

INTERSPECIFIC FEEDING AMONG BIRDS: A REVIEW

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Much recent attention has been devoted to intraspecific helpers at the nest. Skutch (1935, 1961, 1976) listed several instances of interspecific helping, but a thorough consideration of this topic is lacking. The purpose of this paper is to give a comprehensive survey of the occurrence of the feeding of one bird by another of a different species and to describe the conditions under which the behavior has tended to occur. The subject is potentially of considerable evolutionary interest since in interspecific helping, kin selection is impossible.

Certain instances have been omitted from the discussion and the list. They include captive and parasitic birds and situations where a clutch has been partially or fully replaced with that of another species by an experimenter. Common names for bird species will be used throughout the paper; a list of scientific names appears in Appendix I.

RESULTS

The list of instances of interspecific feeding shown in Table 1 was compiled by searching the literature (Appendix II) and requests made through several ornithological journals. Table 1 summarizes 140 cases of interspecific feeding. Adopting species are represented by 22 families and 65 species, and birds that were fed by 22 families and 71 species (Tables 2, 3). There were 95 cases of nestlings fed, 30 cases of fledglings, 11 cases of both nestlings and fledglings, and 4 cases where no age was given.

I have classified instances of interspecific feeding into 8 categories related to their probable proximate causes (Table 2): (1) for some reason, the bird was raising a mixed clutch; (2) the original nest and brood of the bird were destroyed; (3) the nest of another species was very close to that of the bird performing the behavior; (4) young birds calling stimulated another species to feed them; (5) orphaned birds were adopted temporarily or permanently; (6) a male bird fed another species while his mate incubated; (7) finding a mateless bird, or being mateless itself, a bird joined a heterospecific individual or pair with young; (8) a miscellaneous category: none of the above reasons were evident. Not all of the categories are mutually exclusive.

Mixed clutches.—Mixed clutches have been frequently observed, especially among hole-nesting species when competition for nesting sites is severe. Mackenzie (1954) deliberately removed half of 60 boxes in an area during the fall in an attempt to study effects of competition on cavity-nesters. The following spring, a Redstart presumably laid eggs in 2 tits' nests. The Great Tit and Coal Tit parents raised the young Redstarts along with their own. Great Tits have been thought to usurp Blue

TABLE 1. A list of occurrences of interspecific feeding among birds, arranged by family of adopter.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
GAVIIDAE				
Arctic Loon—Spectacled Eider	close nest	F	B	Abraham 1978
ACCIPITRIDAE				
Goshawk—Red-tailed Hawk	close nest	N	F	Gammon pers. comm.
FALCONIDAE				
American Kestrel—Screech Owl	mixed clutch	B	B	Summer 1933
COLUMBIDAE				
Mourning Dove—White-winged Dove	misc.	N	F	Neff 1945
Mourning Dove—American Robin	mixed clutch	N	F	Raney 1939
STRIGIDAE				
Screech Owl—Common Flicker	nest lost	N	F	Lyon 1922
Great Horned Owl—Red-tailed Hawk	misc.	N	F	Hovingh and Ponshair 1951
TROCHILIDAE				
Green Violet-ear—White-eared Hummingbird	unknown	U	U	Wagner in Skutch 1976
PICIDAE				
Red-bellied Woodpecker—Tufted Titmouse	calling young	F	U	Curry 1969
Hairy Woodpecker—Downy Woodpecker	calling young	F	M	Davis 1973
Northern Three-toed Woodpecker—Black-backed Three-toed Woodpecker	calling young, mate-less	N	F	Hickey pers. comm.
Common Flicker—Starling	misc.	N	F	Lott 1939

TABLE I. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
TYRANNIDAE				
Eastern Phoebe—Tree Swallow	misc.	N	F	Deck 1945
Scissor-tailed Flycatcher—Common Grackle	close nest	N	U	Lowther 1975
Eastern Kingbird—Northern Oriole	misc.	B	F	Bragg 1968
Eastern Wood Pewee—Eastern Kingbird	calling young, orphan	N	U	Snyder 1973
Least Flycatcher—Chipping Sparrow	close nest	N	U	Burgess 1964
HIRUNDINIDAE				
Tree Swallow—Eastern Bluebird	mixed clutch	N	B	Chapman 1955
Tree Swallow—American Robin	close nest	N	M	Munro 1929
Purple Martin—House Sparrow	misc.	F	M	Brown 1977b
Purple Martin—Starling	misc.	N	B	Van Velzen 1960
MOTACILLIDAE				
Gray Wagtail—Song Thrush	close nest	N	U	Pike 1930
Pied Wagtail—Robin	mixed clutch	N	B	Lack 1953
TROGLODYTIDAE				
Carolina Wren—Great Crested Flycatcher	close nest, mate incubating	N	M	Wight 1934
Carolina Wren—Tufted Titmouse	misc.	N	U	Pullman 1970
Winter Wren—Townsend's Solitaire	misc.	B	U	Robinson 1962
Wren—Willow Warbler	misc.	F	U	Pike 1932
Wren—Spotted Flycatcher	close nest	F	U	Heaven <i>in</i> Armstrong 1955
Wren—Coal Tit	misc.	N	U	Betts 1958

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
Wren—Great Tit	close nest, mate incubating	N	M	Heybrook <i>in</i> Armstrong 1955
Wren—Blue Tit	misc.	N	U	Armstrong and Whitehouse 1977
Wren—Linnet	close nest	N	B	Steiniger <i>in</i> Armstrong 1955
House Wren—Common Flicker	close nest, mate incubating	N	M	Royall and Pillmore 1968
House Wren—Black-headed Grosbeak and House Sparrow	mateless	B	M	Hills 1924
MIMIDAE				
Gray Catbird—Common Flicker	orphan	N	U	Hayward 1937
Gray Catbird—House Wren	misc.	N	F	Nolan and Schneider 1962
Gray Catbird—American Robin	mixed clutch	N	F	Benton 1961
Gray Catbird—Cardinal	mixed clutch	N	F	Brooks 1922
MUSCICAPIDAE				
Robin—Pied Wagtail	mixed clutch	N	B	Lack 1953
Robin—Wren	misc.	F	B	Lack 1953
Robin—Wren	misc.	N	U	Duval <i>in</i> Armstrong 1955
Robin—Wren	misc.	F	F	Eckermann <i>in</i> Armstrong 1955
Robin—Blackbird	mate incubating, orphan	N	M	Armstrong and Whitehouse 1977
Robin—Blackbird	misc.	F	B	Lack 1953

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
Robin—Song Thrush	nest lost	N	B	Lack 1953
Redstart—Pied Flycatcher	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Redstart—Great Tit	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Eastern Bluebird—House Wren	close nest, mate incubating	N	M	Forbush 1929
Eastern Bluebird—House Wren	close nest	N	M	Batus 1958
Eastern Bluebird—Mockingbird	misc.	B	B	Carr and Goin 1965
Eastern Bluebird—Mountain Bluebird	mateless	N	M	Scott 1971
Swainson's Thrush—American Robin	calling young	N	U	Jewett 1928
Blackbird—Pied Wagtail	calling young	F	M	Russell 1973
Blackbird—Robin	misc.	F	F	Lack 1953
Blackbird—Song Thrush	mateless	B	M	Moore 1973
American Robin—Mourning Dove	mixed clutch	N	F	Raney 1939
American Robin—Gray Catbird	close nest	N	B	Wetherbee 1930
American Robin—Gray Catbird	mixed clutch	N	F	Benton 1961
American Robin—Brown Thrasher	unknown	U	U	Warren 1930
American Robin—House Finch	close nest	N	B	Henderson 1925
American Robin—House Finch	mixed clutch	N	B	Bailey and Niedrach 1936
Tropical Gnatcatcher—Golden-masked Tanager	close nest	N	F	Skutch 1960
Karoo Prinia—Layard's Titbabbler	close nest	N	B	Martin 1968
Spotted Flycatcher—Blackbird	close nest, lost nest	N	B	Southern 1952

TABLE I. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
AEGITHALIDAE				
Long-tailed Tit—Great Tit	mateless	N	U	Possert 1955
PARIDAE				
Marsh Tit—Coal Tit	mixed clutch	N	B	Gustavsson <i>in</i> Mackenzie 1954
Marsh Tit—Blue Tit	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Willow Tit—Blue Tit	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Carolina Chickadee—Eastern Bluebird	mixed clutch	N	B	Murphy 1968
Mountain Chickadee—Williamson's Sapsucker	close nest, lost nest	N	B	Russell 1947
Mountain Chickadee—Plain Titmouse	mixed clutch	N	F	Jensen 1925
Coal Tit—Redstart	mixed clutch	N	B	Mackenzie 1954
Great Tit—Redstart	mixed clutch	N	B	Mackenzie 1954
Great Tit—Redstart	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Great Tit—Blue Tit	mixed clutch	N	B	Mackenzie 1954
Great Tit—Blue Tit	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Great Tit—Blue Tit	mixed clutch	N	B	Arm 1955
Great Tit—Blue Tit	mixed clutch	N	B	Weinzierl 1954
Blue Tit—Wren	misc.	N	B	Armstrong 1955
Blue Tit—Robin	close nest	N	B	Lonsdale 1935
Blue Tit—Robin	mixed clutch	N	F	Lack 1953

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
Blue Tit—Redstart	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Blue Tit—Marsh Tit	mixed clutch	N	B	Amann <i>in</i> Mackenzie 1954
Blue Tit—Great Tit	mixed clutch	N	B	Arn 1955
Blue Tit—Trecreeper	close nest	B	M	Antoine 1959
SITTIDAE				
Nuthatch—Great Tit	mixed clutch	N	B	Arn 1955
Nuthatch—Starling	close nest	N	U	Powell 1946
Nuthatch—Starling	close nest	N	U	Svensson 1955
Pygmy Nuthatch—Mountain Bluebird	calling young, close nest	N	M	Pinkowski pers. comm.
EMBERIZIDAE				
Song Sparrow—House Wren	orphan	F	U	Jackson 1941
Song Sparrow—American Robin	close nest	B	B	Twombly 1934
Song Sparrow—Cardinal	mixed clutch	N	B	Brackbill 1952
Song Sparrow—Yellow Warbler	close nest	B	B	Jackson 1941
White-throated Sparrow—Dark-eyed Junco	misc.	F	U	Greenlaw 1977
Dark-eyed Junco—Bewick's Wren	close nest, mate incubating	N	M	Williams 1942
Dusky Scaside Sparrow—Red-winged Blackbird	mateless	F	M	Rakestraw pers. comm.
Chipping Sparrow—Purple Finch	close nest, orphan	F	B	Jackson 1941
Field Sparrow—Rufous-sided Towhee	close nest	N	U	Hoyt 1948

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
Rufous-sided Towhee—Mockingbird	misc.	F	F	Westwood 1946
Rufous-sided Towhee—Field Sparrow	close nest	N	M	Hoyt 1948
Rufous-sided Towhee—Field Sparrow	misc.	F	F	Wright 1956
Rufous-sided Towhee—House Finch	misc.	F	B	Olendorff 1974
Brown Towhee—Curve-billed Thrasher	misc.	F	U	Sutton 1968
Brown Towhee—Cardinal	misc.	F	M	Antevs 1947
Towhee—Dark-eyed Junco	calling young	N	M	Thaxter 1930
Cardinal—Gray Catbird	calling young	F	M	Warriner 1937
Cardinal—American Robin	lost nest, mate incubating	F	M	Logan 1951
Cardinal—Song Sparrow	mixed clutch	N	B	Brackbill 1952
Cardinal—Yellow-breasted Chat	close nest	N	M	Nolan 1965
Scarlet Tanager—Chipping Sparrow	mate incubating	N	M	Hales 1896
Blue Honeycreeper—Scarlet-rumped Black Tanager	misc.	F	M	Skutch 1976
Blue Honeycreeper—Yellow-green Vireo	unknown	U	F	Skutch 1961
PARULIDAE				
Black-and-white Warbler—Ovenbird	calling young, orphan	F	B	Kendeigh 1945
Black-and-white Warbler—Worm-eating Warbler	misc.	N	M	Rea 1945
Blue-winged Warbler—Field Sparrow	misc.	N	U	Saunders 1918
Blackburnian Warbler—Yellow-rumped Warbler	calling young, close nest	N	F	Lawrence 1948
American Redstart—American Robin	close nest	N	B	Allen <i>in</i> Williams 1942
Worm-eating Warbler—Ovenbird	mateless	N	U	Maciula 1960

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
Worm-eating Warbler—Kentucky Warbler	calling young	F	U	Hickey pers. comm.
Prothonotary Warbler—Pine Warbler	misc.	F	U	Beck 1925
ICTERIDAE				
Common Grackle—Chipping Sparrow	misc.	B	U	Baillairge 1930
FRINGILLIDAE				
Chaffinch—Hawfinch	calling young	F	M	Mountfort 1957
House Finch—American Robin	mixed clutch	N	B	Bailey and Niedrach 1936
House Finch—American Robin	misc.	N	B	Bailey and Niedrach 1936
PLOCEIDAE				
House Sparrow—Eastern Kingbird	misc.	F	F	Fitch 1949
House Sparrow—Eastern Kingbird	misc.	F	F	Hamilton 1952
House Sparrow—Tree Swallow	misc.	N	U	Porcher pers. comm.
House Sparrow—Cliff Swallow	close nest	N	F	Hofman pers. comm.
House Sparrow—Hedge Sparrow	calling young	B	F	Brindley 1937
House Sparrow—Blackbird	misc.	F	F	Parker 1973
House Sparrow—Tufted Titmouse	calling young, close nest	N	F	Prescott 1967
House Sparrow—Spotted Flycatcher	misc.	N	F	Powell 1927
House Sparrow—Yellow Warbler	misc.	N	U	Brewer pers. comm.
House Sparrow—Red-eyed Vireo	misc.	N	U	Austin 1958
House Sparrow—Serin	misc.	N	F	Hoehl 1940

TABLE 1. Continued.

Species involved ^a	Proximate reason	Age of birds fed ^b	Sex of feeding bird ^c	Source
STURNIDAE				
Starling—Common Flicker	close nest	N	B	Prescott 1971
Starling—Purple Martin	lost nest	N	U	Brown 1977a
Starling—American Robin	lost nest	N	B	Putnam 1961
Starling—American Robin	misc.	N	U	Herbert 1971

^a First species listed fed second species.

^b F = fledgling, N = nestling, B = both nestling and fledgling, U = unknown age.

^c Under Sex of Feeding Bird: F = female, M = male, U = unknown, B = both sexes.

TABLE 2. Incidence of proximate reasons for interspecific feeding.

Reason	No. of cases	Percent ^a
Mixed clutch	32	21.2
Original nest destroyed	7	4.6
Close nest of another species	36	23.8
Calling by young	15	9.9
Orphaned birds	6	4.0
Mateless birds	7	4.6
Male, mate incubating	8	5.3
Miscellaneous	40	26.5

^a Percentages reflect reasons cited; in some cases more than one reason was given.

Tit nests (Arn 1955, Weinzierl 1958). Occasionally, Great Tits have laid in other nests, including those of the Blue Tit and Nuthatch (Arn 1955).

Amann (1949) found a number of similar cases in previous years. Gustavsson (*in* Mackenzie 1954) found a banded Coal Tit and banded Marsh Tit had laid in the same nest; the Marsh Tits ended up raising a mixed clutch of 4 Marsh Tits and 2 Coal Tits. It was unclear whether the Marsh Tits ousted the originally nesting Coal Tits, or the Coal Tits deserted or were killed and the Marsh Tits took over the nest.

At least 3 cases of American Robins sharing a nest with another species have been observed: with a Mourning Dove (Raney 1939); with a Gray Catbird (Benton 1961); and with a House Finch (Bailey and Niedrach 1936). A Robin shared a nest with a Pied Wagtail (Lack 1953), and a Cardinal and Song Sparrow raised a combined brood (Brackbill 1952).

Nest or brood destroyed.—There are several instances of birds feeding another species after their own nest was destroyed. In one, a pair of Robins fed Song Thrushes (Lack 1953). Southern (1952) observed a pair of Spotted Flycatchers feeding Blackbirds after their nest was destroyed in a storm. After a pair of Starlings repeatedly lost a nest placed on a drainspout, they fed nearby nestling American Robins (Putnam 1961). A male Cardinal fed American Robins after his first nest was destroyed and while his mate incubated their second clutch (Logan 1951). Song Sparrows fed Yellow Warblers while nearby there was a Song Sparrow nest with dead young in it, presumably belonging to this pair (Jackson 1941).

When a researcher took the eggs of a Screech Owl, the owl brooded flickers in a hole in the same tree, and even brought a small bird for the nestlings to eat (Lyon 1922). A Starling fed nestling Purple Martins after 4 Starling eggs were taken from the martin-house and destroyed (Brown 1977a). This category is probably larger than it appears. In many observations, summarized later, the nesting history of the birds performing the behavior was unknown.

Close nesting of another species.—There are many examples of 2 species nesting close to each other and one or both taking an interest in the nest of the other. In some cases, a pair has attacked another species

bringing food to their nestlings; at other times the pairs took turns feeding all young with no antagonism.

It is not known how frequently a nest might fail due to one or both parents neglecting it for another nest. A male Pygmy Nuthatch fed nestling Mountain Bluebirds in a nest .5 m above his own; his own nest failed as he was attracted to the bluebirds calling before his eggs hatched (Pinkowski pers. comm.). A male Eastern Bluebird fed nestling House Wrens as his mate incubated and later neglected his own young; he even fought the wren parents to feed the young birds (Forbush 1929).

A pair of Arctic Loons raised a brood of 5 Spectacled Eiders (Abraham 1978). Initial observations included the locating of the loon and duck nests 10 m apart. One month later, the ducks were being fed by the loons, although Spectacled Eiders are self-sufficient upon hatching. The fate of the original loon nest was not known.

The timing of the hatching of the 2 nests seems to be a critical factor. If 2 pairs of birds nest close to each other, the nestlings that hatch first may receive the attention of one or both of the birds of the other pair. This was the case when a male Tree Swallow was observed feeding young American Robins in a nest atop the house in which his own nest was located (Munro 1929). The nestling swallows were about 1 week younger than the robins. Males will sometimes feed at another nest while their own nest is being incubated. A House Wren fed nestling Common Flickers while his mate incubated and continued to do so after his own eggs hatched (Royall and Pillmore 1968) and a Wren fed Great Tits under similar circumstances (Armstrong 1955). This will be discussed further in a separate category.

In one sense, the fact that one nest is close to another cannot be considered a reason for the interspecific feeding behavior since in any given area, there will always be a number of species nesting close to each other. Only those instances are cited where the original author believed it significant enough to mention. Its importance is due to the fact that it indicates that the bird is breeding; in some cases individuals performing the behavior may not be.

Young birds calling as a stimulus.—In certain cases of interspecific feeding, the observers believed the calls of the young were an important factor triggering the behavior. In some cases, fledglings or nestlings were fed as another bird was foraging nearby. Fledglings have directly solicited food from adults of a different species. A Tufted Titmouse begged and ran toward a Red-bellied Woodpecker, which fed it (Curry 1969). While a male Hairy Woodpecker was feeding at a suet holder, an immature Downy Woodpecker called for food and was fed by the Hairy (Davis 1973). A fledgling Pied Wagtail chased a Blackbird and the Blackbird fed it 6–7 times (Russell 1973). A Worm-eating Warbler fed a fledgling Kentucky Warbler as it called from the ground (Hickey pers. comm.).

Of course, when a nest of one species is near the nest of a second (as in the preceding category), the visual and auditory signals could together trigger food-bringing behavior. Begging by nestlings must rarely elicit

feeding by heterospecific birds, based on the scarcity of such observations in the many published studies of nesting behavior. Studies of the feeding of fledglings are much rarer, so it is uncertain whether feeding of fledged young is a rare event. It is not likely that unsuccessful panhandling attempts will be reported in the literature; however, they do occur. Brewer (pers. comm.) saw a fledgling Yellow Warbler beg from a female House Sparrow, which pecked at it.

Orphaned birds.—In several cases, one species has brought food to orphaned broods or individuals of another species. This could be triggered by the presumably loud calling of unsatiated youngsters. Snyder (1913) noticed a brood of Eastern Kingbirds calling loudly after an electrical storm. The parents were not seen afterward. An Eastern Wood Pewee fed the orphans for 10 days, until they fledged. A male Robin fed motherless Blackbirds while his mate was incubating, after which the male Blackbird deserted the nest. The Blackbirds fledged under the Robin's care (Armstrong and Whitehouse 1977). Black-and-white Warblers fed an Ovenbird fledgling which had become separated from its parents (Kendeigh 1945). A pair of Chipping Sparrows fed a brood of fledgling Purple Finches while continuing to feed their own brood in a nest in a small spruce one tier of branches below the finch nest (Jackson 1941).

Male feeding another species while mate incubates.—Two previous sections include several cases of males feeding nestlings of another species while their mates were incubating. Wight (1934) noted a Carolina Wren feeding Great Crested Flycatchers for a short time, although after a few fights with the parents, the wren gave up the attempt. A male Scarlet Tanager fed Chipping Sparrows before his own eggs hatched (Hales 1896), and a Dark-eyed Junco fed Bewick's Wrens as his mate incubated (Lonsdale 1935).

Skutch (1961) noted certain males are so eager to begin feeding their nestlings that they offer food to the unhatched eggs. He suggested that feeding of another species "may provide an outlet for repressed energy."

Mateless birds.—A few cases of interspecific feeding have been documented that involved a bird that had been unsuccessful in finding a mate, or had joined a parent bird whose mate had disappeared. A female Northern Three-toed Woodpecker, out of the known breeding range of this species, fed nestling Black-backed Three-toed Woodpeckers while they called loudly from the nest (Hickey pers. comm.). After several days of observation, Possert (1955) concluded that only 2 birds were attending a Great Tits' nest, a male Great Tit and a Long-tailed Tit. A male House Wren that could not secure a mate, although he had filled a birdhouse with nesting material, fed 3 Black-headed Grosbeaks until they fledged, and then fed nestling House Sparrows (Hills 1924). A male Blackbird fed 2 nestling Song Thrushes, assisting the female thrush; the nestlings fledged and were observed for several days with the Blackbird (Moore 1973). A banded male Dusky Seaside Sparrow that had bred successfully in previous years, could not locate a mate due to a lack

of females (Rakestraw pers. comm). (At that time there was only one female in the entire area of St. John's National Wildlife Refuge near Titusville, Florida.) It fed 2 fledgling Red-winged Blackbirds for 4 days. A male Eastern Bluebird joined a Mountain Bluebird who had lost her mate and helped her raise her brood (Scott 1971). A Worm-eating Warbler fed nestling Ovenbirds at a nest where only one parent Ovenbird was observed (Maciula 1960).

Miscellaneous category.—This is a large category (Table 2) but may only appear so due to omissions in either observations or records of observers. There are, nevertheless, some unusual circumstances surrounding certain instances of interspecific feeding in this category.

Under the category of mixed clutches, it was mentioned that some birds are thought to usurp nests, in some cases with a partial clutch, especially in cases of severe competition for nest sites. Hovingh and Ponshair (1951) cited this as a possible reason for a Great Horned Owl raising a brood of 3 Red-tailed Hawks. A female Common Flicker may have usurped a Starling nest, as she was observed caring for 3 nestling Starlings in what appeared to be a typical Starling nest (Lott 1939). A Mourning Dove, whose own eggs failed to hatch, began to care for a brood of White-winged Doves, who had been neglected by their own parents (Neff 1945).

Perhaps one of the most unusual cases is that of a female Blackbird that, after rearing her own young, continued to offer food for 2–3 weeks to any bird coming near. A Robin accepted the food (Lack 1953).

Taxonomic and ecological distribution.—Of the 65 species that were observed feeding another species, 25 have multiple records (Table 3). The highest number of observations for a species was 10, for the House Sparrow, although it was observed only twice to be fed by another species. Of species that were fed, there are multiple records for 29. Most frequently observed was the American Robin, with 11 records. The 22 families of birds fed are listed in Table 4.

There are 4 instances of one species feeding another, with the reverse situation also being observed. These species pairs are (excluding cases of mixed clutches) Common Flicker—Starling, Purple Martin—Starling, Robin—Blackbird, and American Robin—House Finch.

Comparisons by habitat, diet, and type of nest, indicate similarities between "adopters" and species being fed (Table 5). Edge species were most often observed. This is likely due to the nature of the observations, many made by suburban backyard birdwatchers. Of 8 cases of warblers feeding another species, 5 were ground-nesters. Perhaps the list of observations reflects birds that are most easily seen, and implies the possibility of other, not so visible species, being just as likely to engage in the behavior.

DISCUSSION

The interspecific feeding observed as a result of mixed clutches cannot be considered in the same way as under the other conditions. Peek et al. (1972) have shown that Red-winged Blackbirds do not appear to

TABLE 3. Species with multiple records.

Species	No. of cases	
	Adoptors	Birds fed
Red-tailed Hawk	0	2
Mourning Dove	2	0
Common Flicker	0	4
Eastern Kingbird	0	3
Tree Swallow	2	2
Purple Martin	2	0
Pied Wagtail	0	2
Carolina Wren	2	0
Winter Wren, Wren	7	4
House Wren	2	4
Gray Catbird	4	3
Mockingbird	0	2
Robin	7	4
Redstart	2	4
Eastern Bluebird	4	1
Mountain Bluebird	0	2
Blackbird	3	5
Song Thrush	0	2
American Robin	6	11
Spotted Flycatcher	0	2
Marsh Tit	2	0
Mountain Chickadee	2	0
Coal Tit	0	2
Great Tit	6	5
Blue Tit	7	7
Tufted Titmouse	0	3
Nuthatch	3	0
Song Sparrow	4	0
Dark-eyed Junco	0	2
Chipping Sparrow	0	3
Field Sparrow	0	3
Rufous-sided Towhee	4	0
Brown Towhee	2	0
Cardinal	4	3
Black-and-white Warbler	2	0
Yellow Warbler	0	2
Ovenbird	0	2
Worm-eating Warbler	2	0
House Finch	0	3
House Sparrow	10	2
Starling	4	4
Total number of species with multiple records	25	29

recognize their own young either in or out of the nest until they are 10 days old. In 2 of 3 albatross species, parents did not appear to recognize a strange chick put into their nests to replace one of their own chicks (Tickell and Pindar 1972). Since the chicks rarely leave their own nests, there seems to be no advantage in learning to recognize a bird's own

TABLE 4. Families of adoptors and birds fed, and number of species for each.

Family	No. of adopting species	No. of species of birds fed
Gaviidae	1	0
Anatidae	0	1
Accipitridae	1	1
Falconidae	1	0
Columbidae	1	2
Strigidae	2	1
Trochilidae	1	1
Picidae	4	4
Tyrannidae	5	2
Hirundinidae	2	3
Motacillidae	2	1
Troglodytidae	3	3
Mimidae	1	4
Prunellidae	0	1
Muscicapidae	9	13
Aegithalidae	1	0
Paridae	7	6
Certhiidae	0	1
Sittidae	2	0
Emberizidae	11	9
Parulidae	6	7
Vireonidae	0	1
Icteridae	1	3
Fringillidae	2	5
Ploceidae	1	1
Sturnidae	<u>1</u>	<u>1</u>
Total number of species	65	71

young until later, perhaps upon fledging. This idea is supported in a study of factors relating to the timing of parent-chick recognition in swallows (Burt 1977). Birds may feed almost anything that happens to be in their nests under the right conditions. It is of interest that birds fed and, in some cases, successfully reared another species in their own nests, but it does not explain spontaneous interspecific feeding.

Because there are so many cases of what seems to be an unusual and not easily observed phenomenon, especially for fledglings, it would appear the behavior requires an evolutionary explanation. One possibility is that the behavior is non-adaptive, and a consequence of other adaptive features. For example, it may be ordinarily advantageous to have such a strong drive to care for young that it overcomes heavy deterrents. If this is so, feeding inappropriate young may be rare enough, and carry a small enough penalty, that no evolutionary modification of the strong drive occurs.

Arguing against this possibility is the fact that it is difficult to provoke the feeding of alien young in any fashion except by placing them in the parental nest. When parent swallows begin actively to discriminate their

TABLE 5. Number of species of adoptors and birds fed, according to habitat, diet, and type of nest.

	No. of adopting species	No. of species of birds fed
Habitat		
Edge	41	50
Forest	19	17
Water	3	2
Grass	2	1
Desert	0	1
Primary Diet		
Insectivorous	45	51
Granivorous	13	16
Other	7	4
Type of Nest		
Open	39	45
Cavity	26	26

own young from others (upon fledging) they are aggressive to alien chicks (Burt 1977).

Dawkins (1976) suggested that adoption should be a rare mistake, since it confers no benefits upon the foster parents, but instead wastes time and energy that could be invested in their own kin. He did, however, allow that adoptors could benefit by gaining practice in the "art of childrearing." From this hypothesis, one would predict younger birds to be more likely to engage in interspecific feeding than older birds, since the experience they would gain by the feeding practice would directly benefit them and enable them to be better parents.

That experience does improve nesting success is suggested by a study conducted by DeStevens (1978). She found that younger female Tree Swallows have lower fledging rates for their broods than older female Tree Swallows. Lehrman and Wortis (1967) presented conclusive evidence of experience improving parental care in Ringed Turtle Doves, and a number of similar observations support this idea as well (Hediger 1950, 1955, Lehrman 1961).

In most cases of interspecific feeding, the age of the helper is, unfortunately, unknown. Porcher (pers. comm.) mentioned a case of a juvenile House Sparrow feeding nestling Tree Swallows. He observed older sparrows being driven off by swallows, and believed the young sparrow was allowed to approach the nest because it was not yet mature. Several cases report definitely older, experienced birds feeding another species. Rakestraw's (pers. comm.) observation of the Dusky Seaside Sparrow that had bred successfully in previous years is a case in point. The bird had had ample experience in raising young. The male Blackbird who assisted a mateless Song Thrush was "mature" (Moore 1973).

It may be more advantageous for a young bird to feed another species

than not to engage in the feeding behavior at all if experience improves an organism's parental abilities. In certain cases, this might be especially true, for example, when a bird's own nest failed and it was too late for it to renest, or when its own mate had been lost and it could not readily find another, or when a male bird, possibly inexperienced, has time to practice on its neighbors' offspring while his mate incubates. Other hypotheses explaining interspecific feeding are conceivable, such as reciprocal altruism (Trivers 1971), but the currently available information seems not to provide any ready way of approaching them.

Although accepting food no matter who the donor is should be advantageous in most circumstances, being raised by foster parents may lead to later problems. When a pair of Common Terns raised a Herring Gull, it did not behave as a normal gull (Kuhlemann 1939). A Mourning Dove remained with its foster family of Ringed Turtle Doves rather than joining its own species (Grewe 1959). Female Zebra Finches raised by Bengalese Finches showed no clear preference for their own species in choosing a mate (Sonnemann and Sjölander 1977). Herring and Lesser Black-backed gulls showed abnormal migration and hybridization after cross-fostering experiments (Harris 1970). These types of reactions indicate that cross-fostering may not be totally beneficial to the adopted bird.

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APPENDIX I. Common¹ and scientific names of avian species mentioned in paper and list arranged in taxonomic sequence (Morony et al. 1975).

Common name	Scientific name
Arctic Loon	<i>Gavia arctica</i>
Spectacled Eider	<i>Somateria fischeri</i>
Goshawk	<i>Accipiter gentilis</i>
Red-tailed Hawk	<i>Buteo jamaicensis</i>
American Kestrel	<i>Falco sparverius</i>
Herring Gull	<i>Larus argentatus</i>
Lesser Black-backed Gull	<i>Larus fuscus</i>
Common Tern	<i>Sterna hirundo</i>
Ringed Turtle Dove	<i>Streptopelia risoria</i>
Mourning Dove	<i>Zenaida macroura</i>
White-winged Dove	<i>Zenaida asiatica</i>
Screech Owl	<i>Otus asio</i>
Great Horned Owl	<i>Bubo virginianus</i>
Green Violet-ear	<i>Colibri thalassinus</i>
White-eared Hummingbird	<i>Hylocharis leucotis</i>
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>
Downy Woodpecker	<i>Picoides pubescens</i>
Hairy Woodpecker	<i>Picoides villosus</i>
Northern Three-toed Woodpecker	<i>Picoides tridactylus</i>
Black-backed Three-toed Woodpecker	<i>Picoides arcticus</i>
Common Flicker	<i>Colaptes auratus</i>
Eastern Phoebe	<i>Sayornis phoebe</i>
Scissor-tailed Flycatcher	<i>Muscivora forficata</i>
Eastern Kingbird	<i>Tyrannus tyrannus</i>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>
Eastern Wood Pewee	<i>Contopus virens</i>
Least Flycatcher	<i>Empidonax minimus</i>
Tree Swallow	<i>Tachycineta bicolor</i>
Purple Martin	<i>Progne subis</i>
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>
Gray Wagtail	<i>Motacilla cinerea</i>
Pied Wagtail	<i>Motacilla alba</i>
Bewick's Wren	<i>Thryomanes bewickii</i>
Carolina Wren	<i>Thryothorus ludovicianus</i>
Winter Wren, Wren	<i>Troglodytes troglodytes</i>
House Wren	<i>Troglodytes aedon</i>
Gray Catbird	<i>Dumetella carolinensis</i>
Mockingbird	<i>Mimus polyglottos</i>
Brown Thrasher	<i>Toxostoma rufum</i>
Curve-billed Thrasher	<i>Toxostoma curvirostre</i>
Hedge Sparrow	<i>Prunella madularis</i>
Robin	<i>Erithacus rubecula</i>
Redstart	<i>Phoenicurus phoenicurus</i>
Eastern Bluebird	<i>Sialia sialis</i>
Mountain Bluebird	<i>Sialia currucoides</i>
Townsend's Solitaire	<i>Myadestes townsendi</i>
Swainson's Thrush	<i>Catharus ustulatus</i>
Blackbird	<i>Turdus merula</i>
Song Thrush	<i>Turdus philomelos</i>
American Robin	<i>Turdus migratorius</i>
Tropical Gnatcatcher	<i>Poliopitila plumbea</i>

APPENDIX I. Continued.

Common name	Scientific name
Willow Warbler	<i>Phylloscopus trochilus</i>
Karoo Prinia	<i>Prinia maculosa</i>
Layard's Tit-babbler	<i>Parisoma layardi</i>
Pied Flycatcher	<i>Ficedula hypoleuca</i>
Spotted Flycatcher	<i>Muscicapa striata</i>
Long-tailed Tit	<i>Aegithalos caudatus</i>
Marsh Tit	<i>Parus palustris</i>
Willow Tit	<i>Parus montanus</i>
Carolina Chickadee	<i>Parus carolinensis</i>
Mountain Chickadee	<i>Parus gambeli</i>
Coal Tit	<i>Parus ater</i>
Great Tit	<i>Parus major</i>
Blue Tit	<i>Parus caeruleus</i>
Plain Titmouse	<i>Parus inornatus</i>
Tufted Titmouse	<i>Parus bicolor</i>
Nuthatch	<i>Sitta europaea</i>
Pygmy Nuthatch	<i>Sitta pygmaea</i>
Treecreeper	<i>Certhia familiaris</i>
Song Sparrow	<i>Zonotrichia melodia</i>
White-throated Sparrow	<i>Zonotrichia albicollis</i>
Dark-eyed Junco	<i>Junco hyemalis</i>
Dusky Seaside Sparrow	<i>Ammodramus maritimus</i>
Chipping Sparrow	<i>Spizella passerina</i>
Field Sparrow	<i>Spizella pusilla</i>
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>
Brown Towhee	<i>Pipilo fuscus</i>
Black-headed Grosbeak	<i>Phœucticus melanocephalus</i>
Cardinal	<i>Cardinalis cardinalis</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Scarlet-rumped Black Tanager	<i>Rhamphocelus passerinii</i>
Golden-masked Tanager	<i>Tangara nigrocincta</i>
Blue Honeycreeper	<i>Cyanerpes cyaneus</i>
Black-and-white Warbler	<i>Mniotilta varia</i>
Blue-winged Warbler	<i>Vermivora pinus</i>
Yellow Warbler	<i>Dendroica petechia</i>
Pine Warbler	<i>Dendroica pinus</i>
Blackburnian Warbler	<i>Dendroica fusca</i>
Yellow-rumped Warbler	<i>Dendroica coronata</i>
Kirtland's Warbler	<i>Dendroica kirtlandii</i>
American Redstart	<i>Setophaga ruticilla</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Worm-eating Warbler	<i>Helmitheros vermivorus</i>
Prothonotary Warbler	<i>Protonotaria citrea</i>
Kentucky Warbler	<i>Geothlypis formosa</i>
Yellow-breasted Chat	<i>Icteria virens</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Yellow-green Vireo	<i>Vireo olivaceus flavoviridis</i> ²
Northern Oriole	<i>Icterus galbula</i>
Red-winged Blackbird	<i>Agelaius phoeniceus</i>
Common Grackle	<i>Quiscalus quiscula</i>
Chaffinch	<i>Fringilla coelebs</i>
Serin	<i>Serinus canaria</i>
Linnet	<i>Acanthis cannabina</i>

APPENDIX I. Continued.

Common name	Scientific name
Purple Finch	<i>Carpodacus purpureus</i>
House Finch	<i>Carpodacus mexicanus</i>
Hawfinch	<i>Coccothraustes coccothraustes</i>
Zebra Finch	<i>Poephila guttata</i>
Bengalese Finch	<i>Lonchura striata</i>
House Sparrow	<i>Passer domesticus</i>
Starling	<i>Sturnus vulgaris</i>

¹ Common names for North American records follow the AOU Checklist (AOU 1957 and supplements).

² According to Peters (1931).

APPENDIX II. List of journals reviewed. Following the title of each journal listed is the date of earliest volume reviewed followed by volume or issue numbers. Parentheses indicate that the volumes enclosed were incomplete or missing. A dash between numbers indicates a continuous run. A dash not followed by a number indicates all volumes were reviewed after the last one listed. The literature reviews were conducted in Waldo Library at Western Michigan University, Kalamazoo, and the Josselyn Van Tyne Memorial Library at the University of Michigan, Ann Arbor and reflect their journal holdings.

Alabama Birdlife. (1953)—1—	Iowa Birdlife. (1931)—1—
Audubon (formerly Bird Lore). (1899)—1—(12, 13)—	The Jack-Pine Warbler. (1933)—13—
The Auk. (1884)—1—(54)—	The Kingbird. (1950)—1—
Bird-Banding. (1939)—8—	The Loon (formerly The Flicker). (1929)—1—
Bird Lore. See Audubon.	Maryland Birdlife. (1945)—(1, 4, 5)—
Bird Study. (1954)—1—	The Murrelet. (1920)—1—
The Blue Jay. (1942)—1—	The Oriole. (1936)—1—
The Cardinal. (1971)—1—	The Ostrich. (1968)—39—
The Chat. (1937)—1—	The Raven. (1930)—1—
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