LEMON, R. E. 1971. Analysis of song of red-eyed vireos. Can. J. Zool. 49: 847–854.
MARSHALL, A. J. 1950. The function of vocal mimicry in birds. Emu 50: 5–16.
MORTON, E. S. 1975. Ecological sources of selection on avian sounds. Am. Natur. 109: 17–34.
———. 1976. Vocal mimicry in the Thick-billed Euphonia. Wilson Bull. 88: 485–487.
MURRAY, J. W. 1974. A check-list of the Birds of Montgomery County, Virginia. Raven 45: 55–70.
REMSEN, J. V., JR. 1976. Observations of vocal mimicry in the Thick-billed Euphonia. Wilson Bull. 88: 487–488.
ROBINSON, F. N. 1974. The function of vocal mimicry in some avian displays. Emu 74: 9–10.
SNOW B. K. 1974. Vocal mimicry in the Violaceous Euphonia, *Euphonia violacea*. Wilson Bull. 86: 179–180.
THORPE, W. D. 1967. Vocal imitation and antiphonal song and its implications. Proc. 14th Intern. Ornithol. Congr.: 245–263.
WILDENTHAL, J. L. 1963. Structure in primary song of the Mockingbird, *Mimus polyglottos*. Unpublished M.S. thesis, Lawrence, Univ. of Kansas.

Received 31 March 1977, accepted 14 October 1977.

Two Successive Male Eastern Bluebirds Tending the Same Nest

BENEDICT C. PINKOWSKI
245 County Line Road, Bridgeville, Pennsylvania 15017 USA

Many instances of apparently altruistic behavior have been reported for the Eastern Bluebird (*Sialia sialis*). Some of the reports involve bluebird fledglings feeding siblings of a later brood (Wetherbee 1933, Laskey 1939) or additional adult helpers at the nest (Laskey 1947, Pinkowski 1975) and may be interpretable in terms of kin selection and inclusive fitness (Hamilton 1964, Wilson 1975). There are also reports of a male bluebird feeding the offspring of an unrelated pair (Pinkowski 1976) and a male attempting to courtship-feed another male prior to the breeding season (Pinkowski 1977a); these instances, as well as others involving bluebirds feeding the young of other species (Bent 1949, Batts 1958, Carr and Goin 1965), probably represent reproductive errors. Here I describe the behavior of a male Eastern Bluebird that replaced a lost male at a nest and cared for the widowed female's offspring. I also suggest an explanation for this behavior.

On 16 May 1977 a pair of bluebirds was tending a nest containing four 6-day-old young. The nest was located in a nest box in Macomb County, Michigan, and I banded the male bluebird on 16 May. On 21 May the nest contained only two young and the resident male was missing, its territory occupied by an unbanded male new to my study area. Two young fledged on 31 May. On 21–30 May I observed the nest for 17.3 h (seven observation periods of 2–3 h each) and found that the female fed the young on 97 occasions, removed fecal sacs on 28 of her feedings, and drove off intruders such as Tree Swallows (*Iridoprocne bicolor*) 12 times. Corresponding figures for the male were 15, 4, and 2, respectively. Only one fledgling was observed on 1–13 June when, during 10 h of observations (six observation periods of 1.5–2 h each), the male fed twice and the female fed 13 times. Thus the male offered only 17 of 127 feedings (13.4%) at a time when both adults normally contribute about equally to the nutritional requirements of the young (Pinkowski 1978). However, occasionally the male fed the female and she took the food to the nestlings; two of nine female feedings observed on 21 May occurred in this fashion. Alarm notes, often in response to my presence, were only given by the female during both the nestling and the fledgling periods. The female always went to the nest box and fed the young with much less hesitancy if the male was with her than if she was alone.

The male appeared to alternate periods of courtship activity with periods of caring for the young, especially at first. Thus male feedings were erratic; five were observed in one 26-min period on 28 May but none occurred during six of the 13 entire observation periods. Courtship activities included displays about the nest box, singing, and various aerial and non-aerial displays such as "Butterfly Flight" and "Wing-waving" (Krieg 1971). These became less common as the fledgling reached independence. During the nestling period the male entered the nest box without food on 16 occasions, often as part of a display and when the female was nearby. The female did not do this, and such behavior is rarely observed in other male bluebirds at nests containing nestlings (pers. obs.). The female did not respond to these displays, nor did she behave aggressively toward the male. The male usually followed the female on her trips back and forth to the nest until fledging. After fledging the pattern was occasionally reversed as the

female followed the male on nest site inspections, five of which occurred on 5 June. After 9 June the male was not seen near the fledgling but spent much time defending the nest site against other species as well as a male bluebird that attempted to usurp the site on 13 June.

Although the male bluebird fed the young infrequently and did not give alarm notes, he appeared to increase the likelihood of a successful nest by the widowed female in three ways: 1) by feeding the juveniles and cleaning the nest; 2) by offering food to the female who in turn delivered it to the young; and 3) by enhancing the female's feeding rate because she fed with less hesitancy if the male was present.

The pair began a new nest in the same nest box on 15 June. Four eggs were laid on 19–22 June and all four hatched on 5 July. During the period 11–19 July I observed 38 male feedings and 30 female feedings (four observation periods of 1.5–2.5 h each), and the proportion of feedings offered by the male to the second brood (55.9%) was significantly greater than the proportion he offered to the first brood ($\chi^2 = 37.4, P < 0.001$). While tending the second brood the male gave alarm calls in response to potential predators and rarely approached the nest except to feed the nestlings. Alarm notes from the male were especially common after 13 July, when three of the four young were taken by an unidentified mammalian predator. The remaining nestling fledged on about 25 July.

Power (1975) experimentally removed male Mountain Bluebirds (*S. currucoides*) and found that none of eight male "consorts" arriving at nests containing nestlings fed the young; although one female did so, he interpreted the behavior as a reproductive error. The male Eastern Bluebird that I observed, however, arrived after the latest date on which bluebirds in my study area can still rear two broods (15 May) and at a time when few other bluebirds are entering the study area (Pinkowski 1977b). Thus the male acquired a mate, territory, and nest site for a later brood, and because these nesting requisites are in relatively short supply after the season begins, the male enhanced his chances for gene perpetuation by behaving in an apparently altruistic manner. Had the first nest failed the female may have left the territory, perhaps without the male (Pinkowski 1977b), and the nest site may have been usurped before the male could obtain a new mate.

The apparently altruistic behavior of the male bluebird may, therefore, be interpretable as reciprocal altruism (Trivers 1971) or, more appropriately, reciprocity (Konecni and Power 1976). In a multi-brooded species this behavior would be most advantageous early in the season; late in the season widowed adults might be expected to rear young alone because potential consorts would derive little benefit from providing aid. Hamilton (1943) observed a female Eastern Bluebird incubate a clutch of eggs laid by another female that was killed by a cat and his observation, like the present one, occurred early in the season (May). Of three other cases I have observed wherein male bluebirds disappeared at nests containing nestlings and the young were reared by the female alone, all disappearances occurred late in the season (20 June, 15 July, 1 August). My only record of a male bluebird rearing a brood alone involved a female disappearance that also occurred late in the season (7 July).

The reciprocal benefits obtained by early season consorts belonging to multi-brooded species may also be available to consorts of single-brooded species that establish lasting pair bonds or breed in the same areas during successive breeding seasons. Thus reciprocity may be the correct interpretation of the observations by Kilham (1977) of apparently altruistic behavior in the Yellow-bellied Sapsucker (*Sphyrapicus varius*), a single-brooded species that often retains the same range during its lifetime (Lawrence 1967).

I thank Harry W. Power for criticizing this manuscript and my wife, Phyllis, for her assistance in the field.

Literature Cited

Batts, H. L. 1958. The distribution and population of nesting birds on a farm in southern Michigan. Jack-Pine Warbler 36: 131–145.

Bent, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. 196.

Carr, T., & C. J. Goin, Jr. 1965. Bluebirds feeding Mockingbird nestlings. Wilson Bull. 77: 405–407.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I and II. J. Theoret. Biol. 7: 1–16, 17–52.

Hamilton, W. J. 1943. Nesting of the Eastern Bluebird. Auk 60: 91–94.

Kilham, L. 1977. Altruism in nesting Yellow-bellied Sapsucker. Auk 94: 613–614.

Konecni, V. J., & H. W. Power. 1976. Altruism: methodological and definitional issues. Science 194: 562–563.

Krieg, D. C. 1971. The behavioral patterns of the Eastern Bluebird (*Sialia sialis*). New York State Mus. Sci. Serv. Bull. 415.

LASKEY, A. R. 1939. A study of nesting Eastern Bluebirds. Bird-Banding 10: 23–32.
———. 1947. Evidence of polyandry at a bluebird nest. Auk 64: 314–315.
LAWRENCE, L. D. 1967. A comparative life-history study of four species of woodpeckers. Ornithol. Monogr. No. 5.
PINKOWSKI, B. C. 1975. Yearling male Eastern Bluebird assists parents in feeding young. Auk 92: 801–802.
———. 1976. Further observations on a family of Eastern Bluebirds. Bird-Banding 47: 160–161.
———. 1977a. "Courtship feeding" attempt between two male Eastern Bluebirds. Jack-Pine Warbler 55: 45.
———. 1977b. Breeding adaptations in the Eastern Bluebird. Condor 79: 289–302.
———. 1978. Feeding of nestling and fledgling Eastern Bluebirds. Wilson Bull. 90: 84–98.
POWER, H. W. 1975. Mountain Bluebirds: experimental evidence against altruism. Science 189: 142–143.
TRIVERS, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46: 35–57.
WETHERBEE, K. B. 1933. Eastern Bluebirds in juvenal plumage feed young of second brood. Bird-Banding 41: 199–200.
WILSON, E. O. 1975. Sociobiology: the new synthesis. Cambridge, Massachusetts, Harvard Univ. Press.

Received 27 September 1977, accepted 10 December 1977.

Effects of Interspecific Dominance Among Egrets Commensally Following Roseate Spoonbills

JAMES K. RUSSELL
Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514 USA

Egret species participate as followers in several "beater-follower" associations (Rice 1954, Christman 1957, Parks and Bressler 1963, Emlen and Ambrose 1970, Leck 1971, Courser and Dinsmore 1975). This type of relationship in which one species, the "follower," increases its foraging efficiency through exploitation of prey items disturbed by the foraging activities of another species, the "beater," may be important in the evolution of many mixed-species associations (Rand 1954, Moynihan 1962, Friedmann 1967). To understand the composition of this kind of association we need to know both the benefits animals obtain by participating in them and the factors that limit the magnitude of these benefits. In associations with a single follower species Heatwole (1965) and Dinsmore (1973) showed that egrets increase their foraging efficiency by following, and Grubb (1976) showed that intraspecific aggression limits the number of followers that can take advantage of any beater. Where there are multiple follower species interactions between them will affect the advantages each can obtain by following and will thereby influence the tendency for members of each species to occur in the association. This paper compares the increase in feeding efficiency achieved by interspecifically dominant Great Egrets (*Casmerodius albus*) with that achieved by interspecifically subordinate Snowy Egrets (*Egretta thula*) when they both participate as followers in a feeding aggregation.

From 26 to 29 January 1975 I observed feeding aggregations of Great Egrets, Snowy Egrets, Roseate Spoonbills (*Ajaia ajaja*), White Ibises (*Eudocimus albus*), Glossy Ibises (*Plegadis falcinellus*), immature Little Blue Herons (*Florida caerulea*), and American Jacanas (*Jacana spinosa*) in a marsh in Costa Rica. The aggregations form when a group of Roseate Spoonbills begins foraging in emergent water hyacinth. In contrast to the slow lateral sifting movements they use while foraging over submerged vegetation, in emergent hyacinth the spoonbills move rapidly and jerk their bills forward through the vegetation, acting as beaters. Roseate Spoonbills, White Ibises, Great Egrets, and Snowy Egrets are regularly present in the aggregations, the other species irregularly. There is considerable variation in the composition of the aggregations, but typically the spoonbills and White Ibises are present in roughly equal numbers and form one or more clumps that the egrets surround and frequently attempt to penetrate. Snowy Egrets are usually at least as numerous as the spoonbills and roughly five times as numerous as Great Egrets.

Great Egrets and Snowy Egrets also feed solitarily in the same area. Therefore, I could observe each species foraging in and away from the aggregations under similar conditions and compare the increase in foraging efficiency they obtained by joining the aggregations.