

HELPER EFFECTS ON VARIANCE COMPONENTS OF FITNESS IN THE COOPERATIVELY BREEDING RED-COCKADED WOODPECKER

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ABSTRACT.—Studies of how avian helpers influence reproduction have concentrated on mean effects. We examined the effects helpers have on variance in reproductive success and breeder survival in the Red-cockaded Woodpecker (*Picoides borealis*). Variance in reproduction and survival are components of fitness, and increased variance results in decreased fitness. We found that helpers did not affect variance in breeder survival, but variance in reproductive success was affected by helpers at nests that produced young. When we exclude groups in which breeding failed or was not attempted, reproductive success is more variable among groups with one helper than among groups with no helpers or groups with two helpers, regardless of the age of the female breeder. A survey of the literature showed no clear pattern in other cooperative breeders, although the presence of helpers often was associated with higher variances. Like helper effects on mean reproductive success, helper effects on variance in reproductive success might be confounded by effects of habitat quality. Received 24 April 1995, accepted 6 September 1995.

HELPING BEHAVIOR in cooperatively breeding birds has been studied extensively for the past 20 years (Brown 1978, 1987; Emlen and Vehrencamp 1983; Emlen 1991). A major issue is the extent to which helpers derive indirect fitness benefits by improving reproduction of breeders, which generally are their relatives (Brown and Brown 1981; Emlen 1982; Brown 1985; Emlen and Wrege 1988, 1989; Ligon and Stacey 1989). The presence of helpers is not associated with increased reproductive output in some species (e.g. Vehrencamp 1978, Craig 1979, Birkhead 1981, Bednarz 1987). However, in most species, groups with helpers produce more young on average than groups without helpers (e.g. Stacey and Koenig 1990, Emlen 1991). Helper effects might be confounded with effects of territory quality and breeder age (Brown and Brown 1981, Brown 1987, Koenig and Mumme 1987). A helper effect independent of territory-quality and breeder-age effects rarely has been demonstrated either observationally

(Woolfenden and Fitzpatrick 1984, Austad and Rabenold 1985) or experimentally (Brown et al. 1982; but see Koenig and Mumme 1987:162). A less-explored possibility is that the presence of helpers increases breeder survival (Reyer 1984, Woolfenden and Fitzpatrick 1984, Austad and Rabenold 1986, Koenig and Mumme 1987, Curry 1988).

One common theme among all studies of effects of helpers on breeder fitness is that only mean effects have been considered. Gillespie (1977) introduced the idea that variance in reproductive success reduces the fitness of a genotype below that of another genotype that has the same mean reproductive success but less variance. This effect is depicted in Figure 1, where fitness, defined as contribution of offspring to subsequent generations, is plotted as a function of reproductive success. Other life-history parameters, such as survival, might be substituted for reproductive success. Gillespie (1977) showed that this function is convex (i.e. there is a greater increase in fitness by having one young rather than none, when compared with having 20 young rather than 19; Fig. 1). A population in which individuals always have exactly X young will have a corresponding fitness $f(X)$ (Fig. 1). If, in a second population, the same mean number of young is produced, but one-half of the individuals produce $X - \delta$ young and one-half produce $X + \delta$ young, the

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population will have an average fitness that is lower than that of the first population:

$$\frac{[f(X + \delta) + f(X - \delta)]}{2} < f(X) \quad (1)$$

This results from the asymmetric effect of variance on fitness (an individual with $X - \delta$ young has a disproportionately greater decrease in fitness than the increase in fitness of an individual with $X + \delta$ young; Gillespie 1977). This "variance discounting" has been applied extensively in foraging theory (Oster and Wilson 1978; Caraco 1980; Real 1980a, b; Real and Caraco 1986), and also has been applied to mating strategies (Powell 1989).

Lacey et al. (1983) applied this concept to life-history evolution and found the variance to be an important component of fitness that was independent of the mean. Therefore, fitness based on reproductive success is better measured by the mean reproductive output minus some function of its variance (Gillespie 1977, Lacey et al. 1983). If helpers can decrease variance in reproductive success (or survival) of breeders, they will increase breeder fitness. If breeders are related to helpers, the inclusive fitness of helpers also is increased. Therefore, it is worthwhile to consider how helpers influence variance components of fitness. Our objective here is to report on the effects of helpers on the variability in reproductive success and breeder survival of Red-cockaded Woodpeckers (*Picoides borealis*).

STUDY SPECIES AND METHODS

Once distributed almost continuously across the southeastern United States, the Red-cockaded Woodpecker now exists in relatively small, isolated populations (Jackson 1971) and has been on the Federal Endangered Species List since 1970 (Federal Register 35:16047, 1970). This species lives in year-round territories, preferring mature open pine forests (U.S. Fish and Wildlife Service 1985, Walters 1990). The Red-cockaded Woodpecker lives in family groups consisting of a breeding pair and zero to four nonbreeding helpers, most of which are males (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988). Information on natural history of the species can be found in Thompson (1971), Wood (1983), Walters (1990), and Kulhavy et al. (1995).

Red-cockaded Woodpecker helpers engage in a wide variety of activities that have the potential to influence fitness of breeders. Helpers incubate eggs (Lay et al. 1971, Lennartz and Harlow 1979), brood nest-

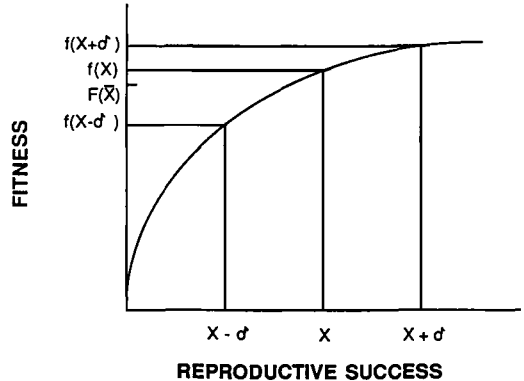


FIG. 1. Fitness as function of reproductive success. With increased reproductive success, fitness increases at decreasing rate. In a population where all individuals produce same number of young, fitness is higher $f(X)$ than average fitness in second population ($F[\bar{x}]$) with same mean reproductive success, but in which one-half of individuals produce $X + \delta$ young and one-half produce $X - \delta$ young.

lings (Ligon 1970, Lennartz and Harlow 1979), feed nestlings (Ligon 1970, Baker 1971, Lennartz and Harlow 1979), and feed fledglings (Ligon 1970). They also assist in territory defense and cavity construction (Ligon 1970). The effects of these activities on breeder fitness are unclear. Ligon (1970) and Lennartz and Harlow (1979) found that the presence of helpers was associated with increased reproductive output, but small sample sizes prevented conclusive results. Lennartz et al. (1987) and Walters (1990) found a significant correlation between the presence of helpers and reproductive success. However, territory quality is confounded with helper presence (Lennartz et al. 1987). Moreover, the effects of breeder age, which can be large in this species (Walters 1990), were not considered. A recent analysis indicates that controlling for territory quality reduces the increase in reproductive success in the presence of helpers by about half, to 0.39 fledglings per helper per year (Heppell et al. 1994). This analysis may still be confounded by effects of breeder age. Effects of helpers on breeder survival have not been determined for this species.

Our study area encompassed more than 110,000 ha in the Sandhills of south-central North Carolina. About 1,100 Red-cockaded Woodpeckers occur in the Sandhills, making it one of the largest extant populations of this species (U.S. Fish and Wildlife Service 1985). Over one-half of the population is included within our study area. The habitat is primarily second-growth pine, with scattered old-growth pines and varying amounts of deciduous hardwood understory and mid-story. Details of the study sites and data collection are in Walters et al. (1988).

Data were collected from 1980 through 1987. Censuses were conducted annually during the breeding

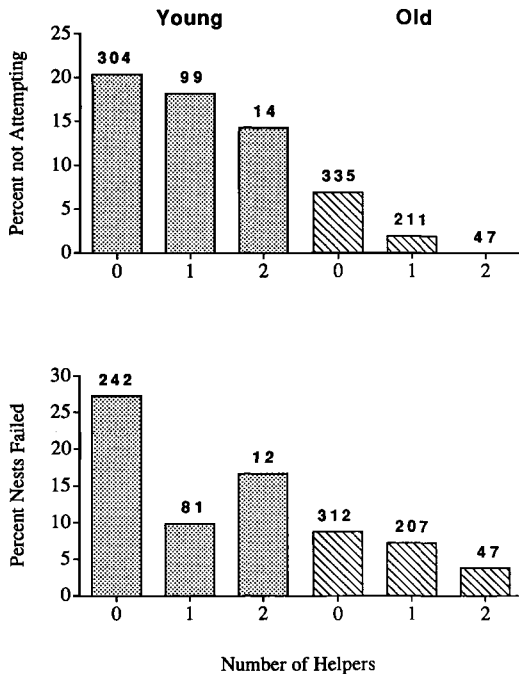


FIG. 2. Percent of times in which breeders failed to nest (upper) and percent of nests that failed (lower) as function of number of helpers for old and young breeding females. Numbers of groups indicated above bars.

season to identify all members of each Red-cockaded Woodpecker group on our study sites. Each individual was marked with a unique combination of an aluminum leg band (U.S. Fish and Wildlife Service) and three or four plastic, colored leg bands. Reproduction was monitored by visiting the cavity trees of each group every 9 to 14 days during the breeding season. Nestlings were banded and fledglings identified by following groups after the projected fledging date. We used the number of fledglings as our measure of reproductive success. Breeder survival was measured from one breeding season to the next.

We looked for an association between the number of helpers and variance in reproductive success. Because groups with more than two helpers were rare, we confined our analyses to groups with zero, one, or two helpers. We first analyzed data with all years and breeder ages combined, dividing groups according to the number of helpers present. Because there is a correlation between breeder age and reproductive success (Walters 1990), we also divided the data into two groups based on the age of the female breeder: (1) one or two years old; and (2) more than two years old. Individuals of unknown age were omitted from these analyses.

To assess variability, we used analysis of variance (ANOVA) on suitably transformed data (O'Brien 1981). We concluded that use of the coefficient of variation

was inappropriate for these data (Simpson et al. 1960). The values we used were the absolute deviations from the median, rather than deviations from the mean, because the former produce asymptotically distribution-free and robust tests (O'Brien 1981). We examined variation in reproductive success among three sets of breeders. First, we examined all breeders, including those for which we did not record a nesting attempt. Any group containing at least one adult male and one adult female was considered a breeding group, and the dominant member of each sex was the breeder. Second, we examined only those groups that attempted to nest. Third, we evaluated only those groups that nested successfully (i.e. produced at least one fledgling).

Within each sex, mortality of breeders appears to be independent of age, except that those few males that breed at age 1 have an increased chance of not surviving (Walters 1990). Therefore, to test for effects of helpers on variability in breeder survival, we combined all age classes for a given sex and calculated the annual survival of breeders both with and without helpers. We compared the variance in survival across years between these two groups using a Levene test (Miller 1986).

RESULTS

Fledgling production.—Groups without helpers were more likely to fail to attempt to breed (14.8%) than groups with one (6.1%) or two (4.5%) helpers ($\chi^2 = 26.2$, $df = 2$, $P < 0.001$). Younger birds were much less likely to nest than older ones (Fig. 2). Within each age class, groups with more helpers were more likely to nest, but this trend was significant only among older birds (old females, $\chi^2 = 10.3$, $df = 2$, $P < 0.01$; young females, $\chi^2 = 0.6$, $df = 2$, $P = 0.7$). Among those groups that nested, nests of groups with no helpers were more likely to fail (21.3%) than those of groups with one (11.5%) or two (6.0%) helpers ($\chi^2 = 25.1$, $df = 2$, $P < 0.001$). Older birds had a lower probability of nest failure than young birds (Fig. 2). The presence of helpers was associated with a reduction in this probability for young females ($\chi^2 = 10.7$, $df = 2$, $P = 0.005$) but not for old females ($\chi^2 = 2.8$, $df = 2$, $P > 0.2$; Fig. 2). Among groups that reproduced successfully, there was a trend for the number of young fledged to increase with number of helpers if the breeding female was old, but not if she was young.

Despite helper effects that reduced the likelihood of producing no young, helpers had no effect on variation in reproductive success among all groups ($P = 0.28$; Fig. 3), or among groups that nested ($P = 0.46$; Fig. 4). Among

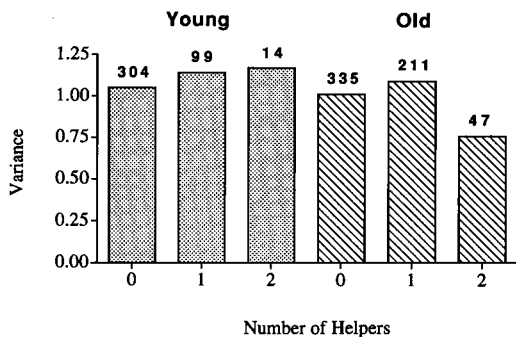


FIG. 3. Variance in reproductive success for groups with 0, 1 and 2 helpers, for old (>2 years old) and young females. Numbers of groups indicated above bars.

groups that nested successfully, helpers affected variation in reproductive success ($P = 0.002$), but in a non-linear fashion. Groups with one helper were more variable than groups with no helpers or groups with two helpers (Fig. 4).

Annual survival.—Annual survival for breeding females averaged 0.684 (variance = 0.675) for those without helpers and 0.658 (variance = 0.225) for those with helpers. Mean annual survival for males was 0.740 (variance = 0.734) without helpers and 0.692 (variance = 0.644) with helpers. Although variances were lower when helpers were present, the difference was not significant for females ($P > 0.14$) or males ($P > 0.8$).

DISCUSSION

Our results indicate that although helpers increase the probability of producing young, their presence is not associated with reduced variability in reproductive success. We conclude that helpers contribute to breeder fitness primarily through effects on mean reproductive success, and that any variance effects are small compared with mean effects.

The age of the male breeder, as well as that of the female breeder, is correlated with reproductive success in Red-cockaded Woodpeckers (Walters 1990); reproductive success is more variable, as well as lower, at younger ages in both sexes. We included only female age in the analyses presented here because it is difficult to assess effects of both male age and female age simultaneously. When we analyzed data for male breeders only, the patterns were unaffected.

We examined the literature for evidence of a

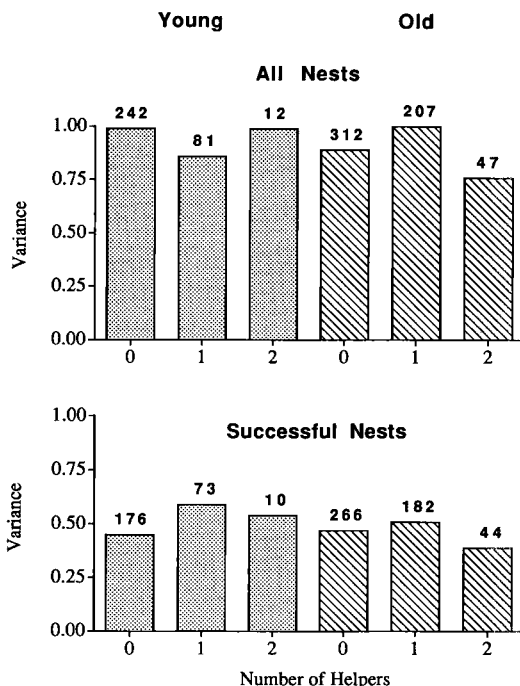


FIG. 4. Variance in reproductive success for old (>2 years old) and young (≤2 years old) breeders among all nesting groups (upper), and among groups that nested successfully (lower), for groups with 0, 1, and 2 helpers. Numbers of groups indicated above bars.

relationship between helpers and variance in reproductive success for other singularly breeding, cooperative birds. *A priori*, we did not expect helpers to affect variance in reproductive success in all cooperatively breeding systems. We found adequate data for eight species (Table 1). For the Pied Kingfisher (*Ceryle rudis*), the presence of a single helper was associated with less variance than the presence of no helpers in two different years. With the addition of another (unrelated) helper, variance was higher. Among species for which data from groups with and without helpers were available for a single year only, helpers were associated with higher variance in two cases and lower variance in three. In Harris' Hawk (*Parabuteo unicinctus*), helpers were associated with higher variance in two years and lower variance in one. Only for the Florida Scrub-Jay (*Aphelocoma coerulescens*) were there sufficient data for statistical testing. In this species, there was a tendency for helpers to be associated with increased variance in reproductive success (Wilcoxon signed-ranks test, $T = 44$, $n = 10$, $P = 0.053$).

TABLE 1. Examples of the relationship between the presence of helpers and variance in fledgling production in other singularly breeding, cooperative species (number of nests in parentheses). Multiple lines under a species present data from different years.

Species	No. of helpers					
	None	1	2	3	4	5
Harris' Hawk (<i>Parabuteo unicinctus</i>) ^a	0.91 (7)	1.69 (8)				
	0.58 (6)	3.24 (12)				
	1.44 (16)	1.09 (10)				
Hoatzin (<i>Opisthocomus hoazin</i>) ^b	0.11 (?)	0.15 (?)	0.33 (?)	0.29 (?)	0.38 (?) ^c	
Pied Kingfisher (<i>Ceryle rudis</i>) ^d	0.36 (14)	0.25 (12)	1.00 (6)			
	0.81 (9)	0.25 (4)				
Green Woodhoopoe (<i>Phoeniculus purpureus</i>) ^e	0.39 (17)	0.32 (33)	0.32 (35)	0.35 (32)	0.39 (25)	0.50 (14)
Dunnoch (<i>Prunella modularis</i>) ^f	3.76 (5)	2.92 (4)				
Splendid Fairy-Wren (<i>Malurus splendens</i>) ^g	2.07 (81)	1.48 (64)	2.07 (55)	2.00 (28)	2.41 (12)	
White-browed Sparrow-Weaver (<i>Plocepasser mahali</i>) ^h	0.82 (11)	0.28 (7)				
Florida Scrub-Jay (<i>Aphelocoma coerulescens</i>) ⁱ	1.23 (7)	1.99 (18)				
	1.99 (4)	0.72 (13)	1.96 (15)			
	2.25 (14)	2.07 (12)	2.07 (12)			
	1.61 (13)	2.56 (15)				
	1.44 (16)	2.99 (11)				
	1.49 (11)	2.25 (19)				
	1.46 (13)	1.42 (13)				
	2.46 (14)	2.96 (18)				
	2.07 (12)	3.35 (24)				

^a Faaborg and Bednarz (1990); ^b Strahl and Schmitz (1990); ^c ≥ 4 helpers; ^d Reyer (1980); ^e Ligon and Ligon (1990); ^f Birkhead (1981); ^g Birkhead and Russell (1990); ^h Lewis (1981); ⁱ Woolfenden and Fitzpatrick (1984).

More comprehensive analyses of data from other species are needed to determine whether effects of helpers on the variance in reproductive success are widespread among cooperative breeders. Results of our initial examination are equivocal, although they suggest that helpers may actually increase variance in reproductive success (thereby countering mean effects by reducing breeder fitness) in some species. This could occur if helpers promote the fledging of unusually large broods. Effects of helpers on variability in reproduction are likely to differ among species in magnitude and direction, because the degree to and manner in which helpers influence reproduction varies widely among cooperative breeders.

For the Red-cockaded Woodpecker data, we could control for effects of breeder age but not for those of territory quality. Thus, with respect to variance effects, our results are subject to the same confounding influence of a relationship between territory quality and presence of helpers found in analyses of mean effects (see above). We doubt that this was a major factor in our analyses because when we examined only breeding pairs that had helpers in some years but not in others (i.e. the sets of territories in help and no-help groups were identical), the patterns in the data did not differ noticeably from those observed in the complete data set. Still, effects of territory quality and helpers on variance in reproductive success need to be examined concurrently using sufficiently large data sets, in Red-cockaded Woodpeckers and in other species. Variance effects due to territory quality are, of course, of interest in their own right, as this dimension of territory quality has not been addressed previously. Territory quality is thought to be a key factor in group formation in Red-cockaded Woodpeckers and other cooperative species (Stacey and Ligon 1987, 1991; Emlen 1991; Walters et al. 1992). We suggest that reduced variance in reproductive output might be another factor (in addition to increased survival and reproductive success) that favors life-history strategies that increase the chance of acquiring a high-quality territory.

Fry (1972) and Parry (1973) suggested that a consequence of the presence of helpers is that populations could be buffered against breeder mortality by acting as replacements for breeders, thus keeping the number of breeders at a relatively constant level from year to year. This buffering is an artifact of the breeding system

rather than an adaptation. For example, Woolfenden and Fitzpatrick (1984) witnessed an epidemic in a Florida Scrub-Jay population that resulted in the death of 45% of the breeding birds and 92 of 93 fledglings produced that year. Two years later, the number of breeding birds was similar to that before the epidemic because helpers replaced the dead breeders. Helpers might buffer groups in another way. The more a population, or a group, fluctuates in size, the greater its chances of extirpation (Diamond 1985, Pimm et al. 1988; but see Schoener and Spiller 1992, Tracy and George 1992). In Stripe-backed Wrens (*Campylorhynchus nuchalis*) and Florida Scrub-Jays, as well as Red-cockaded Woodpeckers, the presence of helpers decreases the probability of a family group leaving no young at all (Rabenold 1984, Woolfenden and Fitzpatrick 1984). This conceivably could increase the probability of family group survival and lineage survival, because offspring inherit territories (Woolfenden and Fitzpatrick 1978).

Helpers, therefore, might affect evolution in ways not previously realized. They might affect a breeder's fitness by stabilizing (or destabilizing) reproductive success and also could affect family group and lineage survival. These concepts of variance components of fitness can be applied readily to existing data sets for cooperative breeders, and we encourage their use.

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