A TEST FOR CONSPECIFIC EGG DISCRIMINATION IN THREE SPECIES OF COLONIAL PASSERINE BIRDS

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ABSTRACT.—Naturally occurring populations of three species of colonial passerine birds, the Piñon Jay (*Gymnorhinus cyanocephalus*), Great-tailed Grackle (*Quiscalis mexicanus*), and Barn Swallow (*Hirundo rustica*), were tested for conspecific egg discrimination and the presence of intraspecific brood parasitism that such discrimination would imply. Current theory predicts that intraspecific brood parasitism, or cheating, might occur when a brood parasite's fitness is enhanced relative to a nonparasite's. Due to the high cost of parental care in altricial birds, selection for defenses against such cheaters should also be intense. Egg rejection is the most common selection mechanism against interspecific brood parasites, and I tested for the presence or absence of this mechanism.

Single eggs were switched between pairs of 19 Piñon Jay nests, 15 Great-tailed Grackle nests, and 14 Barn Swallow nests, and a fifth egg was added to each of 8 Piñon Jay nests. No significant level of rejection of introduced eggs was found, possibly either because the cost of cheating is too great or because egg discrimination and rejection are not the mechanisms of selection against cheaters in the populations tested. *Received 8 August 1979, resubmitted 19 May 1981, accepted 7 January 1982.*

INTRASPECIFIC brood parasitism, a reproductive strategy wherein a parasitic bird uses another individual of its species to rear its young, apparently is rare among altricial birds, even though a conspecific should be an ideal host due to the nutritional requirements of the young parasite, the compatibility of parental behavior and egg size (Payne 1977), and the synchrony of egg laying by the host and parasite (Hamilton and Orians 1965). Intraspecific brood parasitism has been positively demonstrated, however, in only five species: the House Sparrow (*Passer domesticus*; Manwell and Baker 1975), the Fairy Martin (*Petrochelidon ariel*; Manwell and Baker 1975), the African Village Weaverbird (*Ploceus cucullatus*; Victoria 1972), the Starling (*Sturnus vulgaris*; Yom-Tov et al. 1974), and the Dead Sea Sparrow (*Passer moabiticus*; Yom-Tov 1980).

The question of why intraspecific brood parasitism isn't more prevalent in altricial birds gains added importance when viewed in light of the hypothesis of Hamilton and Orians

(1965) regarding the evolution of brood parasitism. Their evolutionary scenario is: (1) accidental destruction of the protoparasite's nest during the egg laying phase; (2) the protoparasite then being stimulated by a neighbor's nest containing eggs to lay in that or a nearby nest; and (3) subsequent renesting by the protoparasite. The likelihood of these events occurring is greater in colonial than in noncolonial species due to the number and proximity of similar nests (Hamilton and Orians 1965).

In altricial birds the frequency of brood reduction by starvation of some nestlings (e.g. Ricklefs 1969) suggests that the cost of raising even one of another bird's young would often be great. Selection might therefore favor a defense against parasitism by any altricial bird that is regularly subjected to any degree of brood parasitism, whether it be inter- or intraspecific. The most common host adaptation to interspecific parasitism is egg rejection (versus denying access to the nest, deserting a parasitized nest, or refusing to care for or rejecting the young parasite) (Rothstein 1975a). Any host defense involving egg rejection implies that the host has the ability to discriminate its eggs from those of a parasite. Examination for egg recognition and rejection of alien eggs is a relatively simple means of testing for inter-

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specific (Rothstein 1975a) and intraspecific (Peek et al. 1972, Hoogland and Sherman 1976, Burtt 1977) brood parasitism.

The goal of this study was to examine three species of colonial, altricial birds, the Piñon Jay (*Gymnorhinus cyanocephalus*), Great-tailed Grackle (*Quiscalis mexicanus*), and Barn Swallow (*Hirundo rustica*), for the presence or absence of intraspecific egg recognition as indicated by the rejection of a foreign egg or desertion of the nest. *Inter*specific brood parasitism has not been reported for the Piñon Jay or Great-tailed Grackle, and the Barn Swallow is a rare host for the Brown-headed Cowbird (*Molothrus ater*; Friedmann et al. 1977).

METHODS AND MATERIALS

SPECIES AND STUDY SITES

Piñon Jay.—Piñon Jays are colonial, monogamous birds inhabiting the piñon-juniper woodlands of the western United States (Balda and Bateman 1972). The two colonies used in this study occupied woodlands about 20 km west of Magdalina, New Mexico (see Ligon 1978 for a more detailed description of this study site). Fieldwork was conducted from February through April of 1978. Nests were usually built in the upper halves of piñon (*Pinus edulus*) and juniper (*Juniperus monosperma*) trees. The female incubates almost continuously and is fed by the male (Balda and Bateman 1972). Female Piñon Jays probably stay on their nests from the onset to protect their eggs from the cold, as snow flurries and cold rains are not uncommon during the egg-laying and incubating stages, which occur in late February and early March. Nests within a colony are spread over a wide area, with 24 nests in one colony covering about 20 ha and 7 nests in a second covering about 12 ha.

Great-tailed Grackle.—This species, both colonial and polygynous, ranges from the south-central United States south into Mexico (Selander and Giller 1961). The colony used in this study occupied a small marsh (about 8 ha) adjacent to New Mexico State Highway 85, approximately 23 km south of Albuquerque, New Mexico on the Isleta Indian reservation. Fieldwork was conducted from April through June of 1977 and 1978. Nesting was underway when fieldwork started in both years. Some nests were being constructed, others already contained eggs, and a few contained young. Nests were constructed in cattails (*Typha latifolia*) and bulrushes (*Scerpus californicus*), with 13 nests occupying about ⅓ ha in 1977 and 19 nests occupying about the same area in 1978. The female alone builds the nest, incubates her eggs, and cares for the young. Unlike female Piñon Jays, female Great-tailed Grackles do not remain on the nest continuously during the egg-laying and incubation stages. The difference in attentiveness may be related to environmental factors. Great-tailed Grackles begin nesting in late spring when weather conditions are dry and temperatures mild.

Barn Swallow.—The Barn Swallow, ubiquitous in most of the United States, is a colonial, monogamous species. The cup-shaped nests of the colony used in this study were constructed under a wooden bridge across the Rio Grande on New Mexico State Highway 60, about 80 km south of Albuquerque, New Mexico. As with the grackles, nesting was underway in May of 1977 when fieldwork with this species started, with some nests under construction, a few with eggs, but none containing young. Fieldwork was halted in July of 1977. Samuel (1971) reported that both sexes participate in nest construction, but the male only occasionally assists in incubation. Both parents participate in rearing the young. Female Barn Swallows do not remain continuously on the nest during egg-laying and incubation stages. The same reasons for inattentiveness in grackles probably apply to Barn Swallows.

Procedures.—Standard procedure consisted of removing an egg from a nest containing n eggs and replacing it with an alien but conspecific egg. These experimental nests then contained $n - 1$ of their own eggs and one alien or test egg. Host eggs had small numbers (1–2 mm) and test eggs had small "T's" written on them in indelible ink. Control nests consisted of n of their own eggs and were subjected to the same manipulations and visits as experimental nests in order to establish an index of desertion due to human interference.

After test eggs were added, nests were checked within 24 h for any initial response by the host, with subsequent checks being made at 48 h, 7 days, and 14 days. These checks ended (1) when a response to the parasitism was noted, (2) when eggs were taken by predation, (3) following the 14 day check, or (4) when the eggs hatched. All experiments were scored as either acceptance or rejection, following Rothstein's (1975a) criteria for rejection. Three responses were considered as rejections: (1) chipped or damaged eggs, (2) disappearance of the test egg, and (3) nest desertion. Missing test eggs were assumed to have been successfully ejected, and a chipped or damaged test egg was assumed to have been damaged during an attempted ejection. If a nest contained an entire clutch but lacked any evidence of activity (warm eggs or presence of an incubating female) on at least two consecutive visits, it was considered deserted. Nests in which both a test egg and one or more of the host's eggs were missing could have resulted from either rejection or predation and were not counted. All data were analyzed by use of Fisher's Exact Probability Test (Sokal and Rohlf 1969). A significance level of 0.05 was used for this study.
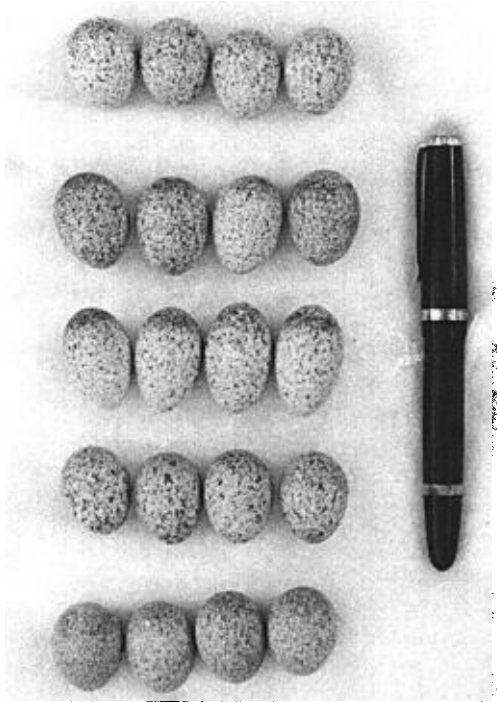
Fig. 1. Comparison of size, shape, and pattern variation among eggs of Piñon Jay clutches.

Fig. 2. Comparison of size, shape, and pattern variation among eggs of Great-tailed Grackle clutches.

RESULTS

Piñon Jay.—Of 30 nests located, 19 had eggs exchanged (an egg removed and an alien egg added), 5 were controls, and the remaining 6 were not used, either because they were destroyed prior to egg laying or because they were inaccessible. Although clutches were visibly different to me in size, shape, coloration, and pattern of streaking (Fig. 1), no eggs were rejected. Two experimental nests were deserted ($P = 0.57$) by the 24-h and 48-h checks, but no controls were deserted. One of the desertions may have occurred prior to my finding the nest and placing an alien egg in it. I never saw a female on or near the nest as I did at all other nests of this species. Nest desertion occurs regularly at low frequencies (8–20%) in Piñon Jays (Balda and Bateman 1972, Ligon 1978). No unusually large clutches, which might suggest egg dumping, were found. Mean clutch size, 3.44 ± 0.96, was smaller than the means found by Balda and Bateman (1972) or Ligon (1978).

At 8 nests, when no response had been not-

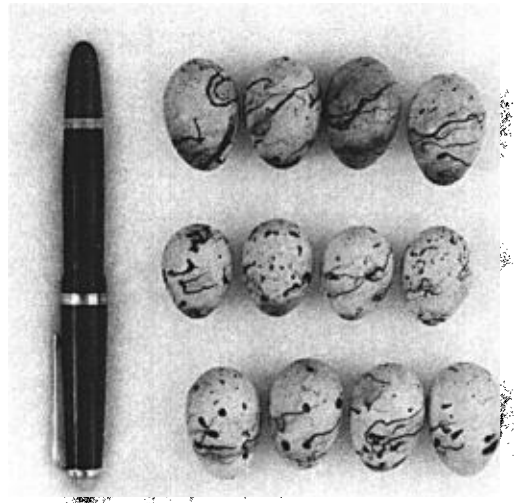ed by the 48-h check, a second test egg was added (each of these nests then contained $n - 2$ of its own eggs and 2 alien or test eggs), and checks were made 24 and 48 h later. Except for one desertion (the other of the two desertions mentioned previously), no rejections were noted. As with the case of single test eggs, females readily accepted the addition of the second alien egg and incubated it.

Great-tailed Grackle.—Of 20 nests located during the study, 15 were used as experimental nests, 4 as controls, and 1 was not used, due to being inaccessible. Three rejections were recorded. In one nest the test egg had a hole pecked in it, while in the other two, test eggs were missing at the 24-h check. The latter two rejections might be explained on bases other than defense against brood parasitism. Both nests were located on the same day and eggs were switched between them. At the 24-h check, one nest had two newly hatched young but no test egg. The other nests had only the host's eggs present and no test egg. It is possible that the egg from the first nest was placed in the second, younger clutch and hatched prior to the host female's being physiologically and behaviorally ready to care for any young, and the host female ejected it. This, however, is unlikely (e.g. Emlen 1941). In the case of the older clutch, the younger test egg may have
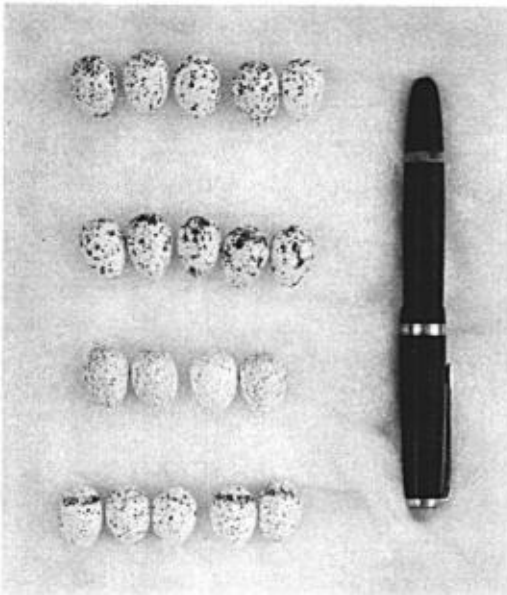
Fig. 3. Comparison of size, shape, and pattern variation among eggs of Barn Swallow clutches.

been ejected after it failed to hatch at the same time as those of the host. In no nests did I ever see unhatched eggs and young together after the majority of the clutch had hatched. The probability of obtaining three rejections by chance is 0.36. If the two nests just discussed are discounted, the probability is 0.72.

As with the Piñon Jay, female grackles seemed readily to accept eggs from other clutches. Also, like Piñon Jays, variation existed between clutches in egg size, shape, depth of color, and general pattern of scrolling (Fig. 2). No unusually large clutches, suggesting egg dumping, were found. Mean clutch size was 3.12 ± 0.44. Desertions were not observed, either of experimental nests or of controls. In this species, no additional test eggs were added to nests where no response to one alien egg was noted. Nest predation in 1978 was much higher (42%) than in 1977 (23%), with 5 experimental and 2 control nests being predated. In 1977 1 experimental and 2 controls were similarly lost.

Barn Swallow.—Of 22 nests located for this species, 14 were utilized as experimental nests, 7 served as controls, and 1 was inaccessible. Only one egg rejection was observed, the test egg being gone at the 24-h check ($P = 0.66$). Like the clutches of jays and grackles, there

appeared to me to be some variation between clutches in egg size, shape, coloration, and pattern of marking (Fig. 3). Due to the small size of swallow eggs, however, this variation was on a smaller scale and therefore less obvious than for the jays and grackles. No test or control nests were deserted during the study of this species, and no unusually large clutches, which might suggest egg dumping, were found. Clutch sizes ranged from 2 to 5 for this species (as compared to 2–4 for grackles and 3–5 for the jays), with a mean clutch size of 4.00 ± 0.84.

DISCUSSION

Selection for and against intraspecific brood parasitism.—Payne (1977) states that, due to prolonged care in altricial birds, intraspecific brood parasites should experience severe adverse selection due to host responses, which would cause such parasitism to be rare. He further states that such selection is suggested by the ability of some colonial birds to discriminate alien eggs from their own. It should be noted that most discrimination tests reported in the literature deal with precocial or semi-precocial birds (e.g. Buckley and Buckley 1972) or with the use of artificial or real eggs of species other than the one being tested (e.g. Rothstein 1975a, b). Because conspecific eggs have not been used by most investigators, any arguments that intraspecific brood parasites are experiencing severe adverse selection, at least through the mechanism of egg discrimination, are somewhat weakened. I can find only three studies of altricial birds (Peek et al. 1972, Hoogland and Sherman 1976, Burtt 1977) in which eggs of conspecifics have been used.

The most extensive testing for egg discrimination in altricial birds is that of Rothstein (1975a, b). His results have direct bearing on the problem of intraspecific brood parasitism. Instead of using conspecific eggs, however, Rothstein (1975a, b) placed artificial or real cowbird eggs in the nests of 31 species of North American passerines, including the Barn Swallow. He found that 8 species were rejectors, while 23 species were acceptors. Rothstein divided the latter into two types: Type I acceptors, those species not normally parasitized by cowbirds and that have no known selective pressure to evolve a defense; and Type II acceptors, those species parasitized by cowbirds

but that have not yet evolved egg rejection as a defense.

Rothstein suggests (1975b) that Type II acceptors should exhibit zero rejection frequencies. He reasons that selection pressure for egg rejection should be high and that, once rejection evolves in a population, the substitution of the gene (or genes) associated with this behavior would be rapid. He concludes that the large selection coefficient that results for egg rejection should preclude intermediate levels of this behavior except in those species that have only recently evolved egg rejection as a host defense. Rothstein (1975a) found low levels of rejection frequencies, however, for both types of acceptors. This, as he points out (Rothstein 1975b), causes problems with his hypothesis. If his hypothesis is correct, the presence of low egg-rejection frequencies means that all acceptor species have recently and simultaneously evolved this behavior. For Type II acceptors this is entirely possible if Brown-headed Cowbirds have only recently invaded most of North America (Mayfield 1960). Rothstein (1975b) rejects this on two accounts. First, low levels of rejection behavior can exist in those species having a low probability of being parasitized or that have a high reproductive rate in the face of parasitism. Second, low frequencies of egg rejection may be due, not to an evolved response to parasitism, but rather to behaviors associated with other aspects of breeding. He points out that some acceptor species that show rejections build shallow nests from which the test egg may simply have been accidentally pushed out, in other words, that the rejections among Type I acceptors may have been artifacts (Rothstein 1975b), just as I suggest that two of the three grackle rejections were possibly artifacts.

Either supposition may be correct. Low levels of egg rejection may have resulted from past intraspecific brood parasitism, however, accounting for the rejection exhibited by Type I acceptors. If so, then one must wonder why no rejection of conspecific eggs was observed either in this study or in those of Peek et al. (1972), Hoogland and Sherman (1976), or Burtt (1977). Two possible explanations come to mind: (1) sample size may have been too small to detect very low frequencies of occurrence of egg rejection within the populations examined; or (2) other defensive strategies might have been employed by these species.

Robertson and Norman (1978) argue that a better method of defense than egg rejection should be aggressive behavior toward the parasite, thus denying it access to a potential host's nest by driving the parasite from the vicinity of the nest. These investigators presented models of Brown-headed Cowbirds to Type II acceptors as well as rejectors by placing the models near the test species' nests and observing aggressive responses toward the models. A positive correlation was found between the degree of aggression exhibited and the incidence of brood parasitism, suggesting that those species exhibiting strong defensive behavior had good reason to do so.

The problem of egg discrimination tests.—Although positive findings of egg discrimination and rejection are good evidence for the presence of brood parasitism (e.g. Rothstein 1975a), the negative results of this study and those of Peek et al. (1972), Hoogland and Sherman (1976), or Burtt (1977) do not have such power in rejecting the existence of intraspecific brood parasitism. First, if we conclude that an absence of egg discrimination implies an absence of brood parasitism, we would then have to conclude that many acceptor species (Rothstein 1975b) are not parasitized interspecifically by cowbirds because they accept cowbird eggs. Rothstein's work (1975a, b) has shown that this is not the case. While the presence of an adaptation such as egg discrimination implies current or previous selective pressure, the absence of the adaptation does not imply, anywhere near as strongly, an absence of the selective pressure. There is no reason to assume that all animals respond adaptively to all selective pressures that affect them [e.g. the seeming lack of a response by Kirtland's Warblers (*Dendroica kirtlandii*) to heavy parasitism by the Brown-headed Cowbird].

A second problem with this study and those of Peek et al. (1972), Hoogland and Sherman (1976), and Burtt (1977) is that none of the results of these tests excludes the possibility of any colonial species' containing a proportion of highly adapted, partially parasitic individuals. If such individuals occurred in species with little or no egg variation and if they usually deposited one egg and removed one host egg per nest, the techniques used in this study would not detect their existence. These individuals might be maintained at low frequencies by some type of frequency-dependent selection.

The question of intraspecific brood parasitism.— Current evolutionary theory maintains that, because of the intensity of selective forces, individuals maximize personal fitness at all times (e.g. Dawkins 1976). Intraspecific brood parasitism might therefore be expected in all bird populations in which such a parasite stands to gain relative to nonparasitic individuals. Yet this and the other studies suggest that parasitism of this type may indeed be rare and possibly a negligible selective force as regards colonial species. If the intensity of selective pressure to become a parasite or cheater (e.g. Dawkins 1976) has been overestimated—cheating must have certain costs associated with it— then it might occur very infrequently, and no mechanism counteracting such cheating would exist in most populations. When a gene for intraspecific brood parasitism does occur in the absence of selective pressure against it (as evidenced by the lack of host defensive behaviors), then that gene would become rapidly fixed in that population and species (Payne 1977) if it led to a gain in fitness by the parasite relative to other members of the population. Payne (1977) points out that those species parasitizing only conspecifics, and not other species as well, would become extinct. Such extinction would account for the relative rarity of intraspecific brood parasitism, especially in altricial birds for which one would predict high rates of adverse selection, due to the cost of producing offspring.

The cost of parental care should increase in the face of low nesting success due to heavy nest predation pressure or nest destruction, as should the importance of being a good parent. During this study, no accurate data on nesting successes were recorded. Ligon (1978), however, reported spring and fall nesting successes ranging from 36% to 54% during 4 yr of study of the Piñon Jay. Tutor (1962) reported nesting success for Great-tailed Grackles to be 20.4% for first nestings and 65% for second nestings. Samuel (1971) does not mention nesting success as such but does report egg and nestling mortality as 18.9% for first nestings and 14.9% for second nestings in the Barn Swallow.

Considering the high nest loss of Piñon Jays and the moderately high losses of grackles, intraspecific brood parasitism would appear to be, at first glance, an ideal way to spread the risks of nest failure (Payne 1977); it would also place a premium, however, on superior paren-

tal care and behavior. Only those individuals constructing first-rate nests in well-hidden sites and providing abundant care and food for young would be successful. If we assume that the lack of any demonstrable defense against eggs of parasites, such as egg rejection, implies an absence of intraspecific brood parasitism, the question is raised as to why so few birds "cheat" but instead seem to focus all their reproductive efforts on caring for their own young. The answer may simply be that under most circumstances natural selection has favored those individuals exhibiting superior parental behavior rather than those that might be inclined to deposit eggs in the nests of others, especially at some cost to the offspring they attempt to rear on their own. This seems likely for those species for which nest failure is very high. And this may be why, although nest failure is a common occurrence among birds (Hamilton and Orians 1965), only 1% of all birds are brood parasites (Payne 1977).

LITERATURE CITED

BALDA, R. P., & G. C. BATEMAN. 1972. The breeding biology of the Piñon Jay. Living Bird 12: 5–42.

BUCKLEY, F. G., & P. A. BUCKLEY. 1972. Individual egg and chick recognition of adult Royal Terns (*Sterna maxima maxima*). Anim. Behav. 20: 457–462.

BURTT, E. H., JR. 1977. Some factors in the timing of parent-chick recognition in swallows. Anim. Behav. 25: 231–239.

DAWKINS, R. 1976. The selfish gene. New York, Oxford Univ. Press.

EMLEN, J. T., JR. 1941. An experimental analysis of the breeding cycle of the Tricolored Red-wing. Condor 43: 209–219.

FRIEDMANN, H. 1960. The parasitic weaver bird. Washington, D.C., U.S. Natl. Mus. Bull.

———, L. F. KIFF, & S. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. No. 235.

HAMILTON, W. J., III, & G. H. ORIANS. 1965. Evolution of brood parasitism in altricial birds. Condor 67: 361–382.

HOOGLAND, J. L., & P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46: 33–58.

LIGON, J. D. 1978. Reproductive interdependence of Piñon Jays and piñon pines. Ecol. Monogr. 48: 111–116.

MANWELL, C., & C. M. A. BAKER. 1975. Molecular genetics of avian proteins XIII. Protein polymorphism in three species of Australian passerines. Australian J. Biol. Sci. 28: 545–557.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci. Bull. No. 40.

PAYNE, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1–28.

PEEK, F. W., E. FRANKS, & D. CASE. 1972. Recognition of nest, eggs, nest site and young in female Red-winged Blackbirds. Wilson Bull. 84: 243–249.

RICKLEFS, R. E. 1969. An analysis of nestling mortality in birds. Smithsonian Contrib. Zool. 9: 1–48.

ROBERTSON, R. J., & R. F. NORMAN. 1978. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78: 166–173.

ROTHSTEIN, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250–271.

———. 1975b. Evolutionary rates and host defenses against avian brood parasitism. Amer. Natur. 109: 161–176.

SAMUEL, D. E. 1971. The breeding biology of Barn and Cliff swallows in West Virginia. Wilson Bull. 83: 284–301.

SELANDER, R. K., & D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed grackles. Condor 63: 29–86.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. B. Freeman and Co.

TUTOR, B. M. 1962. Nesting studies of the Great-tailed Grackle. Auk 79: 77–84.

VICTORIA, J. K. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaverbird *Ploceus cucullatus*. Ibis 114: 367–376.

YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. Biol. Rev. 55: 93–108.

———, G. M. DUNNET, & A. ANDERSON. 1974. Intraspecific nest parasitism in the Starling *Sturnus vulgaris*. Ibis 116: 87–90.