

HELPERS AMONG BIRDS

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Twenty-five years ago, I published a paper (1935) on "Helpers at the Nest," in which I gave short accounts of the breeding of three species of birds whose nestlings were attended by individuals other than the two parents. In addition, I mentioned one other species in which I had found a helper and a few instances of similar behavior that had come to my attention in books. In the quarter-century that has elapsed since this paper was written, I have watched helpers of 16 additional species, and scores of similar instances have been described in print.

The purpose of the present paper is to give a comprehensive survey of the occurrence of helpers among birds, indicating the range of their activity and analyzing the circumstances that promote it. The first part contains a general discussion of the subject, and this is followed in the second part by a systematic list of instances of helpers known to me. This listing of cases which have come to my notice over the years does not pretend to be complete. Although most of the examples presented come from ornithological books and journals, others were found in books of a more general nature, in popular magazines of natural history, and even in the daily press. I doubt if I have noticed a third or even a quarter of the helpers which have been reported in print in all parts of the world. However, I believe that the examples cited give a fair notion of the range and variety of helpfulness among birds and indicate the groups and the circumstances in which helpers are most likely to be found.

To avoid needless duplication, I have omitted scientific names and citations of literature in the first part of this paper whenever these are to be found in the Annotated List which immediately follows.

THE STATUS AND ACTIVITIES OF HELPERS

Status of helpers.—A "helper" is a bird which assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age which is neither its mate nor its dependent offspring. Helpers may be of almost any age; they may be breeding or nonbreeding individuals; they may aid other birds of the most diverse relationships to themselves, including those of distinct species; and they may assist in various ways. Hence the complete analysis of this subject involves attention to three questions: (1) The status or condition of the helper, whether young or old, a parent or a nonbreeder; (2) its relationship to the bird or birds which it assists; and (3) the activities in which it engages.

Although we commonly distinguish immature birds from breeding adults, there is, in many species, an intermediate group for which we lack a convenient designation because this class of individuals is not found in man and because our language developed with special reference to ourselves and our activities. Humans and other familiar mammals are, as a rule, able to reproduce before they cease to grow, often while they are far below their adult size. Many kinds of birds which are fully grown in one or a few months must wait almost two years, or in some species much longer, before they are ready to breed. Thus they pass through one or more nesting seasons, subsequent to that in which they hatched, without themselves nesting. To designate these intermediate individuals, we often use a phrase of several words, such as "full-grown, sexually immature individual."

To fill this gap in our nomenclature, I propose the term *innubile* (the negative of the Latin *nubilis*—marriageable) to designate birds which in a breeding season subse-

quent to that in which they hatched are still sexually inactive. We have, then, the following developmental stages in the life of a bird:

1. Nestling, from hatching to leaving the nest.
2. Fledgling, in nidicolous birds, or chick, in precocial birds, from leaving the nest to the cessation of parental care.
3. Immature, from the attainment of independence to the approach of the following breeding season. The bird may also be designated as juvenile while in the early part of this stage and while still bearing most of its juvenal plumage.
4. Innubile, from the beginning of the breeding season following hatching to the attainment of reproductive activity. Many small birds, which mature in a year or less, omit this stage, passing directly from the immature to the adult stage.
5. Adult or, if one wishes, "nubile"—mature individuals engaged in breeding or fully able to reproduce. Although in many small species innubiles are lacking, in numerous sea fowl and other larger birds, and even in some passerines, they form a large proportion of the total population.

Classification of helpers.—Helpers fall into two great classes with regard to their relationship to the birds they assist. There are "intraspecific helpers," who aid others of their own kind, and "interspecific helpers," who assist individuals of different kinds. With these distinctions, we may attempt a classification of helpers:

I. In reproductive activities

A. Intraspecific helpers

1. Immature helpers
2. Innubile helpers
3. Adult helpers
 - a. Nonbreeding adult helpers
 - b. Breeding helpers
 - Unilateral helpers
 - Mutual helpers

B. Interspecific helpers

The subdivisions under this heading are theoretically the same as under A, but actual records are lacking for some of them.

II. In non-reproductive activities

A. Intraspecific helpers

B. Interspecific helpers

(The examples under both A and B that are at present available are so few that no subdivision seems advisable.)

Ways of helping.—The most common way in which birds help each other is by sounding the alarm at the approach of danger and by repelling animals of all kinds that intrude upon the nesting area. The warning cry which an alert bird raises when a hawk appears is recognized and heeded by individuals of other species, which dive into sheltering vegetation or try to escape detection by immobility. A hush falls over the countryside until the dangerous raptor passes. Indeed, not only do birds warn each other, they sometimes alert mammals that have learned the meaning of the cries or the attitudes of the birds frequently associated with them (Riney, 1951). Birds whose nests are close together, whether of the same or of different species, sometimes unite in threatening or attacking dangerous trespassers; or, more rarely, they try to lure them away by simultaneous distraction displays (Skutch, 1954–1955:563–564). Since helpfulness of this sort (other than the simultaneous distraction displays) is so common, and since it may be unintentional (each bird trying merely to deflect the intruder from its own nest or young), we shall say little about it in the remainder of this paper.

The next most common mode of helpfulness among birds is in feeding. Since the survival of most species depends upon the parents' placing sufficient food into the mouths of their young, the urge to give food to other individuals has become very strong in birds. It is one of the first forms of parental behavior to become manifest in the young and it has been observed even in nestlings. It persists in parent birds who have lost their young hours or even days earlier (Skutch, 1956:364). It has acquired importance in relationships other than parental, especially in courtship and maintaining the bond between mates, and in nourishing the incubating female. It turns up in the most unexpected contexts, as in the captive Raven which passed food through the bars of its cage to a free Black Vulture (*Coragyps atratus*), the Cardinal which fed goldfish, and the Jackdaw which, regarding Dr. Konrad Lorenz as his mate, pushed food into that ornithologist's mouth or even into his ear (Lorenz, 1952:136). Finally, it is one of the last modes of parental behavior to disappear when a species becomes parasitic and depends on others to rear its progeny; there are a number of recorded instances of the feeding of the young of their own kind by parasitic cuckoos (Moreau, 1944) and cowbirds (Bent, 1958:441, 462).

Less frequent forms of helpfulness are nest building, incubation, and brooding. In mature birds, building usually leads to laying and incubation; hence helpers who assist in nest construction generally belong to the class of "mutual helpers," who build, lay, and incubate with other individuals of the same or sometimes different species. There are, however, a few records of immatures or even nestlings helping to build or maintain the nest, as in European Cormorants, Crowned Hornbills, and Barn Swallows. Immature birds who feed nestlings not infrequently brood them, as in the Black-shouldered Kite, Eastern Bluebird, and Purple Martin mentioned beyond. There is even a record of a month-old Rock Dove attempting, not very successfully, to incubate the eggs of his mother's next brood. But most instances of the incubation of other birds' eggs or the brooding of their young by mature individuals fall under the heading of "mutual helpers."

Crèches.—One mode of helpfulness that was reported by earlier observers has not been substantiated by the most careful recent studies. In a number of species that breed on the ground, usually in colonies, the young, after they leave the nest and move around somewhat freely, gather into "crèches," where the offspring of several or many parents are mixed together and guarded by some of the adults while others go off to forage. Such aggregations of young birds have been described in penguins of several kinds, in flamingos, in eider ducks, and in the Sheld-duck, *Tadorna tadorna* (Coombes, 1950:409). In the latter the downy young of several parents form a flotilla on the water. It was formerly believed that in these nurseries the parents fed the young indiscriminately, rather than each his or her own. That each parent feeds its own offspring and not others, even when the young of many families are mixed together, has been demonstrated, or at least made probable, by the observations of Sladen (1953; 1955:245) on the Adelle Penguin (*Pygoscelis adeliae*) and the Chinstrap Penguin (*P. antarctica*), by Prévost (1955:251) on the Emperor Penguin (*Aptenodytes forsteri*), and by Brown (1958:410-412) on the Greater Flamingo (*Phoenicopterus antiquorum*). The parent Adelle Penguins studied by Sladen fed strange chicks only in exceptional circumstances.

A little reflection makes it clear that the indiscriminate feeding of the young by the parents, which at first glance appeals to us as an admirable mode of cooperation, would hardly be practicable without a degree of regimentation of the young which birds could hardly achieve, and which would be difficult even with human children in the open air. Unless the young penguins, flamingos, or other birds in the crèches lined up to receive their meals in turn, the largest and most aggressive of them would take more than their

share, and the smaller and more timid would go hungry. The system of individual attention to its own young by each parent insured that even a broken-winged young flamingo received its meal, although in a general melee to get food it would probably have lost out (Brown, *loc. cit.*).

Relative frequency of intraspecific and interspecific helpers.—Although there are many recorded instances of birds feeding or otherwise assisting members of distinct species, this form of helpfulness appears to be far less common than that which is given to other birds of the same species. In 30 years of bird watching in Central America, I have discovered intraspecific helpers at or near 31 nests of 18 species. No less than 55 individuals of these species were serving as helpers. I have excluded from these figures the communal nests of the anis and the mutual helpers that I watched there, because I knew beforehand of their peculiar breeding habits and made a special effort to study them. All the other helpers that I found were unexpected discoveries. As against this total of 55, I have seen only two individuals of two species—the Tropical Gnatcatcher and the Blue Honeycreeper—helping birds of different kinds. In the records of helpers published by others, interspecific helpers figure far more prominently, accounting for nearly 40 per cent of the reports that refer to free birds. If the computation were made on the basis of the number of individual birds serving as helpers, the percentage of interspecific helpers would be smaller but still quite substantial. But we should bear in mind that interspecific helpers are more likely to be noticed and reported by the casual bird watcher than are the intraspecific helpers. It usually requires sustained and careful observation to learn how many individuals of the same kind are attending a nest, but anyone who notices a bird feeding an individual of another species, or sharing a nest with it, is interested by the extraordinary occurrence.

Immature intraspecific helpers.—The Annotated List contains records of about 20 species in which free young birds of early broods helped with later broods in the same year, and a number of instances of helpfulness by captive immatures are also given. The groups in which immature or juvenal helpers have been most frequently observed are the Common or Florida Gallinule, Barn or European Swallow, House Martin, fairy wrens of Australia (*Malurus* spp.), bluebirds of North America (*Sialia* spp.), and Golden-masked Tanager. The activity in which these young birds most often engage is feeding nestlings and removing their droppings. On rare occasions they help, mostly rather ineffectually, to build, as has been witnessed in the Barn Swallow and the Red-throated Ant-Tanager. Sometimes they toy with building material but seem not to know what to do with it, as I have seen in the Golden-masked Tanager. Their dedication to their self-imposed task of feeding the nestlings is likely to be sporadic, spurts of activity alternating with periods of neglect, so that the nestlings would fare badly but for the steadier application of their parents. Juveniles may even brood, as in the Rock Dove, Purple Martin, and Eastern Bluebird; but this appears to have been observed only in captive birds.

Although in an aviary immatures may attend unrelated younger individuals of their own species and even nestlings or fledglings of different species, in the free state they seem usually to feed their younger brothers and sisters. Hence we should expect to find immature helpers chiefly in species which rear two or more broods in a single nesting season. Moreover, they are likely to occur only in the more sociable species, which do not, in the manner of many birds, repel the young of their previous brood as they prepare for the following brood or when this later brood hatches. When a young Cardinal brought food to a late nest, the female parent tried to drive it away, although the male was more tolerant.

Perhaps an unusual degree of precocity is also necessary to make helpers of the immature individuals of some species. In the family of Southern House Wrens whose fortunes I followed carefully for two years, the parents seemed to be more vigorous in the second year, when they began to breed exceptionally early, and their offspring likewise appeared to be more precocious in the second year. Although young Southern House Wrens are usually driven away about the time the following brood hatches, the first brood of the second year stubbornly refused to be evicted, and soon they were feeding the single nestling which remained from the four eggs of the second brood. With this assistance in the care of the second brood, the parents began to build a nest for the third brood. This was the only instance of this overlap of nestings that has come to my attention in this species. Even while building the third nest, the parents continued to bring food to the nestling of the second brood. But the young female helper, only 73 days old, became antagonistic to her mother and tried to keep the latter out of the gourd that sheltered the nestling. This gave rise to the fiercest struggle that I have ever witnessed among birds, in which the precocious young female was defeated and driven away. Her more pacific brother continued to feed the nestling.

Frequently young helpers, who have not completely outgrown their infantile ways, solicit food from their parents, then pass it on to the still younger individuals which they attend, or sometimes they eat it themselves. In the Common Gallinule or Moorhen, this appears to have become a ritual (see Annotated List, p. 209). I have seen helpers take food from their parents in the Southern House Wren, and Brackbill has witnessed the same in the Cardinal. Probably many young birds only a month or two old have difficulty in finding more food than is needed to satisfy their own hunger. In captivity, where an abundance of food is spread before them, they may indulge as freely as they like in the adult activity of feeding helpless young without stinting themselves. Hence a large share of the records of young helpers refer to captive or semi-captive birds, who fed young of their own or of other species that were closely associated with them in the aviary. Among the more interesting instances are those of the Purple Martin and the Eastern Bluebird recorded later in this paper.

Even nestlings may pass food to their nest mates, as has been recorded for the European Cormorant, the American Flamingo, the Crowned Hornbill, and a hybrid dove only 12 days old (Nice, 1943:79). A captive Chipping Sparrow about 39 days old fed a still younger Redwinged Blackbird. All of these extremely precocious birds evidently had superabundant food supplied to them by their parents or human attendants. Apparently not until they are somewhat older and more self-sufficient do birds offer to others food for which they have themselves foraged. A Golden-masked Tanager was first seen to do so when 46 days old, a Smooth-billed Ani when 48 days old, and a Southern House Wren when 54 days old.

Innubile intraspecific helpers.—Although the distinction between innubile and adult individuals is clear and the ascription of helpers to the correct category is indispensable for the full understanding of the behavior that now occupies our attention, in practice it is frequently difficult to decide with which class of helpers we are dealing. Often we cannot tell whether a nonbreeding bird is innubile or mature unless it has been banded as a nestling or fledgling and its history followed for several years. Whenever one sex far outnumbered the other and the helpers are all of this more numerous sex, as in the Black-eared Bushtit, the Pygmy Nuthatch, and the Brown-headed Nuthatch, there is a strong suspicion that they are mature individuals who lack nests of their own because mates are not available to them. Because of this practical difficulty, in my earlier paper (1935) I lumped together, under the heading of "unmated helpers," innubile helpers and mature helpers who lacked mates.

My conclusion (1935:265) that the helpers in the Brown Jay are sexually immature or inactive yearlings has recently been confirmed by Selander (1959:394). Probably the helpers in the White-throated Magpie-Jay are also innubiles. It is likely that at least some of the helpers at the nests of the Blue Fairy Wren, and of related species, belong to this class; for at some nests Rowley found, in addition to the parents, attendants of both sexes which were one year or more old and were in full breeding plumage. If these helpers were sexually mature, as their plumage suggested, why should a male and female be attending the nest of another pair instead of mating with each other and rearing their own brood? I am also inclined to include among the innubile helpers those of the Collared Araçari and the Banded-backed Wren, and at least some of the Chimney Swifts that assisted mated pairs.

To judge by my experience with the Brown Jays, innubile helpers are likely to be found at the majority of the nests of those species in which they are present, whereas most other classes of helpers are of more sporadic occurrence. The conditions which favor the occurrence of innubile helpers are not only the postponement of reproductive maturity until the second nesting season following hatching or even later, which is found in many species, but likewise a higher degree of sociability in the breeding season and more tolerance of extra individuals at the nest than most birds exhibit. Since innubile individuals have long been full grown and are well able to take care of themselves, they are likely to become efficient helpers; and they may be even more zealous in the defense of the nest and young than are the parents, as I found in Brown Jays.

Nonbreeding adult intraspecific helpers.—The best examples of this class are four species in which males are substantially more numerous than females: Arctic Tern, Black-eared Bushtit, Pygmy Nuthatch, and Brown-headed Nuthatch. In at least the three last-mentioned species, male helpers were found at a number of nests but no female helpers were noticed, which points strongly to the conclusion that the males had remained unmated because no partners were available. In the Golden-masked Tanager, in which the sexes are often indistinguishable by plumage, a third individual in adult plumage is found at such a small proportion of the nests that one can hardly surmise the helper's status; possibly it is an individual that cannot find a mate, but it is equally probable that it is a breeding bird that has lost its mate and offspring. The same difficulty of interpretation applies to all those species, including the Wheatear, Kentucky Warbler, Blue Dacnis, and Speckled Tanager, for which there is a single record of a helper in adult plumage. Possibly some of these helpers are individuals suffering from some physiological derangement that prevents breeding.

Breeding unilateral intraspecific helpers.—Unilateral helpers attend the eggs or young of other parents who do not reciprocate. The services which these unrequited breeding helpers render to the offspring of other parents of their own kind are usually occasional or sporadic rather than sustained, although at times lost or orphaned young may be adopted and reared until they become self-supporting. Kentish Plovers and Avocets sometimes brood their neighbors' chicks; although this kind office may be reciprocated, probably more often it is not. A female Purple Martin fed the hungry young in a neighboring nest from which the female parent had been carried off for a homing experiment. Adoption of strayed or orphaned young of their own kind has been reported for European Blackbirds (*Turdus merula*), American Robins, Winter Wrens, and Great Tits; occasional feeding has been observed in the Wood Thrush, Scarlet-rumped Black Tanager, and Rose-breasted Grosbeak. Most inconsistent was the behavior of a breeding Buff-throated Saltator that tried hard to drive away another female whose nest had been built unusually close to her own. The eviction of the more timid female would have

been fatal to the newly hatched nestling of that female, whereas the destruction of this nestling would have hastened the departure of the timid female. Yet the dominant female sometimes fed this nestling—a most convincing demonstration of the strength of a parent bird's impulse to feed.

Parents whose young have just been lost continue to bring food to the vicinity of their nest, and if responsive young of other families are close by, they may become the beneficiaries of the thwarted parental impulses. This has been reported for terns of several species, for Murres, and for Tree Swallows. The helpers that are often found at nests of the Long-tailed Tit may be breeding birds whose nests have been destroyed too late in the season for renesting.

Mutual intraspecific helpers.—Mutual helpers are necessarily breeding individuals. They are on rare occasions found in species which normally rear their broods alone: two Wood Ducks incubated in the same box; two pairs of Cardinals shared the same nest, as did two pairs of Song Sparrows. In a few species, cooperation among breeding pairs has become a frequent, if not an invariable, habit. Among these we may include all those which build bulky nests containing a number of compartments, such as the Gray-breasted Parakeet of southern South America, the Social Weaver of South Africa, the Palm-Chat of Hispaniola, and possibly the Rufous-fronted Thornbird of tropical South America. The construction of the framework of these avian apartment houses is certainly a community project, although each pair may finish its own chamber and rear its family without help from its neighbors. Even more complete cooperation is not improbable in these gregarious birds, of which, unfortunately, we lack detailed studies.

The best known examples of complete mutual helpfulness are the anis (*Crotophaga*), in which the several cooperating pairs share the labors of the nest at every stage of building, incubating, and rearing the young. Fragmentary observations suggest that equally close cooperation may occur among breeding pairs of certain barbets and helmet shrikes. Under this heading we may also include those megapodes in which a number of pairs construct the mound in which the eggs are incubated by the heat generated by fermenting vegetable tissues. These mound builders pay no attention to the exceptionally precocious young.

Immature interspecific helpers.—Although wild immature birds not infrequently attend younger individuals of their own kind, the only instances of immatures helping members of other species that have come to my notice refer to birds in aviaries. Well fed captive young, only a month or two old, often give food to the nestlings or fledglings closely associated with them in the same compartment. One of the most remarkable of these young helpers was an Eastern Bluebird, only six weeks old, which helped to nourish 15 nestlings of half a dozen kinds. A captive young Black-shouldered Kite, after rearing to independence nestlings of her own species, adopted a day-old buzzard chick and fed it until it was three times her own size.

Nonbreeding adult interspecific helpers.—No case of an innubile interspecific helper has come to my attention, and even nonbreeding mature interspecific helpers appear rarely to have been recognized. A wild male Canada Goose that guarded a brood of ducklings provides one of our few examples of this behavior. An old, unmated Wood Thrush, which in an aviary helped to feed 15 nestlings of various kinds, seems likewise to fall under this heading.

Breeding unilateral interspecific helpers.—A nonreciprocal relationship between breeding birds of distinct species is the form of helpfulness that has been most frequently reported by bird watchers everywhere. In addition to the numerous cases of helpers definitely known to be breeding, it is probable that most of the birds of un-

known status that were found feeding the young of some other species were, or recently had been, engaged in reproduction. Although usually passerines are discovered attending other passerines, the helpers and the helped sometimes represent different orders. The combinations are so diverse that one suspects that each species of altricial bird has occasionally helped every other altricial species of about the same size with which it has been associated over a wide area for many generations. Unlike some of the examples of intraspecific helpers that we have noticed, these instances of interspecific aid are too sporadic to be of importance in the economy of any species, but they give us fascinating glimpses into the psychology of birds.

Sometimes the helper is a male whose mate is incubating, as has been reported for the Eastern Bluebird, Winter Wren, Carolina Wren, Scarlet Tanager, and Oregon Junco. Such males are often so impatient to begin feeding their nestlings that they offer food to the unhatched eggs. This latter behavior I have called "anticipatory food bringing" (Skutch, 1953*a*). The feeding of a neighbor's offspring may provide an outlet for repressed energy; and in all territorial birds, the nearest nests are more likely to belong to some other species than to other individuals of the same species.

In other cases, the helpers have lost their own nestlings, or they have reared their fledglings to independence without exhausting their impulse to feed or otherwise attend young birds. Among these may be mentioned the Mourning Dove that mothered nestling White-winged Doves (*Zenaida asiatica*), the Eastern Phoebe that fed Tree Swallows, the European Blackbird that offered food to any bird who came near, the European Robins that fed nestling Song Thrushes (*Turdus ericetorum*), the male Cardinal that fed fledgling American Robins, and the Brown Towhee that nourished fledgling Cardinals. Sometimes a parent bird gives food to young not its own because its intention to feed its own offspring is temporarily thwarted, as in the case of the female American Redstart which, when her own young were held by children to be photographed, gave her billful of food to American Robins in a neighboring nest. At other times, a parent bringing food to its offspring may fly past other young birds, whose gaping mouths appeal irresistibly to parental instincts, as in the case of the Gray Wagtail that fed thrushes. The calls of a neighbor's nestlings may be similarly impelling, as in the case of the European Nuthatch that often took food to young Starlings (*Sturnus vulgaris*) in a hole three feet distant from its own nest.

More surprising are the instances of breeding birds that neglect their own nests to attend those of other species. Among these we may mention the female Tropical Gnatcatcher that became so engrossed in caring for a brood of Golden-masked Tanagers that she ignored the nest which her mate was building a few feet away, and the Blue Tits that abandoned their own eggs in order to feed European Robins in a nest built on the roof of their box.

Sometimes parent birds become helpers by accident, as appears to be true of a pair of Mountain Chickadees. Their nest in a rotting pine trunk had been separated from a hole of Williamson Sapsuckers (*Sphyrapicus thyroideus*) by a thin partition which collapsed, dropping their nest down into the sapsuckers' chamber. Thereupon, the chickadees began to feed the young woodpeckers.

The relations between the helpers and the parents of the young which they attend are various. Sometimes the helper is belligerent toward the parents, as in the case of the male Oregon Junco that fed nestling Bewick Wrens (*Thryomanes bewickii*) and the Tropical Gnatcatcher that attended a Golden-masked Tanagers' nest. More often, the parents are troubled by the presence of the uninvited assistant, and they may try to drive it away. Examples of this are the Mourning Dove at the White-winged Doves'

nest, the Eastern Phoebe at the Tree Swallows' nest, the Black-and-White Warbler at the Worm-eating Warblers' nest, and the Eastern Bluebird at the Northern House Wrens' nest. In other instances, the parents and helpers work together in concord, as happened when a Worm-eating Warbler fed nestling Ovenbirds (*Seiurus aurocapillus*), when a male Cardinal attended fledgling American Robins, and when a Brown Towhee attended fledgling Cardinals. Rarely the parents take food directly from the helper and either pass it to their nestlings or eat it themselves; Black-headed Grosbeaks accepted food from a Northern House Wren, and Yellow Warblers (*Dendroica petechia*) from Song Sparrows.

The same contrasts in the attitude of the parent birds to their assistants, and of the latter toward the parent birds, are found in intraspecific associations, and they suggest the two distinct routes by which birds are led to attend the nests of other individuals. In some species, prolonged close association between the parent birds and their offspring brings the latter into intimate contact with subsequent broods of the parent birds, in the same breeding season or, in the case of birds which pass through an innubile stage, in some following year. Most immature and innubile intraspecific helpers, and even some mature intraspecific helpers, are led in this way to assist at others' nests. In these cases, it is difficult to decide whether the nonbreeding birds are stimulated to engage in parental activities by seeing the parent birds do so or by the direct appeal of eggs or nestlings to their latent parental impulses.

The other route is that followed by most interspecific helpers and even some intraspecific helpers; these birds are not closely associated with the parent birds until accidental contact with their nest or young, at a time when they are particularly susceptible, releases parental activity, in the course of which they come into close contact with the parents themselves. The attitude toward each other of the birds thus suddenly brought together may be either friendly, hostile, or indifferent. In the first group of helpers, the social bond is primary and participation in parental offices arises secondarily from it. In the second group of helpers, the appeal to parental impulses is primary and mutual accord may in some instances develop from it, as when parents and helpers cooperate amicably in the care of the nestlings, the former sometimes even accepting food directly from their assistants. In other cases, however, participation in a common endeavor fails to overcome the antagonism between the parents and the intruding collaborators.

Mutual interspecific helpers.—These most curious cases of mutual helpfulness arise when two birds of distinct species build their nests close together or even lay in the same nest. A Rufous-sided Towhee and a Field Sparrow had nests only 18 inches apart in the same tree, and both nests contained nestlings of about the same age. The male towhee frequently fed the young sparrows and removed their droppings, and a parent sparrow likewise brought food to the nestling towhees. More often, the mutual helpers lay eggs in the same nest, and the parents of both species incubate alternately or even together, sitting side by side, or perhaps one upon the other. When successful in hatching out the mixed family, they may cooperate in brooding and feeding the nestlings. These disparate nesting partners have consisted of a Mourning Dove and a Yellow-billed Cuckoo, a Mourning Dove and an American Robin, a European Robin and a Willow Warbler (*Phylloscopus trochilus*), a European Robin and Pied Wagtails (*Motacilla alba*), a Cardinal and a Song Sparrow, and House Finches and American Robins.

Unless the nestlings of the two cooperating species hatch at about the same time, are of approximately equal size, and have similar food requirements, it is unlikely that both kinds will be successfully reared. The mixed brood of Mourning Doves and American Robins survived until they were eight days old, and I suspect that the very different

feeding responses of doves and thrushes insured that each nestling received nourishment only from its own parents. In the joint nesting of Cardinals and Song Sparrows, only the young of the larger Cardinal were fledged. When House Finches and American Robins nested together, the nestling robins smothered their smaller nest mates. But when European Robins shared a nest with Pied Wagtails, the nestlings of both species appear to have been successfully reared. No mutual partnership of this sort has proved sufficiently profitable to give rise to habitual symbiotic nesting by two species, corresponding to the intraspecific communal nesting of the anis. The fostering of the young of parasitic cuckoos, honeyguides, and cowbirds by a wide variety of other species is a wholly unilateral relationship. As in the numerous instances of birds hatching the eggs of other nonparasitic species occasionally deposited in their nests, such unintentional service to other birds falls beyond the scope of this paper. Helpers do more than incubate the eggs which some other bird has dropped into their nest, and which perhaps they do not distinguish from their own; in one way or another, they deviate from the typical breeding pattern in order to serve, or enter into close association with, individuals other than their own mate and offspring.

Intraspecific helpers not associated with reproduction.—To this group belong adult birds, unable to forage for themselves, which have remained alive and well and which have been sustained by food supplied by their companions. Recorded instances of this sort are not numerous. One of the most celebrated is that of a blind American White Pelican, alive and well in a breeding colony of its kind. Since its condition made fishing impossible, it was obviously nourished by its neighbors. Similar care of crippled or incapacitated individuals has been reported for an adult Brown Booby with only one wing, an adult Magnificent Frigate Bird in the same plight, blind Indian crows, a wounded crow attended by its companions in a hollow tree, and an adult male Black-headed Grosbeak with a deformed bill that evidently made foraging difficult. In captivity, a male European Robin fed a rival after the latter broke his leg.

Once I saw, in a band of Fiery-billed Araçaris (*Pteroglossus frantzii*) an adult, in apparently good condition, whose bill was so grotesquely deformed that it seemed impossible that it could feed itself. Apparently it depended on offerings from its companions to sustain its life. This is not improbable, since adult araçaris have been seen to feed each other (Skutch, 1958:209). But we must not too hastily conclude that because a bird's bill is misshapen it cannot forage. A Common or Bronzed Grackle (*Quiscalus quiscula*), whose upper mandible was about twice as long as the lower and otherwise malformed, managed by its own efforts to thrive for at least two years, despite this severe handicap (Bent, 1958:412).

Apparently the helpless birds I have just mentioned persuaded their companions to feed them by begging in the manner of fledglings. In species in which the male passes food to his mate, an intensification of this usual behavior, stimulated by the more persistent pleading of the hungry, helpless partner, might suffice to keep the latter alive. In the case of the Black-headed Grosbeak with a deformed bill, the female seems to have assumed the role that normally belongs to the male. Yet even in normal birds without visible defect, one occasionally notices such a reversal of nuptial feeding; I have seen it in the White-flanked Antwren (*Myrmotherula axillaris*) and in the Tawny-bellied Euphonia (*Tanagra imitans*).

Interspecific helpers not associated with reproduction.—A Raven that passed food through the bars of its cage to a free Black Vulture is my only example of this class in which both of the participants were birds. Nuptial feeding is common in the Corvidae, and possibly the well-fed captive Raven was treating the other big black bird as its

mate. But what shall we say of the free Cardinal which fed goldfish? Had this bird lost its nestlings or fledglings, and did the open mouths of the fish provide a stimulus for feeding? The motive of this Cardinal was evidently quite different from that of the Green Heron (*Butorides virescens*) that gave bread to fish in order to spear them when they approached to nibble at it (Lovell, 1958).

Helpers and the rate of reproduction.—In view of the widespread tendency of immature birds to engage in parental occupations, one may well ask why natural selection has not seized upon and elaborated this habit to increase the reproductive potential of those species in which maturity is delayed for several years, or even of more rapidly maturing species which rear two or three broods in a season. Parents with two or more yearling helpers should be able to rear twice as many young as unaided parents of the same kind; hence strains with helpers should increase more rapidly than those which lack them, finally supplanting the latter. Yet helpers are exceptional even among species which do not begin to breed until two or more years of age; and no species that I know lays more eggs than one would expect from its systematic position and environment because of the fact that helpers are available. Brown Jays, for example, lay two or three eggs in a set, although four, five, or even seven grown birds may attend the nestlings.

The answer to the foregoing question seems to be that if a higher rate of reproduction were advantageous to a species, putting the immature individuals to work at the nests of mated pairs would not be the most efficient method of achieving it. The more bustle and activity there is at a nest, the more likely it is to draw the attention of predators. In the tropical forest, where breeding birds have more enemies than in many other environments, nests rarely contain more than two eggs or young, and the parents as a rule bring large but infrequent meals, thereby minimizing the likelihood of directing hostile eyes to the nest. Helpers seem to be most frequent among birds whose eggs and young are somewhat inaccessible, as in the enclosed nests of Banded-backed Wrens and bushtits, or in those species whose size and strength enable them to repel at least the less powerful predators, as in jays. Yet even nests of the large and aggressive Brown Jays are by no means immune to predation.

If an accelerated rate of reproduction were highly advantageous to any species whose young mature slowly, it appears that this could be more efficiently achieved by hastening the advent of the adult state than by making helpers of the innubiles. Being more efficient, the former is the course which natural selection should favor. Why birds which have long been fully grown should pass from one to six breeding seasons without themselves reproducing, certainly poses a problem to one who reflects that the mammals with which we are most familiar are ready to beget offspring even before they have attained adult size. It would seem to require relatively slight physiological adjustments to advance by one or several years the attainment of reproductive maturity by all those penguins, albatrosses, fulmars, gulls, terns, swifts, crows, jays, and others which now pass one or more breeding seasons as innubiles. The existence of this large nonbreeding class is impressive testimony that its members are not needed as breeders; that, in fact, it would be disadvantageous to the species to have them engage in reproduction. The presence of helpers, and especially of innubile helpers, is, then, one more link in the lengthening chain of evidence pointing to the conclusion that birds have a considerable store of unused reproductive potential and that their reproductive rate has, in many cases, been delicately adjusted to the conditions of their lives rather than pushed to the limit of their power to rear offspring, as some have contended (Skutch, 1949; 1953c).

AN ANNOTATED LIST OF HELPERS

Pelecanus erythrorhynchus. White Pelican. An old, blind pelican was found alive in a breeding colony. Since it could not feed itself, it must have been fed by its neighbors (Baird and Stansbury, 1852:193; frequently quoted by other authors).

Sula leucogaster. Brown Booby. An adult that had lost a wing was kept alive by the food which its neighbors in a breeding colony supplied to it (Murphy, 1936).

Phalacrocorax carbo. Great or European Cormorant. Nestling cormorants sometimes feed each other, and they help to work loose material into the nest (Kortlandt *in* Armstrong, 1947:192; Nice, 1943:79).

Fregata magnificens. Magnificent Frigate Bird. An adult lacking a wing was supplied with food by its neighbors in a breeding colony (Murphy, 1936).

Phoenicopterus ruber. American Flamingo. Young flamingos feed each other (Chapman *in* Armstrong, 1947:192).

Branta canadensis. Canada Goose. A wild male goose accompanied and guarded a brood of 13 (domestic?) ducklings, along with the female duck, who "seemed to welcome the gander." He followed the family in the rear and stayed with them all day (Messenger, 1949).

Aix sponsa. Wood Duck. Two females laid in the same nest box and incubated side by side. For several days, each had her own position in the box; but later they shifted about, showing no attachment to any particular part of the box or cluster of eggs (Bellrose, 1943).

Melanitta deglandi. White-winged Scoter. "In all species of ducks, one parentless brood may on occasion join another in its entirety, and the process may repeat itself until finally a large aggregation results. An extreme case is that of a white-winged scoter that I saw with eighty-four young, all under two weeks of age! Lesser scaups [*Aythya affinis*] are commonly seen with broods of twenty or more, sometimes with two or more hens attending such combined families" (Hochbaum, 1960:56).

Elanus caeruleus. Black-shouldered Kite. A captive fledgling fed and brooded nestlings of her own kind, rearing them from the age of one day to independence. She also adopted a day-old buzzard, which she continued to feed for nearly two months, until it was three times her own size. She "brooded" a red notebook and other inanimate objects of the same color (van Someren, 1956:68-69).

Megapodius freycinet. Scrub Fowl. A mound, in which the eggs are incubated by heat generated by the fermentation of a great mass of vegetation kicked together by the birds, is sometimes attended by several pairs (Frith, 1956:633).

Gallinula chloropus. Common or Florida Gallinule, Moorhen. On a weedy pond near Cartago in the Costa Rican highlands, I found, on July 1, 1952, a family consisting of two adults, two full-grown young birds in grayish plumage with dark bills and foreheads, and four downy chicks, which kept up a constant peeping. The full-grown young birds seemed to give as much attention to them as the parents did, and once one of the former appeared to pass food to a downy chick. The feeding of younger siblings by gallinules has also been reported by McIlhenny (Nice, 1943:79) and for the British form by Finn (Armstrong, 1947:192) and by Grey (1927:155-157). Grey watched the parents give pieces of bread to full-grown young hatched in May, who then passed this food to the downy chicks born in July. When a parent gave bread directly to a chick, one of the older young took it from the downy one's bill and then replaced it there.

Fulica atra. European Coot. The feeding by immatures of still younger birds has been reported by Ruthke (Nice, 1943:79).

Laterallus leucopyrrhus. Rail. In captivity, young individuals fed younger siblings (Meise *in* Nice, 1943:79).

Charadrius alexandrinus. Snowy or Kentish Plover. Some birds of both sexes take an interest in chicks of other birds of their own and related species and may even brood them (Walters, 1959).

Recurvirostra avosetta. European Avocet. Parents brood recently hatched chicks of their neighbors (Selous, 1927:223-224).

Sterna paradisaea. Arctic Tern. Some of the younger males, unable to breed because of a shortage of females, attached themselves to nesting pairs and helped to feed the chicks (Cullen, 1957). In time of scarcity, when mortality among young is high, terns of various species feed chicks belonging to other individuals (Palmer *in* Armstrong, 1947:190).

Uria aalge. Common Murre or Guillemot. Bereaved adults, and even those with chicks, brood

and feed others' chicks; but the parents of the latter resent neighbors' attentions to their young. Parents that have lost chicks also "feed" imaginary ones (Perry, 1946:174-200).

Columba livia. Rock Dove or Domestic Pigeon. A fledgling about 25 days old regurgitated food to a younger companion. Another young pigeon, about a month old, took sticks to the nest where its mateless mother incubated and presented them to her as an adult male does to his mate. After some initial difficulties, it daily incubated its mother's eggs for about two hours at a stretch (Goodwin, 1947).

Zenaidura macroura. Mourning Dove. One of these doves brooded and fed nestling White-winged Doves (*Zenaida asiatica*) a few days old, which had been neglected through most of the day by their own parents. When at last the female White-winged Dove returned in the late afternoon, she fought and drove away the fostering Mourning Dove. The latter, however, continued to minister to the young White-wings until they fledged. Apparently her own eggs had failed to hatch. In aviaries, Mourning Doves and several other kinds of doves are quick to adopt and assist in the care of young doves of any species (Neff, 1945). See also Yellow-billed Cuckoo and American Robin.

Myiopsitta monachus. Gray-breasted Parakeet. Many pairs unite to build a huge arboreal structure of interwoven thorny twigs. This communal nest may weigh a quarter of a ton; it contains many chambers, apparently each the nest of a single pair (Hudson, 1920, 2:30-33).

Coccyzus americanus. Yellow-billed Cuckoo. This species and the Black-billed Cuckoo (*C. erythrophthalmus*) often lay eggs in each other's nests, as likewise in the nests of a number of other small birds, possibly because their own poorly built structures have capsized while their eggs were ready for deposition. On one occasion, a Yellow-billed Cuckoo laid two eggs in a nest of the American Robin (*Turdus migratorius*), in which the robin also laid an egg. Then a Mourning Dove added two eggs to the mixed set and incubated along with the cuckoo. Both birds were found sitting side by side on the eggs of three kinds (Bent, 1940:56).

Crotophaga sulcirostris. Groove-billed Ani. Although about half the nests belong to single pairs, two, three, or rarely more pairs may join in building a communal nest, in which all the females lay their eggs in a single mass. All the cooperating parents take turns at incubating and brooding, one at a time, and a single male takes charge of the nest through the night. All the parents feed the nestlings, without distinguishing their own. Beginning at the age of 72 days, a young ani of the first brood fed and defended nestlings of its parents' second brood (Skutch, 1959).

Crotophaga ani. Smooth-billed Ani. In its communal nesting arrangements, this species resembles the Groove-billed Ani, but the cooperating group may be larger, containing up to five females in some instances. At the age of 48 days, a young bird of the first brood fed nestlings of the second brood (Davis, 1940). When about six weeks old, a hand-reared ani carried and arranged sticks and straws (Merritt, 1951:229).

Crotophaga major. Greater Ani. This large ani nests communally, like the smaller species (Davis, 1942).

Guira guira. Guira Cuckoo. Pairs may nest alone, or several may attend a communal nest, as in the anis (Davis, 1942).

Caprimulgus europaeus. Nightjar. An extra adult helped to feed nearly grown young (Stülken and Brüll, 1938).

Chaetura pelagica. Chimney Swift. Extra birds frequently assist parents in incubation, brooding, and feeding the nestlings. Some nests have two of these helpers simultaneously, in addition to the two parents. The assistants are of both sexes but more often males than females. Some are yearlings, others old birds apparently in their last year of life; but some are of intermediate age and engage in active reproduction in later years. The helpers roost clinging to the wall of the chimney or air shaft near the nest, in company with the parent or parents who are not incubating or brooding. Sometimes they roost with the fledglings (Dexter, 1952; Sherman, 1952:47, 56).

Lophoceros melanoleucos. Crowned Hornbill. After the emergence of the female from the nest cavity in which she is sealed from the start of laying until the nestlings are half grown, the young birds, working from within the hole, plaster up the doorway again, leaving a gap just wide enough for the parents to pass food to them. Captive nestlings placed in a box with a small opening proceeded to reduce its size with mud supplied to them, with particles of food, and with their own drop-

pings. They attended efficiently to the sanitation of their box. One of them proffered food to its nest mates (Moreau and Moreau, 1940:641-644; Moreau, 1936:25-26).

Lophoceros deckeni. Red-and-White-billed Hornbill. After the emergence of the mother from a nest hole, two nestlings, 21 to 25 days old, replaced the plaster seal with material they found inside the hole (Moreau, 1936:22-24).

Bycanistes subcylindricus. Casqued Hornbill. On several occasions, intruding individuals offered food to a female of the same species who was enclosed in her nest hole in a tree. When the mate of the enclosed female returned, he chased the trespassers away (Kilham, 1956:26-27).

Buccanodon leucotis. White-eared Barbet. In tropical Africa, four adults brought food to a hole containing four nestlings. Since other nests of this species contained only two or three eggs, this is, apparently, an instance of communal nesting (Moreau and Moreau, 1937:171-172).

Lybius albicauda. Pied Barbet. In addition to the parents, two birds occasionally brought food to nestlings (van Someren, 1956:209-212).

Pteroglossus torquatus. Collared Araçari. Early in the year, six grown individuals of this small toucan slept in a high, inaccessible hole in a tree in the Panamanian forest. After eggs were laid in this hole, a single individual passed the night in it. Later, when the eggs hatched, there were, in addition to the nestlings, five lodgers, all of whom brought food to the young, of which there were at least three. These attendants probably consisted of the two parents and three innubile helpers (Skutch, 1958:201-207).

Tripsurus chrysauchen. Golden-naped Woodpecker. As I described in an earlier paper (1948), fledglings return to sleep with their parents in the hole in which they were reared. The entire family may continue to lodge together in this hole, or in others built to replace it, until the following breeding season, when the parents move into a newly finished hole and the young of the preceding year depart. In El General, this woodpecker usually rears a single brood; but in 1960, after an exceptionally early first nesting, a pair undertook to raise a second brood in a neighboring hole. The three young females of the first brood slept with the two parents in the nest cavity while the eggs of this later brood were being incubated and the nestlings were growing up. Apparently the young birds did not help their parents to incubate the eggs with which they were thus closely associated, but after the eggs hatched, they sometimes entered the hole with the nestlings by day and probably brooded them. This seemed at first to upset the parents, and the adult female was mildly antagonistic toward the young females when they approached the nest. After the nestlings began to look through the doorway, at least two of the young females, then in their fourth month, brought small particles of food. But they seemed to fear the grasping thrust with which older nestlings take their meals. Instead of delivering their offerings from the outside with head turned sideways to facilitate its transfer, as the parents did, after considerable hesitation the young females pushed quickly through the doorway with their heads bent down to avoid the nestlings' bills. Since all the food which the young woodpeckers brought was taken inside, I could not learn how much of it the nestlings actually received. It was evident, however, that the parental behavior of these helpers was imperfectly developed. They brought to feathered nestlings particles of the size that should be given to newly hatched ones, and they did not present this food in the proper manner.

After two young of this second brood were fledged, the hole in which they were reared was entered each evening by seven woodpeckers, including the two parents, three females of the first brood, and a male and a female of the second brood. Soon the stub that contained this hole fell, and the parents proceeded to carve a new dormitory. At least one female of the first brood helped in this work; and even the male of the second brood, now about 57 days old, three weeks out of the nest, and still receiving occasional meals from his parents, took part in the undertaking. I could not see how much carving he did inside the cavity, but one morning he threw out ten billfuls of chips in about half an hour. Each billful was smaller than those which adults customarily remove while carving.

In its family life, the Golden-naped Woodpecker stands between species of *Centurus*, whose habits I briefly outlined in an earlier paper (1943), and the following species.

Balanosphyra formicivora. Acorn Woodpecker. Leach (1925) reported that in California a whole flock of these woodpeckers participates in a nesting. Apparently more than two individuals help to carve the nest hole and take turns incubating the eggs. At least five, and possibly more, brought food to a single brood of nestlings. In Costa Rica, this woodpecker has similar customs. In an inaccessible

nest, four males and one female were taking turns at incubation and changing over very frequently. At another nest, at least two males and one female were incubating. At yet another nest, at least two males and two females were bringing food to an undetermined number of well-grown nestlings (Skutch, 1943, and later observations). Unfortunately, neither Leach nor I was able to learn the contents of the nests that we watched. Without this information, we cannot decide whether several pairs nest communally, as in anis, or a single breeding pair is assisted by helpers.

Phacellodomus rufifrons. Rufous-fronted Thornbird. In Venezuela, four birds were seen working on a bulky nest of interwoven sticks that had three entrances, apparently giving access to separate chambers (Gilliard, 1959:19-20).

Sayornis phoebe. Eastern Phoebe. A female whose first brood was becoming independent brought food to nestling Tree Swallows, continuing this for about a week, while the parent swallows tried to drive her away (Deck, 1945).

Progne subis. Purple Martin. At the age of 54 days, a hand-reared female tried to brood nestlings and soon began to bring insects to them (Richmond, 1953:245-246). When a female parent was carried away for a homing experiment, the mother of a brood in an adjoining compartment in the bird house fed the absent mother's nestlings as well as her own. The mate of the absent female accepted this assistance without protest (Southern, 1959).

Delichon urbica. House Martin. As many as 14 martins may cooperate in building a single nest. Four or more individuals often feed a single brood. Some of these attendants are the young of earlier broods (Bent, 1942:435-436; Witherby *et al.*, 1938, 2:236).

Petrochelidon pyrrhonota. Cliff Swallow. Three individuals sometimes build together and take turns incubating the eggs (Bent, 1942:474).

Hirundo rustica. Barn Swallow. In both Europe and North America, young swallows appear not infrequently to feed the nestlings of their parents' subsequent brood. Sometimes they may even help to build the nest for this brood; in one instance they engaged in this work about a week after they took wing. Occasionally a third adult helps to feed the nestlings (Nice, 1943:79, 243; Armstrong, 1947:191-192).

Riparia riparia. Bank Swallow or Sand Martin. The excavation of burrows is a communal activity, the climax of an elaborate aerial display, in which many swallows participate. The number of holes is at first approximately the same as the number of individuals present. At one display, from three to six birds may be active at a single burrow, while at the next display, excavation is carried on at quite different holes. The same swallow may move from hole to hole, digging at several in succession (Hickling, 1959).

Iridoprocne bicolor. Tree Swallow. More than two attendants at a nest are not uncommon. The nestlings in one box were attended by four to six adults, of which at least three were males and at least one a female. In another locality, at least three broods had an extra attendant, a female whose own young had died (Bent, 1942:387).

Tachycineta thalassina. Violet-green Swallow. Sometimes two or even three females bring food to the young in a single nest (Shirling *in* Bent, 1942:378-379).

Corvus corax. Common Raven. In freezing weather, a captive in a zoo passed food through the bars of its cage to a free Black Vulture, *Coragyps atratus* (Davis, 1952).

Corvus monedula. Jackdaw. A captive young bird fed younger individuals (Strauss *in* Nice, 1943:79).

Corvus brachyrhynchos. American Crow. Three crows were watched building one nest in Boston, and three were seen feeding the young in one nest in Connecticut. Nests containing two sets of eggs have been reported (Forbush, 1927:395).

Corvus sp. "Indian crow." "Mr. Blyth, as he informs me, saw Indian crows feeding two or three of their companions which were blind; and I have heard of an analogous case with the domestic cock" (Darwin, 1871, ch. 4).

Corvus sp. Crow. "Brehm himself saw two crows feeding in a hollow tree a third crow which was wounded; its wound was several weeks old" (Kropotkin, 1902:59).

Psalorhinus mexicanus. Brown Jay. The bills of young birds are yellow, and they turn black gradually and irregularly, providing patterns which facilitate the recognition of individuals. Pied-billed innobles, apparently about a year old, assist the darker-billed parents in the duties of the nest,

sometimes bringing sticks during construction or feeding the incubating female, often bringing food to the nestlings, and guarding them, at times more zealously than the parents. At a nest with eggs, at least two helpers fed the incubating female; and at four other nests with young, one, two, three, and five helpers were distinguished (Skutch, 1935; 1960:231-257).

Calocitta formosa. White-throated Magpie-Jay. An incubating female was attended by at least two, and probably more, other individuals, who fed her 47 times in 13¾ hours, keeping her so well supplied that she found it unnecessary to forage for herself (Skutch, 1953*d*; 1960:258-259).

Cyanocorax dickeyi. Tufted Jay. Three individuals were interested in a nest, and two of them sat side by side on the eggs for a short while (Moore, 1938:238-239).

Aphelocoma ultramarina. Mexican Jay. Two pairs sometimes breed in the same tree, and three or four birds may join in building a nest (Bent, 1946:118-123). Seven or eight individuals, including two yearlings, collaborated in building a nest (Gross, 1949:242-244).

Aphelocoma coerulescens. Scrub Jay. A nest with two young was attended by three adults, at least two of whom brooded (Grimes, 1940).

Cyanocitta cristata. Blue Jay. "Occasionally, in winter or early spring, one of these birds is seen to feed a companion. They are said to care for the aged and infirm" (Forbush, 1927:380).

Corcorax melanorhamphus. White-winged Chough. These Australian corvids live in flocks of up to 12 individuals. The whole group may join in building the nest, a very bulky structure that is repaired year after year (Mathews, 1925-1927:414-420).

Parus major. Great Tit. A male fed the nestlings of a female Great Tit whose mate had died. A pair of these tits adopted eight fledglings which were the offspring of another pair. A young bird placed food within reach of a young male of the same brood whose leg was broken (Howard, 1952:25, 31, 102).

Parus caeruleus. Blue Tit. A pair built a nest in a box, on top of which a pair of European Robins already had a nest. The female robin laid five eggs and the tit laid three. When the robin's eggs hatched, the tits covered their own eggs with feathers and fed the young robins. At first there was a little fighting, but soon the two pairs settled down to attend the nestlings in concord. After the robins were fledged, the tits laid another set of seven eggs over the original three and raised a brood (Lonsdale in Williams, 1942:246-247).

Parus bicolor. Tufted Titmouse. Parents rearing a second brood were assisted in feeding the nestlings by two other titmice, apparently young of their first brood (Wight in Laskey, 1957:142). For two weeks, a banded unmated yearling helped to feed the three nestlings of its female parent, whose mate had died and who was now paired with another male. Although its attendance was less regular than that of the nestlings' parents, it brought food at least 89 times, while the male brought food at least 120 times and the female 126. The female parent was friendly with the helper, but the male tried to drive it away (Brackbill, 1958).

Parus gambeli. Mountain Chickadee. A pair fed nestling Williamson Sapsuckers (*Sphyrapicus thyroideus*) which were also being attended by their own parents. This situation apparently resulted from the collapse of the partition which separated the holes of these two species in the same decaying pine trunk (Russell, 1947).

Aegithalos caudatus. Long-tailed Tit. There are many records of nests at which more than two individuals were in attendance. Some of these nests held unusually large sets of eggs, which had probably been laid by two females; but often the nests with extra attendants had sets of normal size. Although most often there was only one extra bird, sometimes there were two. At one nest with a set of normal size there were certainly two and possibly four helpers. Usually these assistants feed the nestlings, but sometimes they are present during incubation. It is probable that many of these helpers are breeding birds that have lost their own brood and fail to renest because of the shortness of the tits' breeding season. In the absence of territorial defense, they readily attach themselves to parents with young (Lack and Lack, 1958:14). At one nest the attendants were two males and one female, and all three were feeding the ten young in complete harmony (Robertson and Porter, 1952). Immatures also feed younger broods (Morbach in Nice, 1943:79).

Psaltriparus melanotis. Black-eared Bushtit. In the breeding season, males are greatly in excess of females, and those who do not find mates assist the mated couples at the nest. At times they bring downy material to the pensile pouch while incubation is in progress, but far more often they help to attend the nestlings, feeding and even brooding them. At three nests there were one, one, and three

male helpers, most of whom slept in the cozy pouch along with the parents and the four nestlings (Skutch, 1935; 1960:211-225).

Psaltriparus minimus. Common Bushtit. At some nests a third individual helps the parents to incubate and to feed and brood the nestlings (Addicott, 1938).

Sitta pygmaea. Pygmy Nuthatch. Of 36 nests in California, eight were attended by three individuals. The extra individual was invariably a male, usually a yearling but sometimes older, who was not actually mated to the female. This helper assisted in nest construction, in feeding the female while she incubated or brooded, in feeding the nestlings, and cleaning the nest. He also fed the young birds after their emergence from the nest, and at all stages of the breeding cycle he roosted in the nest with the other members of the family. In this species, parents and offspring continue to sleep together in a suitable cavity over the winter. Many of the helpers are young males who have been for many months thus closely associated with their parents. Their failure to rear families of their own is evidently caused by the paucity of females, since the sex ratio is strongly unbalanced in favor of the males. When two family groups forage together, an adult of one family sometimes feeds fledglings of the other family. Up to six individuals have been found excavating a nest cavity, which was later used by a single pair (Norris, 1958:177, 197, 240). Nine nestlings, not an abnormally large brood, were fed by four adults (Bleitz, 1951).

Sitta pusilla. Brown-headed Nuthatch. As in the Pygmy Nuthatch, there are far more males than females in this species. An unmated male sometimes assists a mated pair at all stages of the nesting, although the helper was not found sleeping in the hole with the parents when they had eggs or nestlings. A pair which lost its nest helped to feed the nestlings of a neighboring pair (Norris, 1958:178, 187, 191). Houck and Oliver (1954) studied a nest in which seven young were fed by four adults, which they believed to be two pairs.

Sitta europea. European Nuthatch. When a pair of nuthatches nested three feet away from a pair of Starlings (*Sturnus vulgaris*), one of the former often carried food into the nest box of the latter. It also removed droppings of the nestling Starlings (Powell, 1946).

Certhia brachydactyla. Garden Tree Creeper. Captive young birds fed still younger ones (the Heinroths in Nice, 1943:79).

Argya malcolmi. Large Gray Babbler. As soon as fledglings leave the nest, they join in a band and are apparently fed and protected by the band as a whole. As a rule, only the parents attend young still in the nest, but an exception was noticed at a late nest with two nestlings. Here, five adults with food in their bills were seen in the nest tree at one time, and three of them were at the nest feeding the young (Hutson, 1947:574-575).

Armstrong (1947:191-192) mentions several other species of babblers in which small bands cooperate in building the nest or attending young, but details are not available to me. In the Jungle Babbler or "Seven Sisters" (? *Turdoides striatus*) six adults fed three young in a nest (Lowther, 1951).

Campylorhynchus zonatus. Banded-backed Wren. In the nonbreeding season, these large wrens live in family groups, which lodge in bulky covered nests, sometimes as many as 11 occupying the same dormitory. In the following breeding season, some of these birds remain with the mated pair and help them to attend the nest. At a nest with three nestlings, there was a single helper; at another nest, with five young, there were certainly two and possibly five attendants bringing food, in addition to the two parents. The status of the helpers is not known, but apparently they are innubile yearlings (Skutch, 1935; 1960:186-201).

Thryothorus ludovicianus. Carolina Wren. A male whose mate was incubating in a nest box fed not only her but likewise young Great Crested Flycatchers (*Myiarchus crinitus*) in a neighboring box (Wight in Laskey, 1948:118).

Troglodytes troglodytes. Winter or European Wren. A pair adopted fledglings of their own kind which had been hatched and partly reared by a pair of Great Tits. A wren fed two Spotted Flycatchers (*Muscicapa striata*) after they had left their nest which was close to that of the wren. Another wren fed nestling Great Tits while his mate incubated, continuing to do so at least four days. Winter Wrens have also been known to feed young Willow Warblers (*Phylloscopus trochilus*) and Linnets and to nourish a European Cuckoo (*Cuculus canorus*) that was attended by Hedge Sparrows, *Prunella modularis* (Armstrong, 1955:104-105, 233-234, 242). A wren fed nestling Coal Tits (*Parus ater*) that were nearly ready to leave their nest box, and twice it passed food to a parent of the tits (Betts, 1958:427-428).

Troglodytes aedon. Northern House Wren. A wren gave food to parent Black-headed Grosbeaks of both sexes while they brooded their nestlings; the grosbeaks ate some of this food and fed some to the nestlings. After the young grosbeaks left the nest, the wren fed them directly. A few days later, this wren brought food to a family of House Sparrows, *Passer domesticus* (Hills *in* Bent, 1948:125-126).

Troglodytes musculus. Southern House Wren. Fledglings newly emerged from the nest are, as the day ends, led by their parents to sleep in some sheltered nook, sometimes in the nest space itself. If the young continue to lodge in the nest space, the parents usually evict them about the time the following brood hatches; but sometimes they refuse to be driven away and sleep close to the nestlings. In these circumstances, they may help to feed their younger brothers and sisters. In one family, two immatures of the first brood attended nestlings of the second brood, and the single survivor of the second brood brought food to the third brood, beginning this activity at the age of 54 days. While attending the second brood, the young female of the first brood became antagonistic to her mother, who drove her away after a day of fierce fighting (Skutch, 1953*b*:137-140).

Dumetella carolinensis. Catbird. A brood of orphaned Cardinals was fed and mothered by a Catbird. Another Catbird fed a half-grown flicker (*Colaptes*) that had been dislodged from its nest and separated from its parents in a severe storm (Bent, 1948:328).

Turdus merula. European Blackbird. After rearing two of her own young, a female blackbird continued for two or three weeks to offer food to any bird that came near, and an adult European Robin was among those who accepted (Lack, 1953:99). On two occasions, a fledgling, that strayed rather far from its nest in the first day after leaving it, came into the territory of a neighboring pair that also had fledged young. In both cases, the male of the new pair promptly adopted the wanderer and fed it until it could care for itself; it was never seen to be fed by its own parents. Usually, however, young that beg from strange adults receive nothing. When two families have become mixed, the parents have always been seen feeding only their own young (Snow, 1958:22).

Turdus migratorius. American Robin. Fledglings that become separated from their parents are sometimes adopted by other adults (Young, 1955:339). Captive young robins fed still younger birds of other species (Favell *in* Nice, 1943:79). Robins sometimes share a nest with another individual, of the same or a different species. The most curious of a number of instances that have come to my attention is that of a robin and a Mourning Dove, each of whom laid two eggs in the same robin's nest. They took turns incubating, then fed and brooded the nestlings until they were eight days old. On the following day, the four nestlings died (Raney, 1939). A robin and a Catbird each built a nest in the same clump of lilacs. Both took turns at incubating the Catbird's eggs, and when the young hatched they were brooded by both the robin and the Catbird (Bent, 1948:328). See also House Finch.

Hylocichla mustelina. Wood Thrush. Nine days after her first brood left the nest, a female fed a strange young bird which with its parents had entered her territory (Brackbill, 1943:79). In an aviary, an old, unmated thrush helped to feed 15 nestlings of various species, including Wood Thrushes, Veeries (*Hylocichla fuscescens*), Bobolinks (*Dolichonyx oryzivorus*), Cardinals, and orioles. Her co-worker was the young Eastern Bluebird mentioned under that species (Ivor, 1944*b*).

Hylocichla ustulata. Swainson Thrush. A thrush assisted in feeding nestling American Robins, bringing food to the nest at least 12 times in four hours. The parent robins were present (Jewett *in* Bent, 1949:167).

Hylocichla minima. Gray-cheeked Thrush. Three adults fed the young in one nest (Wallace *in* Bent, 1949:205).

Sialia sialis. Eastern Bluebird. Five birds of the first brood, all less than two months old, diligently cared for the four nestlings of the second brood, beginning when the latter were three days old. These helpers also cleaned the nest (Laskey, 1939:28). Other instances of bluebirds feeding younger siblings are cited by this author and by Nice (1943:79). A six-week-old female bluebird fed young Wood Thrushes, Veeries, Bobolinks, Cardinals, orioles, and a cowbird, 15 in all, which were being hand reared in the same aviary. When slightly older, this same female helped to feed and to brood a nestful of young Eastern Bluebirds, sometimes sitting in the nest beside the female parent (Ivor, 1944*b*). An adult male fed nestling Northern House Wrens, upsetting their parents, until his mate hatched young wrens, when he transferred his attention to his own offspring (Forbush, 1929).

Sialia mexicana. Western Bluebird. Young birds fed the next brood of their parents (Finley, 1907).

Sialia currucoides. Mountain Bluebird. Three young birds of the first brood fed their siblings of the second brood (Mills, 1931:9).

Oenanthe oenanthe. Wheatear. In two instances, young birds of the first brood helped their parents to feed the second brood (Nicholson, 1930:306; Wynne-Edwards, 1952:378). On Baffin Island, a fully adult male, somewhat less boldly colored than the male parent, helped a mated pair to feed seven nestlings. Once the helper was mildly chased by the male parent (Sutton and Parmelee, 1954:298-299).

Phoenicurus ochrurus. Black Redstart. A second adult male, in better plumage than the father, helped to feed young and clean the nest. The parents, although not hostile, were disturbed, and "their efficiency in feeding the nestlings was impaired" (Ashby *in* Nice, 1943:243).

Erithacus rubecula. European Robin. Parents of fledglings sometimes feed strange fledglings, even those that differ considerably in age. Robins that had lost their own young fed a brood of nestling Song Thrushes (*Turdus ericetorum*). Other robins have fed young Song Thrushes, Blackbirds, and, in several instances, European Wrens. When two males were placed in the same aviary, they fought often, but after one broke his leg, his rival fed him (Lack, 1953:98-99, 82; Armstrong, 1947:168; 1955:233). A story told by Eckermann in his "Conversations with Goethe" has been frequently quoted. He found two newly fledged wrens and wrapped them in a handkerchief to take home, but they escaped while he was passing through a wood. Three days later, he found them in a robin's nest, being fed together with the nestling robins. Evidently the wrens, when seeking a snug lodging for the night as is their habit, found the robin's nest, entered it, and were accepted by the parent robins. "A robin and a willow warbler were found, each sitting on six eggs in a nest built by the latter species, and another pair raised a combined brood with a pair of pied wagtails [*Motacilla alba*]" (Lack, 1953:86).

Sylvia communis. Common Whitethroat. Captive young birds fed still younger ones (the Heinroths *in* Nice, 1943:79).

Malurus cyaneus. Blue Fairy Wren. Of 18 breeding groups that were color-banded, 12 consisted of one male and one female only. Of the remaining six, four had a second male, one had both a second male and a second female, and one had two males and a female in addition to the mated pair. All these birds were entering their second year, if not older, and all were in full breeding plumage. At these six nests, each of the extra birds helped the parents to feed the young, both before and after they fledged. This was true even of the group with five attendants. Besides this assistance from other older birds, the young of earlier broods frequently feed their more recently fledged siblings. In this multiple-brooded species, the female, occupied with a new nest, may cease to feed the young after they have been out of the nest about ten days; and as the fledglings are still dependent, care by other attendants is important to them. Moreover, if a parent is killed, the helpers may rear the brood (Rowley, 1957).

Malurus lamberti. Variegated Fairy Wren. "This species is double-brooded, and very often the young of the first brood assist the parents in feeding those of the second" (Cayley, 1949:42). "A young male helps nearly every pair . . . to feed their young" (Armstrong, 1947:192, citing Waterhouse).

Malurus amabilis. Lovely Fairy Wren. At one nest, a male and three birds in female plumage fed the young, and all the attendants gave a distraction display simultaneously (Cayley, 1949:51, 55).

Malurus splendens. Splendid Fairy Wren. "At one nest, a single male and two females or immatures fed the young; at another, two fully plumaged males and only one female; while elsewhere there appeared to be only one bird of each sex" (Warham, 1954:138).

Poliophtila plumbea. Tropical Gnatcatcher. A female fed and brooded two nestlings of the Golden-masked Tanager and likewise cleaned the nest. As days passed, she became increasingly hostile to the parent tanagers, devoting more time to her futile attempt to keep these slightly larger birds away and less to attending the nestlings. The parents usually ignored her, unless she became very annoying, when they chased her mildly. Her attendance at the nest continued at least 12 days and was terminated only by the nestlings' departure. While the female gnatcatcher was so engaged, her mate built a nest in the same tree without her help, but she apparently failed to lay in it. He, in turn, took no interest in his neighbors, the tanagers (Skutch, 1960:49-52).

Muscicapa hypoleuca. Pied Flycatcher. "Helpers that are strangers sometimes associate with feeding pairs without being driven off" (von Haartman, 1956:464). A male was attending alone nestlings that had lost their mother. A strange female arrived and, despite mild attacks by the male, helped to bring food to the young. When strange young flycatchers, already self-supporting, rested atop an experimental nest box in which hungry nestlings called for food, but were inaccessible to their parents, the latter sometimes fed these strangers (von Haartman, 1953:157, 162).

Motacilla cinerea. Gray Wagtail. As a parent wagtail flew over a brood of young thrushes, they opened their mouths, whereupon the wagtail faltered in flight, turned, alighted, and gave all its food to them (Pike in Armstrong, 1947:61).

Motacilla capensis. Cape Wagtail. A third individual, possibly the young of an earlier brood, sometimes took a turn at incubating the eggs of a mated pair (Skead, 1954:98).

Anthus trivialis. Tree Pipit. Captive young birds fed still younger ones (the Heinroths in Nice, 1943:79).

Dulus dominicus. Palm-Chat. Bulky nests of interwoven sticks containing several chambers, each probably occupied by a breeding pair, are built by the combined exertions of a small flock (Wetmore and Swales, 1931:347-349).

Artamus maximus. Papuan Wood-Swallow. Three nestlings were fed by four or five adults (Gilliard, 1958:304).

Cracticus nigrogularis. Pied Butcherbird. An individual in immature plumage brought food to a nest which was also attended by two birds in adult plumage (Thomas, 1951).

Prionops poliocephalus. White Helmet Shrike. Several nests may be built close together, and sometimes two females lay in the same nest. The members of a small flock share incubation and feeding the young (Gilliard, 1958:298).

Prionops plumata. Spectacled Shrike. Four birds out of a flock of six brought material to a nest which the flock was building (Gilliard, 1958:299).

Eurocephalus rüppellii. White-crowned Shrike. Two or more females take turns on the eggs (Moreau and Moreau in Armstrong, 1947:192).

Meliphreptes lunulatus. White-naped Honeyeater. Two pairs of adults fed one lot of young. In another instance, two obvious sets of eggs were found in one nest (Mathews, 1924:250).

Cyanerpes cyaneus. Blue Honeycreeper. On April 23, 1958, my wife saw a male in full nuptial attire give food to a fledgling Scarlet-rumped Black Tanager on the feeding shelf beside our house. For the next three days, the brilliant honeycreeper continued to attend the tanager, which was at least twice his size, giving it chiefly pieces of banana or plantain from the shelf and sometimes insects caught in the foliage. Again and again, this strange pair returned to the feeding shelf; and the honeycreeper stuffed the tanager with fruit, once passing it six billfuls of banana in rapid succession. The honeycreeper insisted on pushing his long, sharp bill well into the throat of the short-billed tanager, who seemed not to relish this method of delivering food. When sated, the young tanager would turn its head away, whereupon the honeycreeper would flit over its back from side to side, presenting the morsel alternately on the right and on the left, until the tanager flew away with its attendant following. Often the young bird pursued the honeycreeper through the neighboring trees, begging; but when the attendant started off on a high flight, the tanager, a member of a species which does not travel so high and far, did not follow. The tanager was beginning to feed itself, and it also received at least occasional food from a male of its kind, probably its parent. It seemed, however, to prefer the attentions of the more complaisant honeycreeper. No female tanager was seen to feed the fledgling.

Dacnis cayana. Blue or Turquoise Dacnis. In May, 1959, I found a nest of this honeycreeper 18 feet up in a guava tree close by my house. It was a light-colored open cup attached by its rim (not a covered structure as has been stated in print), excellently concealed by clustering foliage. While the female incubated her two white, speckled eggs, her mate sometimes fed her, and a second male, also in full nuptial attire, was sometimes nearby. After one of the eggs hatched, both males helped the female to feed the nestling. One male sometimes mildly chased the other; yet at other times they were at the nest together with food. When I made visits of inspection, both protested my intrusion along with the female, all uttering low, weak notes. Although this may have been a case of polyandry, I think it probable that the second male was a helper rather than another mate of the female. One of the males associated with her far more closely than the other.

Mniotilta varia. Black-and-White Warbler. One of these warblers repeatedly fed nestling Worm-eating Warblers, although the parents attacked him when he approached the nest. Once they tore food from his bill and themselves gave it to the young. The helper gave a distraction display when the observers visited the nest (Rea, 1945). A pair of Black-and-White Warblers fed a young Ovenbird (*Seturus aurocapillus*) that had recently left the nest and had apparently become separated from its parents. They cared for the fosterling for several days (Kendeigh, 1945:147).

Helminthos vermivorus. Worm-eating Warbler. Over a period of at least five days, a Worm-eating Warbler fed four nestling Ovenbirds and sometimes cleaned the nest. Although the helper and the female parent were occasionally at the nest together, no hostility was noticed (Maciula, 1960).

Oporornis formosus. Kentucky Warbler. At one nest, a second male, which seemed to be abnormal, brought food to the incubating female, although occasionally he was chased by another male that sang better and seemed to be her mate (De Garis, 1936:423).

Setophaga ruticilla. American Redstart. While young redstarts were being photographed in the hands of children, the male parent brought them food, but the more timid female gave her food to young American Robins in a nest 25 feet away (Allen *in* Williams, 1942:246). A nest with a double set of eggs was attended by two females, while two males were in the vicinity (Wood *in* Bent, 1953: 665-666).

Passer domesticus. House or English Sparrow. In Kansas, a female sparrow brought food to three fledgling Eastern Kingbirds (*Tyrannus tyrannus*), whose parents were not seen. For at least a week, the sparrow continued to bring bread and other food to the flycatchers, although her head was usually caught by the closing of the wide mouth into which she placed the morsels and she had to struggle to release herself (Fitch, 1949). An almost identical episode is reported from Louisiana. In this case, also, no adult kingbird was seen to take an interest in the three fledglings that were fed by the female sparrow. At least one of the kingbirds was attended by the sparrow over a period of 10 days (Hamilton, 1952). A sparrow cooperated with a pair of Red-eyed Vireos (*Vireo olivacea*) in feeding and defending their nestlings (Bent, 1958:17).

Spermestes nigriceps. Black-headed or Rufous-backed Mannikin. Both adult and immature auxiliaries help to build the nest (Armstrong, 1947:192). "Several birds will combine and construct a sleeping nest capable of holding a number of birds . . . If more than two birds are taking part in nest building, the nest is probably temporary sleeping quarters. If in a week or so it does hold eggs, you will find that the occupants are now only two; the helpers in the nest building have gone off" (van Someren, 1956:477).

Quelea quelea. Black-faced or Red-billed Weaver. In an aviary, more than two adults may nourish the young in one nest, although this is not known to occur among birds in the wild (Morel and Bourlière, 1956:118).

Philetairus socius. Social Weaver. Under a roof constructed of small twigs and dried grasses by the flock as a whole, each pair builds its own nest chamber. Large communal nests may measure more than 25 by 15 feet at the base and about five in height; they contain 95 or more individual nests (Friedmann, 1930).

Quiscalus quiscula. Common Grackle. A female grackle fed and protected nestling Chipping Sparrows whose parents could not be found (Bent, 1958:412). This behavior is unexpected in a bird which sometimes preys on smaller birds.

Agelaius phoeniceus. Redwinged Blackbird. A female, whose young were lost two days after they left the nest, helped a neighboring female to feed her fledglings. She continued to do this for at least ten days (Strosnider, 1960).

Tangara larvata. Golden-masked Tanager. At one nest in Panamá and two in Costa Rica, a young tanager in juvenal or transitional plumage helped a mated pair to feed nestlings. One of these young birds, 46 days old, was noticed helping its parents to feed their next brood. At first it brought food as often as either of the parents, although often it came with a smaller portion. But after the novelty of this adult occupation wore off, it was far less regular in its attendance (Skutch, 1954:209-210). On three occasions, I have watched trios of adults, in full breeding plumage, attending nestlings. One of these trios was bringing food to a nest that contained one nestling and one unhatched egg, so that evidently this was not a case of two females laying in the same nest. The relationship of the helper to the parents is unknown.

Twice I have seen individuals in juvenal plumage gather material while their parents were building a nest for a later brood. On the second of these occasions, the young tanager tried to pull a long, strong fiber from an abandoned nest of a Blue Honeycreeper. When the fiber resisted, the tanager hung from it with closed wings until it finally came loose; but the bird then dropped the piece that it had tried so hard to obtain. The second young tanager of this family sat in the honeycreeper's nest and made movements such as a building bird uses to shape its structure.

Tangara chrysophrys. Speckled or Yellow-browed Tanager. In late May of 1959, a pair of these tanagers built in a poró tree near our house. The female was lame, with a right leg that hung uselessly; yet, despite this handicap, she managed to hatch a single nestling. Before this young bird left the nest, I noticed that two birds of the same species were feeding it, along with its lame mother. I could not distinguish the helper from her mate. In nine hours of watching, the lame female brought food 52 times and the other two attendants 62 times. Although sometimes all three came to the nest tree together, more often the helper was alone. After the fledgling left the nest, I repeatedly saw its three attendants carry banana from the feeding shelf.

Tangara inornata. Plain-colored Tanager. Four grown birds, who could not be distinguished from each other, fed two nestlings, often coming in a little flock (Skutch, 1954:214-216).

Thraupis episcopus. Blue Tanager. In May of 1954, I discovered a nest with four eggs, which is twice the usual number found in El General, Costa Rica. It was attended by two females, who had a single mate—the only instance of bigamy that has come to my attention in this species. The dominant female, which was in better plumage than the submissive female, incubated when she wished; the other sat on the eggs when she was permitted to do so. This submissive bird spent much time hopping restlessly about the nest or preening close by it while her more forceful partner sat. She took over the eggs the moment the latter left and promptly made way for the dominant female when she returned. If the submissive tanager was slow in leaving the eggs, she received a mild peck from the dominant one. In four hours, the dominant female sat for 77.2 per cent of the time, which is about normal assiduity for a Blue Tanager. The submissive female incubated for 22.8 per cent of the time. The eggs were constantly covered, but the two females never incubated simultaneously. After the nestlings hatched, the male and two females fed them in perfect harmony, bringing 142 meals to the three nestlings in four hours. At least two young were fledged.

Ramphocelus passerinii. Scarlet-rumped Black Tanager. A full-grown, young bird, afflicted with paralysis, was fed at least once by two different females, one of whom appeared to be its own parent, while the other was the mother of fledglings just out of the nest (Skutch, 1954:127).

Piranga olivacea. Scarlet Tanager. A male fed young Chipping Sparrows until his own nestlings hatched (Hales, 1896).

Habia gutturalis. Red-throated Ant-Tanager. Immature birds sometimes help to build and more often to feed nestlings, probably later broods of their parents (Edwin Willis, *in litt.*, September 28, 1957).

Saltator maximus. Buff-throated Saltator. Although nests of this large, plain-colored finch are usually well separated, I once found two pairs nesting in neighboring coffee bushes, only eight feet apart. One female, who was clearly dominant, repeatedly chased her neighbor from the latter's eggs and nestling. The dominant female sometimes went to the other's nest to make sure that her rival was absent, and if she happened to be carrying food for her own nestling, she might give it to the offspring of the female she was trying to drive away. Twice I saw her feed her enemy's nestling, and once she brooded it for five minutes (Skutch, 1954:74).

Richmondia cardinalis. Cardinal. A juvenile, probably a female, whose age was estimated at about 78 days, brought food to a late nest of her own species. She also begged from the nestlings' parents and was occasionally fed by the male. The female parent tried to drive her away, yet on one occasion, while both rested on the nest's rim, she took food from the young helper and passed it to a nestling (Brackbill, 1944). A male Cardinal, whose nest had been destroyed, fed four fledgling American Robins a few days younger than his own lost nestlings. For a week, he was almost as active in bringing food to the young robins as were their own parents; and perfect harmony prevailed among the three attendants. After the replacement brood of the Cardinals hatched, the male apparently brought food to both families simultaneously. His mate took no interest in the robins (Logan, 1951).

Sometimes two female Cardinals lay in the same nest and attempt to incubate simultaneously, sitting side by side, facing in opposite directions. In one instance, these doubly incubated eggs failed to hatch; in another, they hatched (Hawksley and McCormack, 1951).

A male Cardinal fed seven goldfish, bringing food to them repeatedly for some days and standing on the pool's edge while he placed it in their open mouths, slightly raised above the water. This strangest of all the instances of "helpfulness" that have come to my attention is corroborated by an excellent photograph (Lemmons, 1956). See also Song Sparrow.

Peucecticus ludovicianus. Rose-breasted Grosbeak. A semicaptive male, arriving with food for his own nestlings, gave it to nestling grosbeaks in a neighboring nest, who were calling loudly because their parents had neglected them. He did this several times (Ivor, 1944a:99).

Peucecticus melanocephalus. Black-headed Grosbeak. An adult male with a deformed bill, which evidently made it difficult for him to feed himself, was fed by a female, by whose care he had apparently been kept in good condition for an extended period (Fox, 1952:160-161).

Passerina cyanea. Indigo Bunting. Juveniles fed still younger birds in captivity (Sanborn *in* Nice, 1943:79).

Carpodacus mexicanus. House Finch. A nest in Colorado contained four half-grown American Robins, two newly hatched finches, and four finch eggs. It was attended by two adult robins and two female finches apparently mated to the same male, all five of which fed the young regularly. The large robins smothered their small nest mates. After the robins were fledged, the three finches continued to feed them. At another nest in the same locality, adult robins and adult finches fed young robins. There was no evidence, however, that the finches had laid eggs in this nest (Bailey and Niedrach *in* Bent, 1949:56).

Carduelis cannabina. Linnet. An injured adult was fed by a companion in a cage (Lack, 1953:82).

Fringilla coelebs. Chaffinch. Persistent calling for food by newly fledged Hawfinches (*Coccothraustes coccothraustes*) attracted a male Chaffinch, which fed them six times (Mountfort, 1957:91).

Pipilo erythrophthalmus. Rufous-sided Towhee. A female fed two young Mockingbirds (*Mimus polyglottos*), continuing this for hours. When she gave seeds, they were rejected, but insects were accepted (Westwood, 1946). A towhee and a Field Sparrow had nests 18 inches apart in the same tree, and both held nestlings of about the same age. The male towhee frequently fed the young sparrows and removed their droppings, and a parent sparrow likewise brought food to the nestling towhees (Hoyt, 1948). A towhee cared for a young Brown-headed Cowbird (*Molothrus ater*) which had been hatched in a nest of an Orchard Oriole, *Icterus spurius* (Neff, 1945).

Pipilo fuscus. Brown Towhee. A male whose own first brood had just become independent joined a pair of Cardinals in feeding three fledglings of the latter. These three adults worked together in complete harmony for about three weeks. A month after helping to feed the Cardinals, the towhee and his mate reared a second brood (Antevs, 1947).

Junco oreganus. Oregon Junco. When a pair of juncos and a pair of Bewick Wrens (*Thryomanes bewickii*) nested on opposite sides of the interior of the same garage, the juncos often chased the wrens as they came with food for their young. Yet, while his mate incubated, the male junco fed the nestling wrens and also cleaned their nest. The wrens did not try to drive away the juncos (Williams, 1942:245-246).

Spizella passerina. Chipping Sparrow. Juveniles about 39 days old fed a younger Redwinged Blackbird in captivity (Laskey *in* Nice, 1943:79).

Spizella pusilla. Field Sparrow. A case of reciprocal helpfulness with a Rufous-sided Towhee is given under the latter species.

Melospiza melodia. Song Sparrow. A pair of Cardinals and a pair of sparrows nested simultaneously in a nest built by the former and lined by the latter. Both females laid eggs and both incubated and brooded, the Cardinal sometimes sitting upon the sparrow. Three Cardinals were hatched and reared to nest-leaving, fed by all four of the adults cooperating closely. No antagonism between the Cardinals and Song Sparrows was noticed (Brackbill, 1952). A pair of sparrows helped a neighboring pair of American Robins to feed their nestlings and clean the nest, continuing until their own eggs hatched. One or two sparrows helped Yellow Warblers (*Dendroica petechia*) to feed a brood. When the female warbler was on the nest, she took the food from the sparrow and passed it to the nestlings. Two sparrows laid in the same nest and incubated alternately, then all four parents fed the eight young (various authors cited by Brackbill, 1952:306).

SUMMARY

A "helper" is a bird that assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age that is neither its mate nor its dependent offspring. Helpers may be of almost any age; they may be breeding or non-breeding individuals; they may aid other birds of the most diverse relationships to them-

selves, including those of distinct species; and they may assist in various ways. The many recorded instances of this behavior are classified according to whether the helpers are immatures, innubiles (individuals sexually immature or inactive in a breeding season following that in which they hatched), nonbreeding adults, or breeding adults; whether they assist other birds of their own species or of different species; and whether their helpfulness is or is not associated with reproduction.

Aside from giving warning of the approach of danger, the most common mode of helpfulness is in feeding. Less often the helpers participate in nest building, incubation, and brooding. Some "mutual helpers" share rather equally in all the labors of building a nest and rearing a brood.

Contrary to earlier reports, when the young of several families gather in "crèches," the parents as a rule do not feed them indiscriminately, but each nourishes his or her own offspring.

Although interspecific helpers are most likely to attract attention, especially of the casual bird watcher, intraspecific helpers are more numerous in both species and individuals and they occur more regularly.

Examples of the several classes of helpers are given and the conditions which favor their occurrence are discussed.

Helpers point to the existence of much unused reproductive potential in birds and furnish additional evidence that their reproductive rate has, in many cases, been delicately adjusted to the circumstances of their lives rather than pushed to the limit of their capacity to rear sturdy offspring.

Helpers would doubtless occur far more frequently if superfluous assistants, and the increased activity inseparable from their presence, did not increase the likelihood of attracting predators to nests.

Brief accounts of the activities of helpers in over 130 species are given in an annotated list.

LITERATURE CITED

- Addicott, A. B.
1938. Behavior of the bush-tit in the breeding season. *Condor*, 40:49-63.
- Antevs, A.
1947. Towhee helps cardinals feed their fledglings. *Condor*, 49:209.
- Armstrong, E. A.
1947. *Bird display and behaviour: an introduction to the study of bird psychology* (Lindsay Drummond, London).
1955. *The wren* (Collins, London).
- Baird, S. F., and Stansbury, H.
1852. *Exploration and survey of the valley of the Great Salt Lake of Utah* (Philadelphia).
- Bellrose, F., Jr.
1943. Two wood ducks incubating in the same nesting box. *Auk*, 60:446-447.
- Bent, A. C.
1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. *U. S. Nat. Mus. Bull.* 176.
1942. Life histories of North American flycatchers, larks, swallows, and their allies. *U. S. Nat. Mus. Bull.* 179.
1946. Life histories of North American jays, crows, and titmice. *U. S. Nat. Mus. Bull.* 191.
1948. Life histories of North American nuthatches, wrens, thrashers and their allies. *U. S. Nat. Mus. Bull.* 195.
1949. Life histories of North American thrushes, kinglets, and their allies. *U. S. Nat. Mus. Bull.* 196.
1953. Life histories of North American wood warblers. *U. S. Nat. Mus. Bull.* 203.

1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Nat. Mus. Bull. 211.
- Betts, M. M.
1958. The behaviour of adult tits toward other birds and mammals near the nest. Brit. Birds, 51:426-429.
- Bleitz, D.
1951. Nest of pygmy nuthatches attended by four parents. Condor, 53:150-151.
- Brackbill, H.
1943. A nesting study of the wood thrush. Wilson Bull., 55:73-87.
1944. Juvenile cardinal helping at a nest. Wilson Bull., 56:50.
1952. A joint nesting of cardinals and song sparrows. Auk, 69:302-307.
1958. Titmouse mother's helper. Baltimore Evening Sun, June 18.
- Brown, L. H.
1958. The breeding biology of the greater flamingo *Phoenicopterus ruber* at Lake Elmenteita, Kenya Colony. Ibis, 100:388-420.
- Cayley, N. W.
1949. The fairy wrens of Australia: blue birds of happiness (Angus and Robertson, Sydney and London).
- Coombes, R. A. H.
1950. The moult migration of the sheld-duck. Ibis, 92:405-418.
- Cullen, J. M.
1957. Plumage, age, and mortality in the arctic tern. Bird Study, 4:197-207 (Abstract in Ibis, 102, 1960:336).
- Davis, D. E.
1940. Social nesting habits of the smooth-billed ani. Auk, 57:179-218.
1942. The phylogeny of social nesting habits in the Crotophaginae. Quart. Rev. Biol., 17:115-134.
- Davis, M.
1952. Captive raven carries food to non-captive black vulture. Auk, 69:201.
- Darwin, C.
1871. The descent of man and selection in relation to sex (J. Murray, London).
- Deck, R. S.
1945. The neighbors' children. Nature Mag., 38:241-242, 272.
- De Garis, C. F.
1936. Notes on six nests of the Kentucky warbler (*Oporornis formosus*). Auk, 53:418-428.
- Dexter, R. W.
1952. Extra-parental cooperation in the nesting of chimney swifts. Wilson Bull., 64:133-139.
- Finley, W. L.
1907. American birds (C. Scribner's Sons, New York).
- Fitch, H. S.
1949. Sparrow adopts kingbirds. Auk, 66:368-369.
- Forbush, E. H.
1927. Birds of Massachusetts and other New England states. Vol. 2 (Mass. Dept. Agr., Boston).
1929. Birds of Massachusetts and other New England states. Vol. 3 (Mass. Dept. Agr., Boston).
- Fox, W.
1952. Behavioral and evolutionary significance of the abnormal growth of beaks of birds. Condor, 54:160-162.
- Friedmann, H.
1930. The sociable weaver bird of South Africa. Nat. Hist., 30:205-212.
- Frith, H. J.
1956. Breeding habits in the family Megapodiidae. Ibis, 98:620-640.
- Gilliard, E. T.
1958. Living birds of the world (Doubleday and Co., Garden City, N.Y.).
1959. Notes on some birds of northern Venezuela. Amer. Mus. Novit. No. 1927:1-33.

- Goodwin, D.
1947. Breeding-behaviour in domestic pigeons four weeks old. *Ibis*, 89:656-658.
- Grey of Fallodon, Viscount
1927. *The charm of birds* (Frederick A. Stokes, New York).
- Grimes, S. A.
1940. Scrub jay reminiscences. *Bird-Lore*, 42:431-436.
- Gross, A. O.
1949. Nesting of the Mexican jay in the Santa Rita Mountains, Arizona. *Condor*, 51:241-249.
- Hales, H.
1896. Peculiar traits of some scarlet tanagers. *Auk*, 13:261-263.
- Hamilton, G. D.
1952. English sparrow feeding young eastern kingbirds. *Condor*, 54:316.
- Hawksley, O., and McCormack, A. P.
1951. Doubly-occupied nests of the eastern cardinal, *Richmondia cardinalis*. *Auk*, 68:515-516.
- Hickling, R. A. O.
1959. The burrow-excavation phase in the breeding cycle of the sand martin *Riparia riparia*. *Ibis*, 101:497-500.
- Hochbaum, H. A.
1960. The brood season. *Nat. Hist.*, 69(6):54-61.
- Houck, W. J., and Oliver, J. H.
1954. Unusual nesting behavior of the brown-headed nuthatch. *Auk*, 71:330-331.
- Howard, L.
1952. *Birds as individuals* (Collins, London).
- Hoyt, J. S. Y.
1948. Observations on nesting associates. *Auk*, 65:188-196.
- Hudson, W. H.
1920. *Birds of La Plata*. 2 vols. (J. M. Dent, London).
- Hutson, H. P. W.
1947. Observations on the nesting of some birds around Delhi. *Ibis*, 89:569-576.
- Ivor, H. R.
1944a. Bird study and semi-captive birds: the rose-breasted grosbeak. *Wilson Bull.*, 56:91-104.
1944b. Aye, she was Bonnie. *Nature Mag.*, 37:473-476.
- Kendeigh, S. C.
1945. Nesting behavior of wood warblers. *Wilson Bull.*, 57:145-164.
- Kilham, L.
1956. Breeding and other habits of casqued hornbills (*Bycanistes subcylindricus*). *Smiths. Misc. Coll.*, 131(9):1-45.
- Kropotkin, P.
1902. *Mutual aid: a factor in evolution* (William Heinemann, London).
- Lack, D.
1953. *The life of the robin* (Pelican Books, London).
- Lack, D., and Lack, E.
1958. The nesting of the long-tailed tit. *Bird Study*, 5:1-19.
- Laskey, A. R.
1939. A study of nesting eastern bluebirds. *Bird-Banding*, 10:23-32.
1948. Some nesting data on the Carolina wren at Nashville, Tennessee. *Bird-Banding*, 19:101-121.
1957. Some tufted titmouse life history. *Bird-Banding*, 28:135-145.
- Leach, F. A.
1925. Communism in the California woodpecker. *Condor*, 27:12-19.
- Lemmons, P.
1956. Cardinal feeds fishes. *Nature Mag.*, 49:536.
- Logan, S.
1951. Cardinal, *Richmondia cardinalis*, assists in feeding robins. *Auk*, 68:516-517.

- Lorenz, K. Z.
1952. King Solomon's ring (Methuen and Co., London).
- Lovell, H. B.
1958. Baiting of fish by a green heron. *Wilson Bull.*, 70:280-281.
- Lowther, E. H. N.
1951. A bird photographer in India (Oxford Press, London).
- Maciula, S. J.
1960. Worm-eating warbler "adopts" ovenbird nestlings. *Auk*, 77:220.
- Mathews, G. M.
1924. The birds of Australia. Vol. 11 (Witherby and Co., London).
1925-1927. The birds of Australia. Vol. 12 (Witherby and Co., London).
- Merritt, J. H.
1951. Little orphan ani. *Audubon Mag.*, 53:225-231.
- Messenger, W. H.
1949. Goose baby-sitter. *Nature Mag.*, 42:79.
- Mills, E. A.
1931. Bird memories of the Rockies (Houghton Mifflin Co., Boston and New York).
- Moore, R. T.
1938. Discovery of the nest and eggs of the tufted jay. *Condor*, 40:233-241.
- Moreau, R. E.
1936. The breeding biology of certain East African hornbills (Bucerotidae). *Jour. East Africa and Uganda Nat. Hist. Soc.*, 13:1-28.
1944. Food-bringing by African bronze cuckoos. *Ibis*, 86:98-100.
- Moreau, R. E., and Moreau, W. M.
1937. Biological and other notes on some East African birds. *Ibis*, ser. 14, 1:152-174.
1940. Hornbill studies. *Ibis*, ser. 14, 4:639-656.
- Morel, G., and Bourlière, F.
1956. Recherches écologiques sur les *Quelea quelea quelea* (L.) de la basse vallée du Sénégal II. La reproduction. *Alauda*, 24:97-122.
- Mountfort, G.
1957. The hawfinch (Collins, London).
- Murphy, R. C.
1936. Oceanic birds of South America (Amer. Mus. Nat. Hist., New York).
- Neff, J. A.
1945. Foster parentage of a mourning dove in the wild. *Condor*, 47:39-40.
- Nice, M. M.
1943. Studies in the life history of the song sparrow. II. *Trans. Linn. Soc. New York*, 6:1-328.
- Nicholson, E. M.
1930. Field notes on Greenland birds. *Ibis*, ser. 12, 6:280-313, 395-428.
- Norris, R. A.
1958. Comparative biosystematics and life history of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. *Univ. Calif. Publ. Zool.*, 56:119-300.
- Perry, R.
1946. Lundy: isle of puffins (Lindsay Drummond, London).
- Powell, H.
1946. Nuthatch feeding nestling starlings. *Brit. Birds*, 39:316 (Abstract in *Ibis*, 89, 1947:152).
- Prévost, J.
1955. Observations écologiques sur le manchot empereur (*Aptenodytes forsteri*). *Acta XI Congr. Int. Ornith.*, 1954:248-251.
- Raney, E. C.
1939. Robin and mourning dove use same nest. *Auk*, 56:337-338.
- Rea, G.
1945. Black and white warbler feeding young of worm-eating warbler. *Wilson Bull.*, 57:262.

- Richmond, S. M.
1953. The attraction of purple martins to an urban location in western Oregon. *Condor*, 55:225-249.
- Riney, T.
1951. Relationships between birds and deer. *Condor*, 53:178-185.
- Robertson, A. W. P., and Porter, S. C.
1952. Long-tailed tits' unorthodox nesting arrangements. *Brit. Birds*, 45:257-258 (Abstract in *Auk*, 70, 1953:107).
- Rowley, I.
1957. Co-operative feeding of young by superb blue wrens. *Emu*, 57:356-357.
- Russell, W. C.
1947. Mountain chickadees feeding young Williamson sapsuckers. *Condor*, 49:83.
- Selander, R. K.
1959. Polymorphism in Mexican brown jays. *Auk*, 76:385-417.
- Selous, E.
1927. Realities of bird life: being extracts from the diaries of a life-loving naturalist (Constable and Co., London).
- Sherman, A. R.
1952. *Birds of an Iowa dooryard* (Christopher Publishing House, Boston).
- Skead, C. J.
1954. A study of the cape wagtail, *Motacilla capensis*. *Ibis*, 96:91-103.
- Skutch, A. F.
1935. Helpers at the nest. *Auk*, 52:257-273.
1943. The family life of Central American woodpeckers. *Sci. Monthly*, 56:358-364.
1948. Life history of the golden-naped woodpecker. *Auk*, 65:225-260.
1949. Do tropical birds rear as many young as they can nourish? *Ibis*, 91:430-455.
1953a. How the male bird discovers the nestlings. *Ibis*, 95:1-37, 505-542.
1953b. Life history of the southern house wren. *Condor*, 55:121-149.
1953c. Delayed reproductive maturity in birds. *Ibis*, 95:153-154.
1953d. The white-throated magpie-jay. *Wilson Bull.*, 65:68-74.
1954. Life histories of Central American birds. *Pac. Coast Avif. No.* 31:1-448.
1954-1955. The parental stratagems of birds. *Ibis*, 96:544-564; 97:118-142.
1956. A nesting of the collared trogon. *Auk*, 73:354-366.
1958. Roosting and nesting of araçari toucans. *Condor*, 60:201-219.
1959. Life history of the groove-billed ani. *Auk*, 76:281-317.
1960. Life histories of Central American birds. II. *Pac. Coast Avif. No.* 34:1-593.
- Sladen, W. J. L.
1953. The Adelie penguin. *Nature*, 171:952-961.
1955. Some aspects of the behaviour of the Adelie and chinstrap penguins. *Acta XI Congr. Int. Ornith.*, 1954:241-247.
- Snow, D. W.
1958. The breeding of the blackbird *Turdus merula* at Oxford. *Ibis*, 100:1-30.
- Southern, W. E.
1959. Foster-feeding and polygamy in the purple martin. *Wilson Bull.*, 71:96.
- Strosnider, R.
1960. Polygyny and other notes on the redwinged blackbird. *Wilson Bull.*, 72:200.
- Stülken, K., and Brüll, H.
1938. Vom Nestleben der Nachtschwalbe (*Caprimulgus e. europaeus*). *Jour. für Ornith.*, 86:59-73 (Abstract in *Bird-Banding*, 9, 1938:108).
- Sutton, G. M., and Parmelee, D. F.
1954. Nesting of the Greenland wheatear on Baffin Island. *Condor*, 56:295-306.
- Thomas, H.
1951. Notes on the pied butcher-bird. *Emu*, 51:165-168 (Abstract in *Auk*, 69, 1952:346).

van Someren, V. G. L.

1956. Days with birds: studies of habits of some East African species. *Fieldiana: Zoology*, 38:1-520.

von Haartman, L.

1953. Was reizt den Trauerfliegenschnäpper (*Muscicapa hypoleuca*) zu füttern? *Vogelwarte*, 16:157-164.
1956. Territory in the pied flycatcher *Muscicapa hypoleuca*. *Ibis*, 98:460-475.

Walters, J.

1959. [Observations on two broods of Kentish plovers, *Charadrius alexandrinus*, on Texel.] *Ardea*, 47:48-67 (Abstract in *Ibis*, 102, 1960:338).

Warham, J.

1954. The behaviour of the splendid blue wren. *Emu*, 54:135-140.

W[estwood], R. W.

1946. Contents noted. *Nature Mag.*, 39:399.

Wetmore, A., and Swales, B. H.

1931. The birds of Haiti and the Dominican Republic. *U. S. Nat. Mus. Bull.* 155.

Williams, L.

1942. Interrelations in a nesting group of four species of birds. *Wilson Bull.*, 54:238-249.

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F., and Tucker, B. W.

1938. The handbook of British birds. Vols. 1 and 2 (H. F. and G. Witherby, London).

Wynne-Edwards, V. C.

1952. Zoology of the Baird expedition (1950). I. The birds observed in central and south-east Baffin Island. *Auk*, 69:353-391.

Young, H.

1955. Breeding behavior and nesting of the eastern robin. *Amer. Midl. Nat.*, 53:329-352.

San Isidro del General, Costa Rica, July 3, 1960.