

CONSPECIFIC NEST PARASITISM IN THREE SPECIES OF NEW WORLD BLACKBIRDS¹

KYLE E. HARMS,² LES D. BELETSKY AND GORDON H. ORIANIS

Department of Zoology, NJ-15, and Institute for Environmental Studies,
University of Washington, Seattle, WA 98195

Abstract. We determined the rate of conspecific nest parasitism (CNP) that occurred in populations of Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), and Brewer's Blackbirds (*Euphagus cyanocephalus*), and tested the hypothesis that females whose nests are destroyed during laying may deposit physiologically committed, subsequent eggs in nearby conspecific nests. CNP occurred in only 0.5% of Red-winged Blackbird nests, in 1.1% of Yellow-headed Blackbird nests, and in about 3% of Brewer's Blackbird nests. Nearby nests were destroyed during the laying period within three days of detected CNPs in less than 50% of the cases for both Red-winged and Yellow-headed Blackbirds. We discuss possible options of female songbirds for resorbing, aborting or laying physiologically committed eggs after their nests are destroyed during laying, and the potential costs and benefits to these females of CNP.

Key words: *Conspecific nest parasitism; Red-winged Blackbirds; Yellow-headed Blackbirds; nest destruction; brood parasitism.*

INTRODUCTION

Interspecific nest parasitism has evolved independently a number of times among birds, but its origins are still obscure. The major theoretical problem is to determine the conditions that lead to high enough success for females that parasitically deposit eggs for the trait to spread. Parasitically laid eggs need not have higher success than the average of eggs laid in a facultatively parasitic female's own nest; they need only lead to higher total success. For example, a female might experience higher total reproductive success if she deposits one or more eggs parasitically in addition to tending her own clutch. Also, females whose nests are destroyed during laying may improve their success by laying any physiologically committed eggs in another nest ("egg-dumping"), conspecific or heterospecific, rather than depositing them in the environment (Hamilton and Orians 1965). Because nest destruction is a universal phenomenon, it could provide a common starting point for the evolution of brood parasitism, both conspecific and interspecific.

Recently, ornithologists discovered that at least occasional conspecific nest parasitism (CNP) is

widespread among birds (Yom Tov 1980, Rohwer and Freeman 1989). In a few cases the females responsible for the CNP have been identified (Emlen and Wrege 1986; Brown and Brown 1988, 1989) and, in at least two species, disturbing the nests of laying females has been shown to influence CNP (Emlen and Wrege 1986, Feare 1991). However, for most species, the extent of CNP and the conditions under which it occurs are unknown. The purposes of this study are (1) to assess the nature and extent of CNP among several species of New World blackbirds (Family Emberizidae, Subfamily Icterinae), (2) to test Hamilton and Orians' (1965) hypothesis in these species, and (3) to consider the options of female songbirds, concerning disposal of their subsequent eggs, when their nests are destroyed during laying.

METHODS

We assessed the occurrence of CNP and associated events in populations of marsh-nesting Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) breeding within and adjacent to the Columbia National Wildlife Refuge in south-central Washington state. The area and the breeding biology of these species are described by Orians (1980) and Orians and Christman (1968). Our study of egg-laying and nest parasitism was part of a long-term investigation of

¹ Received 13 March 1991. Final acceptance 2 July 1991.

² Present address: Dept. of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544.

reproductive success in the two species (Orians and Beletsky 1989).

We monitored nesting of Red-winged Blackbirds during 14 consecutive breeding seasons, from 1977 through 1990, during the period over which at least 95% of annual breeding was completed, usually 1 March–30 June. Yellow-headed Blackbirds were monitored only in 1977, 1981, and 1988–1990. Various numbers of breeding marshes were monitored each year (Table 1). This analysis is based on marshes that had ≥ 5 nests in a given year (marshes with < 5 nests were considered poor breeding habitat and were not closely watched), and upon nests reaching the stage of completed construction. Data from all marshes were pooled within years (Table 1) because initial analyses indicated that the frequency of egg dumping did not vary with size or shape of marsh or blackbird breeding population size or density.

In most years, marshes were searched thoroughly for new nests every six days and nests were checked for progress every three days. In 1980 and 1981, most nests were checked daily. We counted eggs and nestlings, noted unusual conditions, and touched eggs to determine if they were warm (being incubated) or cold. Most checks were conducted during mid to late morning. Nests were marked with colored tape placed in nearby vegetation. Between 40% and 50% of Red-winged Blackbird nests in the area are destroyed annually by predators (Orians and Beletsky, unpubl. data), a rate similar to that found in other populations (Case and Hewitt 1963, Haigh 1968, Robertson 1972).

Female Red-winged Blackbirds and Yellow-headed Blackbirds usually lay clutches of 3–5 eggs, with the mode being 4 (Willson 1966, Orians and Beletsky 1989); 6-egg clutches occurred only rarely during the study. Red-winged and Yellow-headed Blackbird females laid their eggs usually in the early morning. Like other songbirds, they initiate incubation after laying their penultimate egg. Female birds lay, at most, one egg/day (Sturkie 1976); two eggs appearing in a nest within a single 24-hr period, therefore, constitutes evidence of egg dumping, or CNP (Yom-Tov 1980). Other evidence of CNP used in this study are eggs appearing in active nests after completion of the clutch (Yom-Tov 1980) and single, unincubated eggs appearing in unused or previously used nests.

For this paper, we analyzed the histories of

7,805 Red-winged Blackbird and 1,227 Yellow-headed Blackbird nests. We determined the number of (1) nests that received at least one egg as part of the regular clutches of the females who built the nests; (2) nests destroyed during laying (as the potential source of females needing to dump eggs); (3) CNPs during laying; (4) CNPs after laying; (5) nests with exceptional delays between eggs laid; and (6) reused nests. Because eggs were not marked in this study, we cannot assess the success of parasitically-laid eggs.

NESTS DESTROYED DURING LAYING

Nests were classed as "destroyed during laying" if, after 1–3 eggs had been laid, the next check revealed the nests to be either empty, destroyed, or never incubated; that is, they were depredated or deserted. Due to the 3-day check interval, over half the nests in this category could not be assigned unequivocally, because it was possible they were destroyed or abandoned immediately *after* the termination of laying. These equivocal assignments were termed "probable" cases of nests destroyed during laying (Table 1). The percentage of nests each year destroyed during laying is the sum of the definite and probable cases divided by the total number of nests that received ≥ 1 egg.

CNPS DURING AND AFTER LAYING

A CNP during laying was operationally defined as the appearance of two eggs in a nest within a 24-hr period. For example, a nest receiving four eggs in 3 days (the check interval) was considered to contain one egg from a female other than the nest-owner. A CNP after laying was defined as an extra egg (in one case, two) appearing in a nest after a completed clutch had been incubated for at least 3 days, but before hatching. (New eggs never appeared in nests containing nestlings.)

OTHER CASES OF CNPS

Other possible cases of CNPs after laying, recorded separately, were: (1) when the number of eggs in a completed clutch was reduced but increased again during the next check. (In these cases, unless a counting error occurred, the nest-owner presumably lost an egg and then had an egg dumped in her nest.); (2) when a single new egg appeared in a nest after fledging or after the nest had been depredated while it contained eggs or nestlings; and (3) when an unused nest received a single egg long (≥ 20 days) after its con-

TABLE 1. Occurrences of CNP and associated events in a breeding population of Red-winged Blackbirds, 1977-1990.

Year	Total no. of nests built	No. of nests that received ≥ 1 egg	No. of marshes	No. of nests destroyed during laying		No. of CNPs during laying		No. of associated nests destroyed ¹		No. of other possible CNPs after laying	Total no. of associated nests destroyed ²		No. of nests with delays during laying	No. of nests reused after depredation or fledging
				Definite	Probable	(%) ¹	CNPs after laying	associated nests destroyed ¹	CNPs after laying		associated nests destroyed ¹	CNPs		
1977	688	622	11	34	82	(18.6)	0	—	0	2	2	2	6	13
1978	522	470	6	13	31	(9.4)	1	0	0	0	1	1	6	5
1979	468	412	7	31	43	(18.0)	0	—	0	1	0	0	6	5
1980	578	503	8	43	13	(11.1)	0	—	1	0	1	1	16	4
1981	610	563	9	69	20	(15.8)	2	1	2	0	4	1	21	1
1982	723	622	9	55	72	(20.4)	0	—	1	1	2	1	9	7
1983	606	486	8	60	64	(25.5)	0	—	1	4	3	4	2	5
1984	608	535	8	50	48	(18.3)	0	—	0	0	0	0	1	6
1985	574	497	8	42	62	(20.9)	0	—	0	0	—	0	3	2
1986	507	388	8	66	68	(34.5)	0	—	4	0	4	1	6	1
1987	502	449	8	38	39	(17.1)	0	—	2	1	2	1	4	1
1988	556	471	8	30	76	(22.5)	0	—	2	0	2	2	5	3
1989	524	467	9	39	52	(19.5)	0	—	2	1	3	1	8	4
1990	339	302	8	22	19	(13.6)	0	—	1	6	2	7	6	1
Total	7,805	6,787	592	689	3	1	16	5	15	9	34	15	99	58

¹% is the sum of definite and probable divided by the total number of nests that received ≥ 1 egg.

²These values are the numbers of nests destroyed during the laying phase on the same marshes as the detected CNPs, 1-3 days before the CNPs (see text).

TABLE 2. Occurrences of CNP and associated events in a breeding population of Yellow-headed Blackbirds.

Year	Total no. of nests built	No. of nests that received ≥ 1 egg	No. of nests destroyed during laying		No. of CNPs during laying		No. of CNPs after laying		No. of other possible CNPs after laying		Total no. of associated nests destroyed ²	Total no. of associated nests destroyed ²	No. of nests with delays during laying	No. of nests reused after production or fledging
			Definite	Probable (%) ¹	CNPs during laying	associated nests destroyed ²	CNPs after laying	associated nests destroyed ²	CNPs after laying	associated nests destroyed ²				
1977	152	141	7	9 (11.3)	0	—	0	0	0	—	0	—	6	1
1981	45	43	1	1 (4.7)	0	—	1	1	0	—	0	—	1	0
1988	447	426	3	21 (5.6)	0	—	1	0	0	—	0	—	2	1
1989	353	343	6	6 (3.5)	0	—	3	0	3	—	0	—	4	2
1990	230	298	2	14 (7.7)	2	1	2	1	0	—	1	—	1	3
Total	1,227	1,161	19	51	2	1	7	1	4	—	13	—	14	7

¹ % is the sum of definite and probable divided by the total number of nests that received ≥ 1 egg.

² These values are the numbers of nests destroyed during the laying phase on the same marshes as the detected CNPs, 1–3 days before the CNPs (see text).

struction. None of the eggs in the latter two types of cases were ever incubated. Total number of CNPs/year was determined by summing all definite and possible cases.

ADDITIONAL DETERMINATIONS

To test whether CNP could be the result of laying by females whose nests were destroyed during egg-laying, we also determined for each case of detected CNP the number of nests destroyed during the laying stage on the same marsh during the previous three days (Tables 1 & 2, "associated nests destroyed").

We also noted two other types of unusual nesting events: (1) To determine the frequency of irregular laying sequences, we noted *nests with delays during laying*. These were cases in which a clutch not yet being incubated (i.e., still incomplete) had at least one egg appear more than one day after the previous one—usually 1–3 days later (range 1–8 days). (2) To determine whether females lay eggs in nests that they did not themselves build, we noted *nests reused within the same breeding season* after initially being depredated or fledging young—either by the same female or by a different one.

We also present nest data from an earlier study (1964–1965) of Brewer's Blackbirds (*Euphagus cyanocephalus*) nesting on the Columbia National Wildlife Refuge.

RESULTS

RED-WINGED BLACKBIRDS

Only 34 cases of CNP were detected in 7,805 nests (0.4%), 3 during the host laying period and 31 after laying (or 0.5%, 34/6787, if only those nests that received ≥ 1 egg from a normal clutch is used in the calculation). The percentage of Red-winged Blackbird nests destroyed during laying each year ranged from 9.4 to 34.5%, with an average of $18.9 \pm 6.2\%$ ($n = 14$ years). If females whose nests are destroyed during laying are committed to laying their next egg, well over 1,000 eggs were potentially available to be laid in conspecifics' nests. In 15/34 cases of Red-winged Blackbird nests receiving CNPs (44.1%), at least one nest was destroyed during laying on the same marsh within 1–3 days before the dump (Table 1). But in over half of the cases of CNP, no local female should have needed to dump an egg.

Data from 1980 and 1981 (Table 1), when daily nest checks were made, indicate that we missed detecting few CNPs due to three-day in-

terval checks in other years. The modal clutch size for Red-winged Blackbird nests with CNP was five ($n = 19$ nests with CNP during or after laying; 15 other cases of possible CNP after laying are not included here because we were less certain about clutch size or they involve nests that never received normal clutches—see above), one more than for unparasitized nests.

The owner apparently delayed laying an egg mid-way through the laying period in only about 1.5% of nests (99/6,787 nests that received eggs). Also, very few nests were reused for "normal" nesting activities after being used previously (58/6,787 = 0.9%; Table 1). Most nests in the latter cases were reused after eggs were depredated; there were only 13 instances in which nests were reused after depredation of nestlings (7 cases) or after successful fledging (6 cases).

YELLOW-HEADED BLACKBIRDS

The percentage of nests destroyed during the laying period was less for Yellow-headed Blackbirds than for Red-winged Blackbirds ($\bar{x} = 6.6 \pm 3.1$, $n = 5$ years; Table 2). CNP was also rare for Yellow-headed Blackbirds—13 cases in 1,161 nests that received \geq one egg = 1.1% of nests. In only 3 of the 13 cases (23.1%) was a nest destroyed on the same marsh within 1–3 days of the suspected CNP.

The modal clutch size was four for $n = 9$ Yellow-headed Blackbird nests with CNP during or after laying, but four of the nine nests did have five-egg clutches. Delays between successive eggs during laying were also rare for Yellow-headed Blackbirds, occurring in only 1.2% (14/1161) of the clutches (Table 2). We found only seven cases of nests being reused after predation had occurred (7/1,161 = 0.6%; Table 2). No Yellow-headed Blackbird nests were reused after fledging young.

BREWER'S BLACKBIRDS

Our records of check schedules are incomplete for data collected in 1964 and 1965 on Brewer's Blackbirds. Nonetheless, they also indicate a low percentage of CNP, 3.1% of nests (1964: 45 nests checked, 2 CNPs detected; 1965: 117 nests checked, 3 CNPs detected).

DISCUSSION

The frequency of occurrence of CNP among all three species of blackbirds is evidently very low. Our estimates are biased downward for two rea-

sons: (1) some eggs laid parasitically during the laying period may not have been detected by three-day nest checking intervals; and 2) even daily nest checks miss detecting parasitic eggs laid one day prior to the start of laying or one day after its termination (Frederick and Shields 1986). We also included all "probable" cases of nests destroyed during laying in our estimation of the number of dumped eggs potentially available. Nonetheless, we still should have observed many more cases of CNP than we did if the Hamilton and Orians (1965) hypothesis was correct for these populations (at least an order of magnitude more cases for the Red-winged Blackbird). Also, the low number of CNPs detected in 1980 and 1981, when we checked nests daily, suggests that we did not miss detecting many CNPs with three-day checks.

Our results raise two questions of theoretical interest. The first concerns the fate of physiologically committed eggs of females whose nests are destroyed mid-way through their laying sequence. If most eggs are not dumped in nearby conspecific nests, as our results demonstrate, where are they going? Four possibilities are that: (1) *Eggs are dropped more or less indiscriminately in the environment.* Even though eggs dropped in the environment would be very difficult to detect, we believe that a female with an egg she must deposit is likely to seek out another nest in which to lay it (see also Yom-Tov 1980). The success of eggs dropped randomly is guaranteed to be zero, whereas eggs deposited in a conspecific nest may survive. It is true that 91% of cases of Red-winged Blackbird CNP we detected represent eggs deposited during incubation, a time when they had no chance of hatching. However, this is an inflated estimate because we had a better chance of detecting CNP during incubation, which lasts 11–12 days, than during laying.

(2) *Eggs are laid in nests on other marshes or of other species.* These scenarios are doubtful because females should know more about the locations of nests in their own marshes than in other areas. Also, if females do dump eggs in other, distant breeding marshes, we still should have found many more dumped eggs, produced by females nesting in surrounding areas. On the other hand, we did find more CNP than could be accounted for by the set of females who had nests destroyed during laying on the same marsh at the times of the CNPs. This suggests that some

females may dump eggs on marshes other than their own. We have no evidence that female Red-winged or Yellow-headed Blackbirds laid eggs in heterospecific nests. Blackbird nests generally outnumbered any other passerine nests in the general area. Therefore, because we found no eggs of any of the three blackbirds in the nests of another species, it is extremely unlikely that female blackbirds laid any eggs in nests of other passerines in the study area. Also, other than those of the brood parasitic Brown-headed Cowbird (*Molothrus ater*), we found no eggs of other species in blackbird nests. (Thus, even though there are five species of interspecific brood parasites in the Icterinae, there is no evidence of incipient interspecific nest parasitism in the three species we studied.)

(3) *The eggs are resorbed or aborted.* The assumption that females whose nests are destroyed during laying must lay at least one additional egg may be incorrect. If depredation occurs during the day, as is the case with most nests on our study area, a female has the remaining daylight hours plus the entire night during which to resorb or abort any partly formed eggs already ovulated. If that is sufficient time for resorption or abortion, then most females whose nests are destroyed during laying need not lay additional eggs. According to this hypothesis, our cases of CNP were due to females whose nests were destroyed during the night or very early in the morning, leaving them insufficient time to resorb/abort the eggs they were to lay that morning. Under this view, females may seek out conspecific nests even though the fraction of females whose nests are destroyed during laying that need to do so is much lower than Hamilton and Orians assumed. We did find that over 40% of CNPs in our Red-winged Blackbird nests were closely associated in time with at least one nest destroyed during laying on the same marsh. As far as we can determine, although it is known that not all ovulated avian ova are necessarily oviposited (Gilbert and Wood-Gush 1971), and that avian oocytes are at times resorbed, even after ovulation (Johnson 1986), the precise timing and constraints on songbirds' abilities to induce resorption or abortion of ova already in the oviduct are, at present, unclear.

4) *Eggs are laid in a nest or on land and then consumed.* If resorption or abortion of eggs is physiologically impossible shortly after ovulation, and given that only a tiny fraction of dumped

eggs in this study could have been successful, i.e., led to fledged young (see below), females might avoid the cost of the energy lost in a dumped egg by laying the egg and eating it. This type of "auto-ovophagy" has been observed in captive Brown-headed Cowbirds (Dufty 1983, Fleischer 1985).

The second question concerns the reasons why blackbird females do not regularly dump eggs. Many of their nests are destroyed during laying and, because they breed colonially or at high densities, there are usually other nests with eggs nearby. Three hypotheses present themselves. Hypothesis 1 is that other nests are not available to lay in or are difficult to gain access to or locate. This is unlikely because during much of the breeding season in these colonial blackbird species there are other nests nearby at the same nesting stage (i.e., laying). For Red-winged and Yellow-headed Blackbirds at least, nearby nests are easily locatable, both because females are very vocal near their nests (Beletsky and Orians 1985) and because nesting densities are often so high that many nests are within a few meters of each other. Additionally, Brown-headed Cowbirds frequently parasitize Red-winged Blackbird nests in the study area (Orians et al. 1989), apparently having little trouble locating and gaining access to Red-winged Blackbird nests during their laying periods. Sealy et al. (1989) recently found only 11 CNPs in over 1,500 Yellow Warbler (*Dendroica petechia*) clutches over a 14-year period—a ratio comparable to those we found in blackbirds. Sealy et al. suggest that one explanation for the low rate of CNP they observed is intraspecific aggression, i.e., nest-guarding, by potential host pairs. This explanation is unlikely for Red-winged Blackbirds because females during laying and incubation spend long periods away from their nests and territories. Thus, on balance, we do not believe Hypothesis 1 holds for these blackbird species.

Hypothesis 2 is that female blackbirds simply do not possess in their repertoire behaviors allowing them to lay eggs in nests other than their own. This hypothesis can be rejected because: (1) we did detect a few definite cases of CNP; and (2) we did find a low frequency of females laying in and conducting normal nesting activities at nests that had been previously used. In fact, in at least 12 of the 58 Red-winged Blackbird cases (Table 1), the females laying in reused nests were not the original builders. (In a few of the remaining cases we know that the same female

reused her own previous nest, but for most of the cases we do not know the identity of one of the users, either the first or the second.)

Hypothesis 3 is that the costs to females of dumping committed eggs are larger than potential benefits. Costs to a female dumping an egg include time and energy spent searching for an appropriate host nest, possible aggressive interactions with the host female and with the male territory owner, and the loss of energy contained in the egg itself. Given these costs, we could postulate that female blackbirds should pursue CNP as a strategy only if there is a real advantage, i.e., a chance for successful fledging of the parasitic egg. Our information is scanty on the success of parasitic eggs in our study. Most of the cases of CNP we detected occurred during mid-incubation and therefore these eggs had no chance to hatch and lead to fledged offspring. Two of the three Red-winged Blackbird nests with CNP during laying fledged young, but because less than the full clutch fledged in both cases, we cannot determine if the parasitic young fledged. The other Red-winged Blackbird nest was depredated during the egg stage. Only one of the two Yellow-headed Blackbird nests with CNP during laying fledged young, but again, not all of them; the other Yellow-headed Blackbird nest was depredated. Thus, for thousands of nests, at most only three CNP eggs could have produced fledged young. If these data are typical, it is not difficult to understand why genes leading to CNP do not spread in these blackbirds.

In a species with an evolved strategy of CNP, delays during laying between eggs in a clutch may arise when females deliver their parasitic egg midway through their laying period (Brown 1985). Therefore, apparent delays between eggs during laying may be common in populations employing regular CNP. In accordance with the low rate of CNP that we found for these blackbirds, we also found low between-egg delay rates. Some of the delays could be weather-related. There was apparently no relationship between unseasonal temperatures in the study area and laying delays, but approximately 25% of the Red-winged Blackbird delays were associated with rain dates. We have no information on wind effects.

Tests of the hypotheses that eggs can be resorbed or aborted less than 24 hr before laying or that they are consumed would not be difficult. Nests could be destroyed during incubation and their owners captured and held for 24 hr to de-

termine if they lay eggs and, if so, whether they are then eaten. Further physiological research on the question of how many hours after ovulation resorption can occur would also be of value. The results of these investigations would be of interest, not only for the evolution of brood parasitism, but also for our understanding of the physiological control of avian reproduction.

ACKNOWLEDGMENTS

We thank the many field assistants who collected nesting data for us during the years of this study, and Bruce Lyon for helpful comments on this manuscript. Refuge Manager Dave Goeke kindly provided permission to work on the Columbia National Wildlife Refuge. This work was supported by National Science Foundation grant BSR 8614620 and National Institute of Mental Health grant MH44609 to Gordon Orians.

LITERATURE CITED

- BELETSKY, L. D., AND G. H. ORIANS. 1985. Nest-associated vocalizations of female Red-winged Blackbirds, *Agelaius phoeniceus*. *Z. Tierpsychol.* 69:329-339.
- BROWN, C. R. 1985. The costs and benefits of coloniality in the Cliff Swallow. Ph.D.diss., Princeton University, Princeton, NJ.
- BROWN, C. R., AND M. B. BROWN. 1988. A new form of reproductive parasitism in Cliff Swallows. *Nature* 331:66-68.
- BROWN, C. R., AND M. B. BROWN. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Anim. Behav.* 37:777-796.
- CASE, N. A., AND O. H. HEWITT. 1963. Nesting and productivity of the red-winged blackbird in relation to habitat. *Living Bird* 2:7-20.
- DUFTY, A. M. 1983. Variation in the egg markings of the Brown-headed Cowbird. *Condor* 85:109-111.
- 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.
- FEARE, C. J. 1991. Intraspecific nest parasitism in Starlings *Sturnus vulgaris*: Effects of disturbance on laying females. *Ibis* 133:75-79.
- FLEISCHER, R. C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behav. Ecol. Sociobiol.* 17:91-99.
- FREDERICK, P. C., AND M. A. SHIELDS. 1986. Corrections for the underestimation of brood parasitism frequency derived from daily nest inspections. *J. Field Ornithol.* 57:224-226.
- GILBERT, A. B., AND D.G.M. WOOD-GUSH. 1971. Ovulatory and ovipository cycles, p. 1353-1378. In D. J. Bell and P. M. Freeman [eds.], *Physiology and biochemistry of the domestic fowl*, Vol. 3. Academic Press, New York.
- HAIGH, C. R. 1968. Sexual dimorphism, sex ratios and polygyny in the Red-winged Blackbird. Ph.D.diss., Univ. Washington, Seattle.

- HAMILTON, W. J., AND G. H. ORIANIS. 1965. Evolution of brood parasitism in altricial birds. *Condor* 67:361-382.
- JOHNSON, A. L. 1986. Reproduction in the female, p. 403-431. *In* P. D. Sturkie [ed.], *Avian physiology*. Springer-Verlag, New York.
- ORIANIS, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, NJ.
- ORIANIS, G. H., AND L. D. BELETSKY. 1989. Red-winged blackbird, p. 183-197. *In* I. Newton [ed.], *Lifetime reproduction in birds*. Academic Press, New York.
- ORIANIS, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Yellow-headed, and Tricolored Blackbirds. *Univ. Calif. Publ. Zool.* 84:1-85.
- ORIANIS, G. H., E. RØSKAFT, AND L. D. BELETSKY. 1989. Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds? *Wilson Bull.* 101:599-605.
- ROBERTSON, R. J. 1972. Optimal niche space in the Red-winged Blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. *Can. J. Zool.* 50:247-263.
- ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* 67:239-253.
- SEALY, S. G., E. A. HOBSON, AND J. V. BRISKIE. 1989. Responses of Yellow Warblers to experimental intraspecific brood parasitism. *J. Field Ornith.* 60:224-229.
- STURKIE, P. D. 1976. *Avian physiology*. Comstock Associates, Ithaca, NY.
- WILLSON, M. F. 1966. Breeding biology of the Yellow-headed Blackbird. *Ecol. Monogr.* 36:51-77.
- YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. *Biol. Rev.* 55:93-108.