CONSPECIFIC BROOD PARASITISM IN THE HOUSE SPARROW

PAUL E. KENDRA,[1,2] ROLAND R. ROTH[1,3] AND DOUGLAS W. TALLAMY[3]

ABSTRACT.—We studied 94 clutches of the House Sparrow (*Passer domesticus*) in Newark, Delaware, to determine: (1) the frequency of apparent conspecific brood parasitism (CBP); (2) if the laying of eggs in a conspecific's nest is truly a parasitic interaction with the recipient; and (3) that indeterminate laying can predispose a species to CBP. Eight clutches yielded evidence of CBP; electrophoresis of egg albumin detected a genetically odd egg in 4 of 42 clutches, while 4 other clutches provided indirect evidence of CBP—visibly odd eggs in other than the ultimate position and two eggs laid in one day. An egg-removal experiment suggested that House Sparrows are indeterminate layers before the third egg is laid; thus a female can increase her fecundity by laying one or more parasitic eggs before completing her own clutch of normal size. A complementary egg-addition experiment showed that a recipient female may reduce her contribution to her own clutch by one egg if an egg is inserted before she lays her third one. Insertion after the third egg can result in an enlarged clutch to the potential detriment of both host and parasite. *Received 19 May 1987, accepted 10 Sept. 1987.*

Females of over 50 species of birds are known to lay eggs in the nests of conspecifics (Yom-Tov 1980a, Andersson 1984). This behavior, variously termed intraspecific (or conspecific) nest (or brood) parasitism (e.g., Yom-Tov 1980a, Andersson 1984, Emlen and Wrege 1986), has been recognized since about 1900 (Weller 1959, Yom-Tov 1980a), but until recently it was treated largely as incidental, aberrant behavior. Its brief treatment under "dump nesting" and its exclusion from "brood parasitism" by Terres (1980) and Campbell and Lack (1985) are evidence of past perspectives. Our terminology throughout will refer to parasitism, even though the purist would object that we have not demonstrated cost and benefit of the behavior to the recipient and donor, respectively.

Several recent authors have hypothesized which individuals should be parasitic and under what circumstances (Yom-Tov 1980a, Andersson and Eriksson 1982, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). We summarize these as the: (1) "last resort hypothesis"—a female lays parasitically because, as a result of inexperience, social status, or accident, she lacks a nest of her own; (2) "enhancement hypothesis"—a female lays a clutch in her own nest and increases her fecundity by laying one or more eggs in other nests; (3) "pure parasite hypothesis"—a female lays all her

[1] Order of authorship determined by coin-toss.
[2] Myrtle Bell Lane Lab., Dept. of Medicine, Duke Univ. Medical Center, Durham, North Carolina 27710.
[3] Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, Delaware 19717-1303.

eggs in other conspecifics' nests; and (4) "the accident hypothesis"—a female mistakenly lays in a nest not her own (Hamilton and Orians 1965, referring to interspecific parasitism).

Scant testing of these hypotheses exists. Emlen and Wrege (1986) provide limited experimental support for the "last resort hypothesis" in the White-fronted Bee-eater (*Merops bullockoides*). Petrie (1986) and Gibbons (1986) report nonexperimental data supporting the enhancement hypothesis for the Common Moorhen (*Gallinula chloropus*). Their findings are exceptions in a literature that has asked and tested few selection-based questions about egg dumpers. Most efforts instead have focused on effects of conspecific brood parasitism (CBP) on egg recipients (hosts).

Most verified conspecific parasites are precocial species (Yom-Tov 1980a). Among the small number of altricials are the European Starling (*Sturnus vulgaris*) (Yom-Tov et al. 1974, Power et al. 1981, and others summarized by Andersson 1984); Cliff Swallow (*Hirundo pyrrhonota*) (Brown 1984); Eastern Bluebird (*Sialia sialis*) (Gowaty and Karlin 1984); White-fronted Bee-eater (Emlen and Wrege 1986); Fairy Martin (*Petrochelidon ariel*) (Manwell and Baker 1975); and several passerids (Yom-Tov 1980a, Dhindsa 1981), including the House Sparrow (*Passer domesticus*) implicated in an aside to a genetics study (Manwell and Baker 1975).

House Sparrows exhibit the following qualities of potential hosts (H) and parasites (P) proposed by Hamilton and Orians (1965) as conducive to the development of interspecific parasitism: (1) hole nesting (H) (Bent 1958, Summers-Smith 1963:52); (2) colonial nesting (H) (Summers-Smith 1963:102, McGillivray 1980); (3) indeterminate laying (H, P) (Witschi 1935, Klomp 1970, this study, but see Brackbill 1960); and (4) limited or no nest-building role for female (P) (Summers-Smith 1963:55). One should expect CBP in a species with those features because conditions conducive to parasitism exist in each female as both host and parasite.

Anecdotal evidence suggests that parasitic laying occurs among House Sparrows. First, reports of enlarged clutches, possibly "dump nests" or joint efforts, exist (Bent 1958, Summers-Smith 1963:75–76, Fleischer 1982). Second, single clutches usually contain one or two eggs differing in color and spotting pattern from the rest of the clutch (Bent 1958, Brackbill 1960, Dawson 1964, Murphy 1978, Lowther, 1988). Most authors state or assume that these are the ultimate and penultimate eggs in a clutch. However, Seel (1968:270) refers to the "most recently laid" egg as being paler and brighter, a condition that "generally lasted less than 24 hours." Lowther (1988) invokes an effect of fortuitous hormonal shifts at the end of laying in speculating on the proximate cause of the

oddness. Electrophoretic evidence shows that odd-appearing eggs in at least some clutches, however, are from females other than the nest owners (Manwell and Baker 1975, this study). Thus, two kinds of oddness may be involved.

In this paper we report initial tests of the hypothesis that laying in a conspecific's nest increases the fitness of an egg donor at a reproductive cost to the egg recipient. We confirm the occurrence of CBP in the House Sparrow, examine indeterminate egg production as a catalyst for CBP, and provide preliminary evidence that CBP can reduce fitness in host females.

METHODS

The study nests were at two sites 300 m apart on the University of Delaware Farm in Newark, Delaware. Nests were in farm sheds at one site and in several nest boxes (erected in March, 1983) and an adjacent row of bushes (*Cupresso cyparis leylandi*) at the other. We checked the contents of the nests daily (mid- to late-afternoon) on 29 April–11 June 1983 and 30 May–10 July 1984. All of the 1983 nests were in the sheds. Completed clutches were collected, photographed, and refrigerated for later electrophoresis. In 1983 we delayed collection of some clutches until embryonic development had started. By comparatively aging the embryos in such clutches, we determined the position of the odd-appearing egg in the laying sequence. We examined electrophoretically only those clutches lacking macroscopically visible embryonic development to insure that only maternal proteins were sampled.

Albumin is entirely of maternal origin and therefore reflects the female genotype (Brush 1968). Electrophoresis of albumin resolves the House Sparrow genotype into a distinct banding pattern of four proteins, of which one, transferrin (conalbumin), is polymorphic, consisting of three patterns (Manwell and Baker 1975). Though like patterns cannot distinguish parentage, the occurrence of an odd transferrin pattern within a single clutch indicates an egg of different maternal origin (Fleischer 1985). Thus, electrophoresis does not reveal all cases of House Sparrow dumping, but it is a useful index of occurrence and minimum relative frequency. Gowaty and Karlin (1984) list additional reasons why the frequencies would be underestimates.

Our electrophoretic technique was a nondenaturing, polyacrylamide gel system: 12% separatory gel and 4.5% stacking gel with a pH 9.0 Tris/boric acid buffer (modified from Allen 1974). Gels were run overnight at constant current (10 ma). Proteins were stained and fixed in the gels with 0.1% Coomassie brilliant blue in 50% TCA. Entire clutches were run on single gels to allow direct comparison of eggs for protein polymorphism.

Two manipulative experiments were conducted in 1984. An egg-removal experiment used six active nests in boxes to determine if House Sparrows are indeterminate layers. From three nests, we removed one egg/day (always the oldest one) beginning after the laying of the second egg, leaving one egg in the nest. Eggs were removed from the remaining three nests after a third egg had been laid, leaving two eggs in the nest.

To determine the effect of a nonhost's egg on host clutch size, we added one egg to each of 17 clutches. The time of addition varied, being after the first, second, third, or fourth egg was laid. The inserted eggs came from other partial, unincubated clutches, including ones abandoned in the egg-removal experiment. The eggs were stored at 4°C until needed and warmed to ambient temperature before being put in a nest. Fifteen unmanipulated nests served as controls. During the daily nest checks, newly laid eggs were numbered to facilitate

identification and to determine the laying sequence and the number of eggs laid in the host nest. Electrophoresis was used to check for natural egg dumping events in all clutches.

RESULTS

Evidence of parasitic laying.—In 1983, 17 of the 54 complete clutches collected were suitable for electrophoresis. Four of those (24%) contained one egg genetically different from its clutch-mates. The genetically unique eggs differed in color and spotting pattern from their clutch-mates in 3 of the 4 cases, but no record was made of their position in the laying order. All were laid during the hosts' laying periods. The first laying dates and final sizes of the clutches in which each appeared were 2 May (4), 30 May (5), 2 June (6), 5 June (7), and 10 June (4). In 1984, 1 of 25 clutches (4%) that were electrophoretically examined contained one egg that was both genetically and morphologically unique. (See item 5 in the next paragraph for peculiar details of that clutch.)

Circumstantial evidence of parasitic laying came from several observations made during daily nest checks. Although not definitive, five results are consistent with such behavior. Two involved genetically odd eggs. (1) An exceptional clutch of 7 eggs was laid 5–11 June 1983. Mean size of 14 other complete clutches begun on 5 June ±7 days was 4.43 ± 0.25 SE. One of the 7 eggs was genetically, but not visibly, odd. (2) Two eggs appeared on the same day in one nest, an unlikely possibility for a single female (but see Nolan 1978:189). The two differed in appearance; one resembled the first egg of the clutch, and the other had a lighter background and fewer spots than the rest of the clutch. Damage of the eggs in storage prevented electrophoretic analyses. (3) In 1983, 41 of the 54 clutches held at least one visibly odd egg as did 11 of 15 control clutches in 1984 (see below). Over the two years, 75% (N = 69) of the clutches held a visibly odd egg. Four clutches in 1983 and one in 1984 held two eggs that differed visibly from the rest of the clutch. In four of those, the two eggs were of similar, lighter background and had fewer, bolder spots than their clutch-mates. In the fifth, the two odd eggs differed from one another as well. This last case, if none other, indicates laying by at least two different females in the nest. (4) A visually odd egg appeared in the penultimate position in one clutch each year and as the second of four eggs in a nest in late April, 1983. This latter result is evidence of parasitic laying even if females typically lay an odd egg last and sometimes next to last. (See the egg-removal experiment below for another case of this type.) (5) One nest received a clutch of three eggs on 27–29 April 1984 and then apparently was abandoned by the owner. The clutch remained unchanged until 5 May, when an egg was missing. On 6 May a new egg visibly different

TABLE 1

SCHEDULE OF LAYING AND EXPERIMENTAL REMOVAL OF EGGS IN HOUSE SPARROW NESTS
IN 1984

Removal schedule	Nest	Day 1 date	Status of clutch on day number[a]																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Before egg 3	1	28 Apr	R	R	R					R	r	N	N	N				N	N	N				
	2	16 Jun	R	R	R	R		r				R	R	R	R	r					R	R	R	r[b]
After egg 3	1	22 Apr	R	R	N	N																		
	2	6 May	R	R	R	R	N	N																

[a] Day number 1 is day when first egg found in nest. R, r = egg removed one or two days after being laid in "before egg 3" and "after egg 3" nests, respectively; r = visually odd egg; N = egg not removed and female allowed to lay and incubate additional eggs.

[b] Single, remaining egg removed to terminate experiment.

from the original eggs appeared. No additional laying or incubation occurred. Electrophoresis confirmed the egg to be of different genetic composition. This case may not represent CBP (see Discussion).

Egg-removal experiment. — When egg removal occurred in the interval between the second and third eggs, two females continued to lay for extended periods (Table 1). One female laid 11 eggs in three pulses over 17 days. The second female laid 14 eggs over a period of 22 days in 3 laying pulses. The latter presumably also had laid five eggs on 4–9 June that were collected from the same box on 9 June in the egg-addition experiment (see below). The first female did not stop to incubate when the last three eggs of the second cycle were not removed, but initiated another cycle and added three more eggs to the clutch. She incubated those six eggs, of which five hatched, and the nestlings fledged. The third female abandoned her nest after laying her fourth egg, which appeared two days after the third was laid and the first removed. A one-day skip followed the third egg.

Two females did not extend laying to replace lost eggs when removal of single eggs occurred after the nest held three eggs, i.e., leaving two eggs in the nest (Table 1). The females incubated the two eggs that remained in the nest after laying stopped. The third female abandoned her nest after her third laying day when we removed her first egg.

The second egg in the second pulse (fifth one laid) of the first extended layer was visually odd, as was the egg laid at the end of each pulse by the second extended layer (Table 1). No odd eggs appeared in the clutches of the nonextended layers. No electrophoretic differences were found among the eggs collected.

Egg-addition experiment. — We combined the data for different laying

TABLE 2

HOST CLUTCH SIZE IN EXPERIMENTAL AND CONTROL NESTS OF HOUSE SPARROWS

Treatment	Clutch size minus inserted egg		
	Mean	SE	N
Unmanipulated (control)	5.13[a]	0.09	15
Egg added before egg 3	4.17[b]	0.32	12
Egg added after egg 3	4.80[a,b]	0.37	5

[a,b] Values with same superscript not significantly different (ANOVA, Duncan's Multiple Range Test, $F_{2,29}$ = 4.99, P = 0.014).

intervals to create two groups: insertions before and insertions after egg 3 had been laid. We term the eggs not inserted by us the "host clutch." They, plus the inserted egg, equal the "final clutch size." We assume any actual parasites had equal access to experimental and control nests.

The host clutch in the "pre-3" nest was smaller than in the "post-3" and control nests (Table 2). "Post-3" clutches were more similar to controls than to pre-3 ones. ANOVA indicated significant differences among the groups (P = 0.01), but a Least Significant Difference test failed to group the post-3 nests solely with controls (Table 2). The small N for the post-3's may have been a factor in that failure. The final clutch size of the pre-3 group equaled the controls while that of the "post-egg 3" group was 0.7 egg larger.

In addition to the premature termination of host laying, the dumping experiment revealed three behavioral responses to egg addition. (1) One host female removed from her nest three different eggs that we had inserted singly after she had laid her first, second, and third eggs. The marked eggs were found on the ground not far from the host nest on the day following addition. (2) At 3 of the 17 manipulated nests, the host female failed to add an egg to the clutch on the day following egg addition. These occurrences were clearly skips in the middle of the normal laying cycle. One control clutch with five eggs had a one-day skip after egg 2. (3) Two of the 17 manipulated nests were abandoned after we added an egg, but none of the 15 control nests was abandoned.

DISCUSSION

Our electrophoretic analyses confirmed the occurrence of parasitic laying in the House Sparrow and corroborated at least one observation, an over-sized clutch, as such. A second case (laying in an apparently abandoned clutch) may have been erroneous parasitic laying. It also could have been an aborted change of ownership (P. Lowther, pers. comm.).

We will not consider it to be CBP hereafter. Manwell and Baker (1975) reported 2 of 32 clutches (6%) contained electrophoretically mismatched eggs. Wetton et al. (1987) found that 8% of nestlings in a population in England were genetically mismatched with their presumed parents. We found 24% and 0% to be genetically odd in the two years, respectively. These values are conservative, because House Sparrows exhibit polymorphism at only one albumin locus. Detection of genetic differences is limited by the degree of protein polymorphism within a species and because different females may possess the same alleles (Gowaty and Karlin 1984). Fleischer's (1985) technique, which we could not attempt, would have permitted estimating the probability that eggs of the same electromorph were from different birds.

Eight of the 94 clutches examined in the study showed evidence of CBP. The evidence included: (1) four clutches with electrophoretic confirmation of parasitic laying; (2) fourth, but not fifth, egg of a five-egg clutch visibly odd; (3) second of four eggs visibly odd in one clutch; (4) two eggs laid in a nest in same 24 h period; and (5) fourth and fifth eggs in a five-egg clutch visibly different from each other and the rest of the clutch. The 8.5% parasitism rate is a crude estimate, because not all nests were tested electrophoretically nor treated equally by virtue of the experiments in 1984. The value is slightly less than estimates for other altricial species: 12–46%, European Starlings (references in Andersson 1984); 10–27%, White-fronted Bee-eaters (Emlen and Wrege 1986); and 0–24%, Cliff Swallows (Brown 1984). Gibbons (1986) found 18% parasitism in Common Moorhens and that 20% of the laying females were parasites.

The visibly odd eggs common to *Passer* clutches (Bent 1958, Yom-Tov 1980b, Lowther 1988) remain enigmatic.` Virtually every writer commenting on the oddness of the last-laid egg has used a qualifier of "usually," "normally," etc. (e.g., Bent 1958, Dawson 1964, Murphy 1978). We found mismatched eggs usually, but not always, to be the last egg in the clutch, as did Lowther (1988). Four of five eggs in our study and 2 of 2 in Manwell and Baker's (1975) data that were genetically odd were also odd-appearing. These results beg a closer look at the origin of the last egg in House Sparrow nests, especially in light of reports that European Starling and White-fronted Bee-eater parasites tend to lay near the end of the host's laying period. One possibility is that the last odd egg is indeed from the resident female and that only the odd eggs detected in other positions are parasitic ones. We failed to distinguish systematically among types of oddity, e.g., darkness, lightness, etc., in relation to clutch-mates and cannot test that point.

Egg-removal experiments indicated that the female House Sparrow is an indeterminate layer up to a clutch size of 3 eggs. After three eggs appear

in a nest, total egg production appears to be determined at 4–6 eggs. These data suggest that a House Sparrow could increase her fecundity through parasitic laying before she has laid three eggs in her own nest. If parasitic eggs achieve reproductive maturity with any regularity, selection should favor the tactic described by the enhancement hypothesis.

Results of the egg-addition experiments indicate indeterminate laying can be a favorable trait for a parasite but a reproductive liability for a host. The host's cost may be reduced fecundity and diluted resources for her own young. If an egg is inserted before the host has laid her third egg, the parasitic egg may stop egg production, prematurely reducing the host's fecundity by one. This consequence has been recognized in the Redhead (*Aythya americana*) (Weller 1959) and the Common Goldeneye (*Bucephala clangula*) (Andersson and Eriksson 1982). If insertion occurs after a House Sparrow lays her third egg, the host can be left with an oversized clutch. The parasite shares this problem, but its young is a "bonus" and a smaller portion of its fecundity than are the host's young of its fecundity. Oversized clutches can result in decreased food delivery per young, lower weights, and decreased survival of nestlings and fledglings (Klomp 1970, Askemo 1977, Schifferli 1978). Notably, we found only one clutch larger than six.

The logical existence of antiparasite defenses has been anticipated (e.g., Lanier 1982, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). We saw limited evidence of the typical defensive responses to parasitic eggs—nest abandonment and egg-removal. Egg-removal has been observed in another passerid, the Village Weaver (*Ploceus cucullatus*) (Victoria 1972), and in White-fronted Bee-eaters (Emlen and Wrege 1986).

Another behavior seen during the egg-addition experiment suggests another type of defense. To avoid an oversized clutch, a host could lay one of her own eggs elsewhere. In three cases in our egg-addition experiment, host females failed to lay an egg in their nests on the day immediately following an egg addition. If eggs are produced consecutively at a rate of one per day, such skips may indicate instances in which the host laid elsewhere. An initial case of parasitic laying could result in a "domino effect," perpetuating the behavior among several females. If this pattern prevailed, most females would end up with a "normal" clutch to raise and would have laid their usual number as well. The advantage would go ultimately to females that were successful at parasitism but that also had defenses against foreign eggs, thereby keeping their own clutches pure and at a lower number.

We did not try to determine the status of the parasites. Possibilities include secondary females of polygamous matings, females disrupted at laying time, mated females contesting the same nest, unmated females

laying in their parents' nests, cooperative breeders, inexperienced females, and any or all females (Summers-Smith 1963:48, Sappington 1977, Yom-Tov 1980a, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). Our results do not permit us to reject any of the possibilities. Likewise, we cannot reject any of the four hypotheses of CBP enumerated in the introduction.

This study confirms the occurrence of CBP in the House Sparrow, provides insight to specifics of reproductive biology of the species which predispose it to such behavior, and supports the hypothesis that the donor-recipient interaction is parasitic in nature. Nevertheless, CBP remains poorly understood both in House Sparrows and as a general phenomenon. A more thorough assessment of the behavior and its costs and benefits for both donor and recipient House Sparrows is in progress. Similar studies of other species are required before the behavior can be accepted or rejected with confidence as parasitism and as a regular adaptive phenomenon.

LITERATURE CITED

ALLEN, R. C. 1974. Polyacrylamide gel electrophoresis with discontinuous buffers at a constant pH. Pp. 105–113 *in* Electrophoresis and isoelectric focusing in polyacrylamide gel (R. C. Allen and H. R. Maurer, eds.). Walter de Gruyter, New York, New York.

ANDERSSON, M. 1984. Brood parasitism within species. Pp. 195–228 *in* Producers and scroungers: strategies of exploitation and parasitism (C. J. Barnard, ed.). Croom Helm, London.

ANDERSSON, M. AND M. O. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: some evolutionary aspects. Am. Nat. 120:1–16.

ASKEMO, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival, and female weight loss in the Pied Flycatcher *Ficedula hypoleuca* (Pallas). Ornis Scand. 8:1–8.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Nat. Mus. Bull. 211.

BRACKBILL, H. 1960. Determinate laying by House Sparrows. Condor 62:479.

BROWN, C. R. 1984. Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. Science 224:518–519.

BRUSH, A. H. 1968. Conalbumin variation in populations of the Red-winged Blackbird *Agelaius phoeniceus.* Comp. Biochem. Physiol. 25:159–168.

CAMPBELL, B. AND E. LACK (EDS.). 1985. A dictionary of birds. Buteo Books, Vermillion, South Dakota.

DAWSON, D. C. 1964. The eggs of the House Sparrow. Notornis 11:187–189.

DHINDSA, M. S. 1981. Intraspecific nest parasitism in two species of Indian weaverbirds, *Ploceus benghalensis* and *P. manyar.* Ibis 125:243–245.

EMLEN, S. T. AND P. H. WREGE. 1986. Forced copulations and intraspecific parasitism: two costs of social living in the White-fronted Bee-eater. Ethology 71:2–29.

FLEISCHER, R. C. 1982. Clutch size in Costa Rican House Sparrows. J. Field Ornithol. 53: 280–281.

———. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. Behav. Ecol. Sociobiol. 17:91–99.

GIBBONS, D. W. 1986. Brood parasitism and cooperative nesting in the moorhen, *Gallinula chloropus.* Behav. Ecol. Sociobiol. 19:221–232.

GOWATY, P. A. AND A. A. KARLIN. 1984. Multiple maternity and paternity in single broods of apparently monogamous eastern bluebirds *(Sialia sialis).* Behav. Ecol. Sociobiol. 15: 91–95.

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

KLOMP, H. 1970. The determination of clutch-size in birds: a review. Ardea 58:1–124.

LANIER, G. A. JR. 1982. A test for conspecific egg discrimination in three species of colonial passerine birds. Auk 99:519–525.

LOWTHER, P. G. Spotting pattern of the last-laid egg of House Sparrows. J. Field Ornithol. In press.

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

McGILLIVRAY, W. B. 1980. Communal nesting in the House Sparrow. J. Field Ornithol. 51:371–372.

MURPHY, E. C. 1978. Breeding ecology of House Sparrows: spatial variation. Condor 80: 180–193.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor.* Ornithol. Monogr. 26:1–595.

PETRIE, M. 1986. Reproductive strategies of male and female moorhens *(Gallinula chloropus).* Pp. 43–63 *in* Ecological aspects of social evolution (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.

POWER, H. W., E. LITOVICH, AND M. P. LOMBARDO. 1981. Male starlings delay incubation to avoid being cuckolded. Auk 98:386–389.

SAPPINGTON, J. N. 1977. Breeding biology of House Sparrows in north Mississippi. Wilson Bull. 89:300–309.

SCHIFFERLI, L. 1978. Experimental modification of brood size among House Sparrows *Passer domesticus.* Ibis 120:365–369.

SEEL, D. C. 1968. Clutch-size, incubation and hatching success in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. Ibis 110:270–282.

SUMMERS-SMITH, D. 1963. The House Sparrow. Collins, London.

TERRES, J. K. 1980. The Audubon Society encyclopedia of North American birds. Knopf, New York.

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

WELLER, M. W. 1959. Parasitic egg laying in the redhead (*Aythya americana*) and other North American Anatidae. Ecol. Monogr. 29:333–365.

WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild house sparrow population by DNA fingerprinting. Nature 327:147–149.

WITSCHI, E. 1935. Seasonal sex characters in birds and their hormonal control. Wilson Bull. 47:177–188.

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

———. 1980b. Intraspecific nest parasitism among Dead Sea Sparrows *Passer montanus*. Ibis 122:234–236.

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

NORTHEAST RAPTOR MANAGEMENT
SYMPOSIUM AND WORKSHOP

The Northeast Raptor Management Symposium and Workshop, hosted by the National Wildlife Federation's Institute for Wildlife Research, will be held 16–18 May 1988 at the Hotels at Syracuse Square, Syracuse, New York. The Symposium will feature technical papers on the status and management of northeastern raptors and land use issues which impact raptor populations. Interactive workshops will encourage participants to discuss raptor management issues in the region and develop management recommendations. For more information, contact the National Wildlife Federation, 1412 Sixteenth St., N.W., Washington, D.C. 20036-2266 or call (703) 790-4264.