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EFFECTS OF HELPERS ON NESTLING CARE AND BREEDER SURVIVAL IN PYGMY NUTHATCHES[1]

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Abstract. I studied nestling care in the cooperative-breeding Pygmy Nuthatch (*Sitta pygmaea*) in 1983 and 1984 to determine how helper participation in providing for nestlings affected breeding success and parental survival. Breeding in 1984 was about 3 weeks earlier than 1983. Mothers and helpers contributed equally, but significantly less than fathers in provisioning the nestlings. Between-nest differences in the onset of breeding determined most of the variation in nestling feeding rates; nests initiated early in the breeding season received more frequent feeding visits. Enhanced reproductive success by breeding units with helpers (Sydeman et al. 1988) was not related to increased feeding rates to the nestlings. Total feeding rates were no greater when helpers supplemented the feeding visits of both parents. At nests with helpers, however, parents and helpers were at the nest cavity more often. The feeding contribution made by helpers proved more beneficial to parents than nestlings, allowing parents to reduce feeding frequency, and presumably energy expenditure. However, this benefit did not lead to increased breeder survival.

Key words: Feeding rate; helpers; seasonal variation; Sitta pygmaea; *fledging success; breeder survival.*

INTRODUCTION

A potentially important feature of avian cooperative breeding is the participation of helpers in caring for nestlings (Brown 1987). There are at least two adaptive hypotheses to explain this behavior. First, annual productivity (fledging success) may be enhanced by more frequent feeding visits to the nestlings. Second, helper contributions may allow the parents to decrease their feeding frequency and the energy expenditure during nestling care (Brown et al. 1978, Lewis 1982, Rabenold 1984). Few studies on cooperative birds have documented increased feeding rates attributable to helpers while controlling for confounding variables (Mumme 1984, Wilkinson and Brown 1984). Moreover, correlations between feeding rates and group size do not provide a mechanism for enhanced fledgling yield unless brood reduction, in the form of nestling starvation, is documented as well. Finally, predator detection and deterrence, rather than feeding frequency, has been linked to annual productivity in some cooperative birds (Rabenold 1984, Woolfenden and Fitzpatrick 1984, Austad and Rabenold 1985).

The Pygmy Nuthatch (*Sitta pygmaea*), a resident passerine of western North American coniferous forests, shows a high degree of cooperation during breeding with helpers found in about 30% of all breeding units (Norris 1958, Sydeman et al. 1988). Genetic relationships between the helpers and breeders were close. Helpers were often progeny of a previous year, but our sample of known-parentage birds ($n = 11$) was too small to be conclusive (Sydeman et al. 1988). Helpers were not always related to an increase in annual productivity. Reproductive success of breeders with helpers was enhanced in only one year of a 4-year study (Sydeman et al. 1988). Annual productivity was also greater in mature rather than disturbed forest. Breeding units which failed to fledge any young caused the difference in reproductive success between habitats and nests with and without helpers. Although total brood loss was a rare phenomenon, these data suggest that factors influencing nest protection are more important than feeding rates in determining annual productivity.

The goals of this paper are to describe and quantify the contributions made by parents and helpers in caring for nestlings. I will focus on feeding rates and time spent at the nest cavity, compare nestling care at nests with and without helpers, and evaluate the adaptive value of cooperative nestling care in Pygmy Nuthatches in relation to annual productivity and survivorship.

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METHODS

I studied nestling care in a color-banded population of Pygmy Nuthatches at Walnut Canyon National Monument (WCNM) and in adjacent Coconino National Forest (CNF) east of Flagstaff, Arizona. WCNM and CNF differed greatly in vegetation characteristics. The habitat of WCNM is mature ponderosa pine forest dominated by high densities of oaks and junipers, and numerous dead trees (snags). The habitat of CNF is disturbed forest, having been selectively logged in 1967. CNF is a mixture of large ponderosa pines with many thickets of small trees, low oak and juniper density, and few snags. Details on marking the birds, the study area, and habitat are described elsewhere (Sydeman et al. 1988).

I recorded annual productivity, breeding phenology and individual survivorship from 1981–1984, and observed breeder and helper behavior in 1983 and 1984. I used fledging dates (based on data from 1981–1984) as an index of the onset of reproduction. Twenty-four breeding units were observed for 94 hr: six units with and six without helpers each year. A total of 2,226 feeding visits were recorded. Nests with a maximum of two helpers were observed. Occasionally, previously unrecorded nonbreeding birds began to participate in feeding young well into the nestling period. I considered the first helper observed within the season at nests that eventually were recorded with two helpers ($n = 3$), the "first" helper. These birds uniformly contributed more to nestling care than "second" helpers (see below). I randomized observations between 07:00 and 12:00 for each nest under study. Nuthatches fed young and behaved normally during observations made without use of a blind. Data were collected on the frequency (number per hour) and duration (seconds) of feeding visits, identity of the providing birds, and fecal sac removals using a 20× spotting scope in observation periods ($n = 86$) usually lasting 60 min ($n = 75$). I selected 60-min observation periods to maximize the number of nests that could be observed by a single investigator per day, rather than increasing the length of observations per nest. During 71 observation periods, I scored food particle size on a scale of 1 to 3: seeds and small insects, 1; larger arthropod food which forced the birds' bill open (spiders and medium-sized insects), 2; food which forced the bill fully open and draped out each side (lepidopteran larvae and moths), 3. I added the food particle size score for each feeding visit to estimate "feeding value" (see below). Samples of observations in which each feeding visit was given a food particle size score were insufficient for inclusion in multivariate analyses.

I measured time at the nest cavity, including time inside and outside, during feeding visits. Visits that did not exceed 2 min in length were summed to estimate the proportion of each hour with adults at the site. This separated female feeding from brooding visits. Observations were not made at all nests when nestlings were brooded, therefore, including these observations might bias the results. Fathers and helpers never stayed at the nest cavity for longer than 2 min.

I used analysis of covariance (ANCOVA) to compare within- and between-nest variation in nestling feeding rates and evaluate the relative strengths of each factor with total, fathers', mothers', and helpers' feeding rates. Feeding rates were analyzed by pooling the data for both years. Day in the season (date), brood size, nestling age, year, helper, and habitat effects were examined. I standardized the observation dates between years by adding 24 days to the date for 1984 (see below for data on annual variation in the timing of breeding). The covariates (date, brood size, and nestling age) were entered into the models first and considered concurrently. Main factors and two-way interactions were considered after covariate effects were controlled. Means are expressed ± one standard deviation.

Mortality was addressed by comparing the number of breeding birds that survived between each breeding season, 1981–1984. Effects were analyzed using a hierarchical log-linear model. Survival rates were based upon disappearances, and the assumption that dispersal following a bird's first breeding season did not regularly occur.

RESULTS

ONSET OF BREEDING

Over the 4 years fledging dates averaged earliest in 1984 (5 June ± 6.51 days, $n = 33$) and latest in 1983 (29 June ± 8.74 days, $n = 20$). Fledging dates averaged earlier for breeding units with helpers (15 June ± 10.54 days, $n = 45$) than units without helpers (19 June ± 10.52 days, $n = 62$). Fledging dates were also earlier in WCNM (16 June ± 10.98 days, $n = 54$) than CNF (19 June ± 10.22 days, $n = 53$). Significant differences

TABLE 1. Hourly feeding rates in the Pygmy Nuthatch.

	$\bar{x}$ ± SD	Range	% of total
Total	23.2 ± 10.59	3–53	
Fathers	13.3 ± 9.17	3–53	60.4 (56.4)[a]
Mothers	5.9 ± 6.17	0–29	24.1 (18.0)
Helpers (total)	5.9 ± 4.79	0–19	12.0 (22.2)
Unidentified	0.8 ± 1.19	0–6	3.5 (3.4)
Helper (primary)	4.8 ± 4.24	0–19	9.7 (17.8)
Helper (secondary)	1.1 ± 3.10	0–14	2.3 (4.4)

[a] Numbers in parentheses show percent contribution at nests with helpers only.

were found in fledging dates between years (Three-way ANOVA; $F = 63.1$, df = 3,91, $P < 0.001$) and between units with and without helpers ($F = 7.8$, df = 1,91, $P < 0.01$).

PROVISIONING NESTLINGS

Feeding rates were significantly different for birds of different breeding status (Table 1; One-way ANOVA; $F = 41.79$, df = 2,216, $P < 0.001$). Males fed more frequently than females ($t = 7.76$, df = 170, $P < 0.001$) and helpers ($t = 7.46$, df = 131, $P < 0.001$). No difference was found between females and helpers ($t = 0.29$, df = 131, $P > 0.05$). The first helper made about 80% of the helpers' feeding visits at nests with two helpers. A total of 3.5% of the feeding visits were made by unidentified birds.

Total and helpers' feeding rates decreased significantly as the season progressed (Table 2); 22% in 1983, and 13% in 1984, of the variation in total feeding rates was explained by date. Feeding rates significantly increased with the number of nestlings. Brood size accounted for 12% of the variation in total feeding rates in 1983, 10% of the variation in male feeding rates in 1984, and 11% of the variation in female feeding rates in 1983. Total and helpers' feeding rates increased with age of nestlings in 1983, but no relationship was found in 1984.

Total and mothers' feeding rates were influ-

TABLE 2. Multiple regressions on feeding rates in relation to nestling age, date, and brood size for each year. Independent variables were entered in the equations simultaneously.

	1983 (n = 45)		1984 (n = 41)	
	Coefficient[a]	t-value	Coefficient[a]	t-value
Total:				
Nestling age	0.418	2.64**	0.004	0.03
Brood size	0.341	2.55**	0.254	1.64
Date	−0.474	2.96***	−0.362	2.07*
Fathers:				
Nestling age	0.118	0.63	−0.022	0.13
Brood size	0.025	0.16	0.315	1.97*
Date	−0.234	1.23	−0.241	1.34
Mothers:				
Nestling age	0.221	1.24	−0.258	1.42
Brood size	0.333	2.21*	0.139	0.80
Date	−0.022	0.12	0.003	0.03
Helpers:				
Nestling age	0.858	3.13***	0.075	0.18
Brood size	−0.311	1.84	0.287	0.85
Date	−0.769	2.82**	−0.128	0.35

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.005$.
[a] Standardized partial regression coefficient.

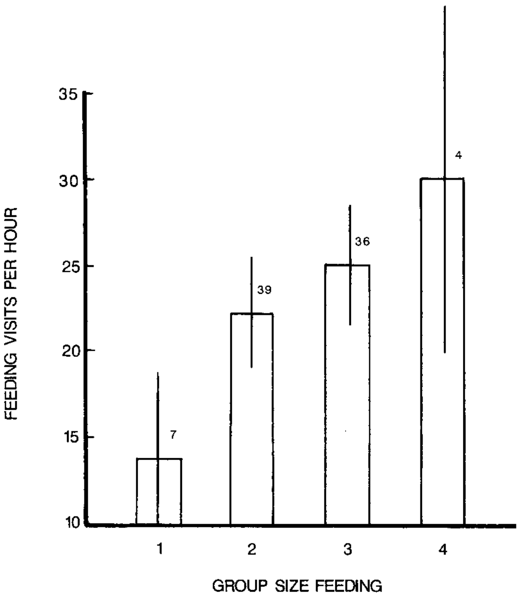

FIGURE 1. Feeding rates ($\bar{x}$ ± 2 SE) of Pygmy Nuthatches by the number of contibuting adults. Student-Newman-Kuels pairwise contrasts showed that this difference was due to the difference between a single adult feeding and 2, 3, or 4 providers.

enced by helpers (Table 3). Total feeding rates were higher and females' feeding rates lower at nests with helpers. Total feeding rates significantly increased with the number of adults providing food (Fig. 1; $F = 5.14$, df $= 1{,}84$, $P < 0.05$). However, no difference was found between 2, 3, or 4 feeding adults (Student-Newman-Keuls test, $P > 0.05$). Often females did not feed at all (12 of 86 observations at 8 of 24 nests). I recorded lack of female feedings at nests with ($n = 4$) and without helpers ($n = 4$). Nine records were made in 1983, and three in 1984. In two cases (at a single nest), these observations were recorded in conjunction with the addition of a second helper and the possible disappearance of the mother. These records were also independent of the age of the nestlings; four were recorded during each week of the nestling cycle. It is also unlikely that observer bias could have caused these results. At each nest, mothers were observed provisioning young during at least one other observation period and in three of 12 observations, mothers visited the nests, but did not bring food. The only significant pattern of mothers not feeding was that none were recorded in WCNM, the section of the study area with greater vegetative cover and diversity (Sydeman et al. 1988). When both parents fed (i.e., excluding the observation periods when females did not feed), no difference was found in total feeding rates at nests with and without helpers ($P > 0.05$).

Food particle size may influence the amount of food young receive at nests with helpers (Royama 1966, Ligon and Ligon 1978, Stallcup and Woolfenden 1978). The average size of food particles significantly increased with nestling age for males ($r^2 = 0.20$, $F = 18.2$, df $= 1{,}74$, $P < 0.001$) and females ($r^2 = 0.23$, $F = 18.0$, df $= 1{,}59$, $P < 0.001$), but no relationship was apparent for first helpers ($r^2 = 0.04$, $F = 1.4$, df $= 1{,}32$, $P > 0.20$) and the sample for second helpers was too small for analysis. Total "feeding value" increased with up to three providing adults ($F = 4.13$, df $= 2{,}33$, $P < 0.05$). However, like results on simple feeding frequencies, if observations in which mothers did not feed are excluded ($n = 5$), no difference in feeding value was found between two and three feeders ($F = 0.87$, df $= 1{,}27$, $P > 0.05$; notes: since $n = 2$ for one providing adult this datum was excluded).

Feeding rates were influenced by habitat (Table 4). Total, males', and females' frequencies were higher in WCNM. These results suggest that habitat characteristics in WCNM facilitate more rapid feeding that may influence the reproductive success of birds.

MULTIVARIATE ANALYSES OF FEEDING RATES

Total feeding rates decreased with date (regression coefficient = −0.398) increased with addi-

TABLE 3. Feeding rates of Pygmy Nuthatches at nests with and without helpers. *F*-value is for one-way ANOVA.

	Without helpers $\bar{x}$ ± SD (*n*)	With helpers $\bar{x}$ ± SD (*n*)	*F*-value
Total	20.55 ± 10.31 (40)	25.55 ± 10.39 (46)	5.0*
Fathers	12.73 ± 5.51 (40)	13.71 ± 6.31 (46)	0.6
Mothers	7.33 ± 7.75 (40)	4.70 ± 4.07 (46)	4.0*

* $P < 0.05$.

TABLE 4. Feeding rates of Pygmy Nuthatches in different habitats. *F*-value is for one-way ANOVA.

	CNF $\bar{x}$ ± SD (*n*)	WCNM $\bar{x}$ ± SD (*n*)	*F*-value
Total	19.95 ± 9.86 (41)	26.60 ± 10.20 (45)	10.7**
Fathers	11.61 ± 5.50 (41)	14.76 ± 5.98 (45)	6.4**
Mothers	4.03 ± 4.93 (41)	7.64 ± 6.72 (45)	8.0**
Helpers	5.10 ± 3.54 (23)	6.74 ± 5.73 (23)	1.4

** $P < 0.01$.

tional nestlings (regression coefficient = 1.196) and increased as the young aged (regression coefficient = 0.487; Table 5). No difference was found in total feeding rates between nests with or without helpers, but total feeding rates were significantly greater in 1984 (adjusted mean = 26.0 feedings/hr) than 1983 (adjusted mean = 19.7 feedings/hr). The difference in total feeding rates between WCNM (adjusted mean = 25.3 feedings/hr) and CNF (adjusted mean = 21.0 feedings/hr) was weakened (refer to Table 4) when considering other variables in relation to habitat ($P = 0.06$).

Year and an interaction between year and helpers affected fathers' feeding rates. Fathers fed more often in 1984 (adjusted mean = 15.2 feedings/hr) than 1983 (adjusted mean = 11.5). The interaction shows that fathers' feeding rates were significantly lower at nests with helpers only in 1983 (Fig. 2). Mothers' feeding rates were significantly higher in 1984 (adjusted mean = 7.9 feedings/hr) than 1983 (adjusted mean = 4.1 feedings/hr), lower at nests with helpers (adjusted mean = 4.2 feedings/hr) than nests without helpers (adjusted mean = 7.9 feedings/hr), and affected by an interaction between year and helpers. The interaction shows that mothers fed less often while aided by helpers only in 1984 (Fig. 3).

Lastly, helper feeding rates decreased with date (regression coefficient = −0.295), increased as the nestlings aged (regression coefficient = 0.473), and were more frequent in 1983 (adjusted mean = 7.5 feedings/hr) than 1984 (adjusted mean = 3.7 feedings/hr).

TIME AT THE NEST

Time spent at the nest cavity during feeding visits averaged 9.4 sec for fathers, 16.9 sec for mothers, 9.8 sec for primary helpers, and 5.7 sec for sec-

TABLE 5. Feeding rates of Pygmy Nuthatches by analysis of covariance.

		Feeding rates			
Source	df	Total *F*-value	Fathers *F*-value	Mothers *F*-value	Helpers *F*-value
Covariates					
Date	1	10.4**	2.6	0.4	4.9*
Brood size	1	6.3*	3.3	1.5	0.2
Nestling age	1	4.8*	0.9	0.2	6.4**
Main effects					
Year (Y)	1	5.5**	7.5**	8.1**	4.7*
Helpers (H)	1	0.2	0.0	5.7*	—[a]
Habitat (L)	1	3.5	1.0	1.3	3.2
Interactions					
Year × helpers	1	0.4	5.1*	4.0*	—
Year × habitat	1	0.9	1.1	0.1	1.0
Helpers × habitat	1	0.3	0.2	1.2	—
Total explained	9[b]	4.5***	3.4**	3.9***	2.5*
Residual	76[b]				

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
[a] Not applicable.
[b] df for ANCOVA on helper feeding rates = 6,39.

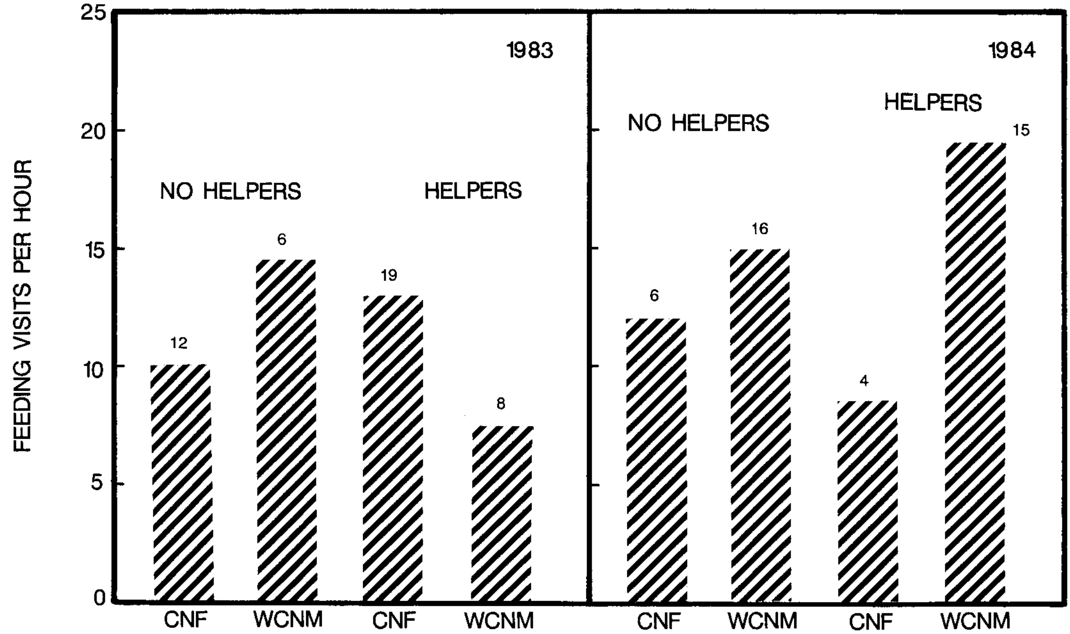

FIGURE 2. Average fathers' feeding rates with and without helpers by habitat and year. Means presented are not corrected for the covariates considered in Table 5. Numbers atop bars show sample size.

ondary helpers. Time at the nest decreased as nestlings aged because the young reached out of the cavity entrance to receive food and voided fecal sacs directly into the parent's bill (ANCOVA; $F = 11.86$, df = 1,76, $P < 0.001$). A significant difference of 59.8 sec/hr was found in the total amount of time with adults at the nest among units with and without helpers ($F = 7.32$, df = 1,76, $P < 0.01$). A significant interaction between helpers and year ($F = 17.03$, df = 1,76, $P < 0.001$) may be the result of differences in the onset of breeding between years and nests with and without helpers. Recall that 1983 was a significantly later year than 1984, breeding units with helpers fledged young earlier in each season, and feeding rates decreased throughout the reproductive period. Therefore, this interaction may simply reflect greater feeding frequency, hence time at the nest cavity, for breeding units with helpers in 1984. Adults were at nests more often in WCNM ($F = 3.77$, df = 1,76, $0.05 < P < 0.10$).

ANNUAL SURVIVORSHIP OF THE BREEDERS

Significant differential disappearance between years was found (Fig. 4, Log-linear partial $\chi^2 = 9.73$, df = 2, $P < 0.01$). Annual survivorship varied from 41% between the 1982 and 1983 breeding seasons to 70% from 1983 to 1984. Survival rates were also lower for females (49%/year) than males (64%/year, partial $\chi^2 = 3.73$, df = 1, $0.05 < P < 0.10$). Two females, however, disappeared and reappeared in subsequent years. These occurrences may bias these results by reducing estimates of female survival. Survival values did not significantly differ among breeders with (55%/year) and without (57%/year) helpers ($\chi^2 = 0.03$, df = 1, $P > 0.10$) or between breeders with territories in WCNM (59%/year) vs. CNF (54%/year; partial $\chi^2 = 0.13$, df = 1, $P > 0.10$).

DISCUSSION

NESTLING CARE AND BREEDING SUCCESS

Helpers may enhance the likelihood of successful nesting in Pygmy Nuthatches by contributing to the protection of nestlings. If adults are at the nest more often, the probability of detecting and driving off potential nest predators before young are lost may be increased. However, Skutch (1961) suggested that one of the principal costs of having helpers may be attraction of predators to the nest site due to increased activity. In this study, time spent at the nest cavity was greater

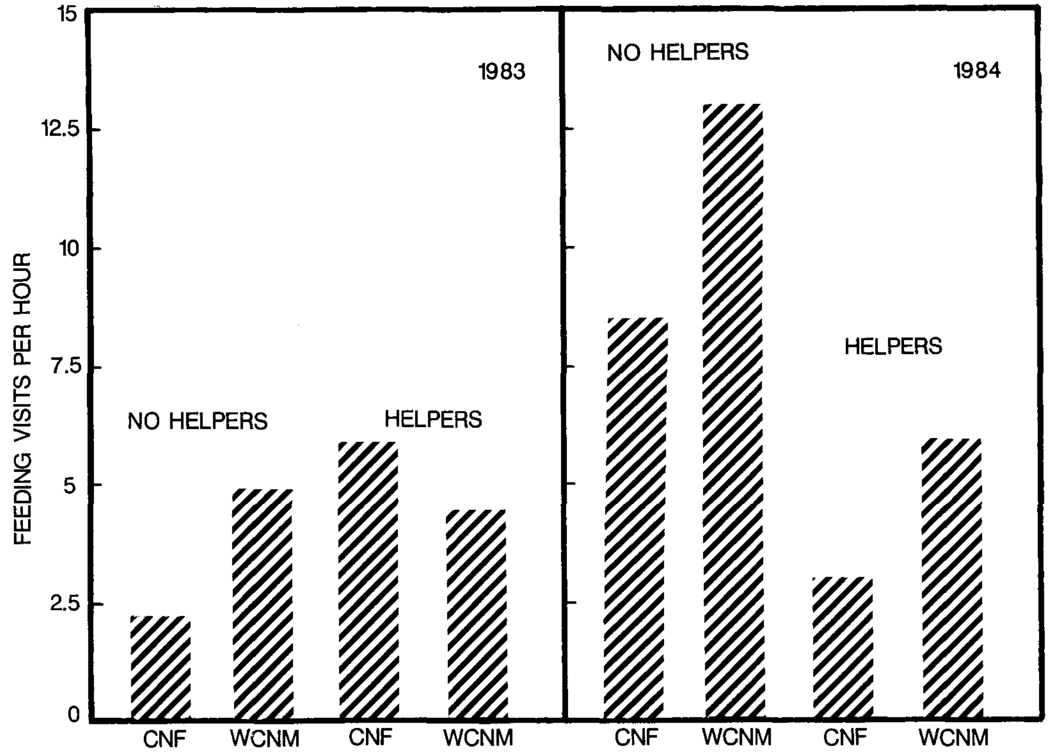

FIGURE 3. Average mothers' feeding rates with and without helpers by habitat and year. See Figure 2 legend for details.

in WCNM and at nests with helpers. Annual productivity was lower in CNF and at nests without helpers, principally due to total brood loss (Sydeman et al. 1988). Helpers were observed chasing and mobbing intruders. However, it is difficult to imagine how three or four nuthatches (weight = 10–11 g) would be more effective than two adults in repelling potential predators. There may be an indirect effect on reproductive success if some adults continue to feed young while others are involved in nest defense (Rabenold 1984). Pygmy Nuthatch breeding males appear to be most attentive and aggressive toward potential nest predators. Although the predator detection hypothesis cannot be rejected here, the behavior and effectiveness of parents and helpers in nest defense is yet to be resolved.

Helpers may also enhance the number of young fledged each year by contributing to the provisioning of nestlings. However, my results on feeding rates, brood reduction, and the effect of timing (date) suggest that feeding rates do not relate to enhanced reproductive success. First, brood size reflected annual productivity for most of the 24 nests in this study. Brood reduction occurred only once. This nest, which began with five nestlings but fledged only four, was not attended by helpers. Complete nest failure also occurred at one nest without helpers. At all other nests the number of fledged young equaled the brood size used in these analyses. Therefore, although it is possible that helpers aid in increasing fledging weight of the young, these data suggest that helpers could have no direct effect on productivity by feeding nestlings. Second, even if brood reduction had occurred, helpers did not increase the total feeding rate to the nestlings (Table 5), especially if both parents participated in feeding young (Fig. 1). Third, nestling feeding rates were primarily affected by the timing of breeding. No significant effect of date was reported for feeding rates in Grey-crowned Babblers, *Pomastomus temporalis,* or Acorn Woodpeckers, *Melanerpes formicivorus* (Brown et al. 1978, Mumme 1984). In Pygmy Nuthatches, the seasonal decrease in total feeding rates was re-

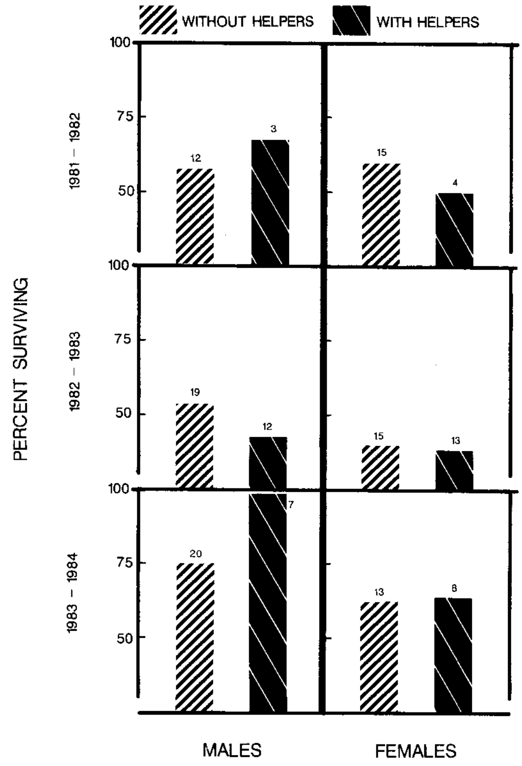

FIGURE 4. Breeder survival of Pygmy Nuthatches with and without helpers by sex and year. The number of birds at risk in the earlier year are shown atop bars.

lated to helpers. No significant relationships were found for fathers' or mothers' feeding rates as the season progressed (Table 5). Moreover, pairs with helpers fledged young earlier in the season than those without helpers. Consequently, the significant date effect on total feeding rates must be due to the contribution of helpers at nests early in the season. The relationship between helpers and timing of breeding is unclear. It is unknown if helpers decreased the length of the nesting cycle, or chose or were recruited by early breeding individuals. However, I suspect that helpers aided early breeders because older birds generally nest before young birds (Nol and Smith 1987 and references therein), individuals that have previously reproduced are most likely to have independent yearlings on territory, and helpers in Pygmy Nuthatches were generally progeny of the breeders from an earlier year (Sydeman et al. 1988). In conclusion, helpers appear to be selectively neutral in relation to feeding rates and enhancement of reproductive success. This matches our data on annual reproductive success which showed that helpers were related to enhanced breeding success in only one of a 4-year study.

Significantly higher feeding rates, however, and greater time by parents and helpers at the nests were documented in the WCNM. These data may help explain variation in reproductive success between disturbed and mature forest (Sydeman et al. 1988). Pygmy Nuthatches are mostly insectivorous during breeding. Larger ponderosa pines and greater Gambel oak patch density in WCNM vs. CNF probably increase available foraging substrate and food resources. In addition the records of females not feeding in the poorer quality habitat suggest that food may be more difficult to obtain.

PARENTAL CARE AND BREEDER SURVIVAL

Pygmy Nuthatch adults fed young an average of once every 2 min in the morning hours. In some cases, nests were visited almost every minute. Feeding rates of this magnitude in cooperative-breeding birds are rare and restricted to species with large numbers of providing adults (Brown et al. 1978, Mumme 1984, Wilkinson and Brown 1984). The feeding rates reported in this paper were made by no more than four adults, and often only three were involved. Presumably, energy expenditure by individual Pygmy Nuthatches during nestling care was high. Individual survivorship and residual reproductive value may vary in relation to this energetic cost.

The participation of helper Pygmy Nuthatches in feeding nestlings supports the hypothesis that parents benefit by a reduction in nesting responsibilities. Reduced feeding rates were found for fathers with helpers in 1983 and mothers aided by helpers in 1984 (Table 5). Brown et al. (1978) suggested that the major consequence of decreased feeding rates is a reduction in energy expenditure. Lifetime reproductive success of individuals that reduce energy expenditure in one reproductive attempt may be enhanced if additional nests can be initiated within a breeding season (Brown et al. 1978; Brown and Brown 1981; Lewis 1981, 1982), or if longevity is increased (Woolfenden and Fitzpatrick 1984, Reyer 1984). Pygmy Nuthatches normally raise only a single brood per season (Norris 1958, Sydeman et al. 1988). Thus, a fitness increase related to additional nesting within a breeding season is usually not possible. Survival rates of breeders with and without helpers were no different (Table

6), although yearly differences in mortality and differences between males and females were detected. Thus, during this relatively brief study, breeder reductions in feeding rates did not influence residual reproductive value.

Breeder survival may be influenced to a greater extent by the size and dynamics of winter groups than spring breeding units. Pygmy Nuthatch winter groups are critical for survival. Individual survivorship through winter is enhanced by communal roosting and huddling in tree cavities (Knorr 1957, Sydeman and Guntert 1983, Guntert 1988). Helpers may benefit by gaining access to a winter group for communal foraging and roosting (Sydeman et al. 1988). Parents that expend less energy during breeding may also maintain a quality position in a winter group. Birds in advantageous roosting positions show larger reductions in energy expenditure by decreasing convective heat loss through greater body contact with other birds and by entering a deeper state of hypothermia (D. B. Hay, unpubl.). A thorough analysis of winter group dynamics and other variables affecting survival such as population density and territory quality (Koenig and Mumme 1987) and age (Woolfenden and Fitzpatrick 1984) is needed to reject the hypothesis that helpers serve to reduce the reproductive costs of breeding.

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LITERATURE CITED

AUSTAD, S., AND K. RABENOLD. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren. Behav. Ecol. Sociobiol. 17:19–27.

BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, NJ.

BROWN, J. L., AND E. R. BROWN. 1981. Kin selection and individual selection in babblers, p. 244–256. *In* R. D. Alexander and D. Tinkle [eds.], Natural selection and social behavior: Recent research and new theory. Chiron Press, New York.

BROWN, J. L., D. D. DOW, E. R. BROWN, AND S. D. BROWN. 1978. Effects of helpers on feeding of nestlings in the Gray-crowned Babbler, *Pomatostomus temporalis*. Behav. Ecol. Sociobiol. 4:43–59.

GUNTERT, M. 1988. Communal roosting in the Pygmy Nuthatch: A winter survival strategy. Proc. XIX Ornithol. Congr. (1986).

KNORR, O. A. 1957. Communual roosting in the Pygmy Nuthatch. Condor 59:398.

KOENIG, W. D., AND R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton Univ. Press, Princeton, NJ.

LEWIS, D. M. 1981. Determinants of reproductive success in the White-browed Sparrow Weaver. Behav. Ecol. Sociobiol. 9:83–93.

LEWIS, D. M. 1982. Cooperative breeding in a population of White-browed Sparrow Weaver. Ibis 124:511–522.

LIGON, J. D., AND S. H. LIGON. 1978. The communal social system of the Green Woodhoopoo in Kenya. Living Bird 17:159–197.

MUMME, R. A. 1984. Competition and cooperation in the communally breeding Acorn Woodpecker. Ph.D.diss. Univ. California, Berkeley.

NOL, E., AND J.N.M. SMITH. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J. Anim. Ecol. 56:301–313.

NORRIS, R. A. 1958. Comparative biosystematics and life history of the nuthatches, *Sitta pygmaea* and *Sitta pusilla*. Univ. Calif. Publ. Zool. 56:119–300.

RABENOLD, K. 1984. Cooperative enhancement of reproductive success in tropical wren societies. Ecology 65:871–885.

REYER, U. H. 1984. Investment and relatedness: A cost/benefit analysis of breeding and helping in the Pied Kingfisher, *Ceryle rudis*. Anim. Behav. 32: 1163–1178.

ROYAMA, I. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits (*Parus major*). Ibis 108:313–347.

SKUTCH, A. F. 1961. Helpers among birds. Condor 63:198–226.

STALLCUP, J. A., AND G. E. WOOLFENDEN. 1978. Family status and contributions to breeding by Florida Scrub Jays. Anim. Behav. 26:1144–1156.

SYDEMAN, W. J., AND M. GUNTERT. 1983. Winter communal roosting in the Pygmy Nuthatch, p. 121–124. *In* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels [tech. coords.], Snag habitat management: Proceedings of the symposium. U.S. For. Serv. Gen. Tech. Rep. RM-99.

SYDEMAN, W. J., M. GUNTERT, AND R. P. BALDA. 1988. Annual reproductive yield in the cooperative Pygmy Nuthatch. Auk 105:70–78.

WILKINSON, R., AND A. E. BROWN. 1984. Effects of helpers on feeding rates of nestlings in the Chestnut-bellied Starling, *Spreo pulcher*. J. Anim. Ecol. 53:301–310.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1984. The Florida Scrub Jay: Demography of a cooperative breeding bird. Princeton Univ. Press, Princeton, NJ.