

off of excess energy through nest building (Forbush 1929). These explanations have all been dismissed (see Welter 1935; Verner 1963, 1965). Verner (1965) hypothesized that dummy nests may be built as shelters for adults and newly fledged young. This does not explain why males should build many more nests than the number of young fledged and why females do not select males that build more shelters for their young. Nor does this hypothesis explain the variation among males in the number of nests built. None of the hypotheses proposed to date adequately explain the persistence of this phenomenon.

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## Facultative Helping by Pygmy Nuthatches

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In many cooperatively breeding birds, helping is a compulsory stage in the social development of individuals. Helpers enhance their chances of breeding in future years by increasing dominance status (Woolfenden and Fitzpatrick 1977), position in social queues (Woolfenden and Fitzpatrick 1978, Wiley and Rabenold 1984), or the probability of successful dispersal (Koenig 1981, Ligon and Ligon 1983, Hannon et al. 1985). Once individuals breed, reversal of social status is rare (but see Emlen 1981, Emlen and Wrege 1988, Curry 1988, P. B. Stacey pers. comm., for Acorn Woodpeckers, *Melanerpes formicivorus*). As an example, the White-fronted Bee-eater (*Merops bullockoides*) is known

to revert to helping after breeding failure within a season or between seasons, a behavior termed redirected helping (Emlen 1981).

Recently, adaptive or functional explanations for helping have been challenged by the idea that helpers merely respond to a stimulus (i.e. nearby begging nestlings), which causes them to feed unrelated young (Jamieson and Craig 1987, Jamieson 1989, see Ligon and Stacey 1989 for a response). In this interpretation, helping behavior may be viewed as a consequence or byproduct of natal philopatry (see Stacey and Ligon 1987), which places young, nonbreeding birds in the proximity of begging nestlings. This hypothesis im-

plies that helping is a response rather than an evolved behavior. Herein, I report a few examples of redirected or "facultative" helping in the Pygmy Nuthatch (*Sitta pygmaea*), a bird with a well-developed cooperative breeding system (Norris 1958, Sydeman et al. 1988, Sydeman 1989). I use these data to evaluate Jamieson and Craig's (1987) "unselected" hypothesis as a possible explanation for helping in Pygmy Nuthatches.

I studied helping behavior and social organization of a large color-banded population of Pygmy Nuthatches on a 250-ha site located 17 km east of Flagstaff, Arizona, from September 1980 to August 1984. Details of the site and habitat are given in Sydeman et al. (1988). During breeding the social organization of Pygmy Nuthatches is similar to that of many cooperative species. Approximately 35% of the breeding pairs are accompanied by one to three nonbreeding helpers (Norris 1958, Sydeman et al. 1988, Sydeman 1989). Helpers are typically male yearlings related to the breeding pairs they help (Sydeman et al. 1988). Breeding units with helpers fledged significantly more young than units without helpers in only 1 year of a 4-year study (Sydeman et al. 1988). Moreover, I found no relationship between helpers, nestling provisioning rates, and reproductive output (Sydeman 1989). During the course of this research, I noted 3 cases of "facultative helping" (Appendix: A). In each case the helper was male. These few cases of facultative helping suggest that this behavior is aberrant. However, of 141 first nesting attempts monitored from 1981 to 1984, only 16 (11%) resulted in failure. Four of the 16 males re-nested. Considering that 12 pairs did not re-nest (Appendix: cases 2-13), 2 instances (cases 2 and 3) of facultative helping represents 16.7% of the failed breeding population.

Each case of facultative helping was different. Case 1 describes a bird that reversed its social status between breeding seasons, while cases 2 and 3 are of birds that helped within a season after reproductive failure. The timing of helping differed in each case. In case 1, the helper joined the breeding effort early in the incubation phase and contributed substantially to the feeding of nestlings. In case 2, the helper joined the nesting effort 13 days before fledging and also made many feeding visits. In case 3, the helper appeared 2 days before the young fledged; he fed infrequently and was initially driven off by the breeding male. Facultative helping may occur at any time during the breeding cycle. Lastly, the behavior of the helpers differed. All helped by feeding the nestlings, but the helper in case 1 fed the incubating female, and the helper in case 3 defended the nest site.

The reason facultative helping occurred in a species where helping is usually associated with unmated male yearlings related to the birds they aid is unclear. In each case, the helpers helped at the closest neighboring nest. In cases 2 and 3, both helpers aided their fathers in a territory adjacent to their own. In case 1,

the filial relationship between the helper and breeders was unknown, but the territory was adjacent to where this helper nested in 1982 and where he attempted to nest in 1983; the helper was familiar with the birds he aided because he foraged and roosted with them over the previous winter.

Relatedness among the 10 males that did not help after reproductive failure (Appendix: B) was unknown, although all of these birds were familiar with their nearest neighbors. Cases 7, 10, 11, and 12 involved males that were probably related to adjacent breeders. In cases 10 and 11, these males were probably the fathers of the nearest neighbors, but I have never found fathers helping sons or daughters. In case 12, perhaps the failed male did not help because there were 3 helpers already provisioning nestlings at his parent's nest. Indeed, the maximum number of helpers I noted over the 4 yr was 3 at a single nest. It is unknown why the male in case 7 did not help after his own nest failed, considering that he had helped the male of the nearest nest in the previous year.

Proximately, facultative helper nuthatches may be responding to the stimulus of nearby nestlings, in support of Jamieson and Craig's (1987) hypothesis. Facultative helpers may be individuals with prior helping experience that are primed to respond to begging nestlings (cases 2 and 3). Ultimately, it is difficult to interpret facultative helping as adaptive. First, helper Pygmy Nuthatches do not relate to enhanced reproductive success of the breeders. Instead, helper provisionings of nestlings serves to reduce the cost of reproduction (Sydeman 1989). Reciprocity (Ligon and Ligon 1983) does not appear to explain these observations because both facultative helpers and males that did not help after reproductive failure were familiar with neighboring birds (see Sydeman and Guntert 1983, Guntert et al. 1989, Appendix). The benefit of increasing indirect fitness is a possible explanation for facultative helping. Helping relatives after reproductive failure may provide for some fractional increase in fitness where none was otherwise possible. However, the helper in case 3 could not have contributed substantially to the production of fledglings because he joined the pair only 2 days before the young fledged. Last, we have proposed that Pygmy Nuthatch helpers help in order to gain membership in a communal foraging and roosting group which can improve the probability of over-winter survival (Sydeman et al. 1988, Guntert et al. 1989). This hypothesis does not account for facultative helpers who were older individuals with established positions within winter groups. In conclusion, facultative Pygmy Nuthatch helpers appear to be responding to a proximate stimulus, namely neighboring breeding birds and nestlings. This behavior may have little adaptive value, or it may be related to indirect fitness gains.

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APPENDIX. Case histories of the behavior of male Pygmy Nuthatches following reproductive failure, 1981-1984.

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A. Males that helped after reproductive failure

Case 1.—Male A mated with an unbanded female in 1982 and successfully fledged 4 young; he foraged and roosted in winter 1983 with 2 different groups, DBe (dark blue east) and R (red); he was alone during territory establishment in spring 1983. Male B's nest (another member of the DB winter group) was found 14 May 1983 with 7 eggs. Male A was first observed at Male B's nest on 18 May; Male A fed the incubating female, and he contributed 21% of the feeding visits to nestlings on 5 June, 43% on 13 June, and 40% on 16 June. Male A was seen throughout the winter of 1984, but he disappeared before the 1984 breeding season.

Case 2.—Males X, Y, and Z were siblings, the sons of Male C and Female D produced in 1981. Male X helped Male Z in 1982; Male Y helped Male C (his father) and an unrelated female in 1982; during winter 1983, Males X, Y, Z, and C foraged and roosted together (winter territory LG, light green); in 1983, Male X nested with an immigrant female in his natal nest cavity; on 13 June Male X fed young at his father's nest

ca. 80 m from Male X's nest site. The nest of Male X was empty on 13 June, apparently preyed upon by chipmunks (*Eutamias* spp.). On 13, 17, and 24 June Male X made 33%, 30%, and 10% of all feeding visits at his father's nest.

*Case 3.*—Juvenile E was banded 27 June 1982 in a roost cavity that contained 2 adults, Male K and Female L, and 6 other unbanded juveniles. Presumably this was a family group because (a) Male K and Female L fledged 7 young, and 7 juveniles were in the roost, (b) the nest and roost cavities were 4 m apart in the same tree, and (c) the young were only 2 days fledged, and juveniles often roost with their parents for a considerable period following fledging (M. Guntert unpubl. data). Male E was not seen for 18 months after banding; in winter 1984 Male E foraged/roosted with the O (orange) winter group; on 31 May 1984 Male E's nest containing nestlings was found, but by 7 June the nest was inactive; the entrance had been enlarged and a second, smaller entrance was found below the original. This was probable Acorn Woodpecker (*Melanerpes formicivorus*) predation. In 1984 the nest of Male K had been observed 22 May to 1 June, and only the parents were seen feeding; on 6 June, Male E was observed at Male K's nest, sometimes with food and sometimes without, and helped mob Acorn Woodpeckers on the nest snag; initially, Male K chased Male E away from the cavity, but by the end of the observation period on 6 June, Male E was feeding Male K's young.

#### B. Males that did not help after reproductive failure

*Case 4.*—Male M mated with an unbanded female in 1982; the nest was depredated during incubation; the female disappeared; at least 5 other active nests from Male M's winter group (LBe = light blue east) were active when his nest failed; relatedness between Male M and others in the LBe group was unknown.

*Case 5.*—In 1983, Male N mated with a yearling female in the same nesting cavity he used in 1981 and 1982; the nest probably failed during incubation; the female disappeared; at least 3 other nests from Male N's winter group (LGe = light green east) were active when his nest failed; relatedness between Male N and others in the LGe group was unknown.

*Case 6.*—Male O was a member of the LBe group during winter 1983; his nest was preyed upon when it contained small chicks in spring 1983; his mate, Female Q, mated with another LBe male in 1984; Male O dispersed to another winter group in 1984 (PW = park west); 3 other nests in the LBe group were active when Male O's nest failed; he was probably unrelated to these individuals.

*Case 7.*—Male P helped Male W and Female T in 1982. He also fed Western Bluebird (*Sialia mexicana*) young in a cavity adjacent to the one that he helped. In 1983, Male P lost his chicks to chipmunk predation; 1 other nest (the nest of Male W) was active in the Ye (yellow east) winter group when Male P's nest failed; Male P was familiar and probably related to his nearest neighbors.

*Case 8.*—Male Q helped in 1981; Male Q successfully bred in 1982; in 1983, Male Q lost his nest during incubation; his unbanded mate disappeared; Male Q was a member of the DBe winter group; only 1 other nest was active at the time his nest was lost (see case 1); the other nest already was tended by a helper; Male Q was familiar, but probably unrelated to the breeders in case 1.

*Case 9.*—In 1984, Male R, a probable yearling, lost his nest with chicks; at least 2 other nests were active from the LBw (light blue west) winter group; Male R was familiar with the breeders at these other nests, but relatedness was unknown.

*Case 10.* Male S lost his nest with chicks in 1984; 2 other nests were active in the territory of winter group LBe when Male S lost his nest; Male S had successfully bred in 1982 and 1983; he was familiar, and probably related (a father) to other LBe breeders.

*Case 11.* Male T lost his nest with eggs in 1984; there was only 1 other active nest in the Ye territory when Male T's nest failed; the male at this other nest had helped Male T in 1983; Male T was familiar and probably related to his nearest neighbors.

*Case 12.* Male U was a yearling breeder in 1984; his nest failed during the egg stage; there was only 1 other active nest in the DBw (dark blue west) group territory, that of his probable mother and father; however, this nest was attended by 3 helpers already; Male U was familiar and probably related to his nearest neighbors.

*Case 13.* Male V was a yearling breeder in 1984; his nest probably failed with chicks; there were 4 other active nests in the LGe group territory when Male V's nest failed; although his probable father was alive, he was not breeding in 1984; Male V was familiar, but probably not related to the other active LGe breeders.

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