

ANNUAL REPRODUCTIVE YIELD IN THE COOPERATIVE PYGMY NUTHATCH (*SITTA PYGMAEA*)

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ABSTRACT.—We studied cooperative-breeding Pygmy Nuthatches (*Sitta pygmaea*) for 4 yr in northern Arizona. Breeding units contained 2–5 birds. Helpers were found at about 30% of all nests. All helpers that later bred on the study area were male. Helpers were mostly yearlings, and offspring or siblings of the birds that they aided, but often aided at least one unrelated breeder. Breeding units with helpers produced significantly more young than those without helpers. Breeding units in habitats with the greatest floral diversity and structural maturity fledged significantly more young than those in other habitats. Habitat did not influence the effect of helpers. Year effects increased the strength of the relationship between helpers and annual reproductive output. Previous breeding experience and pair-bond duration were not related to reproductive success. Total brood loss, although rare, was responsible for the difference in reproductive output among pairs with and without helpers and between habitats.

Breeding birds with helpers benefit by an increase in direct fitness. The advantage to the helpers is not clear but may be an increase in indirect fitness associated with aiding relatives. Helpers may benefit directly, however, by sharing roosting cavities on a group territory thereby enhancing overwinter survival. Received 26 September 1986, accepted 15 September 1987.

COOPERATIVE-BREEDING Pygmy Nuthatches (*Sitta pygmaea*) were first documented in central California. Helper Pygmy Nuthatches aid the breeding birds by feeding the incubating female, feeding the nestlings and fledglings, and defending the nesting territory and cavity (Norris 1958, Sydeman 1985). Norris (1958: 177) attributed the presence of nonbreeders to a biased sex ratio in favor of males. Unlike most cooperative birds (Fry 1972, Brown 1978), Pygmy Nuthatches inhabit cold-temperate environments. Pygmy Nuthatches are social throughout the year. Winter groups average 5–15 birds (Norris 1958, Sydeman 1985, Güntert in press), but larger assemblages have been recorded (Knorr 1957, Sydeman and Güntert, 1983). Winter groups forage as a flock and roost communally in tree cavities located within a group territory. Individual membership in winter groups is consistent within and between years (unpubl. data). Group size may be limited by the size and thermodynamics of roosting

cavities. Communal roosting is a means of reducing nightly energy expenditure by sleeping in cavities, huddling, and hypothermia (Hay 1983, Güntert in press).

Avian cooperative breeding is a model vertebrate system for testing hypotheses relating inclusive fitness (Hamilton 1964, Brown and Brown 1981) to the evolution of helping behavior. Understanding the adaptive significance and selective pressures leading to cooperation, such as helping at the nest in birds, requires examination of the costs and benefits of this behavior to the recipient breeders and donor helpers. Studies on the demography of birds that breed with and without helpers are a crucial step to understanding the benefits of avian cooperation.

We examined several hypotheses regarding variation in annual reproductive yield and inclusive fitness. Inclusive fitness has two components: direct and indirect fitness (Brown and Brown 1981). Breeders with helpers that raise more young than breeders without helpers benefit by an increase in direct fitness. The potential cost of allowing competitors on a territory may then be reduced. Helpers may benefit indirectly if they enhance the reproductive success of relatives (Rowley 1965, 1981; Parry 1973; Stacey 1979; Brown and Brown 1981; Emlen 1981;

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Koenig 1981; Woolfenden 1981; Kinnaird and Grant 1982; Rabenold 1984; Austad and Rabenold 1985; Hunter 1985). However, reproductive enhancement has not been observed consistently (Gaston 1973, Zahavi 1974, Vehrencamp 1978, Craig 1980, Ligon 1981), helpers have been unrelated to the breeders (Reyer 1980, 1984; Emlen 1981; Ligon 1981), and complicating influences have prohibited conclusion of a direct cause and effect relationship between helpers and reproductive output (but see Brown et al. 1982).

Ecological and demographic features intercorrelated with helpers may create spurious relationships among the critical variables. Reproductive success may be affected by territory quality or size (Lack 1968, Zahavi 1974, Brown and Balda 1977, Gaston 1978, Vehrencamp 1978, Brown and Brown 1981, Koenig 1981, Lewis 1981), yearly variation in resources (Stacey 1979, Koenig 1981, Woolfenden and Fitzpatrick 1984), and age or experience of the breeders (Lack 1968, Maynard-Smith and Ridpath 1972, Woolfenden 1975, Koenig 1981, Rowley 1981). These alternative hypotheses are not mutually exclusive and may interact with helper effects. Consequently, we have focused on the interrelationships among these factors.

We compared productivity of birds reproducing with and without helpers. Our objectives were to describe cooperative-breeding Pygmy Nuthatches in northern Arizona, examine the interacting effects of helpers, habitat, year, and breeding experience on annual reproductive yield, and evaluate the role of reproductive yield as a selective force in the evolution of cooperative breeding. Survivorship and nestling care were not considered here.

METHODS

Study area and vegetation measurements.—We studied nuthatches in an extensive (approx. 1,000,000 ha) ponderosa pine (*Pinus ponderosa*) forest. The site, roughly 250 ha, is located 15 km east of Flagstaff, Arizona (elevation 2,195 m) and is bisected by the northern border of Walnut Canyon National Monument (WCNM) and Coconino National Forest (CNF). Other dominant vegetation includes intermittent stands of gambel oak (*Quercus gambelii*), junipers (*Juniperus* spp.), and pinyon pine (*Pinus edulis*).

The environment is cold-temperate with a seasonal climate. Air temperatures at WCNM varied seasonally, with an average monthly low of -4.9°C in the winter and high of 27.1°C in the summer. In May,

TABLE 1. Tree density and diversity in Walnut Canyon National Monument and Coconino National Forest, Arizona.

	Ponderosa pine (no./ha)	Juniper spp. (no./ha)	Gambel oak (no./ha)	Snags (no.)
WCNM	54.1	36.1	27.9	112
CNF	60.9	28.6	18.6	24

June, and July, when Pygmy Nuthatches breed, the mean monthly low was 5.4°C , with a high of 26.0°C . Precipitation also varied seasonally, with snowfall or rain showers in winter and thunderstorms in summer.

The forest of WCNM has been undisturbed for about 70 yr. In comparison, CNF was logged selectively in 1967 and has been cut continually for fuelwood. We sampled features of the vegetation using a modified point-quarter method (Cottam and Curtis 1956). Points were selected at 100-m intervals along 5 east-west transects, spaced 150 m apart through the entire study site. Because of the irregular dimensions of the site, 3 1,500-m transects were established in CNF and 2 1,700-m transects were located in WCNM. Using a Spiegel Relaskop at each point we measured the distance to and height of the closest ponderosa pine with a diameter at breast height (DBH) greater than 10 cm in 4 quadrants. We calculated basal area by counting trees from each point that showed a DBH > 10 cm in the Relaskop. Each point served as the center of a 20-m circular plot in which we tallied the number of oak patches and junipers. We counted the total number of snags in the study area and included fallen snags if they stood for at least 2 of the 4 yr of study.

Marking and censusing.—From November 1980 through August 1984 we captured adult and young nuthatches with mist nets at artificial and natural water holes during dry periods, and at roost and nest cavities as they tried to escape. More than 500 nuthatches were individually color-marked using combinations of 4 bands (a U.S. Fish and Wildlife Service aluminum band and 3 color bands). Two bands were placed on each leg, and color bands were sealed with acetone.

Individual nuthatches were sexed only during the breeding season by brood patch (females only; Norris 1958) and cloacal protuberance (males only). Young of the year were identified up to 3 months after fledging by the color of the base of the mandible (pink to pale off-white vs. gray to black in adults).

We systematically censused the population by ordered visits to group territories. Individual color-band combinations were read every month for 4 yr. The transition from winter to the breeding cycle was characterized when winter groups split into breeding units. At this time we monitored the status of each breeding unit at 3-day intervals. We located nest cavities during

TABLE 2. Characteristics of ponderosa pine in Walnut Canyon National Monument and Coconino National Forest, Arizona.

	WCNM		CNF		t-test ^a
	n	Mean ± SD	n	Mean ± SD	
Basal area (m ² /ha)	34	13.97 ± 8.69	45	10.46 ± 6.04	2.13*
DBH (cm)	136	50.65 ± 23.69	180	40.37 ± 19.96	4.17**
Height (m)	136	18.82 ± 7.99	180	15.36 ± 7.23	4.01**

^a* = $P < 0.05$, ** = $P < 0.001$.

excavation. We determined the number of fledglings produced at each nest at fledging.

The number of young fledged per breeding unit each year and failed nesting attempts for units with and without helpers were recorded. Successful breeding units were defined as those that fledged at least 1 young/yr. We also compared the proportion of 1983 fledglings (banded as nestlings) that were observed in the 1984 breeding season for units with and without helpers. Factorial analysis of variance (ANOVA) was used to examine the effects of year, helpers, and habitats.

RESULTS

Habitat.—The halves of the study area differed in tree density and diversity (Table 1). We presume that the diversity of potential foraging and nesting substrates was considerably greater in WCNM than CNF.

The halves of the study area also differed in pine structure. The ponderosa pines in WCNM covered more ground, were significantly taller, and had larger diameters than trees in CNF (Table 2). If pine age is correlated with tree size, then WCNM may be considered an older, more mature ponderosa-pine community.

Social organization.—Breeding units consisted of a mated pair or a pair with a complement of 1–3 helpers. The average unit size was 2.5 birds. Three observations suggest that helpers did not contribute genetically to the production of young. First, only the breeders participated in cavity excavation and nest building (but see Norris 1958: 209). Second, many helpers were initially followed as “singletons” each year. Singletons were seen calling and roaming in territory unoccupied by other nuthatches. Third, potential helpers occasionally were driven from nest cavities by the breeders before the eggs hatched. Some of these birds were singletons.

Forty-four color-banded birds served as helpers for 51 breeding pairs during 4 breeding seasons; 37 individuals were helpers for only 1 yr,

and 7 served as helpers for 2 yr. The latter group usually aided the same breeders each year ($n = 5$). Genetic relationships between most helpers and nestlings were unknown. For helpers whose parentage was known ($n = 11$), 2 aided both parents, 2 helped their mother and presumably their father (the father was unbanded), 6 aided fathers and an unrelated female, and 1 helped a brother and an unrelated individual.

Twelve helpers that later bred on the study area were males. Most helpers were yearlings. In 1984 we monitored the reproductive activities of 33 yearlings; 7 were breeding females. Of the remaining 26 individuals, 4 were breeding males, 13 helped, and 9 neither helped nor bred (i.e. floated). This last group was larger than observed in earlier years, and we have no data on the fate of these individuals. If we assume that all 1984 helpers were males and omit breeding females and floaters, then 76% of the yearling males helped. Only 2 birds helped for a second time in 1984, but these birds were banded as adults and their ages were unknown.

Annual reproductive yield.—We recorded fledgling production of 141 first nesting attempts during 4 breeding seasons. First attempts of 16 breeding units failed to produce young. Second nesting attempts after nest failure were unusual: only 2 occurred in 1981, 1 in 1982, and 1 in 1983; 3 of these were successful. A total of 13 breeding units failed to fledge any young. Renests after successful first nests occurred twice in 1982; both units successfully produced fledglings. We added the results of first and second breeding attempts to quantify the total reproductive output for each breeding unit per year.

Breeding units in WCNM ($n = 64$) fledged an average of 5.5 young, but units in CNF ($n = 77$) produced an average of 4.4 fledglings (Fig. 1). Pairs with helpers ($n = 56$) fledged an average of 5.2 young/yr, and pairs without helpers ($n = 85$) averaged 4.3 young/yr. Yearly variation

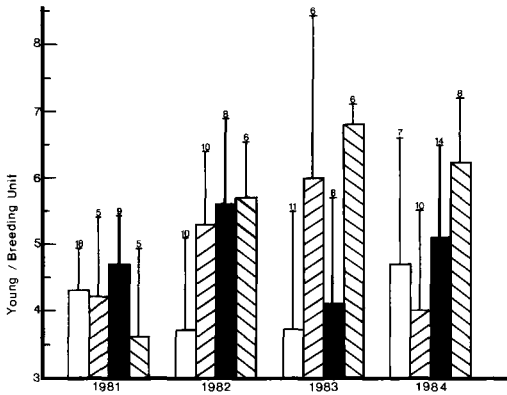


Fig. 1. Annual reproductive yield (mean \pm 2 SE) for breeding units with and without helpers in different habitats. Open boxes show units without helpers in CNF, left hatched boxes show units with helpers in CNF, closed boxes show units without helpers in WCNM, right hatched boxes show units with helpers in WCNM. Sample sizes are given above error bars.

ranged from 4.2 young produced per breeding unit in 1981 ($n = 37$) to 5.0 in 1982 ($n = 34$) and 1984 ($n = 39$). In 1983 ($n = 31$) the average number of young fledged per breeding unit was 4.9.

Annual reproductive yield increased significantly, albeit weakly, with breeding-unit size (Fig. 2). No difference was found between units with 1, 2, or 3 helpers ($F_{2,53} = 0.03, P > 0.05$). Two factors, helpers and habitat (either WCNM or CNF), had significant effects on annual reproductive yield (Table 3). No year effect was found, but a significant interaction between helpers and year was documented. This interaction illustrates the reproductive yield of breeding units with helpers in 1983. Only in this year did units with helpers fledge significantly more young than units without helpers (Table 4).

Variation in reproductive output may be caused by a differential in complete brood loss, even though only 17 of 147 nests were unsuccessful. Nest failure was caused by predation by chipmunks (*Eutamias* spp., $n = 2$ known, 2 suspected), Acorn (*Melanerpes formicivorus*) or Hairy (*Picoides villosus*) woodpeckers ($n = 3$ suspected), and nest abandonment ($n = 2$ known); for 8 failures the cause was unknown. More nests failed in CNF than WCNM (13 of 17; $\chi^2 = 3.46, df = 1, 0.05 < P < 0.10$). Similarly, the

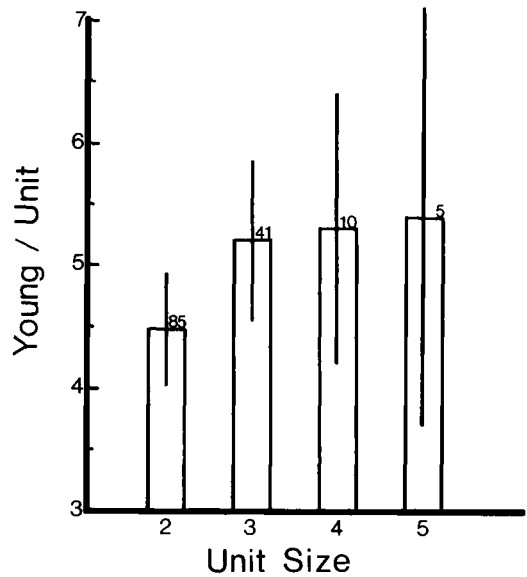


Fig. 2. Annual reproductive yield in relation to breeding-unit size, showing the mean \pm 2 SE and the sample size for each unit.

frequency of failed nests was higher for breeding units without helpers (13 of 17; $\chi^2 = 3.46, df = 1, 0.05 < P < 0.10$).

Breeding units that failed to produce young were responsible for the difference in fledgling yield between units with and without helpers and between habitats. Ten of 13 units that failed in CNF were without helpers. The remaining unit failures, in WCNM, had helpers. The importance of complete unit failure was demonstrated when only successful breeding units were entered in the ANOVA (Table 3). The effects of helpers and habitat were lost, and a highly significant year effect was established. We also found significant interactions between year and helpers and year and habitat. The year effect and its associated interactions may be artificial, the result of increasing the average fledgling productivity in 1983 and 1984. Eleven of the 13 breeding-unit failures occurred in these years.

Neither previous experience of the breeding pair nor pair-bond duration was related to annual reproductive yield (Table 5). We compared novice pairs (both members yearlings with no breeding experience), pairs with mixed levels of experience (one member a yearling, the other with breeding experience), and experienced

TABLE 3. Analysis of variance on factors affecting annual reproductive yield in Pygmy Nuthatches for all breeding units and successful breeding units only (those that fledged at least 1 young/yr).

Effect	All breeding units		Successful breeding units	
	df	F ratio ^a	df	F ratio ^a
Habitat	1	6.20*	1	1.60
Helpers	1	4.07*	1	1.46
Year	3	0.55	3	7.60*
Habitat × helpers	1	0.00	1	0.09
Habitat × year	3	0.54	3	2.72*
Helpers × year	3	2.83*	3	4.15**
Habitat × helpers × year	3	1.25	3	1.06
Residual	125		112	

** = $P < 0.05$, * = $P < 0.01$.

pairs (both members with breeding experience). The influence of pair-bond duration was tested by comparisons of new pairs (members of the pair breeding together for the first time) and old pairs (members of the pair having bred together in the previous year).

Survival of young to one year.—A long-term measurement of the benefit of helping is survivorship to the first breeding season of young reared with and without helpers. In 1983 we marked 48 nestlings, 27 from units with helpers ($n = 5$) and 21 from units without helpers ($n = 6$). These nestlings represented 75% of the total number of young fledged by the 11 breeding units. Forty-eight percent of the young reared with helpers were observed in the 1984 breeding season, while only 38% of those raised without helpers were seen. The difference in these proportions, however, was not significant ($P > 0.05$), and the high survivorship of the 1983 cohort may have been due to a relatively mild winter (Sydeyman 1985).

DISCUSSION

The annual fledgling yield in Pygmy Nuthatches is influenced by helpers, habitat, and the year of observation. We found no relationship between breeding experience or pair-bond duration and reproductive output. The possible interaction between breeding experience and helpers at the nest was not investigated. Other studies also have failed to find significant effects from breeding experience (Rowley 1965, Brown and Brown 1981, Lewis 1981, Brown et al. 1982, Rabenold 1984).

TABLE 4. Analysis of variance on the influence of helpers and habitat on annual reproductive yield in Pygmy Nuthatches for each year of study. See Fig. 1 for data.

Effect	F ratio ^a			
	1981	1982	1983	1984
Habitat	0.15	3.63	0.39	2.93
Helpers	1.35	2.37	7.13*	0.15
Helpers × habitat	1.23	1.49	0.05	1.40

** = $P < 0.01$.

Our data on annual reproductive yield raise a number of points regarding the effect of helpers in varied habitats and different years. The weak correlation between the number of helpers and annual reproductive yield indicates that helpers contribute substantially in only a few cases and years. The 1983 breeding season had a strong effect on the relationship between helpers and annual reproductive yield. Without the 1983 data, significant variation in annual productivity among breeding units with and without helpers would not have been found. Annual variation in reproductive success in some cooperative birds has affected breeding units with and without helpers similarly (Woolfenden and Fitzpatrick 1984). We found that the reproductive success of pairs without helpers did not increase concurrently with helped pairs in 1983.

A relationship may exist between nesting phenology and the effect of helpers. Units with helpers showed the highest reproductive yield in 1983, when breeding occurred at a later date than any other year of study (Sydeyman 1985).

TABLE 5. Annual fledgling yield as related to previous reproductive experience and pair-bond duration of breeding pairs.

	Units with helpers ^a		Units without helpers ^a	
	n	Mean ± SD	n	Mean ± SD
Novice pairs	0		3	5.0 ± 4.58
Mixed pairs	3	4.0 ± 3.46	9	4.7 ± 2.35
Experienced pairs	12	6.8 ± 1.40	9	5.1 ± 3.22
New pairs ^b	20	5.5 ± 2.24	36	4.0 ± 2.68
Old pairs	4	7.3 ± 1.50	6	5.3 ± 3.08

^a All comparisons between experience levels while controlling for the effects of helpers were nonsignificant by Mann-Whitney U -tests; $P > 0.05$.

^b There was a significant difference between new pairs with and without helpers by Mann-Whitney U -test; $P < 0.025$.

Helpers contributed more to feeding nestlings in 1983 than 1984, the latest and earliest years of study, respectively (Sydeman 1985). The timing of breeding may be influenced by the variable climate in the pine forests of northern Arizona. Early spring snowstorms and high precipitation occurred in 1983. Rainfall has been correlated with clutch size and productivity in other cooperative birds (Emlen 1981, Woolfenden and Fitzpatrick 1984). Winter precipitation may increase food availability during the breeding season. If so, then helper Pygmy Nuthatches were most effective under favorable breeding conditions.

We found variation in annual productivity among habitats. The habitat effects were independent of the contribution of helpers, however (see also Brown and Brown 1981, Lewis 1981, Brown et al. 1982). We examined the effects of territory characteristics indirectly by comparing annual productivity in habitats that differed extensively in vegetation structure. Whether this contrast reflects breeding territory "quality," or resource availability, is open to speculation. The smaller territory size in WCNM (Sydeman 1985) supports our contention that this habitat was of higher quality.

Habitat effects may be related to cavity characteristics (Hay and Güntert 1983) or the quantity or quality of nesting sites in WCNM. The age and size of ponderosa pines and snag density may increase the availability of high-quality nest sites. Pygmy Nuthatches can excavate a cavity in the soft wood of snags or dead branches and lightning scars of large live trees, thereby creating a quality nest site if none are available (pers. obs.).

Habitat effects also may be due to variation in the vegetation on breeding territories. Reproductive success of Gray-crowned Babblers (*Pomatostomus temporalis*) was determined in part by the density of a single tree species (Brown and Brown 1981). The importance of gambel oak for Pygmy Nuthatches was suggested by a high percentage of foraging observations on this species (unpubl. data). The larger pines of WCNM may also provide the birds with more foliage on which to forage, and greater tree diversity in WCNM could increase the availability and diversity of prey.

We believe that factors affecting nest defense or abandonment may be the most important determinants of fledgling production. Breeding units that failed to produce young were directly

responsible for the difference in reproductive yield among units with and without helpers and between disturbed and mature habitats. The contribution of unit failure was very strong, even though complete brood loss occurred at less than 12% of the nests we monitored (<10% of the breeding birds).

The advantage of cooperative rearing of offspring to the breeding birds was obvious. On average, breeders with helpers increased annual fledgling productivity by almost 1 young/yr. Our long-term measurement of the significance of helping, survivorship of fledgling to one year of age, is difficult to interpret because mortality after fledging may be confounded by autumn dispersal (pers. obs.).

The benefits of helping behavior to helper Pygmy Nuthatches were not as obvious. Helpers delay reproduction and aid breeding birds. An increase in the reproductive output of breeders that are kin may compensate the potential loss of fitness due to delayed breeding; our data show that helpers and breeders are related. Helper nuthatches always aided breeders from their winter group (unpubl. data), thereby increasing the chance of aiding a genetic relative. Consequently, the benefits of indirect fitness (Brown 1974, Brown and Brown 1981) cannot be immediately discarded as a factor in the evolution of helping behavior in Pygmy Nuthatches.

Some juvenile Pygmy Nuthatches disperse in the autumn of each year, while others remain on natal group territories throughout the winter and breed, help, or float in the following spring. Floaters are unusual in the social organization of cooperative birds (Brown 1978, Koenig and Pitelka 1981), and we have no sound explanation regarding their obvious presence in 1984. The fact that certain young remain with their parents in a winter group argues for extended parental care and sharing of resources as a selective force in the evolution of helping behavior (Ligon and Ligon 1978, Woolfenden and Fitzpatrick 1978, Emlen 1981, Koenig and Pitelka 1981, Ligon 1981, Woolfenden 1981). Communal roosting and group foraging may enhance the probability of overwinter survival (Güntert in press). If dispersal is costly (Brown 1978) and membership in communal roosts is limited (i.e. entrance prohibited by other birds), then Pygmy Nuthatch young that remain in association with their parents may benefit by membership in a winter group. For a small res-

ident species inhabiting an energetically stressful environment, this may be critical to survival and, hence, any measurement of fitness.

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