from captive birds.

In marked contrast to the numbers in Table 1, an extensive search of the literature has produced only two reports of monogamous birds with breeding-male dominance (see below). When more researchers look actively for data on intrapair dominance patterns during the breeding season, I believe that breeding-female dominance will be established as the general pattern in monogamous birds.

ADAPTIVE SIGNIFICANCE OF BREEDING-FEMALE DOMINANCE

For females, the early breeding season is a critical period in their annual cycle. Here their parental investment greatly exceeds that of the males (Trivers, 1972) because they must bear the energetic costs of producing eggs; these costs are often enormous (Perrins, 1970; Emlen and Oring, 1977). If dominance permits a female to obtain more food during this critical period, it could give her a clear selective advantage over more subordinate females. For males, the situation in the early breeding season is different. In order that the eggs he has fertilized be of high quality, a male should do everything possible to maintain his mate in top condition while she is producing them; this is particularly true for the strictly monogamous male whose eggs will literally be all in one basket. It is thus better for both sexes if the female has preferential access to resources such as food at this time; the male that defers to his mate here is actually investing energy indirectly in his own offspring. If those males that defer to their mates at this time have higher reproductive success than those that do not, breeding female dominance will be selected for. It is thus not surprising that females tend to attain their highest rank, if only briefly, at this time of high parental investment—e.g., the report of Crook and Butterfield (1970:238) on the ploceid *Quelea quelea*: "The males' dominance over the female is maintained throughout the year, except possibly during the short period when females occupy nests for laying and early brooding."

WHY REVERSAL?

With such strong selective pressure for breeding-female dominance, why change it in the nonbreeding season? Establishing new dominance relations is costly in time and energy, and even the winner is liable to injury in a fight; nevertheless about two-thirds of the species in Table 1 do show reversal. One possible reason why so many monogamous birds go through dominance reversal twice yearly is the extreme importance to males of obtaining a breeding territory. Males with highest winter rank have been shown to get the best quality breeding territories in many species, while low-ranking males often fail to get any territory at all (Smith, 1976; Verner, 1977). Since males probably outnumber females in most monogamous species (Ward, 1965), only males with the best territories are ensured of getting mates. Low winter rank to a female will have little direct bearing on her reproductive success the following breeding season, but to a male may prevent him from breeding at all. In the breeding season the reverse is true: the advantages of dominance to a female are greater than the disadvantages of subordination to the male, hence reversal twice yearly. This general pattern is shown in Fig. 1.

OTHER PATTERNS

Besides this general avian pattern three other possible combinations exist: breeding-male dominance with reversal to nonbreeding-female

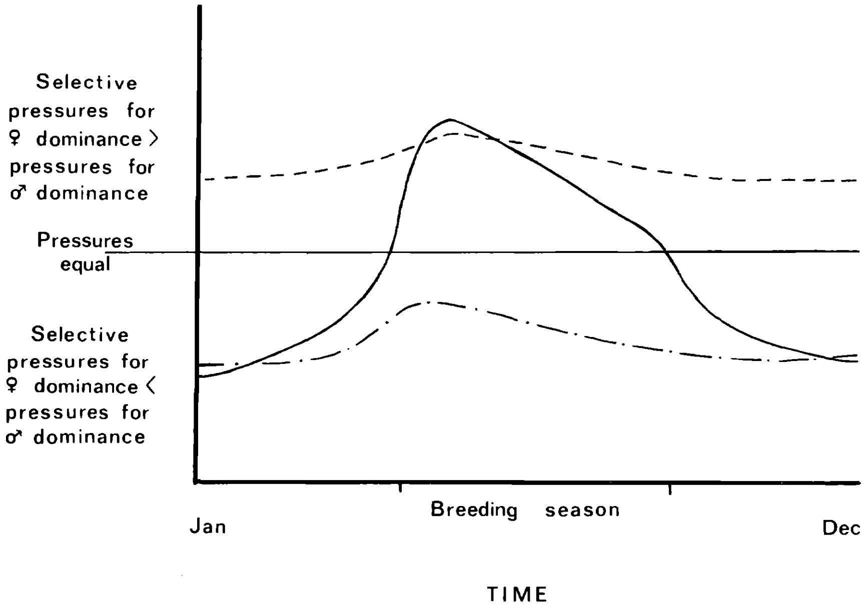

FIGURE 1. Patterns of intrapair dominance as a function of relative selective pressures exerted on the two sexes. The typical patterns in monogamy are breeding-female dominance with reversal to nonbreeding-male dominance (solid line), and less commonly year-round female dominance (dashed line). Year-round male dominance (dots and dashes) is very rare in monogamy, but is the most common pattern for polygynous species.

dominance; females dominant all year; and males dominant all year. Not surprisingly, no example of the first has been recorded for any higher vertebrate. Reports of each of the other two dominance patterns are known in monogamous species.

Theoretically, year-round female dominance can evolve in monogamous species wherever selection pressures for high prebreeding-male rank are lowered while pressures for breeding-female dominance are maintained (Fig. 1). This apparently occurs in the Plain-brown Woodcreeper, and in House, Cassin's, and Purple finches (Table 1). In each case the role of male territoriality in breeding has been reduced, and consequently the importance to males of high prebreeding rank is lessened. In Plain-brown Woodcreepers, breeding occurs in the female's territory which she occupies all year (Willis, 1972). The other three species are loosely colonial, their territories including a small area around the nest but usually not a foraging area. Moreover, the females may actually take the more active role in territorial defence (Thompson, 1960). In such species, behavioral modifications that maintain female dominance all year would be adaptive since individuals with such behavior would twice yearly save the energy and avoid the danger involved in dominance reversal.

Year-round female dominance also occurs in a Costa Rican population of the Rufous-collared Sparrow (Smith, 1978). However, this population has year-round breeding and thus no nonbreeding season is available for reversal. I would predict that more seasonal populations of this species would probably show clear-cut dominance reversal.

The opposite pattern, year-round male dominance, is, in fact, rare in monogamous species. Recently Roëll (1978) stated that Jackdaws (*Corvus monedula*) have year-round male dominance, but this was apparently based on data taken from December to March, and the first eggs were not laid until the second half of April. Since the period of egg production is the time when males are most likely to defer to their mates, data from this critical period are necessary to confirm breeding-male dominance in this species. In contrast to Roëll's conclusions, Lorenz (1931) found no intrapair rank differences in his Jackdaw breeding colony. Theoretically, year-round male dominance could evolve where selection pressures for breeding-female dominance are lowered while those for prebreeding-male dominance are maintained or increased (Fig. 1). These conditions may occasionally be met in species that have helpers at the nest, such as the Florida Scrub Jay (*Aphelocoma c. coerulescens*) (Woolfenden and Fitzpatrick, 1977). Here a typical breeding territory has a breeding pair and several other, usually younger, individuals or "helpers" that share in nest building, incubation, and feeding the young. Such a system evolves primarily where there is a severe, predictable shortage of a resource necessary for breeding, such as suitable nesting territories (Gaston, 1978). Under such circumstances, selection for male dominance at any time of year is greatly intensified. By contrast, the helpers reduce the female's reproductive energy drain, thus perhaps lowering selective pressures for breeding-female dominance.

The Scrub Jay is particularly interesting because Florida birds have helpers whereas California birds do not. This contrast in their social systems may be reflected in their intrapair dominance patterns: Florida birds have year-round male dominance (Woolfenden and Fitzpatrick, 1977), whereas captive male Scrub Jays from California lose their dominance over females in the early breeding season (Brown, 1963). Nevertheless, Woolfenden and Fitzpatrick's claim of year-round dominance is as yet unconfirmed, since they do not present data for the period of egg production. Their data, taken from June through August, were gathered after nesting had ended in their population.

WHY MONOGAMY?

A few scattered reports exist for breeding female dominance in species with polygynous or promiscuous breeding systems. Collias and Collias (1970) found that males of the polygynous African Village Weaverbird (*Ploceus cucullatus*) are subordinate to any of their mates any-where in the breeding territory, even though males of this species dominate females in the nonbreeding season. Recently Willis et al. (1978) suggested that breeding females of *Pipromorpha macconnelli,* a South American tyrannid, may drive males away from the breeding territory, and thus actually cause male promiscuity.

Nevertheless, breeding-female dominance is most strongly correlated with monogamy. Yet egg production is just as costly for females in other mating systems, and male deferral at this critical period would very likely gain them the same benefits in terms of increased egg and/or offspring quality, regardless of the mating system. What, therefore, prevents so many species of other mating systems from showing breeding-female dominance? The answer probably lies in the increased sexual selection experienced by polygynous and promiscuous males, which usually results in males being much heavier than females (Alexander, 1974; Emlen and Oring, 1977). A larger, dominant male may indeed average fewer successful eggs per clutch than a subordinate male would, but if he is consistently chosen by more females, he will still produce more total offspring. For polygynous and promiscuous males, then, the advantages of dominance outweigh the advantages of deferral, and year-round male dominance will be selected for.

All the available data thus suggest that breeding-female dominance is widespread in monogamous birds. Moreover, if selection for male deferral is based on increased egg and/or offspring quality, breeding-female dominance may be common in monogamous species of other animal groups as well. More early breeding season field data from a variety of monogamous species are necessary to see just how general this pattern really is.

SUMMARY

Contrary to statements in many recent reviews on social behavior, breeding-female dominance is widespread in monogamous birds. Intersex dominance patterns are approached by considering the relative selective pressures for dominance on each sex at various times of year. The female must bear an enormous energy burden early in the breeding season; during egg production, only the female can contribute energy directly to the offspring. If males that contribute indirectly to egg quality by deferring to their mates at this time have consistently higher reproductive success than those that do not, then breeding-female dominance will be selected for. In many species the situation changes in the nonbreeding season: here there is no longer any advantage to the male to defer to his mate, and nonbreeding males often dominate females. Breeding-female dominance should be expected wherever male deferral leads via increased egg quality to higher overall reproductive success; this is most likely to occur in monogamous species.

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