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## THE PARASITISM INSURANCE HYPOTHESIS: WHY STARLINGS LEAVE SPACE FOR PARASITIC EGGS<sup>1</sup>

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**Abstract.** We propose that European Starlings (*Sturnus vulgaris*) leave space for intra-specific parasitic eggs in order to prevent parasitism from producing an overcrowded clutch. For this hypothesis to be applicable, a species must have altricial young, determinate laying, and a high frequency of intraspecific brood parasitism. The hypothesis predicts that (1) host clutches will be smaller than would be predicted were only productivity considered, (2) brood parasitism will only moderately depress host reproductive success (RS), and (3) the actual frequency of net brood parasitism will exceed the threshold frequency (where the alternative tactics of leaving space and not leaving space produce equal results). Two models are presented for locating the threshold frequency: the either-or model and the graded model.

The hypothesis was tested on early clutches of starlings in New Jersey, using a combination of nest censusing, weighing, electrophoretic analysis, and analysis of postovulatory follicles. The results were consistent with all predictions. (1) Clutch size five (c/5) was the most common but c/6 was the most productive while c/7 was overcrowded. (2) Parasitism had only a slight dampening effect on host RS. (3) At least 33.3% of clutches suffered net brood parasitism: 21.2% suffered the net addition of one egg while 12.1% suffered the net addition of two or more. These rates are above the threshold frequencies generated by both models. Five alternative explanations for our results were explored but none fit the data as well as the parasitism insurance hypothesis.

**Key words:** *Intraspecific brood parasitism; parasitism insurance hypothesis; reproductive strategy; brood parasitism; clutch size; Sturnus vulgaris; risk aversion.*

### INTRODUCTION

Avian brood parasitism can be thought of as involving two formal players, the parasite and the host. Each evolves a strategy to achieve its goal. The parasite's goal is to lay eggs in the nest of the host at the appropriate time. The host's goal is to avoid being parasitized, but if this is not possible, then to avoid the deleterious consequences of parasitism. These consequences can run the gamut from only slightly stunted growth

of host chicks to their death due to the diversion of resources from host chicks to parasite chicks (Lack 1968, Skutch 1976, Payne 1977). These consequences should favor hosts that implement multiple tactics that collectively reduce as many of the deleterious effects as possible.

The most effective tactic is to prevent parasitism from happening at all. A potential host can do this by guarding its nest and aggressively excluding all potential parasites. Yet guarding cannot be foolproof because the potential host has needs that can only be satisfied away from the nest, e.g., foraging. Individuals can compensate for their inability to guard their nests full-time by enlisting helpers or mates to guard in their absence. Unfortunately, this backup tactic

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cannot be implemented in a species like the European Starling (*Sturnus vulgaris*) where normally there are no helpers (Stouffer et al. 1988), and males accompany females away from the nest during the egg-laying period in order to prevent their own cuckoldry, thus leaving themselves open to intraspecific brood parasitism (Power et al. 1981). In such a species, tactics may evolve that protect a mated pair even if a brood parasite successfully dumps an egg in their nest during their absence.

In this paper we present evidence for a new hypothesis that can account for (1) how starlings protect themselves from the deleterious consequences of successful intraspecific brood parasitism, and (2) why the most common clutch size is smaller than the most productive one in this and possibly other species.

#### THE PARASITISM INSURANCE HYPOTHESIS

*Hypothesis: In species with altricial young, determinate laying, and a high frequency of intraspecific brood parasitism, laying a clutch smaller than expected on the basis of the number and weight of young at fledging will be favored because it will inhibit the production of a clutch where the sum of the host's and parasite's eggs (the gross clutch size) exceeds the size that the host can rear without excess mortality or poor condition of young at the termination of parental care. (We shall hereafter refer to such a clutch as an overcrowded clutch. Excess mortality means mortality beyond that which would occur in the absence of intraspecific brood parasitism.) In this hypothesis hosts are seen as leaving space for parasite eggs in order to protect themselves from reproductive failure as a backup to the tactic of preventing parasites from laying in the first place.*

Care of altricial young is important in the hypothesis because such young require individual care such as feeding one at a time; therefore additional young can exceed the rearing capacity of a host. Species with precocial young are usually hurt less by intraspecific brood parasitism (hereafter simply "brood parasitism") because their young primarily consume resources provided to the group as a whole such as adult body heat. It is of note that super-sized clutches stemming from brood parasitism are most pronounced in precocial species such as ducks (Andersson and Eriksson 1982), i.e., the greatest amount of brood parasitism occurs in those

species under the least selective pressure to prevent it, including some species with precocial young whose chicks may even benefit from it (Eadie and Lumsden 1985).

Determinate laying is necessary to the hypothesis because the arrival of a parasitic egg in the nest of a determinate layer does not automatically inhibit the host's own laying effort as it does with an indeterminate layer. Thus only a determinate layer runs the risk of an overcrowded clutch following parasitism. (In a determinate laying species, the number of eggs laid in a clutch by a female is unaffected by the addition or removal of eggs. In an indeterminate layer, the number is reduced if eggs are added and increased if eggs are removed, keeping the final clutch size approximately constant despite environmental perturbation [Cole 1917, Davis 1955].)

A high frequency of brood parasitism is necessary to the hypothesis because females laying a clutch smaller than predicted on the basis of number and weight of fledglings will have an advantage over those laying larger clutches only if the latter are forced fairly frequently to rear overcrowded clutches because of brood parasitism. Females laying larger clutch sizes will obviously be favored when brood parasitism is rare. Thus the frequency of brood parasitism must exceed some *threshold* in order for leaving space to be favored. (We will define the threshold in the Predictions, and show how to locate it in one model and how to determine whether it has been exceeded in another model in the Discussion.)

#### PREDICTIONS

In application to particular populations of species with altricial young and determinate laying, the parasitism insurance hypothesis will be disproven if the following predictions are *not* met but supported if they are:

- (1) Host clutches will be smaller than they would be were only number and weight of fledglings considered. Moreover, the most productive clutch size(s) (i.e., the one [or ones] producing the most fledglings at the greatest weight per fledgling) will be just smaller than the overcrowded clutch sizes. If this were not true, females would not be disfavored from laying the most productive clutch size(s) because the arrival of a parasitic egg would then inflict no penalty.
- (2) Brood parasitism will seldom produce

overcrowded clutches and therefore seldom depress host reproductive success. Moreover, when host reproductive success is depressed, it will usually be depressed only moderately. Both the low frequency and low magnitude of reduced reproductive success occur because the addition of a parasitic egg generates a gross clutch that is at or close to the most productive size for the host to rear on account of the fact that the host has left space for the parasitic egg.

(3) The actual frequency of "net brood parasitism" will exceed the threshold frequency. Net brood parasitism is the number of eggs added to a nest by parasitism less the number subtracted by removal. Egg removal by brood parasites is important in several species, including starlings (Evans 1988, Lombardo et al. 1989) and Cliff Swallows, *Hirundo pyrrhonota* (Brown and Brown 1988). In so far as a parasite removes one host egg for each egg it lays, the host will not have to rear an overcrowded clutch (although it will still suffer the loss of each of its removed eggs). Thus the frequency of net brood parasitism, not just brood parasitism alone, is what needs to be measured in order to test this prediction.

The threshold frequency is the frequency of net brood parasitism where the alternative tactics of leaving space for parasitic eggs and not leaving space produce equal reproductive success. Leaving space is favored when the threshold is exceeded but disfavored when it is not.

The significance of the first prediction is that when met it gives evidence that birds actually leave space for parasitic eggs. The significance of the second prediction is that when met it shows that leaving space actually provides protection against the consequences of brood parasitism. The significance of the third prediction is that when met it shows that increases in gross clutch size are sufficiently common to favor leaving space for parasitic eggs over the alternative of laying a larger clutch.

If only some of the three predictions are met, then the hypothesis fails and evidence consistent with the other predictions must be accounted for by some alternative hypothesis. (Several alternatives will be considered in the Discussion.)

## METHODS

We tested the hypothesis on the European Starling on the Kilmer Campus of Rutgers University in Piscataway, New Jersey. This is an appropriate test species because starlings have altricial young

(Feare 1984) and are determinate layers (Davis 1958, Kennedy 1989). This study was conducted from 1983 to 1986.

A nest-box trail was established in 1975 by Crossner (1977) and enlarged by Litovich (1982), beginning in 1978. We rebuilt this trail with new nest boxes specially designed to facilitate trapping of birds for biopsy and collecting purposes, beginning in 1983 (Romagnano 1987).

Brood parasitism was detected by a combination of nest censusing, polyacrylamide gel electrophoresis of biopsied blood and pectoral muscle, and examination of postovulatory follicles (POFs) from collected ovaries. Censusing required marking all eggs as they were laid in order to determine their sequence of arrival and possible subsequent removal. Romagnano (1987), Hoffenberg et al. (1988), and Kennedy et al. (1989) describe in detail all techniques used in electrophoresis and POF analysis.

Brood parasitism was detected by censusing when more than one egg was laid per day in a nest. It was detected by electrophoresis when nestlings had electrophoretic phenotypes inconsistent with their putative mothers. It was detected by POF analysis when the number of POFs in an ovary was smaller than the number of eggs in that female's nest.

Egg removal was detected by censusing and POF analysis. It was detected by censusing when a marked egg(s) disappeared from a nest (Lombardo et al. 1989). It was detected by POF analysis when the number of POFs in a female's ovary was greater than the number of eggs in her nest (Kennedy et al. 1989).

Nestlings were not weighed in 1983–1985 at fledging because Crossner (1977) had already experimentally shown that nestlings in broods of sizes four to six (b/4–b/6) were not significantly different from each other in weight at fledging in our population, but that nestlings in larger brood sizes were lighter than those in b/4–b/6. The relevance of Crossner's (1977) results to our study was that they showed that if a bird hatched all of its eggs at those brood sizes it was capable of rearing all of them to the same standard of development at fledging.

However, as we shall show in the Results, only 52–53% of eggs at the three principal clutch sizes (c/4–c/6, collectively accounting for 90% of all clutches) fledged young. Therefore it was important also to know the weight of nestlings at fledging that originated from clutches in which not

TABLE 1. Clutch-size distribution for early broods.

Gross clutch size <sup>a</sup>	No. clutches	% of clutches
1	0	0
2	3	2.17
3	3	2.17
4	27	19.57
5	73	52.90
6	23	16.67
7	7	5.07
8	2	1.45
	138	100.00

<sup>a</sup> Including parasitic eggs.

all eggs hatched and fledged. Accordingly, we weighed 91 nestlings at 27 nests in 1986 1 day before their expected day of fledging. This weighing was more precise than Crossner's (1977) because we used an electronic balance while Crossner had used a Pesola scale. Thus we were more likely to find differences if they existed.

One-hundred-thirty-eight early broods were used to test all three predictions of the hypothesis. They shall hereafter be referred to as the "field sample." Fifty-two females were collected for ovarian examination within 2 days of the laying of their last egg. Of these, 33 laid early clutches. They were used to test the third prediction. They shall hereafter be referred to as the "POF sample."

Early broods were those initiated in April of each season when a highly visible peak of reproductive synchrony occurred (Romagnano 1987). Only early broods were used because (1) 92% of all brood parasitism occurred in those broods, (2) 80% of all large clutches were laid at that time, and (3) 77% of early broods successfully produced at least one fledgling whereas only 45% of later broods did so. The significance of (1) is that brood parasitism is important as a force of selection only in proportion to its frequency; (2) is important because female starlings appeared to treat clutches of six and larger as viable options only during April, thus restricting selection on large clutches mostly to early broods; and (3) is important because the high mortality of later clutches due to causes unrelated to brood parasitism (e.g., ectoparasite infestation of nestlings) made it difficult to biopsy birds for electrophoretic analysis before nest failure, and to evaluate the effect of brood parasitism itself.

For all statistical comparisons, an alpha value of 0.05 was used. Data were pooled over years

TABLE 2. Clutch size and reproductive success.<sup>a</sup>

Clutch size <sup>b</sup>	% successful clutches <sup>c</sup>	% eggs hatching	% eggs fledging	Fledglings per clutch <sup>d</sup>
4	70	73	52	2.07 ± 0.31
5	78	78	53	2.67 ± 0.19
6	88	77	53	3.18 ± 0.31
Groups				
c/4 vs. c/5	ns <sup>e</sup>	ns <sup>e</sup>	ns <sup>e</sup>	ns <sup>f</sup>
c/4 vs. c/6	ns	ns	ns	$P < 0.025$
c/5 vs. c/6	ns	ns	ns	ns

<sup>a</sup> Sample sizes in Table 1.

<sup>b</sup> Where  $n > 20$  in Table 1.

<sup>c</sup> Produced at least one fledgling.

<sup>d</sup>  $\bar{x} \pm SE$ .

<sup>e</sup> Based on  $\chi^2$  tests of actual counts.

<sup>f</sup> Based on Kruskal-Wallis test.

(except where otherwise noted) after tests of homogeneity showed that this was permissible.

## RESULTS

Table 1 shows that c/5 was the most common clutch size, c/4 the next most common, and c/6 the least common among the principal clutch sizes.

Table 2 shows that c/6 was superior to c/4 by all measures of reproductive success, and superior or about equal to c/5 by those same measures. Of greatest importance is the number of fledglings per clutch because it is the most direct measure of reproductive success, and it is the only one where differences between clutch sizes were statistically significant. The distribution as a whole (c/4–c/6) contained significant differences (Kruskal-Wallis test,  $H = 6.4$ ,  $df = 2$ ,  $P < 0.025$ ). The extreme clutch sizes (c/4 and c/6) were significantly different from each other but neither was significantly different from the midpoint clutch size, c/5. This latter probably reflects only the relatively small number of c/4's and c/6's that naturally occurred in early broods (c/4's were very common in later broods and were then reproductively inferior to c/5's). The differences among clutch sizes are interesting: c/5 produced 0.6 more fledglings per clutch than c/4, and c/6 produced 0.51 more fledglings per clutch than c/5 and 1.11 more than c/4.

Table 3 shows that differences among c/4–c/6 in the number of fledglings per clutch were in close agreement with the differences in clutch sizes themselves: c/5 had 1.25 times as many eggs per clutch as c/4 and produced 1.29 times as many fledglings per clutch, while c/6 had 1.5 times as many eggs per clutch as c/4 and pro-

TABLE 3. Clutch size and relative productivity.

Gross clutch size <sup>a</sup>	Expected productivity ratios <sup>b</sup>	Observed productivities <sup>c</sup>	Observed productivity ratios <sup>d</sup>
4	1.00	2.07	1.00
5	1.25	2.67	1.29
6	1.50	3.18	1.54

<sup>a</sup> Including parasitic eggs.

<sup>b</sup> Based on relative clutch size.

<sup>c</sup> Mean no. fledglings per clutch (Table 2).

<sup>d</sup> Based on observed mean no. fledglings per clutch.

duced 1.54 times as many fledglings per clutch. These results suggest that reproductive success was in direct proportion to initial investment in eggs, i.e., the differences between clutch sizes in mean number of fledglings per clutch were as large and real as the differences between clutch sizes themselves.

Figure 1 illustrates the pattern of fledging success: c/6 was superior to c/5 and c/4 in (1) avoiding total failure, and (2) producing larger numbers of fledglings. Despite the fact that no c/6 ever fledged all six eggs, c/6's fledged relatively more broods of five than c/5's did, and relatively more broods of four than either c/5's or c/4's did. Thus c/6 was a better way to fledge five nestlings than c/5 was, and a better way to fledge four nestlings than either c/5 or c/4 was. This makes irrelevant the fact that the c/6's fledged no more broods of six than c/5's or c/4's did.

The superiority of c/6 was also suggested by the fact that c/6 had the lowest total failure rate (i.e., frequency of clutches producing no fledglings) for each of the last 3 years of the study. 1983 is excluded from consideration because there were only two c/6's in 1983, reflecting the fact that we had only 30 nest boxes up in that pilot year (we had 50 nest boxes up in 1984, 75 in 1985, and 68 in 1986). If one assumes that the rank order of failure rate was randomly distributed among c/4–c/6 (the null hypothesis), then the probability that any one of these three clutch sizes would have the lowest failure rate in any 1 year would be 1/3, and the probability that the same clutch size would have the lowest failure rate for three successive years would be  $(1/3)^3 = 0.037$ , a value less than  $\alpha = 0.05$ . Thus the year-to-year superiority of c/6 in avoiding total failure is statistically significant.

The relative superiority of c/6 suggested by Tables 2 and 3, Figure 1, and the year-to-year failure rate was not vitiated by a reduction in quality of fledglings in order to achieve an in-

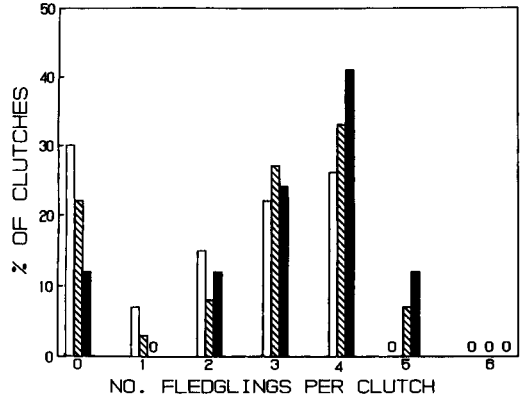


FIGURE 1. Clutch size and fledging success for the principal gross clutch sizes. Open bars = c/4; hatched bars = c/5; black bars = c/6.

crement in their quantity. There was neither a statistically significant difference in fledging weights among c/4–c/6 (two-level nested ANOVA;  $F = 0.756$ ;  $P > 0.25$ ) nor a trend in weight across the progression of clutch sizes. Along with Crossner's (1977) results on fledging weights (see Methods), and Stromborg et al.'s (1988) failure to find a relationship between body mass at fledging and postfledging survival among starlings in Maryland, these results imply that the relative productivity of clutch sizes c/4–c/6 can be legitimately measured by the reproductive success measures of Tables 2 and 3, Figure 1, and the year-to-year failure rate.

Clutches of seven and eight were significantly less productive than c/6 ( $U = 44$ ;  $df = 1$ ;  $P < 0.025$ ). Clutch size seven produced only  $1.43 \pm 0.88$  fledglings ( $\bar{x} \pm SE$ ) while c/8 produced none. This result is also consistent with Crossner (1977). He found that nestlings from experimentally produced broods of seven and larger (1) fledged at significantly lighter weights than nestlings from smaller broods, but that the latter did not fledge at weights significantly different from each other; (2) did not gain weight in the absence of supplemental feeding over the measured part of the nestling period while those from smaller broods did; and (3) responded to supplemental feeding by significant weight gains over almost the entire experimental period while those from smaller broods responded over only the last quarter. Crossner's and our results imply that c/7 and c/8 are overcrowded clutch sizes. These results from our population are reinforced by similar findings in other starling populations. Westerterp et al.

TABLE 4. Parasitism and reproductive success.<sup>a</sup>

Clutch category	% successful clutches	% host eggs fledging	Host fledglings per clutch
Parasitized	74	45	2.08 ± 0.22
Nonparasitized	75	53	2.49 ± 0.16
Differences	ns	ns	ns

<sup>a</sup> Measures and tests as in Table 2.

(1982) in Holland, and Ricklefs and Hussell (1984) in Pennsylvania found that c/7 had higher nestling mortality than smaller broods.

Table 4 shows that starlings whose nests were parasitized were somewhat less successful in producing their *own* young than were starlings whose nests were not parasitized. Although not statistically significant, brood parasitism caused a 16% reduction in the number of host fledglings. But it did not cause a reduction in the fraction of nests that produced at least one host fledgling. This suggests that the overall cost of brood parasitism was small.

In the field sample, 32 of 138 nests (23.2%) received one or more parasitic eggs during the host laying period (Lombardo et al. 1989). However, egg removal matched parasitism in eight cases (5.8%) but exceeded it in none, leaving 24 nests (17.4%) with a gross clutch size larger than the host's clutch size, i.e., net parasitism occurred at 17.4% of nests. Of the 24 nests, 18 (13% of 138 nests) had a net increase of one egg each, and six (4.3% of 138 nests) had a net increase of two to three eggs each.

This is an underestimate of the actual rate of net brood parasitism because of the conservatism of both censusing and electrophoresis in detecting parasitism. Censusing is conservative because it cannot distinguish a host from a parasitic egg if the latter were the last egg in a clutch, or a parasite removed a host egg and substituted one of its own before we marked the host egg (Brown 1984). Electrophoresis was conservative because of the rarity of the second and third alleles at two of the three variable loci we were able to use (Hoffenberg et al. 1988). At one of these (pectoral muscle esterase 1) the most common of three alleles had a frequency of 0.92, and at the other (pectoral muscle esterase 2) the most common of two alleles had a frequency of 0.94. As a consequence, electrophoresis detected only one of 24 cases of parasitism revealed by censusing alone.

The 17.4% net brood parasitism rate in the field sample could be raised to 18.8% (26 of 138 nests) if two ambiguous early brood cases detected by electrophoresis are included. Neither of these had eggs removed. These cases could have been due to either cuckoldry or brood parasitism (Hoffenberg et al. 1988). (The other four ambiguous cases reported in Hoffenberg et al. [1988] involved later broods.)

In the POF sample, 12 of 33 females (36.4%) received one or more parasitic eggs (Kennedy et al. 1989). Only two of the 12 suffered egg removal and one of these still had a net increase in gross clutch size. Thus 11 females (33.3%) experienced net brood parasitism. Of these 11 females, seven (21.2% of 33 females) had a net increase of one egg each, and four (12.1% of 33 females) had a net increase of two to four eggs each.

The estimates of brood parasitism from the POF sample are more accurate than those from the field sample because POF analysis picked up more cases of parasitism than censusing alone did, while electrophoresis detected fewer. Egg removal, the other component of net brood parasitism, was measured by censusing in both samples. Therefore neither is better than the other in estimating the frequency of egg removal. Thus the difference between samples in estimate of net brood parasitism (17.4% vs. 33%) is due solely to the difference in accuracy of measuring parasitism alone. The POF sample provides the more accurate estimate of net brood parasitism by this criterion, and therefore it shall be used to test the third prediction of the hypothesis.

## DISCUSSION

### PREDICTIONS 1 AND 2

The results are consistent with the first two predictions. In an altricial species with determinant laying:

(1) Clutch sizes were smaller than they would have been were they based solely on productivity. This is shown by two lines of evidence:

(a) The most common clutch size (c/5) was smaller than the most productive clutch size (c/6), and the latter was just smaller than the smallest overcrowded clutch size (c/7) (see Results).

(b) The clutch sizes making up nearly 90% of the distribution in Table 1 (c/4-c/6) occurred in a ratio of 22%:59%:19% relative to

each other. Yet the Results show that their productivities were in a 4:5:6 ratio. This should have generated a ratio of 27%:33%:40% relative to each other. The observed distribution is significantly shifted to the left relative to the expected distribution ( $\chi^2 = 40.99$ ;  $df = 2$ ;  $P < 0.0005$ ; based on counts, not percentage). Comparison of the distributions shows that  $c/4$  was about as common as expected on the basis of productivity, but that  $c/5$  was nearly twice as common and  $c/6$  only about half as common as expected.

Actually this comparison underestimates the extent to which the host clutch-size distribution was shifted because it compares the gross clutch-size distribution to the expected one, not the true clutch-size distribution to the expected one. The true distribution is based only on what hosts lay, i.e., it is the gross distribution minus all the parasitic eggs. Because our methods of detection were conservative, we could not find all the parasitic eggs and therefore we cannot specify the true distribution. But we do know that parasitism enlarges clutches and therefore that there are more parasitic eggs in larger clutches (Romagnano 1987). Thus once parasitic eggs are subtracted from the gross distribution, the larger clutch sizes will diminish in frequency more than the smaller ones and the number of smaller ones will be swelled by true clutch sizes made to appear larger by parasitism.

(2) Brood parasitism produced few overcrowded clutches and had little effect on host reproductive success (see Results). This is expected if leaving space for parasitic eggs largely protects a host from nesting failure due to brood parasitism.

#### THE THRESHOLD FREQUENCY AND PREDICTION 3

It is relatively easy to locate the threshold frequency if net brood parasitism is treated as an either-or phenomenon: either a female suffers net brood parasitism or she doesn't. It is more difficult to locate the threshold when net brood parasitism is treated as a graded phenomenon: a female may suffer the addition of one, two, or more parasitic eggs through net brood parasitism. The latter is often more realistic since multiple parasitic eggs overcrowd a clutch more than single parasitic eggs. However, the simplicity of

the either-or treatment makes it useful to consider, and it is applicable to cases where net addition of more than one parasitic egg is truly rare or the consequences of multiple net parasitism are no greater than those of single net parasitism, e.g., when reproductive failure occurs in both cases. Because each treatment has its advantages, both are considered in the form of models and solutions in the Appendix. Only the results of the Appendix are given here.

The either-or model generates a threshold frequency of  $p = 26.4\%$  (see Appendix);  $p$  is an absolute threshold similar to ignition temperature or disease liability (in sensu Falconer 1981). Whenever the actual frequency of parasitism ( $p'$ ) is greater than  $p$  by any amount, the tactic of leaving space is favored. Since the actual frequency of net brood parasitism was 33.3% in the POF sample,  $p' > p$ , and thus leaving space is favored in our population.

The graded net brood parasitism model determines whether the productivity of birds leaving space for parasitic eggs,  $T(x)$ , is greater than the productivity of birds not leaving space,  $T(y)$ , when they are compared across the conditions of (1) not being parasitized, (2) suffering the net addition of one parasitic egg, and (3) suffering the net addition of two or more parasitic eggs. The Appendix shows that  $T(x) > T(y)$  in our population using our best estimates of productivity. Thus the graded model also suggests that leaving space is favored in our population.

#### ALTERNATIVE INTERPRETATIONS

Despite results that were consistent with all predictions, other interpretations must be considered because it may be that factors other than parasitism are responsible for the most common clutch size being smaller than the most productive one. A variety of hypotheses, backed by varying degrees of evidence, have been proposed for other species when this situation has been met (Lack 1968, Klomp 1970, Hussell 1972, Murray 1979). But by and large the special circumstances of many of those hypotheses are not met in our population of starlings. Therefore we shall consider only five alternatives that initially seem applicable to our population: (1) the bad year hypothesis; (2) the iteroparity/longevity hypothesis; (3) the recent superabundant food hypothesis; (4) the individual optimization hypothesis; and (5) the territory quality hypothesis.

(1) The bad year hypothesis states that bad environmental conditions in some years reduce the mean productivity and increase the variance in it more in larger clutches than smaller clutches (Boyce and Perrins 1987). As a result larger clutches do not promote fitness as much as their arithmetic mean productivities suggest because those means do not take into account the balance between reproductive success and variance in reproductive success (M. S. Boyce, pers. comm.). When that balance is taken into account and the bad year hypothesis is correct, the most common clutch size is seen to have the highest fitness.

The way to analyze the trade-off between the fitness effects of arithmetic mean and variance is to calculate the geometric mean (GM) relative fitness (Boyce and Perrins 1987). If the bad year hypothesis is correct, the GM relative fitness of the most common clutch size is greater than that of the arithmetically most productive clutch size. That is not true in our population. We calculated the GM relative fitness for each of the three principal clutch sizes on the basis of the number of fledglings per clutch across years using Boyce and Perrins' (1987) equation (8) and obtained these results:  $c/4 = 0.83$ ,  $c/5 = 0.99$  and  $c/6 = 1.18$ . Thus  $c/6$  had the highest GM relative fitness just as it had the highest reproductive success (Table 2) despite the fact that  $c/5$  was far more common (Table 1).

We believe that our GM relative fitnesses are robust because our study included a record wet year and a record dry year. (Precipitation is probably the most important weather variable because starlings principally feed by probing their beaks into the soil surface. Dry years are probably the worst because very dry soil is hard to probe.) Fledging success was significantly less in the record dry year (1985) (Romagnano 1987) but  $c/6$  was still more productive than  $c/5$ .

(2) The iteroparity/longevity hypothesis holds that females that lay smaller clutches are favored because they avoid exhausting themselves on any single clutch and thereby have the capacity to produce more reproductive descendants in a lifetime than do females that lay larger clutches (Williams 1966, Charnov and Krebs 1974).

For this alternative to be supported, there must be evidence that females which lay the most common clutch size lay more clutches and eggs, and/or fledge more young per lifetime than do females that lay larger clutches (Nur 1988). Table 5 presents the long-term effects of different clutch

sizes laid early in the breeding season. It shows that there were no statistically significant differences among females with different initial clutch sizes in any measure of reproductive success for the years following their initial clutches. Yet  $c/6$  was the best initial clutch size in a rank order sense for five of the six measures, including the single most important measure, number of fledglings per lifetime. In addition, females with an initial clutch of six had the highest rate of return in the following season although there were no statistically significant differences among females with different initial clutch sizes in rate of return. (The rates of return for females with  $c/4$ ,  $c/5$ , and  $c/6$  initial clutches were 73%, 81%, and 83%, respectively.) However, we do not wish to overstate our results. The trade-off between clutch size and iteroparity/longevity cannot be properly evaluated without a formal experimental manipulation (Bell 1984). Therefore our results are not conclusive but they are an important first step and they do suggest that there was no iteroparity/longevity penalty for tending a  $c/6$  rather than a smaller clutch size.

Clobert et al. (1987) published results consistent with ours. They studied the effects of brood size on overwinter survival in a Belgian population of starlings. They found that there were no significant differences in survival after normal winters as a function of brood size in the preceding breeding season, but that after the coldest winter in 20 years females with broods of six had 1.5 times the relative survival rate of females with broods of four or five and more than four times the relative survival rate of females with broods of seven.

(3) The recent superabundant food hypothesis holds that the food supply has grown great enough to make the most productive clutch size larger than the most common one, but where this growth has occurred so recently in evolutionary time that the clutch-size distribution has not caught up with it. This is one interpretation of Vermeer's (1963) finding that the Glaucous-winged Gull (*Larus glaucescens*) can as easily rear six chicks as its normal brood of three. As Klomp (1970) pointed out, these birds largely fed from fish-docks, hardly an evolutionarily normal food source.

For this alternative to be supported, the most productive clutch size must not only be larger than the most common one, there must be evidence that birds have difficulty in laying (or are



TABLE 5. Initial clutch size and subsequent reproductive success.<sup>a</sup>

Initial clutch size	Subsequent <sup>b</sup>					
	Clutch size	Years of nesting	Clutches per season	Clutches per lifetime	Eggs per lifetime	Fledglings per lifetime
4	4.58 ± 0.30 <sup>c,d</sup>	1.64 ± 0.24	1.18 ± 0.08	2.09 ± 0.44	9.36 ± 1.86	6.77 ± 1.55
5	5.05 ± 0.12	1.55 ± 0.17	1.17 ± 0.07	1.86 ± 0.27	9.36 ± 1.35	7.57 ± 0.72
6	4.53 ± 0.32	2.00 ± 0.32	1.57 ± 0.20	3.00 ± 0.45	13.20 ± 1.53	9.30 ± 1.04

<sup>a</sup> Based on nesting attempts after the initial year only ( $n = 38$  returning females).

<sup>b</sup> All intergroup differences statistically insignificant by the Kruskal-Wallis test.

<sup>c</sup>  $\bar{x} \pm SE$ .

<sup>d</sup> Host eggs or fledglings only.

even unable to lay) the most productive clutch size. If this were not so, then females could be expected to respond to the increased food supply by laying larger clutches since it would be within their capacity to lay them.

There is no reason to believe that females in our population have any difficulty in laying a sixth egg: clutches of six occur after parasitic eggs have been subtracted (Kennedy et al. 1989). Moreover, females adjust their clutch sizes downward for replacement and second broods as environmental conditions deteriorate through the breeding season (Romagnano 1987), showing that they are capable of adjusting their clutches to circumstances.

(4) The individual optimization hypothesis states that females lay those clutch sizes which will maximize the number of recruits that they produce in a single season (Perrins and Moss 1975, Pettifor et al. 1988). Thus differences among females in clutch size reflect individual differences in rearing ability. This hypothesis is powerfully supported by artificial brood manipulation experiments on Great Tits (*Parus major*) in England.

For this alternative to be supported, there must be evidence that females whose clutches are manipulated up or down in size produce fewer recruits than those whose clutches are unmolested (Pettifor et al. 1988). We could not directly test this hypothesis on our population because (unlike tits) fledgling starlings disperse, making recruitment into the breeding population virtually impossible to measure, and both brood parasitism and egg removal obscure true clutch size. But we did measure fledging success as a function of clutch size, including naturally manipulated clutch size. (Brood parasitism and egg removal are natural forms of clutch-size manipulation.) Of course such natural manipulation is not an adequate substitute for artificial manipulation because it cannot produce adequate sample sizes

at outlying clutch sizes and parasites are unlikely to choose hosts at random. Nevertheless brood parasitism and egg removal are what happens in nature and thus measuring their effects is an important first step in evaluating the individual optimization hypothesis.

The Results and GM relative fitnesses show that clutches enlarged by net brood parasitism up to c/6 are more productive than smaller clutches. This is not expected under the most straightforward interpretation of the individual optimization hypothesis, i.e., that any change in clutch size reduces productivity. However, this apparent contradiction of the individual optimization hypothesis is misleading because the parasitism insurance hypothesis is really a special case of that hypothesis. Both hypotheses hold that birds "know" what they are doing in making clutch-size decisions. The individual optimization hypothesis is general, referring to "intrinsic or extrinsic differences between individuals" (Pettifor et al. 1988) to account for clutch-size differences without specifying what those intrinsic or extrinsic differences might be or how they might interact in a quantitative manner. The parasitism insurance hypothesis goes beyond the individual optimization hypothesis by specifying (1) brood parasitism as an extrinsic factor aggravating intrinsic differences in rearing ability, and (2) that the optimal clutch size when net brood parasitism exceeds the threshold frequency is smaller than it would be were net brood parasitism to occur less often. This addendum to the individual optimization hypothesis accounts for the apparent contradiction of that hypothesis by our results by noting that when a female takes net brood parasitism into account in making her clutch-size decision, she lays a smaller clutch whose gross productivity is increased if she is parasitized but whose true productivity (production of host fledglings) is not. In fact, her true productivity may decline somewhat but that de-

cline will be less than it would be had she laid a larger clutch. Thus the parasitism insurance hypothesis should be thought of as enriching the individual optimization hypothesis, not opposing it (M. G. Bulmer, pers. comm.).

(5) The territory quality hypothesis holds that differences among females in clutch size reflect differences in the quality of territories (Högstedt 1980, 1981). Thus females with better territories have larger clutches. This hypothesis is also a special case of the individual optimization hypothesis because it specifies an extrinsic difference among females, territory quality, that influences (perhaps determines) their clutch size decisions.

For this alternative to be supported, there must be evidence that females with larger clutch sizes have better territories. Högstedt (1980, 1981) presented evidence for this in the Black-billed Magpie (*Pica pica*), and the senior author has evidence for it in Mountain Bluebirds (*Sialia currucoides*) (Power, unpubl. field data). However, both magpies and bluebirds have Type A territories, providing individual females with separate and largely exclusive resource bases, most importantly with separate feeding areas. By contrast, starlings have Type B territories, making females share all resources except nest sites, including a common feeding ground (Feare 1984, this study). Thus the only differences in territory quality among females are differences in quality of nest sites which could not be expected to produce differences in clutch size, particularly in our population where nest boxes were built to a standard design. It is noteworthy that Högstedt (1980) listed *Sturnus vulgaris* as one of several species expected not to show clutch size variation as a function of territory quality variation.

#### WHY HOST BEHAVIOR STABILIZES BROOD PARASITISM ITSELF

A paradoxical outcome of the host's tactic of leaving space for parasitic eggs is that it enhances the adaptiveness of brood parasitism itself. This is because successful reproduction by the host automatically produces successful reproduction for the parasite (Table 4). But this is purely a by-product of the host's tactic rather than a goal of it. There is no altruism in the host's behavior.

#### DEFENSIVE TACTICS NOT USED

It would appear that starlings should have at least two defensive tactics alternative to the one that

they use: parasitic egg rejection and indeterminate laying. The ease with which we could distinguish host from parasitic eggs at nests III-10 and III-17 in 1985 raises the question of why hosts didn't make the same recognitions and toss out parasitic eggs. Starlings do appear to recognize parasitic eggs as such and to remove them when they are laid before the onset of host laying, but thereafter their removal is erratic (Stouffer et al. 1987). Starlings are not the only birds to have apparent difficulties in regularly implementing the tactic of removing parasitic eggs: Rothstein (1975) found that while parasitic egg rejection is a common response in many species to parasitism by Brown-headed Cowbirds (*Molothrus ater*), it is by no means a universal one. Moreover, he could find no factors that could regularly separate accepters and rejecters, e.g., the eggs of both tactical types are usually easily distinguishable from cowbird eggs, and most or all accepters and rejecters have long histories of sympatry with cowbirds and the physical capability to eject cowbird eggs (Rothstein 1975).

The high frequency of parasitism in our population would seem to favor indeterminate laying because that would prevent overcrowded clutches from ever occurring. We do not know why starlings have not evolved this capability, only that they have not (Kennedy 1989).

The tactic of leaving space for parasitic eggs seems very crude in comparison to the alternative tactics of parasitic egg rejection and indeterminate laying because it is employed whether or not parasitism occurs, whereas the other two tactics are employed only when parasitism actually does occur. We can speculate on why leaving space for parasitic eggs evolved rather than its alternatives, but since we can offer no compelling evidence for our speculations we prefer to leave them be until we have proper evidence. Besides, we may simply be confronted with another case where evolution has yielded a contraption rather than a contrivance (in sensu Ghiselin 1974).

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APPENDIX

Here we derive the either-or and graded net brood parasitism models, and use them to evaluate the alternative tactics of leaving space and not leaving space for parasitic eggs.

In the either-or model, we set:

- p = probability of net brood parasitism.
- 1 - p = probability of escaping net brood parasitism.
- x = most common clutch size (c/x); the one where space is hypothesized to be left for parasitic eggs (e.g., c/5 in our population).
- a = usual number of parasitic eggs per host nest (e.g., 1 in our population).
- x + a = most productive clutch size (c/(x + a)) (e.g., c/6 in our population).
- F<sub>x</sub> = number of host fledglings from c/x when no net brood parasitism occurs.
- F<sub>x+a</sub> = number of host fledglings from c/(x + a) when no net brood parasitism occurs.
- M<sub>x</sub> = decrement in number of host fledglings at c/x when net brood parasitism occurs.
- M<sub>x+a</sub> = decrement in number of host fledglings at c/(x + a) when net brood parasitism occurs.

Then the threshold value of parasitism is found by setting the outcome at c/x equal to the outcome at c/(x + a) and solving for p:

$$(1 - p)F_x + p(F_x - M_x) = (1 - p)F_{x+a} + p(F_{x+a} - M_{x+a}) \tag{1}$$

$$F_x - pF_x + pF_x - pM_x = F_{x+a} - pF_{x+a} + pF_{x+a} - pM_{x+a} \tag{2}$$

$$F_x - pM_x = F_{x+a} - pM_{x+a} \tag{3}$$

$$F_x - F_{x+a} = pM_x - pM_{x+a} \tag{4}$$

$$F_x - F_{x+a} = p(M_x - M_{x+a}) \tag{5}$$

$$p = (F_x - F_{x+a}) / (M_x - M_{x+a}) \tag{6}$$

Equation (6) is used to solve for p, using values presented in the Results.

From Table 2:

$$F_x = 2.67$$

$$F_{x+a} = 3.18$$

The value of M<sub>x</sub> is calculated as the difference between F<sub>x</sub> and 5/6 of F<sub>x+a</sub> (=c/6, the parasitized clutch size when space is left for a parasitic egg) because only 5 of 6 young in the parasitized clutch belong to the host:

$$M_x = F_x - 5/6 (F_{x+a})$$

$$M_x = 2.67 - 5/6 (3.18) = 0.02$$

The value of M<sub>x+a</sub> is calculated as the difference between F<sub>x+a</sub> and 6/7 of F<sub>x+a</sub> (=c/7, the parasitized clutch size when space is not left for a parasitic egg) because only 6 of 7 young in the parasitized clutch belong to the host:

$$M_{x+a} = F_{x+a} - 6/7(F_{x+a+1})$$

Remembering that  $\bar{x} = 1.43$  fledglings per clutch at c/7:

$$M_{x+a} = 3.18 - 6/7(1.43) = 1.95$$

Plugging these values into equation (6) gives:

$$p = \frac{2.67 - 3.18}{0.02 - 1.95} = 0.264 = 26.4\%$$

Since the measured value of net brood parasitism (p') was 33.3% in the POF sample, p' > p. Thus leaving space is favored in our population when the alternatives are assessed by the simple either-or model.

With the graded net brood parasitism model, we begin by recognizing that a nest-holding bird may be in any of three or more circumstances: (1) no net brood parasitism; (2) net brood parasitism adding one egg; and (3) net brood parasitism adding two or more eggs. (The third circumstance could be expanded to include separate listing of three or four added eggs, but net dumping of more than two eggs was too rare in our population for analysis.)

Comparison of the outcomes of the alternative tactics requires a set of definitions taking account of three circumstances:

- F<sub>x</sub> = number of host fledglings at the most common clutch size (c/x, e.g., c/5 in our population) when no net brood parasitism occurs. This is the same as F<sub>x</sub> in the either-or model.
- F<sub>x+1</sub> = number of host fledglings at c/x when net parasitism adds one egg.
- F<sub>x+2</sub> = number of host fledglings at c/x when net parasitism adds two or more eggs.
- F<sub>y</sub> = number of host fledglings at the most productive clutch size (c/y, e.g., c/6 in our population) when no net parasitism occurs. This is the same as F<sub>x+a</sub> in the either-or model.
- F<sub>y+1</sub> = number of host fledglings at c/y when net parasitism adds one egg.
- F<sub>y+2</sub> = number of host fledglings at c/y when net parasitism adds two or more eggs.
- p = probability of net parasitism adding one egg.
- q = probability of net parasitism adding two or more eggs.
- 1 - (p + q) = probability of escaping net parasitism.

Then for birds using either alternative, their total productivity is the sum of their productivities under each circumstance weighted by the probabilities of occurrence of each circumstance. For birds leaving space for parasitic eggs this is:

$$T(x) = F_x(1 - p - q) + F_{x+1}(p) + F_{x+2}(q) \tag{7}$$

and for birds not leaving space it is:

$$T(y) = F_y(1 - p - q) + F_{y+1}(p) + F_{y+2}(q) \quad (8)$$

Leaving space is favored when  $T(x) > T(y)$ .

Before we can solve for  $T(x)$  and  $T(y)$  and compare them, we must have values for the terms of the equations. These are obtained from the discussion of the either-or model above and the Results:

$$\begin{aligned} F_x &= 2.67 \\ F_{x+1} &= 5/6(3.18) = 2.65 \\ F_{x+2} &= 5/7(1.43) = 1.02 \\ F_y &= 3.18 \\ F_{y+1} &= 6/7(1.43) = 1.23 \\ F_{y+2} &= 6/8(0) = 0 \\ \left. \begin{aligned} p &= 0.21 \\ q &= 0.12 \end{aligned} \right\} &\text{POF sample} \\ 1 - p - q &= 0.67 \end{aligned}$$

Plugging these values into equations (7) and (8) we get:

$$\begin{aligned} T(x) &= (2.67)(0.67) + (2.65)(0.21) + (1.02)(0.12) \\ &= 2.47 \\ T(y) &= (3.18)(0.67) + (1.23)(0.21) + (0)(0.12) \\ &= 2.39 \end{aligned}$$

Since  $T(x) > T(y)$ , leaving space is also seen to be

favored in our population when the alternative tactics are assessed by the graded net brood parasitism model.

It should be noted that the threshold frequency is more subtle in the graded model than the either-or model. With the latter, there is but one frequency and either it is sufficiently high to favor the tactic of leaving space or it is not. But with the graded model, the relative impact of single vs. multiple net parasitism, and their relative frequencies need to be considered.

When multiple parasitism has no more impact than single parasitism,  $p + q$  in the graded model reduces to  $p$  in the either-or model. But when multiple parasitism becomes increasingly important relative to single parasitism,  $q$  becomes increasingly important relative to  $p$  in determining whether  $T(x) > T(y)$ . Thus different combinations of  $p$  and  $q$  can produce different selective pressures (and hence different outcomes) even when  $p + q$  remains constant.

Because we have only one equation for determining whether leaving space is favored or not ( $T(x) > T(y)$ ) but two frequency unknowns ( $p$  and  $q$ ), we cannot give a general solution for locating the critical frequencies of  $p$  and  $q$  in the graded model as we could for locating the critical frequency,  $p$ , in the either-or model (equation (6)). Fortunately this does not prohibit use of the graded model because comparison of the empirical solutions to equations (7) and (8) establishes which of the alternative tactics is favored in particular populations of particular species.