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INTRASPECIFIC BROOD PARASITISM IN THE EUROPEAN STARLING

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ABSTRACT.—We studied intraspecific brood parasitism in the European Starling (*Sturnus vulgaris*) in New Jersey. We used three criteria to detect brood parasitism. These were: (1) the appearance of more than one egg/day while the host was laying, (2) the appearance of extra eggs after the host completed its clutch, and (3) the mismatching of protein phenotypes between parent and putative offspring using polyacrylamide gel electrophoresis of blood and pectoral muscle tissue. Based on these methods of detection, one in every four early nests (i.e., clutches initiated in April) contained at least one parasitic egg. Later nests experienced little parasitism. Hosts from parasitized nests of the electrophoresis sample fledged fewer young than nonparasitized nests. Hosts exhibited behaviors that minimized the potential cost of brood parasitism. These behaviors included throwing out the first parasitic egg, initiating incubation midway through laying, laying synchronously, and laying one less egg than the apparent optimal clutch size. Parasites searched for unattended nests in which to lay their eggs. Those parasites laying eggs synchronously with the population fledged more young than those that did not. However, parasites probably laid only one egg to the hosts' four or five. Parasites were probably birds without nests and were therefore adopting a reproductive strategy that was better than total reproductive failure. Intraspecific brood parasitism may be an evolutionary force shaping the current reproductive strategies of our population of European Starlings. *Received 22 Dec. 1988, accepted 27 Aug. 1989.*

Intraspecific brood parasitism (i.e., laying in the nest of an unrelated conspecific host with no subsequent care of egg[s] or offspring) in altricial birds has often been reported anecdotally in the literature (e.g., Kessel 1957, Victoria 1972, Weatherhead and Robertson 1978, Dhindsa 1983). With the advent of electrophoresis, cases of parasitism that would otherwise have remained undetected have been revealed (e.g., Evans 1988, Gowaty and Karlin 1984, Fleischer et al. 1985, Kendra et al. 1988) and suggest that intraspecific brood parasitism in altricial birds is more common than previously thought.

Beyond assessing the frequency of intraspecific brood parasitism, some studies have shown that this behavior may have adaptive value for the parasite. Brown and Brown (1989) have shown that parasitic Cliff Swallows (*Hirundo pyrrhonata*) may produce more young than hosts. Emlen and Wrege (1986) have shown that White-fronted Bee-eaters (*Merops bullockoides*), whose breeding has been interrupted, will parasitize other nests. By doing so, they may regain the chance of fledging young.

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Intraspecific brood parasitism exploits a valuable resource, parental care, and therefore can affect the evolution of parental care and associated behaviors (Hamilton and Orians 1965, Payne 1977). The role of natural selection in shaping the interactions between hosts and parasites was addressed by Brown and Brown (1989). Rather than viewing intraspecific brood parasitism as a random act with little consequence, Brown and Brown (1989) suggest that the behaviors of hosts and parasites have shaped the present reproductive strategies of the population.

We examined intraspecific brood parasitism in an altricial species, the European Starling (*Sturnus vulgaris*), breeding in New Jersey. Other reports of intraspecific brood parasitism in the starling have been both anecdotal (Kessel 1957, Yom-Tov et al. 1974, Power et al. 1981) and well-documented (Evans 1988). Discrepancies in egg-laying patterns and electrophoretic analysis of families enabled us to determine that intraspecific brood parasitism is widespread in our population and not favorable to the reproductive success of hosts. Several behaviors of hosts and parasites suggested that the interactions between hosts and parasites influence the reproductive strategies found in our population of starlings.

METHODS AND MATERIALS

This study was conducted from 1983–1985 on the Kilmer Campus of Rutgers University in Piscataway, New Jersey, on a population of starlings under observation since 1975 (Crossner 1976, Power et al. 1981). Wooden nest boxes were placed on utility poles located along roadways. Utility poles were three to four territory diameters apart (one territory diameter = 10 m; Feare 1984). Vegetation in and around the field site consisted of mowed lawns and scrub and brush. To protect against mammalian predators such as raccoons (*Procyon lotor*) and gray squirrels (*Sciurus carolinensis*), aluminum predator guards 0.61 m wide were placed around all poles directly under the box. In 1983 there were 30 boxes, in 1984 50 boxes, and in 1985 75 boxes.

Three of Yom-Tov's (1980) criteria were used to detect parasitic eggs: (1) The appearance of more than one egg/day before the host completed its clutch indicated that at least two females were laying. Birds normally lay no more than one egg in a day (Warren and Scott 1935, Woodard and Mather 1964, Fraps 1965). (2) The appearance of eggs after the host completed its clutch indicated that another female had laid an egg in a nest after the host was physiologically incapable of further laying (Bullough 1942). Bullough showed that the ovaries of starlings regress rapidly after the completion of a clutch. This was confirmed for our population when post-laying ovaries removed from 52 starlings two to three days after apparent clutch completion showed no active follicles (Kennedy et al. 1989). (3) Genetic nonrelatedness was indicated when there was a mismatch of proteins between putative parents and offspring as detected by electrophoretic analysis.

Nests were checked during the breeding season (mid-April through mid-July). Censuses were performed once daily beginning on 15 April until the first eggs appeared (19 April for all years). Thereafter, nests were checked twice daily in 1983 and 1984 (in the morning and early afternoon) and three times daily in 1985 (07:00–08:00 EST, 11:00–12:00 EST, and 16:00–18:00 EST). In all years, each April clutch was checked at least twice daily until two days after the host completed its clutch. Clutches were considered complete when no new eggs appeared in the nest for two consecutive days. Thereafter, clutches were checked irregularly until hatching, which occurred approximately 12 days after the onset of incubation. The onset of incubation was determined by touching the eggs with the back of the hand to detect warmth (Power et al. 1981). Clutches started after April were checked once daily until completion and irregularly until hatching.

Eggs were numbered sequentially with indelible ink when first detected. In order to maintain the identity of nestlings from egg to fledging, unhatched nestlings were dyed with commercially available food coloring at the time of pipping (Rotterman and Monnett 1984). (This was done in 1984 and 1985 only.) The toenails of newly hatched nestlings were clipped in a unique pattern that allowed identification of their position in the egg-laying sequence for the duration of the nestling period (Romagnano 1987). Broods were visited irregularly until Day 18, at which time nestlings were prevented from fledging until Day 20 (nestlings fledge on or about Day 20; Day 1 = day of hatching of the first egg). To restrict nestlings from fledging but still allow parents to feed, a small rectangular piece of wood with a circular opening of 2.54 cm was placed over the nest box entrance; the entrance itself had a diameter of 5.08 cm. This was done to facilitate tissue collection for electrophoretic studies (see below). After Day 20, the wooden "restrictors" were removed. Nests were visited daily until the fate of all was ascertained (Hoffenberg et al. 1988).

Both blood and pectoral muscle tissue were collected from families for polyacrylamide gel electrophoresis of native proteins. Adult females were captured, banded, and biopsied while brooding young on the sixth night after the first nestling hatched. Only resident females brood young during the night, thus assuring capture of the "correct" female (Litovich 1982). Adult males were captured, banded, and biopsied the next day while feeding young. A radio controlled trap modified from the design of Lombardo and Kemly (1983) was used to capture males in the nest. Nestlings were biopsied on Day 20. See Hoffenberg et al. (1988) for details of tissue collection and preparation and electrophoresis protocols.

Thirty-three presumptive loci were screened in plasma, hemolysate, and pectoral muscle. Three loci were found to be genetically variable and resolvable (Romagnano et al. 1989). These were plasma amylase (two alleles), pectoral muscle esterase 1 (three alleles), and pectoral muscle esterase 2 (two alleles) (Romagnano 1987, Hoffenberg et al. 1988).

A genetic mismatch was considered a case of unambiguous intraspecific brood parasitism if a nestling phenotype mismatched both putative parents or the putative mother only, e.g., if the nestling displayed a BB phenotype and both parents (or the putative mother only) were AA. A genetic mismatch was considered a case of cuckoldry (Power et al. 1981) if the nestling mismatched only the putative father and there was no field evidence of parasitism (see below). Other classes of mismatches were considered ambiguous. One such class consisted of a nestling that partly mismatched both of its putative parents (e.g., a nestling with an AB phenotype and AA parents could have been the result of either cuckoldry or parasitism). Another ambiguous class consisted of a mismatch between a nestling and its putative father in which there was field evidence of the possibility of parasitism. Field evidence included variation in egg shape or color within the clutch (Feare 1984, Evans 1988), egg removal at the nest (parasites sometimes remove eggs preparatory to or while laying their own eggs (Evans 1988, Lombardo et al. 1989), and occurrence of unambiguous cases of parasitism at the same nest, showing that the parasite was active there. Despite such evidence, some cases could not be determined to be either parasitism or cuckoldry, and hence were left in a category called "unassigned" (Hoffenberg et al. 1988).

Clutches were partitioned into three types based on population peaks of laying. These were early clutches (initiated in April), intermediate clutches (initiated in May), and late clutches (initiated in June).

Data were partitioned into two population samples based on methods of data collection.

TABLE 1

FREQUENCY OF BROOD PARASITISM BY YEAR AND CLUTCH TYPE FOR THE CENSUS SAMPLE

	Early				Intermediate				Late			
	N[a]	PL[b]	PA[c]	%[d]	N	PL	PA	%	N	PL	PA	%
1983	22	2	1	13.6	13	0	0	0	2	0	0	0
1984	44	5	5	22.7	21	0	0	0	23	1	1	8.7
1985	45	13	5	35.6[e]	41	1	3	9.8	30	1	0	3.3
Total	111	20	11	26.1[e] (40)[f]	75	1	3	5.3 (5)	55	2	1	5.5 (3)

[a] Total number of clutches.
[b] Number of clutches parasitized while the host was laying.
[c] Number of clutches parasitized after the host completed its clutch.
[d] Percent of clutches parasitized.
[e] Two nests contained parasitic eggs laid both during and after host laying.
[f] Numbers in parentheses indicate the number of parasitic eggs.

The census sample included all clutches that were checked on a daily basis for parasitic eggs. These clutches did not necessarily survive to fledging. The electrophoresis sample (a subset of the census sample consisting of only those clutches whose nestlings survived to be biopsied) included those clutches that were both checked on a daily basis for parasitic eggs and sampled for electrophoretic analysis.

Parasitic eggs were partitioned into two types: those laid while the host was laying and, therefore, likely to hatch and fledge, and those laid after the host completed its clutch and, therefore, not likely to hatch or fledge.

The term "reproductive success" refers to the number of fledglings resulting from a breeding attempt by either hosts or parasites. The term "cost" refers to the loss of fledglings.

RESULTS

Frequency and patterns of occurrence: census sample.—For all three years, 241 clutches were checked for parasitic eggs. On the basis of more than one egg/day and the appearance of eggs after the host completed its clutch, parasitism occurred at 36 nests (48 eggs) with an increase in rate from year to year (Table 1). Early clutches experienced the greatest rate of parasitism (26.1%) with dramatic declines in rates for intermediate and late clutches. More nests were parasitized while the host was laying than after.

There was no evidence that nest checking increased the rate of parasitism by disturbing laying birds and causing them to desert (deserting birds may attempt to lay their eggs in the nests of other birds). Only two cases of nest desertion were attributed to nest checking. In addition, only five nests experienced gaps in their laying sequence, suggesting that nest checking did not cause wholesale temporary desertions. Moreover, these gaps may have been due to egg removal by parasites (Lombardo et al. 1989).

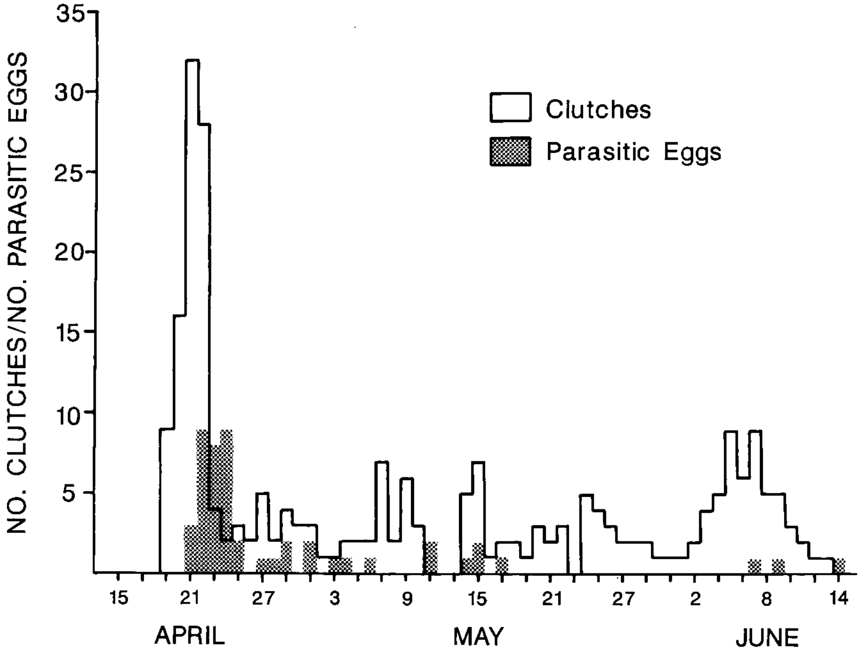

FIG. 1. Dates of clutch initiation (N = 238) and appearance of parasitic eggs (N = 49 including 5 eggs detected by electrophoresis).

Most parasitic eggs coincided with the first peak of laying (Fig. 1). These clutches fledged more young than intermediate or late clutches (Table 2). In addition, most parasitic eggs laid before the host completed its clutch were laid on Days 2 and 3 of the host's laying cycle (Fig. 2). The modal starling clutch was five eggs. Incubation usually started on the third day of laying (Fig. 3). Hatching consequently occurred over a period of two or three days, when clutches were larger than three.

Seventy-six percent of all early eggs (N = 239) from nonparasitized clutches from 1985, the year the time of laying could best be detected, were laid between 07:00 and 11:00 (i.e., detected at the 11:00 census), 6.3% were laid between 11:01 and 16:00 (i.e., detected at the 16:00 census), and 17.6% were laid between 16:01 and 06:59 the next day (i.e., detected at the 07:00 census). However, of 18 parasitic eggs laid while the host was also laying 10 (56%) were detected at different censuses than the ones during which the host's eggs were detected.

Frequency and patterns of occurrence: electrophoresis sample.—A total of 185 adults (102 females and 83 males) and 365 nestlings were biopsied for all years and clutch types. A total of 118 families were analyzed

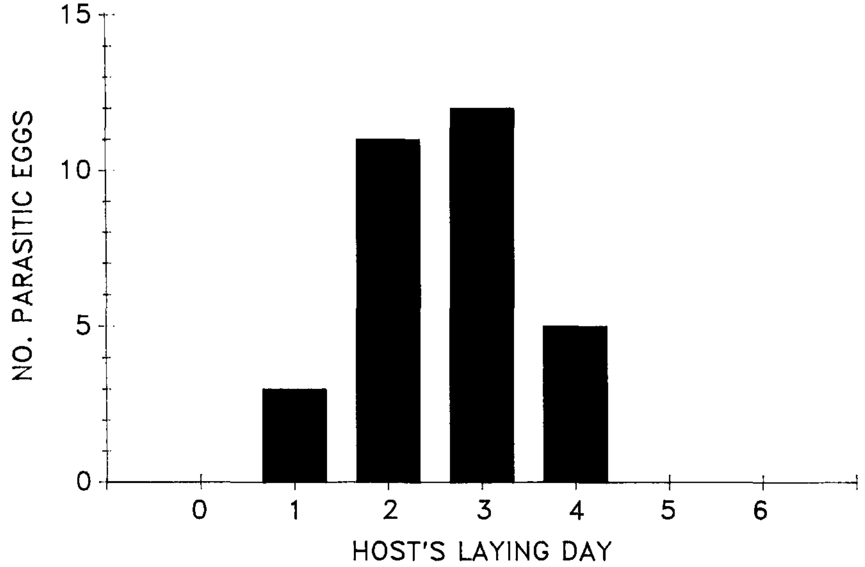

FIG. 2. Day of appearance of parasitic eggs (N = 31 including 5 eggs detected by electrophoresis) with respect to the host's laying cycle. The eggs were not evenly distributed over a five day laying cycle ($\chi^2 = 30.78$, df = 4, $P < 0.001$).

electrophoretically. (Of these, 106 were complete for male, female, and nestlings.) The number of families exceeded the number of males and females biopsied because some birds had more than one brood either within a year or between years.

The frequencies of the alleles at the three loci used for parental exclusion were 0.52 and 0.48 for plasma amylase; 0.92, 0.04, and 0.04 for pectoral muscle esterase 1; and 0.96 and 0.04 for pectoral muscle esterase 2. All loci were determined to be in Hardy-Weinberg equilibrium and to assort independently (Romagnano 1987, Hoffenberg et al. 1988).

Six cases of parasitism were detected electrophoretically in five of 72 early broods (6.9%), all on the basis of amylase (Hoffenberg et al. 1988). Two of the parasitism cases were detected at one nest. One of these was detected by both nest checking and electrophoresis. (The relative efficiency of electrophoresis vs nest checking is discussed in Romagnano et al. (1989)). Six additional mismatches were also detected but could not be unambiguously assigned as cases of parasitism. Two nests contained nestlings resulting from cuckoldry (Hoffenberg et al. 1988).

Fifteen additional early broods in the electrophoresis sample were also parasitized but detected by nest checking only (Table 3). The total rate

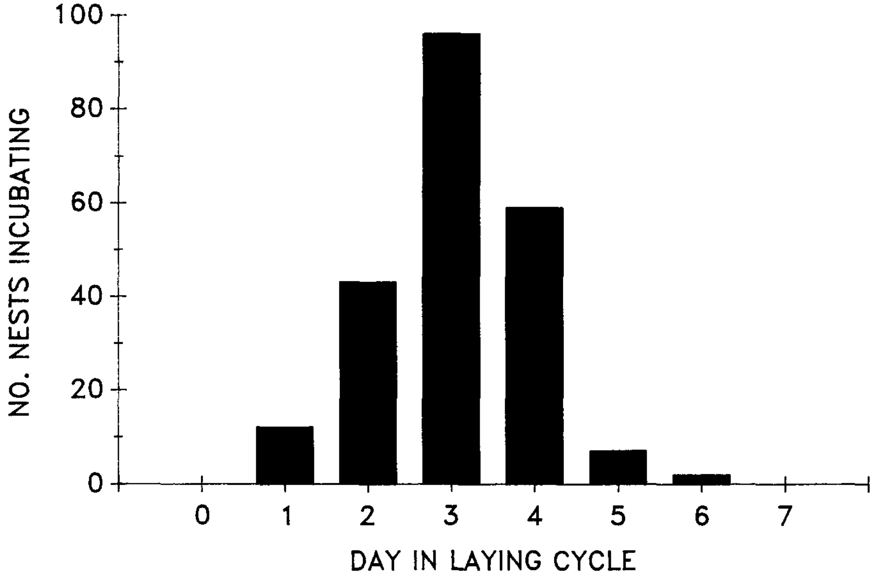

FIG. 3. Day in laying cycle (N = 219 nests) when incubation was begun. Nests with warm eggs two days in a row were considered to have begun incubation on the first of the two days.

of brood parasitism was 27.8% for early broods (20 of 72 early broods). As with the census sample, more nests were parasitized while the host was laying than after.

Effect of brood parasitism on hosts.—Post-laying parasitism often occurred during incubation or after hatching. Since these eggs never fledged they had little or no effect on the reproductive success of the host. Thus, only parasitism during laying was important to the host. Only clutches where the fate of all eggs was known, and clutches that did not experience

TABLE 2

MEAN CLUTCH SIZE, HATCHLING AND FLEDGLING NUMBER FOR ALL CLUTCH TYPES OF THE CENSUS SAMPLE, INCLUDING PARASITIC EGGS

	Clutch size		Hatchlings		Fledglings	
	Mean	SD	Mean	SD	Mean	SD
Early	4.99	0.852	3.77	1.47	2.54	1.71
Intermediate	4.43	1.09	3.43	1.53	1.43	1.54
Late	3.80	0.826	2.69	1.36	0.96	1.30

TABLE 3

FREQUENCY OF BROOD PARASITISM BY YEAR AND CLUTCH TYPE FOR THE ELECTROPHORESIS SAMPLE

	Early				Intermediate				Late			
	N[a]	PL	PA	%	N	PL	PA	%	N	PL	PA	%
1983	12	1	0	8.3	0	—	—	—	0	—	—	—
1984	30	3	5	26.7	9	0	0	0	6	0	1	16.7
1985	30	11[b]	2	36.6[c]	18	0	3	16.7	13	0	0	0
Total	72	15	7	27.8[c]	27	0	3	11.1	19	0	1	5.3
				(28)				(4)				(1)

[a] Symbols as in Table 1.

[b] Five nests contained parasitic eggs detected by electrophoresis.

[c] Two nests contained parasitic eggs laid both during and after host laying.

loss of eggs or hatchlings due to human interference, are included in the following three analyses. No significant differences were found between the mean number of host's young fledged from early clutches that were parasitized ($N = 14$) and clutches that were not parasitized ($N = 66$) in the census sample (Mann-Whitney U-test; $U = 346.5$, $P > 0.10$). In contrast, the electrophoresis sample showed significantly fewer host's young fledged from parasitized ($N = 13$) tha nonparasitized ($N = 47$) early clutches (Mann-Whitney U-test: $U = 136$, $P < 0.01$).

Clutches of four or smaller are often laid by yearlings (Flux and Flux 1981, Feare 1984). These inexperienced breeders might be more affected by brood parasitism if they are not able to care for a larger clutch. However, the mean number of fledglings from host's eggs was the same for parasitized clutches ≤ 4 and ≥ 5 (Mann-Whitney U-test; $U = 9.5$, $P > 0.10$ and $U = 9.5$, $P > 0.10$ for census and electrophoresis samples, respectively).

Relative efficiency of brood parasitism as a reproductive strategy.—Of the 26 parasitic eggs laid in early clutches while the host was also laying, 13 (50%) fledged in the census sample. This is the same fledging rate as for early eggs from nests that were not parasitized ($N = 544$ of which 41% fledged) ($\chi^2 = 0.795$, $df = 1$, $P > 0.30$). However, there was a significant difference between the fledging rate of parasitic eggs laid while the host was laying and those laid after (0%) ($\chi^2 = 9.66$, $df = 1$, $P < 0.01$).

Of the 53 parasitic eggs detected by censusing and/or electrophoresis, 45 occurred singly in nests (84.9%). Multiple parasitism (i.e., the dumping of more than one egg per host nest) occurred at only five of 111 early nests (4.5%). There was no evidence that any one parasitic female was able to lay a complete clutch (4–6 eggs) in any one nest or in several nests.

However, at two nests egg weight and appearance strongly suggested only one parasite for each of the three parasitic eggs at those nests.

During early laying, many eggs were found on the ground either directly below or between nest boxes (Lombardo et al. 1989). Stouffer et al. (1987) found that parasitic eggs laid before the host initiated its clutch were always removed by hosts. This decreased the reproductive success of brood parasites relative to nesting starlings. The actual number of parasitic eggs is probably under-represented because eggs found on the ground were not counted as such.

DISCUSSION

The high frequency of intraspecific brood parasitism in our population has led to some apparent behavioral adaptations on the part of both hosts and parasites. This suggests that intraspecific brood parasitism is a driving evolutionary force that has allowed the coexistence of two alternative, but opposing, reproductive strategies.

The cost of brood parasitism could act as a selective pressure encouraging changes in reproductive behavior. The cost to hosts in the electrophoresis sample was not apparent in the census sample. This could be a function of the methods of data collection. The census sample included both broods that survived to fledging and broods that failed, often for reasons other than parasitism (e.g., weather). The electrophoresis sample included only those families that survived to biopsy. Relative to the census sample, the families of the electrophoresis sample were more likely to experience the detrimental effects of competition between host's young and parasitic young. The electrophoresis sample was thus more likely to demonstrate the effects of parasitism on the reproductive success of hosts.

Reduced fledging success could occur if the host was forced to raise a brood that had been increased beyond optimal size due to the addition of one or more parasitic eggs. Oversize clutches might be more difficult to incubate (Biebach 1981, Westerterp et al. 1982) or to feed (Crossner 1977, Tinbergen 1981). Also, the survival chances of specific host nestlings (e.g., last hatched young) might be decreased by competition with parasitic nestlings (Litovich 1982).

Nesting birds appeared to use several tactics to minimize the cost of parasitism: (1) Eggs were thrown out of the nests if the resident had not begun laying (Stouffer et al. 1987). (2) Incubation was initiated mid-way through laying (Power et al. 1981), most often on Day 3 (Fig. 2). This decreased the amount of time that nests were left unattended, thus making deposition of eggs by parasites more difficult. Alternatively, the incubation behavior of this population may have evolved as a response to the possible benefits of asynchronous hatching (Lack 1954). However, Stouffer (1989) has shown that both synchronous and asynchronous clutches of the same size fledge the same number of young in this population of starlings. (3) Laying was highly synchronous during early clutches when parasitism was occurring at its highest frequency. Yom-Tov (1975) suggested that synchronous breeding may be the result of conspecific interference during breeding: the more synchronous a population, the less chance that any one bird will experience interference such as parasitism. Parasites will have many nests to parasitize over a short period of time, thus decreasing the probability of parasitizing any one nest. Evans (1988) also reports that early clutches of starlings in England are highly synchronous and experience high frequencies of parasitism. Alternatively, synchrony may simply have reflected a common response to environmental conditions (Dunnet 1955). (4) Hosts laid fewer eggs than they could productively rear in an apparent attempt to avoid having to raise an overcrowded brood in the event that they were parasitized (Power et al. 1989). Thus laying a smaller clutch is a form of "insurance" against the crowding effects of intraspecific brood parasitism.

Parasites may counter host defense tactics by actively searching for unattended nests (Norman and Robertson 1975, Payne 1977). This would account for the difference in time of day that host's and parasite's eggs were laid (Feare et al. 1982).

The lack of synchrony between parasites and hosts was costly to parasites. This was also demonstrated by Evans (1988). The reproductive success of parasites was directly dependent on the time at which their eggs were laid, while the reproductive success of hosts was reduced only by parasitic eggs laid while the host was laying. Parasites probably experienced little benefit (i.e., fledglings) from their parasitism relative to the benefits that they would have experienced had they raised their own clutches. Although the parasitic eggs detected while the host was laying had the same fledging rate as host's eggs, parasites probably laid only one such egg to each host's four or five eggs. But if the alternative to parasitism was to lay no eggs, then a parasitic strategy would be favored. Neither the potential long-term benefits, such as increased longevity by postponing reproduction (Evans 1988), nor the potential long term costs of parasitism could be determined from this study.

No parasite was ever observed laying in a host's nest. However, the identity of parasites falls into two broad categories. First, a parasite may be a female that cannot compete well for nest sites when there are more females than nest sites. This category includes birds that already have nests, but lose them to competitors, and birds that never successfully occupy a nest. The latter includes paired as well as unpaired females. The increase in the number of nest boxes from year to year could have attracted an overabundance of females in breeding condition. This would account for the relative increase in the cases of parasitism from year to year.

Second, a female could be a parasite and also raise a clutch of her own (Kendra et al. 1988). This behavior could lead to equal or better reproductive success than rearing only a clutch (Brown 1984). This probably did not occur in this population because intermediate and late clutches were not as successful as early clutches. A female parasitizing early clutches, and then laying a clutch of her own later in the breeding season, would be risking total reproductive failure. An adaptive response to this would be to lay an early clutch and then parasitize a later clutch. But there was no evidence for this. Only seven cases of parasitism were detected during later clutches. Perhaps later clutches would always fail if parasitized, eliminating any advantage to parasitism at that time.

Circumstantial evidence leads us to agree with Evans (1988) that parasites were mostly females without nests. Parasitism can probably be maintained in this population at present levels, because an adult starling will usually have more than one opportunity to breed in a lifetime (Coulson 1960, Romagnano 1987). Thus the events of one breeding season do not spell disaster for a female temporarily forced to be a parasite.

In populations where intraspecific brood parasitism occurs at high levels, it is appropriate to ask questions concerning the evolutionary importance of this behavior in shaping the reproductive strategies of those populations. We have attempted to do this by looking at the reproductive success of both hosts and parasites and by observing patterns of behavior. Although it is usually easier to observe hosts, it is necessary to follow parasites so that accurate measures of their reproductive success can be obtained (Emlen and Wrege 1986, Brown and Brown 1989). The consequences of the interactions between hosts and parasites can then be elucidated.

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