

Tactics of parasitic American coots: host choice and the pattern of egg dispersion among host nests

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Summary. I examined the tactics adopted by a conspecific brood parasite, the American coot (*Fulica americana*), and the degree to which these tactics reflect sources of mortality for parasitic eggs. Only 8% of parasitic eggs produced independent offspring, compared to a 35% success rate for non-parasitic eggs, and most mortality was due to egg-rejection by hosts or the consequences of laying eggs too late in the host's nesting cycle. Parasites usually laid parasitically before initiating their own nests and usually parasitized immediate neighbours. Parasites did not remove host eggs before laying their own egg, and egg disappearance in general was not more common at parasitized nests. I found no evidence for non-random host choice, either on the basis of stage of the host's nesting cycle or the host's brood size. The absence of adaptive host choice is likely a consequence of the fact that, due to host limitation, only a small proportion of parasites had meaningful variation among potential hosts to choose from. The pattern of egg dispersion among host nests by individual parasites appears to be a compromise between constraints imposed by host limitation and the increased success obtained from spreading eggs among nests. Most females laying fewer than five parasitic eggs laid them in a single host nest while females laying five or more eggs normally parasitized two or more hosts. An examination of egg rejection and survival rates showed that parasites would maximize success by laying a single egg per host nest, and the pattern of laying several eggs per host nest is likely a consequence of host limitation. However, no egg that was the fifth laid, or later, parasitic egg in a host nest was ever successful and this probably explains why most females laying five or more eggs parasitized more than one host.

Introduction

Brood parasitism involves a reproductive tradeoff. Parasitism allows females to avoid some of the costs of providing care to offspring and thereby increase their fecundity, but it may also entail a lower success for eggs laid parasitically. Only parasitic eggs laid in suitable host nests at the appropriate stage will be successful and, in some species, parasitic eggs also have to escape defensive host behaviours like egg rejection. Selection is expected to favour traits that reduce these sources of mortality and enhance fitness gained through parasitism. Approximately 1% of all bird species are obligate brood parasites that depend entirely on other species to raise their young (Payne 1977a; Rothstein 1990). The ways these specialized parasites improve survival prospects for their eggs and young have been the subject of numerous studies. Some of the more striking examples include egg and chick mimicry (Nicolai 1974; Davies and Brooke 1988), removal of host eggs and chicks by newly hatched parasitic chicks (Rothstein 1990), and specialized bill hooks on newly hatched parasitic chicks that facilitate the killing of the host chicks (Friedmann 1955).

Brood parasitism within species also occurs but the tactics adopted by conspecific parasites are poorly known. Detailed studies of conspecific parasitism have now been conducted on about a dozen species, but there is no evidence that parasitism within species involves specialized lifelong parasites. Although we would not expect to see the more striking adaptations to a parasitic lifestyle found in interspecific brood parasites, there should nonetheless be a selective advantage to behaviours that increase reproductive success gained through parasitism (Petrie and Møller 1991). For example, depending on the sources of mortality for parasitic eggs, parasites could increase the survival prospects of their eggs by choosing host nests at the appropriate stage in the laying cycle (Emlen and Wrege 1986), by choosing high quality hosts (Brown and Brown 1991), by removing hosts' eggs to reduce competition for host parental care (Lombardo et al. 1989) or by optimizing the disper-

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sion of eggs among host nests (Payne 1977a, b). The tactics that conspecific brood parasites actually adopt are virtually unknown, largely due to the difficulties in identifying parasitic females and following their laying histories. Only one study has examined the pattern of host choice (Brown and Brown 1991) and no previous study has investigated how individual conspecific parasites disperse their eggs among host nests.

In this paper, I examine the sources of mortality of parasitic eggs, and the tactics parasitic American coots (*Fulica americana*) adopt to mitigate these costs and enhance their success as parasites. Parasitism was common during a 4-year study in central British Columbia; over 40% of all pairs were parasitized (Lyon in press). Most parasitism was by nesting females which laid parasitically before initiating their own nests, but roughly a quarter of the parasitic eggs could not be attributed to nesting females and were presumed to have been laid by non-nesting females. I focus on the tactics adopted by nesting parasites here because I have detailed information on when and where individual nesting females laid their parasitic eggs. Specifically, I address five questions concerning the tactics of parasites: (1) What is the temporal pattern of parasitic egg-laying relative to the eggs parasites lay in their own nests? (2) What factors influence the spatial pattern of host use? (3) Do parasites remove host eggs during parasitism? (4) Do parasites choose hosts non-randomly, based on quality or stage of the host's breeding cycle? (5) How do parasites allocate eggs among host nests, and what factors influence the pattern of dispersion?

The issue of how parasites allocate eggs among nests takes on an interesting dimension in coots because of the high frequency of egg rejection by hosts (Lyon 1992), a behaviour absent in most other species with conspecific parasitism. By laying several eggs in the same nest, parasites may make it more difficult for hosts to distinguish parasitic eggs, or possibly even determine that parasitism has occurred at all. Other selection factors, such as increased mortality with increases in clutch size, are thought to favour scattering eggs among nests (Andersson 1984), so there is potential for interesting tradeoffs between these potentially conflicting selection pressures.

Methods

Study area and animal. I conducted the study from 1987 to 1990 at three sites within 60 km of each other in central British Columbia, Canada: (1) Beecher Prairie, 8 km northwest of Riske Creek in 1987 (84 pairs on 12 lakes and ponds), (2) Jaimeson Meadow, 26 km northeast of Big Creek, 1988–1990 (52, 43 and 46 pairs respectively on one large wetland), and (3) Chilco West Marshes (Kloe Lake, Jones Lake and Pond S5) 15 km southeast of Hanceville in 1989 and 1990 (129 and 88 pairs respectively). Coots are monogamous and males help in all aspects of reproduction including nest-building, incubating, feeding and brooding the chicks, and defending the territory (Ryan and Dinsmore 1979). The all-purpose territories are defended throughout the entire reproductive cycle, and fights with neighbours and non-breeding intruders are frequent (Gullion 1953). The chicks are precocial (Nice 1962) but are dependent on the parents for food for at least 10 days (Ryan and Dinsmore 1979; Desrochers and Ankney 1986; Lyon in press). Chicks

are attacked if they stray onto the territories of neighbouring pairs and remain on the parental territory until they are about 50 days old.

Censusing nests and detecting parasitism. I checked the vegetation every 1 or 2 days so that new nests would be discovered early in the laying period. On each visit to nests, all new eggs were numbered with an indelible felt pen, and these numbers were maintained until hatch. Territorial birds were conspicuous so I was certain that I had found all nests on each wetland, except for Kloe Lake. Kloe Lake was too large for me to monitor the entire nesting population, but my study area on the lake was partially isolated from the rest of the lake and I was certain that all nests on the study area were found.

I used three criteria to determine when parasitism had occurred; (1) two or more new eggs per day, (2) new eggs 2 or more days after clutch completion and (3) variation in egg features. These three criteria have been used extensively in other studies of parasitism (e.g. Brown 1984; Gibbons 1986; Møller 1987; Evans 1988). However, because the probability that each criterion will detect parasitism depends on reproductive attributes of the species and on logistic details of the study (Frederick and Shields 1986), I provide this additional relevant information.

Birds are unable to lay more than one egg per day (Sturkie 1965) so two or more new eggs per day is unequivocal evidence that more than one female has laid. However, the proportion of cases that will be detected by this criterion will depend on (1) the laying rate of the females, (2) their clutch size, (3) how early in the laying cycle nests are first discovered and (4) how frequently they are monitored (Frederick and Shields 1986). Female coots normally laid an egg a day in a continuous sequence and "skips" during laying were rare. Clutch sizes are large in this population (8.1 ± 0.09 , $n = 388$). I found most nests early in laying; 52% were found on the day the first egg was laid and 88% by the fourth egg. Depending on the site, nests were checked daily (207 nests) or every 2nd day (210 nests) during the laying and incubation periods.

Egg features like shape, spot colour and pattern and background colour varied considerably among clutches but little within females' clutches (see Appendix), as has been reported for numerous other species (Craig 1980; Fleischer 1985; Gibbons 1986; Møller 1987; Thomas et al. 1989; Jackson 1992). Thus, when parasitized nests were identified by the timing of new eggs, the parasitic eggs could be distinguished by their appearance. In a few cases, egg features alone were used to determine that nests had been parasitized. Arnold (1990) recently demonstrated the accuracy of identifying parasitic eggs in American coot clutches based solely on egg features. He used eggs from nests that were visited frequently during laying, and for which he was fairly sure that parasitism was absent, to assemble 50 clutches of four eggs. Half of these clutches contained a single parasitic egg and three "host" eggs. Visual comparisons correctly assessed whether a clutch was parasitized, and if so, which egg was the parasitic egg, in 94% of the trials. Because I used both the rate of egg-laying and egg features to detect parasitism, I would have missed even fewer parasitic eggs. Only parasitic eggs that were both indistinguishable from host eggs and laid in a continuous sequence with them would have gone undetected.

Egg rejection by hosts could affect the ability to detect parasitism because instances where parasitic eggs were rejected before the nest was visited would be missed (Rothstein 1977). Rejection of parasitic eggs is a common host defence in coots but most rejection was by burial in the nest material, rather than ejection from the nest (Lyon 1992). On average, parasitic eggs were in host nests 5 days before burial and in 90% of burials ($n = 135$), the egg was in the host nest for at least 2 days. In addition, eggs remained buried in the nest material at least a week before falling through the bottom of the nest, and I regularly checked down in the nest material to ensure that eggs had not been buried before their presence was detected. Thus, few cases of parasitism would have been missed as a consequence of egg rejection.

One category of eggs could not be clearly designated as either host or parasitic and I excluded the 56 eggs in this "unknown" category from the analysis. These were instances where one or two eggs appeared in an empty nest and then disappeared before their identity could be established. Some of these were probably cases where nesting females lost the first eggs in their clutch to predators. Others may have been cases where parasites laid in unoccupied nests, quickly followed by predation, or in active nests before the host laid, followed by ejection (e.g. Brown 1984; Emlen and Wrege 1986).

Identifying parasitic females. Striking variation among females in egg features made it possible to visually match parasitic eggs to the females that laid them when parasites also had nests of their own. I also used information about females' laying schedules to help identify parasites: females that laid an egg in their own nest on the day a given parasitic egg was laid on the wetland could be excluded from the pool of potential parasites. In a few cases, I suspected that specific females had laid parasitically, but could not be certain. These females were excluded from any analyses based on parasitic status. This may have resulted in a few parasitic females being excluded from the analysis but this is preferable to misidentifying non-parasites as parasites.

The ability to correctly identify parasitic females is central to this study. However, it is difficult to convey the ease with which parasitic eggs can be visually matched in the field to the females that laid them. I therefore provide an independent, objective demonstration of the degree to which eggs can be matched to the females that laid them based on egg features (see Appendix).

Estimating hatching and fledging success of parasitic eggs. Chicks in most host broods were marked at hatching with nape tags (Foley 1956) containing combinations of coloured seed beads unique within each brood. Nests were normally checked once a day during the hatching period. At nests where parasitic and host chicks were due to hatch on the same day, I pip-marked chicks in the egg (Alliston 1975) on the day before hatch so that parasitic chicks could be identified after hatch. I censused broods from mobile, floating blinds to determine the number of chicks raised to independence, and in marked broods, to determine which chicks survived. Chicks were considered independent, or "fledged", if they were alive after 30 days because virtually no mortality occurred after 30 days. In a few cases, parasitic eggs hatched but their subsequent fate could not be determined, either because the brood was not marked or because tags fell out. I assigned these chicks a fledging success equal to the proportion of hatched parasitic eggs, laid in the same stage of the host's laying cycle, that produced fledged young. I divided the host's cycle into the following stages, based on observed differences among stages (see below); before the host's first egg, days 1-4 of laying, day 5 of laying to 1st day after clutch completion, and the remainder of nesting cycle. Assigning these chicks a proportionate survival was preferable to omitting the eggs from the analysis because most parasitic eggs fail to hatch and omitting these successfully-hatched eggs would underestimate the reproductive success accrued from parasitism.

To examine the relation between the number of parasitic eggs a host received and the proportion of eggs that were rejected, hatched or fledged, I considered the total number of parasitic eggs the host received, including the cases where more than one parasitic female laid in a host nest. When calculating probabilities of egg rejection, I excluded nests that were preyed on because it was not known whether the parasitic eggs would ultimately have been rejected at these nests. Information on the distance between parasite and host territories, in terms of number of territories away, was obtained from the two lakes where territory measurements were obtained (Lyon 1992) and from a third wetland where relative territory positions were known, but actual territory size was not (Lake S5 1990).

Statistical tests follow Siegel and Castellan (1988) or Sokal and Rohlf (1981). I employ one-tailed tests where hypotheses predict a specific direction, otherwise two-tailed tests are used. Wherever

Table 1. Fates of parasitic eggs

Fate	<i>n</i>	(%)
Laid in inactive nests	50	(8.8%)
Preyed on	64	(11.2%)
Rejected by hosts	174	(30.5%)
Failed to hatch	171	(29.9%)
Died after hatch ^a	68	(11.9%)
Fledged ^a	44	(7.7%)
Total parasitic eggs ^b	571	(100%)

^a 41 chicks that hatched but whose subsequent fate was not known were assigned the average success rate for hatched chicks whose fate was known

^b Excludes 9 eggs whose fate was unknown and 12 affected by human disturbance

possible I provide exact probabilities. Values presented with means are standard errors unless indicated otherwise.

Results and discussion

Sources of mortality

Mortality of parasitic eggs and chicks was heavy and only 7.7% of all parasitic eggs produced chicks that survived to independence (Table 1). Egg rejection by hosts and hatching failure were the two most important sources of mortality for eggs and together caused the failure of 60% of all parasitic eggs. The usual method of egg rejection was burial in the nest material. Of the 174 rejected parasitic eggs 80% were buried while 20% were ejected from the nest. Nest predation, brood reduction after hatch and laying eggs in inactive nests were less important sources of mortality and each caused the failure of approximately 10% of the eggs (Table 1). To put the low survival rate for parasitic eggs into perspective, 34.6% of non-parasitic eggs ($n=2183$ eggs from 237 pairs) produced chicks that survived to independence.

The probability of hatching failure or post-hatching mortality for parasitic eggs was closely tied to how early in the host's breeding cycle the parasite laid her eggs (Fig. 1). Hatching success decreased with stage of the host's cycle (Fig. 1a; $\chi^2=72.4$, $P<0.001$, $df=4$), and no egg laid more than 6 days after clutch completion hatched. Considering only eggs that hatched, post-hatching survival decreased with stage of the host's breeding cycle (Fig. 1b; $\chi^2=12.4$, $P<0.01$, $df=3$). Most of this decrease in survival was likely a consequence of the pronounced hatching asynchrony in this species. Post-hatching survival of non-parasitic chicks was closely tied to hatching order (Lyon in press) and later-laid parasitic eggs would have hatched later in the hatching order.

These two components of fledging success, egg rejection and post-hatching survival, combine to produce a clear advantage for parasites that lay early in the host's cycle; the proportion of all parasitic eggs laid that produced independent offspring decreased with stage of the

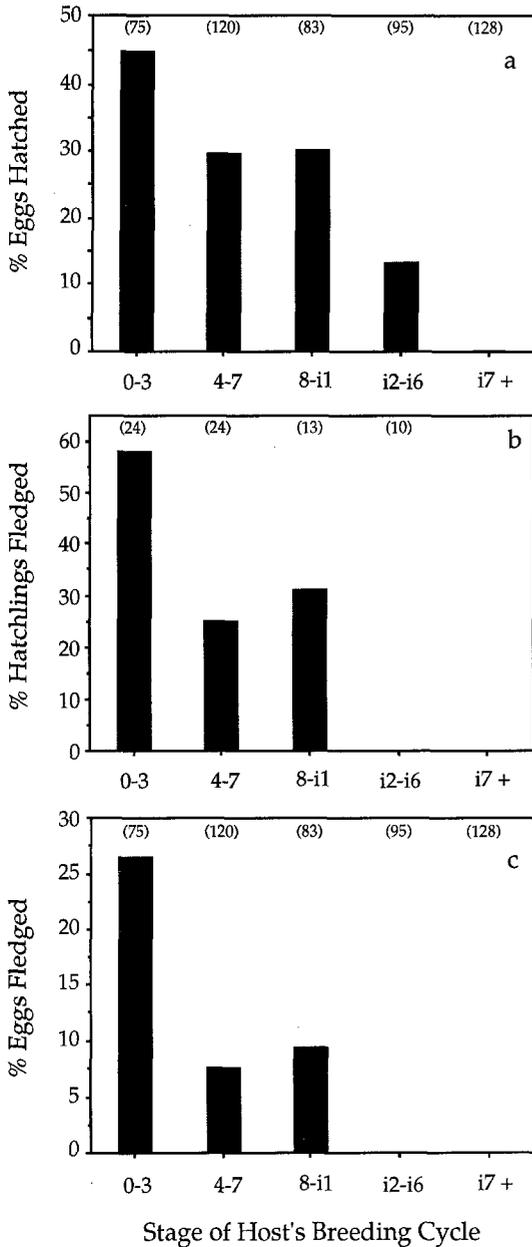


Fig. 1 a-c. The percentage of parasitic **a** eggs that hatched **b** hatchlings that fledged and **c** eggs that produced fledglings as a function of when they were laid in the host's laying cycle. For stage in the host's cycle, 0 is 1 day prior to the host's first egg, 1 to 11 are the laying period, and 11 to i22 are post-laying days. *Numbers above bars* are sample sizes

host's breeding cycle (Fig. 1c; $\chi^2 = 58.6$, $P < 0.001$, $df = 4$). To further illustrate this point, almost 80% of the 24 parasitic chicks known to have reached independence were from eggs laid in host nests by the time the host had laid her fifth egg.

Timing of parasitism in relation to nesting

On average parasitic females laid 3.5 (± 0.31) eggs parasitically ($n = 98$ females), but extremes ranged from 1 to 20. Most females laid parasitically before initiating

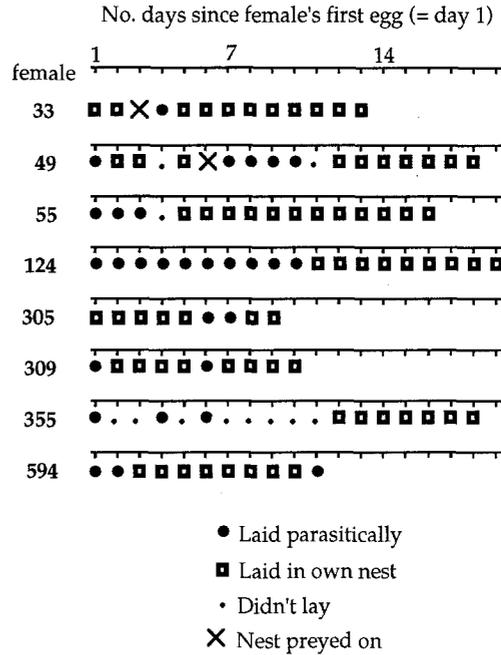


Fig. 2. Representative examples of the timing of parasitic egg-laying in relation to the timing of the parasite's own nest

their own nests (representative examples shown in Fig. 2). Of the 394 parasitic eggs laid by nesting females, 329 (84%) were laid before the parasite initiated her own clutch, 34 (9%) were laid during the interval when the parasite laid her own clutch (e.g. females 305, 309, Fig. 2), and only 3 eggs (1%) were laid after the parasite completed the clutch in her own nest (e.g. female 594, Fig. 2). An additional 28 eggs (7% of total) were laid after nest desertion or immediately following nest destruction (e.g. females 33, 49; Fig. 2). Dates of laying for 69 females were known well enough to establish whether they skipped days while laying parasitically or between parasitism and laying eggs in their own nests. Of these females 40 (58%) laid all of their parasitic eggs in a continuous sequence with their own eggs (e.g. female 124). Most of the females that did not lay in a continuous laying sequence skipped only 1 or 2 days after laying parasitically (e.g. female 55), but a few females skipped several days between parasitic eggs and/or before laying their own eggs (e.g. female 355). For these females that skipped during laying and counting each period between egg-laying as independent, the median number of days skipped was 1 day (1st quartile = 1 day, 3rd quartile = 2 days, range 1-15 days, $n = 33$ skips, 23 females).

The fact that females are capable of skipping several days between successive eggs suggests considerable flexibility in egg-laying, a trait that may facilitate parasitism. It is unlikely that most of these apparent laying skips were instances where eggs were rejected before nests were checked and parasitism could be detected (e.g. Rothstein 1977). Most rejection is by burial, and 90% of rejected eggs remain in the host nest at least 2 days, the maximum interval between nest checks. I cannot rule out the possibility that some of these apparent laying skips were instances where females laid eggs in the water or on unoc-

cupied nest platforms when they were unable to gain access to a host nest. Such eggs are occasionally found and are sometimes even attributable to known parasitic females. However, the apparent laying skips were disproportionately common with females that laid a large number of eggs; rate of parasitic egg laying (total eggs/time interval from first parasitic egg to first egg in own nest) decreased with the number of parasitic eggs laid ($r_s = -0.37$, $P = 0.003$, $df = 65$). This suggests that many of the cases were actual laying skips rather than undetected cases of egg-laying because there is no reason why the proportion of undetected cases of egg-laying should increase with the total number of eggs laid.

The observation that most females that laid parasitically did so before initiating their own nests is similar to findings for most other conspecific parasites studied to date; wood ducks (*Aix sponsa*, Clawson et al. 1979), moorhens (*Gallinula chloropus*, Gibbons 1986), goldeneye ducks (*Bucephala* spp., Eadie 1989), cliff swallows (*Hirundo pyrrhonota*, Brown and Brown 1989), redhead ducks (*Aythya americana*, Sorenson 1991) and bar-headed geese (*Anser indicus*, Weigmann and Lamprecht 1991). The only exception to this pattern is the barn swallow, where females appear to lay parasitically during and after laying, not before (Møller 1987).

This comparative pattern suggests that there is an advantage to laying parasitically before nesting begins, rather than after. There are several possible advantages. First, females may be better able to find and monitor host nests without the competing demands of nesting. Alternatively, laying parasitically while nesting might increase the risk that the parasite's own nest is parasitized (Brown and Brown 1989). Finally, in species with hatching asynchrony, females that laid parasitically after initiating their own clutch, but before clutch completion, would increase the hatching spread and possibly the competitive asymmetries of the chicks in their own nests.

Do parasites remove eggs?

I found no evidence that parasites systematically remove hosts' eggs when laying parasitically. Considering only cases of partial clutch loss, 44 females lost one or more of their own eggs and 8 of these cases occurred on the same night that parasitism occurred. To calculate the probability that at least 8 of 44 cases of egg loss would occur by chance on the same night that parasitism occurred, we need to know the proportion of days that nests are exposed to parasitism during the 28 day period from laying to hatching. On average, each host nest is parasitized on 3.0 of the 28 days (11%) of laying and post-laying. With this exposure to parasitism, the one-tailed binomial probability of observing at least 8 of 44 cases of egg loss associated with parasitism is 0.09. Thus the disappearance of host eggs was not disproportionately frequent on days when parasitism occurred, but there is a trend in this direction. Some of the cases of egg loss were probably instances where eggs were accidentally displaced during the act of parasitism, possibly due to a scuffle or a sudden departure of the parasite

from the host's nest (e.g. Weller 1959). However, even if all eight cases of egg loss during parasitism were cases of egg removal, they would make up less than 6% of the 140 different host-parasite combinations. Egg removal during parasitism is not an important parasitic tactic in coots, if it occurs at all.

This analysis is based on the assumption that parasites would remove eggs on the day the parasitism occurs. It is also possible that parasites visit nests at other times to remove eggs or that parasites damage eggs during their visits and these damaged eggs are later removed by the hosts, as coots do eject damaged eggs from their nests (Lyon 1992). Both of these scenarios predict that partial clutch loss should be more frequent at parasitized nests than non-parasitized nests but this was not observed; 22 of the 44 cases of partial clutch loss occurred at parasitized nests; goodness of fit test with expected values based on 41.2% of all nests being parasitized, $\chi^2 = 1.39$, $P = 0.24$, $df = 1$.

The pronounced hatching asynchrony and subsequent loss of late-hatched chicks would seemingly favour egg removal since it would advance the relative hatching position of the parasite's eggs and thus increase their survival prospects (Lyon 1992). It is therefore worth considering why egg removal does not occur in coots. The fact that most parasites laid several eggs in each host nest provides a probable explanation (Andersson 1984). If egg removal were possible only as an all-or-none behavior, in that parasites could not keep track of previous episodes of parasitism and removed an egg each time they laid parasitically, then females would run the risk of removing their own eggs when parasitizing the same nest more than once.

Although egg removal is commonly seen in interspecific parasitism (Payne 1977a; Davies and Brooke 1988; Rothstein 1990), systematic egg removal by conspecific parasites has been observed in only one species, the starling (*Sturnus vulgaris*; Evans 1988; Lombardo et al. 1989; Feare 1991). It is noteworthy that parasites usually lay one egg per host nest in this species (Lombardo et al. 1989). Similarly, in interspecific parasitism, the common cuckoo (*Cuculus canorus*) normally lays a single egg per host nest and parasites remove host eggs (Davies and Brooke 1988) whereas egg removal is absent in the pied crested cuckoo (*Clamator jacobinus*), a species where female appear to frequently lay more than one egg per host nest (Gaston 1976). These patterns are consistent with the idea that the presence or absence of egg removal is linked to the pattern of egg dispersion by individual parasites. They also suggest that a comprehensive comparative analysis of egg removal by interspecific parasites would be informative.

The spatial pattern of host use

Most parasitism involved immediate neighbours; 85% of host-parasite combinations involved immediate neighbours while 97% were within two territories (Table 2). Why do parasites use such a restricted pool of hosts? One possibility is that parasites are better able

Table 2. The location of the territories of parasitic females in relation to their hosts' territories

Lake	Distance to host territory		
	1 Territory	2 Territories	≥ 3 Territories
Jaimeson 1988	19	4	
S5 1989	21	2	2
S5 1990	15	2	
Total	55	8	2
Cumulative %	84.6%	96.9%	100%

Each parasite-host combination is treated as an independent observation, and values in the table are the number of parasites laying in each distance category

to assess the timing of breeding of immediate neighbours and, thus, lay their eggs earlier in the host's cycle. To test this idea I compared the time in the host's nesting cycle that parasites laid their first egg for host nests on adjacent territories versus host nests on more distant territories. Laying includes days 1–9; day 10 is the first day after clutch completion at all nests, and each unique parasite-host combination was treated as independent. First eggs at host nests one territory away were laid earlier in the host's cycle (day 6.8 ± 0.68 , $n=54$) than parasitic eggs at host nests two or more territories away (day 12.0 ± 3.06 , $n=9$; one-tailed t -test, $t=2.54$, $P=0.007$).

Given that laying accuracy decreases with distance, why do parasites ever lay more than one territory away? A examination of the options available to the ten females that parasitized hosts on more distant territories suggests that parasites may seek more distant hosts when forced to by lack of immediate neighbours as hosts. Two of the ten females had no potential hosts available on adjacent territories (i.e. all of their immediate neighbours either had not begun laying eggs or had already hatched their eggs) and another three females had already parasitized all of their immediate neighbours. Finally, three of the remaining four parasites only had immediate neighbours that were no longer laying.

Do parasites choose hosts non-randomly?

Host choice on the basis of stage of the host's nesting cycle. The higher success rate of early-laid parasitic eggs (Fig. 1) would favour parasites that chose nests in the early stages of laying to parasitize. Do parasitic coots choose host nests non-randomly based on their chronology? I examined the timing of laying of parasitic eggs in host nesting cycles for non-nesting and nesting parasites separately. The timing of laying by non-nesting females did not differ from a random expectation based on the relative exposure of nests during laying and post-laying (10 and 18 days respectively). Non-nesting females laid 56 of 143 eggs (39%) during the hosts' laying period (Fig. 3a) (goodness-of-fit test with an expected 51.1 eggs during laying, $\chi^2=0.71$, $P=0.39$, $df=1$). In contrast,

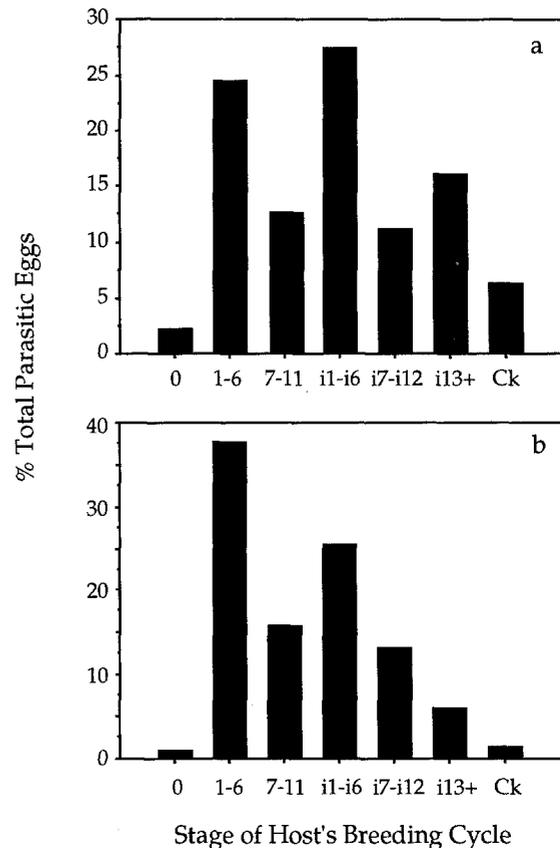


Fig. 3a, b. The frequency with which parasitic eggs were laid in different stages of the host's nesting cycle by **a** non-nesting parasites ($n=143$ eggs) and **b** territorial nesting parasites ($n=355$ eggs). Ck denotes nests where at least one chick has hatched

territorial, nesting parasites laid a disproportionate number of eggs during the hosts' laying period (Fig. 3b); 192 or 355 eggs (54%) were laid during the hosts' laying period and this differs from the expected number of 126.8 ($\chi^2=63.95$, $P<0.001$, $df=1$).

The non-random laying pattern for territorial parasites could result from active host choice by parasites or could simply reflect random host choice coupled with a high degree of breeding synchrony in the population. Because most parasitism by nesting females occurs before they initiate their own nests, random choice of hosts in a synchronous population could result in a high proportion of parasitism during hosts' laying periods.

To determine if parasites choose hosts non-randomly, the pool of hosts available for them to choose from must be determined. Following Brown and Brown (1991), I defined the sphere of "potential" hosts available to each parasitic and non-parasitic female based on the observed spatial and temporal pattern of actual host use. Virtually all parasitism was within two territories (Table 2). Of the 357 parasitic eggs from nesting females 98% were laid in host nests containing eggs, rather than before the host initiated or after hatch, so only nests containing eggs were considered as potential hosts. Finally, parasites usually laid parasitically before initiating their own clutch, so it is necessary to determine host availability on the day females laid their first egg. Based on these observed patterns of host use, "potential

Table 3. Tests for non-random host choice, based on (I) stage in the host's nesting cycle and (II) the host's brood size

Optimal category	% Females choosing hosts in optimal category (<i>n</i>) ^a	<i>P</i> ^b	% Females with variation to choose ^c
I. Nesting stage			
Before incubation	41.3 (29)	>0.83	48.0
Before host's 4th egg	36.8 (19)	>0.76	31.2
Before host's 6th egg	46.4 (28)	>0.62	45.9
II. Brood size			
More than 3 chicks	37.5 (24)	>0.84	70.6
More than 2 chicks	44.4 (18)	>0.64	52.9
More than 1 chick	50.0 (14)	>0.56	41.2

Probabilities for the observed percentage of parasitic females that chose hosts in the "optimal" category were estimated from 1000 simulated random choices (see text)

^a Sample size is the number of parasites that had potential hosts in both the optimal and alternative categories

^b One-tailed probability

^c Number of parasitic females with potential hosts in both categories (*n*) divided by the total number of parasitic females (61 total females for nesting stage, 34 for brood size)

hosts" for each female included any pair within a distance of two territories that had eggs when the female laid her first egg.

Following the approach taken by Emlen and Wrege (1986), I performed random host-choice simulations to determine whether the observed patterns of host choice, with respect to host nesting stage, differed from random expectation. For each individual analysis I chose an arbitrary threshold that differentiated an early, potentially "optimal" category from an alternative late stage category. I calculated the percent of observed instances of parasitism where females parasitized a host in the "optimal" category. Each unique parasite-host combination was considered independent and only parasites that had potential hosts in both categories to choose from were included. I then used simulations to estimate the probability that the observed percentage of "optimal" choices occurred by chance, as follows. For each of the unique parasite-host combination included, I chose one host at random from the pool available to the parasite, and the percent of randomly chosen hosts in the "preferred" category was then calculated for the population of parasites. This was repeated 1000 times to yield a distribution of "percent choices in optimal category", from which I estimated the probability that the observed percentage occurred by chance.

I tested for non-random host choice based on stage of host nest for three different thresholds that defined the optimal category, but there was no evidence for non-random host choice for any of these (Table 3). These tests for non-random choice were based on a radius of potential hosts to within two territories. However, almost 90% of parasitisms involved immediate neighbours. I therefore repeated the three simulations, limiting potential hosts to immediate neighbours, but the

results were unchanged (all *P*'s > 0.6). Restricting the radius of potential hosts to one territory did, however, reduce the proportion of parasites than had hosts in both the early and late categories to choose from; less than 20% of the parasites had such variation to choose from in each of the three tests.

These tests for non-random host choice are based on an *absolute* threshold that differentiates "optimal" from "non-optimal" hosts, but more than half the females in each case did not have variation around this threshold to choose from. However, it is possible that parasites make *relative* choices and choose the best host from the pool available to them. I therefore used matched-pair comparisons to test for non-random choice on a relative scale. For each unique parasite-host combination, I compared the nesting stage at the nest that was parasitized and the median value of the stages at potential host nests that were not parasitized. Chosen host nests were not consistently at an earlier stage than the median values for unchosen hosts; one-tailed Wilcoxon test, $z = -1.06$, $P = 0.14$, $n = 49$. Restricting the pool of potential hosts to adjacent territories does not change the result; one-tailed Wilcoxon test, $z = -1.20$, $P = 0.88$, $n = 24$.

Host choice on the basis of brood size. Parasites could also choose hosts on the basis of parental quality. Larger brood sizes at independence are associated with less brood reduction after hatch (unpubl. data) and, all else being equal, would offer a higher success rate for hatchling parasites. To determine if host choice is random with respect to brood size, I established threshold brood sizes differentiating potentially "optimal" and "non-optimal" brood sizes, tallied the percentage of choices in the optimal category and, as before, ran random host choice simulations to estimate the probabilities for the observed percentage of optimal choices.

The observed pattern of host choice did not differ from random expectations for any of the three thresholds chosen (Table 3). I then restricted the pool of potential hosts to immediate neighbours but the results were unchanged; $P > 0.45$ for comparisons for > 3 chicks and > 2 chicks, insufficient sample for a > 1 chick comparison. Again, restricting the pool of potential hosts to a radius of one territory reduced the number of parasites that had variation to choose from; 29.4%, 20.6%, and 14.7% of the parasites had variation to choose from in the > 3, > 2, and > 1 chick comparisons, respectively. As before, I also checked for non-random host choice on a relative basis. I found no evidence for non-random choice for the comparison based on a pool of potential hosts within a radius of two territories (one-tailed Wilcoxon test, $z = -1.06$, $P = 0.86$, $n = 31$) or within a radius of one territory (one-tailed Wilcoxon test, $z = -1.58$, $P = 0.94$, $n = 15$).

Host value and the number of parasitic eggs. Till now I have considered host choice *per se*, but parasites could also adjust the number of eggs they lay per host nest according to the value of the host nest. For example, parasites could lay more eggs in nests that they parasitize

early in the host's laying cycle. Similarly, if parasites could assess the territory or parental qualities of hosts, they might be expected to lay more eggs in the nests of hosts that raise large broods.

The number of eggs parasites laid per host nest was not correlated with the brood size eventually raised by the host ($r_s=0.05$, one-tailed $P=0.31$, $df=79$). However, there was a negative correlation between the number of eggs laid per nest and the day of the host's cycle on which the parasite laid her first egg ($r_s=-0.14$, one-tailed $P=0.055$, $df=133$). Moreover, parasites that began parasitizing a host nest no later than 1 day after the host finished laying (i.e. in the range where parasitic eggs were successful) laid more eggs in the nest (2.6 ± 0.16 eggs, $n=93$) than parasites that initiated laying 2 or more days after the host's clutch completion (2.1 ± 0.21 eggs, $n=42$; one-tailed Mann-Whitney U -test, $P=0.027$). Thus, parasites appear to adjust the number of eggs they lay according to the stage of their hosts' breeding cycle but not according to expected brood size.

Why do parasites not choose early nests, or pairs that ultimately raise large broods, when they would appear to benefit from doing so? Three factors could be important. First, random host choice may reflect the absence of cues which could allow a parasite to choose. The pronounced brood reduction that most pairs experienced (Lyon in press) suggests that pairs are unable to accurately predict the number of offspring they can rear on their own territories (Lack 1947), and their ability to predict the number of offspring that neighbours can raise would only be worse. However, the observation that parasites adjust the number of eggs they lay according to the stage of the host's nesting cycle suggests that cues are available to assess timing, and that parasites use these cues. Second, most pairs appear to have little to choose from, and less than 20% of the pairs had variation in timing to choose from when the pool of potential hosts was restricted to a radius of one territory. Finally, these analyses implicitly assume that parasites can gain access to all of the potential hosts available to them. Dominance relationships appear to prevent some potential hosts from being utilized (Lyon 1992) and it is unlikely that all parasites can gain access to all of their potential hosts. With this additional constraint, very few parasites may have had meaningful variation among accessible hosts to choose from.

Orians et al. (1989) pointed out that non-random laying patterns at the population level can occur for several reasons and do not necessarily indicate active host choice by individual brood parasites. Their warning is underscored by my findings: the population level analysis revealed that a disproportionate number of parasitic eggs are laid during the host's laying cycle (Fig. 3b), but subsequent analysis showed that this was not the consequence of parasites preferentially parasitizing nests at early stages. Instead, this pattern appears to reflect a fairly high degree of breeding synchrony, coupled with the fact that most parasites laid parasitically before they began laying their own clutches. In support of this idea, parasitism by non-nesting parasites is not constrained by the conflicting demands of nesting, and the popula-

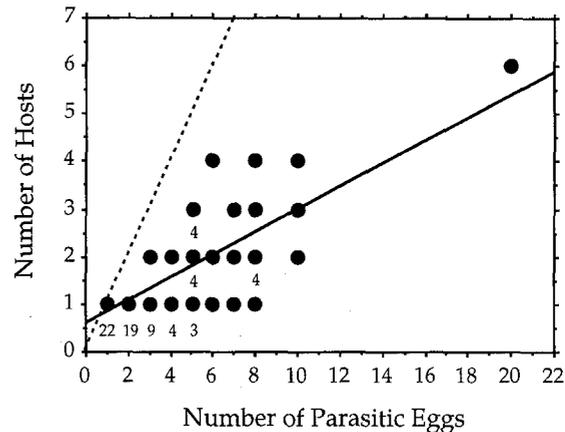


Fig. 4. The relation between the total number of parasitic eggs laid by a parasite and the number of hosts she parasitized. Numbers below points indicate multiple observations. The dashed line represents a slope of 1.0, the slope predicted if birds laid one egg per host nest

tion level comparison for these females did not differ from random expectation (Fig. 3b).

Allocating eggs to nests: single versus multiple laying

The pattern of egg dispersion. Parasites that lay more than one parasitic egg are faced with the decision of how to allocate eggs among nests. They can lay one egg per host nest (scatter laying) or they can lay several eggs in each host nest (multiple laying; Payne 1977b). Parasitic coots showed a strong tendency towards multiply laying (Fig. 4). The slope for the relation between the number of parasitic eggs laid by each female and the number of hosts she parasitized (0.23 ± 0.019 hosts/egg) differs from a slope of zero ($t=12.2$, $P<0.001$, $df=85$), indicating that birds are spreading eggs among nests to some extent. The slope also differs significantly from 1.0 ($t=-41.0$, $P<0.001$, $df=85$), the slope predicted if birds laid one egg per nest.

Whether or not parasites spread their eggs among nests was strongly associated with the total number of parasitic eggs they laid. Most of the females laying four or fewer eggs laid them in a single host nest, while few females laying more than four eggs did so (Fig. 5a). As a result of this pattern of egg dispersion, the average number of eggs laid per host nest increased nearly linearly with increases in the total number of parasitic eggs laid up to four eggs, but then was roughly level for females that laid 4 or more parasitic eggs (Fig. 5b). This levelling off suggests that there is an upper limit to the number of eggs parasites will lay in each nest.

These patterns raise two questions. First, why do parasitic females laying two to four parasitic eggs tend to lay them in a single host nest? Second, why do females that lay more than four eggs tend to lay them in more than one host nest? Post-hatching parental care limits the number of offspring that parents can raise and furthermore, as a consequence of pronounced hatching asynchrony, a chick's probability of survival decreases

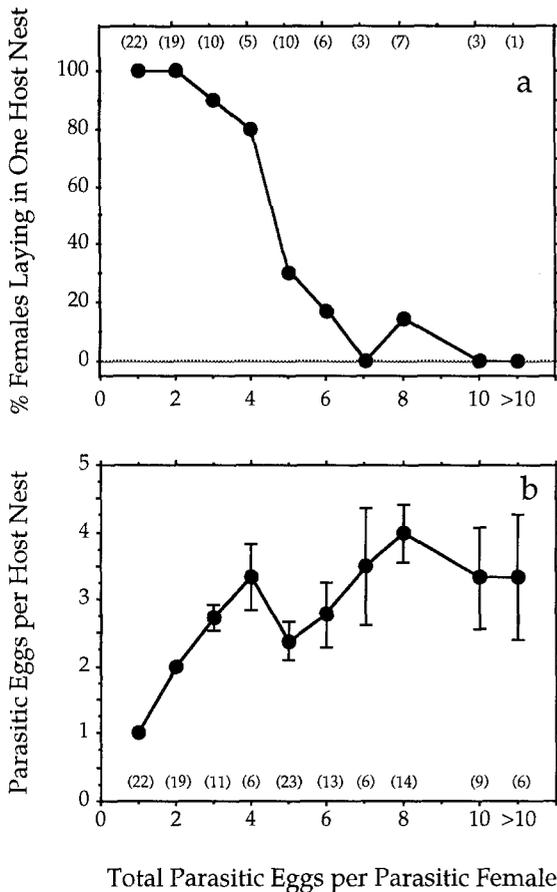


Fig. 5a, b. The dispersion of parasitic eggs among host nests as a function of the total number of parasitic eggs laid, in terms of **a** the proportion of females that laid all of their eggs in a single host nest and **b** the average number of eggs parasites laid per host nest (mean \pm SE). Numbers in brackets are number of parasites (a) and number of host nests (b)

with its hatching order (Lyon in press). Thus, sib competition among parasitic chicks for limited parental care at host nests and/or the effects of hatching order *per se* could favour spreading eggs among host nests. However, the observation that almost all parasites laying four eggs or fewer laid in a single host nest suggests that multiple laying in a single nest is advantageous, at least up to a point. Multiple laying could potentially increase the per capita success of parasitic eggs by affecting the host's ability to recognize and reject parasitic eggs or by affecting the hatching pattern, and consequently, the probability of brood reduction after hatching. Alternatively, multiple laying could be a consequence of host limitation rather than the benefits of clumping eggs. To explore these possibilities further, I investigated the relation between the number of parasitic eggs per host nest and (1) rate of egg rejection, (2) hatching success, (3) post-hatching survival and (4) host availability.

Analyses were done on a per nest basis but the data are summarized graphically in three categories of host nests that are relevant to the issues raised by the observed pattern of dispersion by parasites (Fig. 6); hosts receiving (i) a single parasitic egg (complete scatter laying), (ii) two to four parasitic eggs (the observed pattern

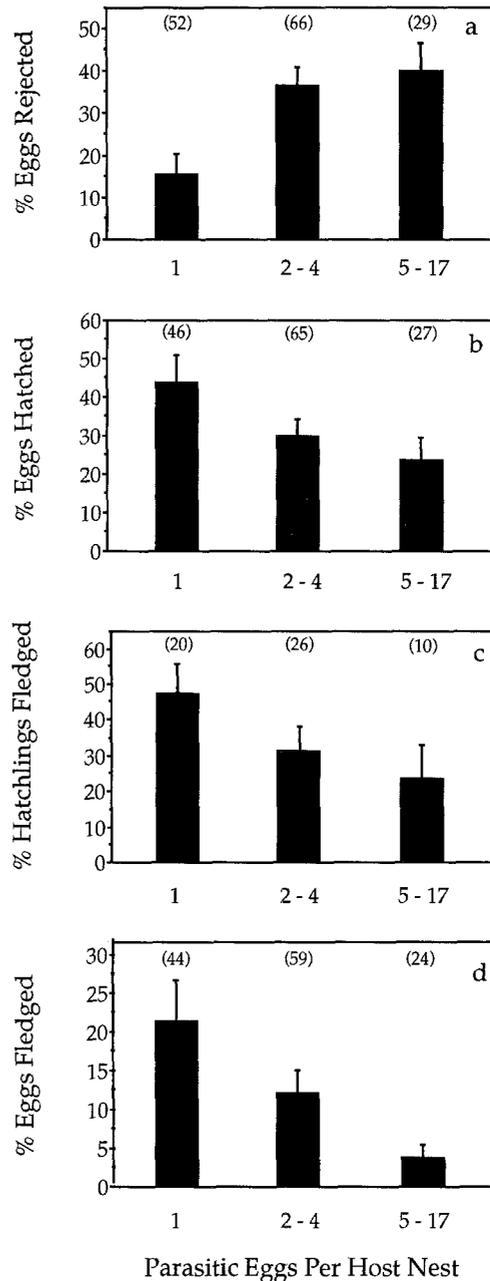


Fig. 6a-d. The relation between the number of parasitic eggs hosts received and the mean percentage of eggs that were rejected or successful per nest; **a** eggs rejected by hosts, **b** eggs that hatched, **c** hatchlings that fledged and **d** eggs that produced fledglings. Values are mean \pm SE. Sample sizes above bars are number of nests

of multiple laying), or (iii) five or more parasitic eggs. Although non-parametric tests were used, I present means because they provide the most meaningful representation of reproductive success.

Multiple laying and parasite reproductive success. The proportion of eggs rejected at each host nest increased with the number of eggs the host received (Fig. 6a, $r_s = 0.33$, $P < 0.001$, $df = 145$). This analysis is not confounded by the number of females parasitizing a host nest because the correlation remains if nests parasitized by more than one parasite are excluded; $r_s = 0.27$, $P =$

0.006, $df=107$. The proportion of eggs rejected per nest differed between nests receiving a single egg ($n=52$) and nests receiving two or more eggs ($n=95$; Mann-Whitney U -test, $z=3.97$, $P<0.001$). Thus, with respect to egg rejection, scatter-laying appears to be more profitable than laying several eggs per nest.

The proportion of parasitic eggs that hatched at a nest was not correlated with the number of parasitic eggs received (Fig. 6b, $r_s=-0.09$, $P=0.31$, $df=136$). However, the proportion of hatchling parasites that survived to independence at each nest decreased with the number of parasitic eggs hosts received (Fig. 6c; $r_s=-0.27$, $P=0.049$, $df=54$). As a consequence of the independent effects of egg-rejection and post-hatching survival, the overall success of parasitic eggs was negatively correlated with the number of parasitic eggs per host nest (Fig. 6d; $r_s=-0.16$, $P=0.07$, $df=125$). There was a trend for eggs to be more successful in host nests receiving a single egg ($n=44$) than in nests receiving more than one egg ($n=83$; Mann-Whitney U -test, $z=1.55$, $P=0.12$). However, there was no difference in the success of eggs in nests receiving two to four eggs ($n=59$) and in nests receiving five or more eggs ($n=24$; Mann-Whitney U -test, $z=0.76$, $P=0.45$).

I have examined the influence of egg number on the average success of parasitic eggs in a host nest but this ignores the possible influence that position in the parasite's laying sequence (i.e. whether a parasitic egg is the first, second, or third parasitic egg laid in the nest) could have on an egg's success. Egg laying position is likely to influence survival because, by necessity, eggs laid later in the parasite's laying sequence at each nest are also laid later in the host's nesting cycle. At the population level, the order in which a parasitic egg is laid in a host nest is strongly associated with how early in the host's cycle the egg is laid; $r_s=0.50$, $P<0.001$, $df=387$. Given that laying order determines hatching order, and that post-hatching survival decreases with hatching order (Lyon in press), first-laid eggs should be more successful than later-laid eggs. Analyses based on average success could provide conservative tests for the benefits of scatter laying because first laid eggs could inflate the average success of eggs in multiply-parasitized nests. I therefore analysed the success of parasitic eggs on the basis of the order in which they were laid in the host nest.

To compare the hatching or fledging success of eggs as a function of their position in the laying sequence at host nests, I pooled all eggs with the same position in the laying sequence and calculated the overall proportion of eggs that were successful. For example, first laid eggs included all eggs from nests receiving a single egg as well as the first laid parasitic eggs in nests receiving more than one parasitic egg to ensure that differences in host quality between singly and multiply parasitized nests would not confound such an analysis I compared the success (% accepted eggs fledged) of first laid eggs in nests receiving one, two to four or five or more eggs, but no difference among categories was observed ($\chi^2=2.27$, $P=0.32$, $df=2$). Similarly, there was no difference in the success of eggs laid second to fourth in nests receiving two to four eggs versus nests receiving five

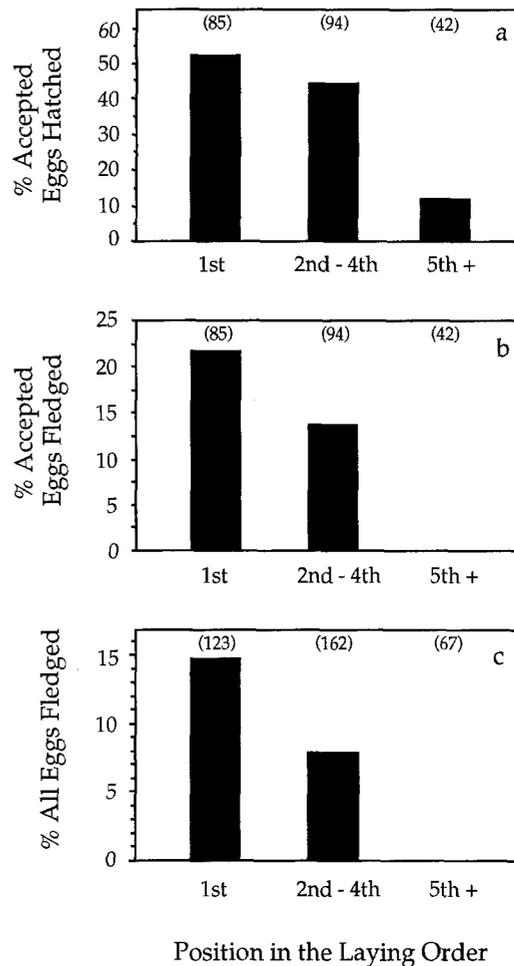


Fig. 7a-c. The relation between the order in which a parasitic egg was laid in a host nest and the percentage of **a** accepted eggs that hatched, **b** accepted eggs that produced fledglings and **c** total eggs that produced fledglings. Sample sizes above bars are numbers of eggs

or more eggs ($\chi^2=0.15$, $P=0.70$, $df=1$). Thus, pooling data from singly and multiply parasitized nests is justified.

Egg rejection was not affected by position in the laying sequence (comparing the three categories first-laid, second- to fourth-laid, fifth- and later-laid eggs; $\chi^2=3.96$, $P=0.41$, $df=2$). Moreover, comparing the rejection rate of first laid eggs versus all later categories combined does not alter the result ($\chi^2=1.33$, $P=0.25$, $df=1$). To examine the influence of position in the laying sequence independent of egg rejection, I removed rejected eggs from the analysis and examined the proportion of accepted eggs that hatched or produced fledged offspring. The proportion of accepted eggs that hatched decreased with position in the laying sequence (Fig. 7a; $\chi^2=19.07$, $P<0.001$, $df=2$), as did the proportion of accepted eggs that produced fledglings (Fig. 7b; $\chi^2=10.67$, $P<0.005$, $df=2$). Examining the success of all eggs, including both accepted and rejected eggs, reveals that the overall success in producing fledglings decreased with position in the laying sequence (Fig. 7c; $\chi^2=12.08$, $P=0.0024$, $df=2$). I employed *post hoc* comparisons with additive partitions of the contingency table (Siegel

and Castellán 1988) to determine which categories differed. The success of first versus second to fourth laid eggs differed ($\chi^2 = 4.07$, $P < 0.05$, $df = 1$) as did the success of first- to fourth-laid versus fifth- and later-laid ($\chi^2 = 8.01$, $P < 0.005$, $df = 1$).

This analysis can explain why, on average, parasites do not lay more than four eggs per host nest (Fig. 5b): no parasitic eggs laid fifth or later was ever successful. The complete lack of success of these eggs makes sense if we consider the minimum hatching order that these eggs could have and the relation between hatching order and post-hatching survival. At best, the fifth egg a parasite laid in a nest would be laid on the same day as the host's fifth egg, if the parasite synchronized her laying perfectly with the host's laying cycle. In this case, the fifth parasitic egg would either be the ninth or tenth egg to hatch, but few ninth-hatched chicks survive (10% of 11 chicks) and no chick that hatched tenth or later survived ($n = 10$; Lyon in press). Thus, laying a fifth egg would never pay for females that began parasitism after a host had laid her first egg, a category which includes virtually all cases of parasitism.

These analyses reject the hypothesis that parasites lay several eggs in the same host nest because multiple laying is advantageous – egg rejection rates were lower at nests receiving a single egg and the analysis of success as a function of laying sequence indicates that reproductive success from parasitism would be maximized by laying a single egg in each host nest. I therefore examine the possibility that host limitation underlies some of the cases of multiple laying.

Host availability and multiple laying. A positive correlation between the number of hosts used by a parasitic female and the number of potential hosts available to her during per period of parasitism suggests that hosts are limiting to some degree (Fig. 8; $r_s = 0.49$, $P < 0.001$, $df = 45$). This relation is based on a pool of potential hosts within a radius of two territories, but almost 90% of parasitism involves immediate neighbours. However, the association between host use and host availability remains if the number of potential hosts available to each parasite is based on a radius of one territory ($r_s = 0.44$, $P < 0.006$, $df = 38$).

I also examined host availability for females that laid more than parasitic egg (range 2–8) but parasitized a single host nest (both host use and availability restricted to a radius of one territory). Of these 15 females 10 (67%) had only one potential host they could parasitize. Moreover, these 15 females that parasitized a single host had fewer hosts available to them (1.33 hosts/parasite, $n = 15$) than the females that parasitized more than one nest (2.60 hosts/parasite, $n = 5$; Mann-Whitney U -test, $z = 2.70$, $P = 0.007$). These patterns all suggest that host limitation underlies many of the cases of multiple laying.

The observed pattern of egg dispersion by parasites appears to be a compromise between the benefits of laying a small number of eggs per host nest and the constraints imposed by host limitation. If hosts were not limiting, parasites would benefit by laying a single egg in each host nest but if host limitation precludes this

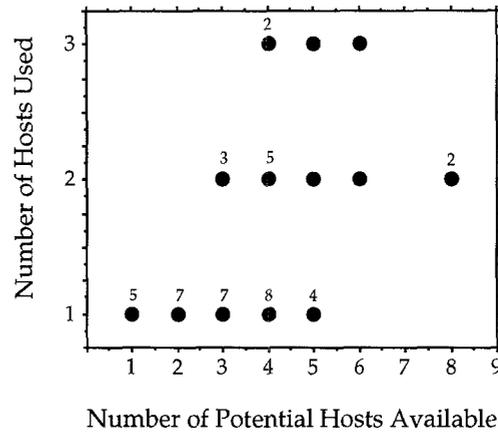


Fig. 8. The number of hosts parasitized by each parasite in relation to the number of potential hosts available to them during the time interval they laid parasitically. Potential hosts includes any pair within a radius of two territories whose nest contains eggs. Numbers above points indicate multiple observations

option, then it appears to be worth laying up to four eggs per host nest. The prediction that parasites should lay a single egg per host nest when hosts are not limiting is supported by a strong positive correlation between the number of hosts a female parasitized and the proportion of those hosts that she parasitized with a single egg; $r_s = 0.55$, $P = 0.004$, $df = 26$ (only females parasitizing two or more hosts are included). This observation, and the dramatic decrease in the use of a single host nest for females laying more than four eggs (Fig. 5a), certainly suggest that the fitness consequences of egg dispersion patterns have shaped the evolution of parasitic tactics to some extent.

There is little information on how conspecific brood parasites in other species disperse their eggs among nests. Evans (1988) showed for starlings breeding in England that the success of parasitic eggs decreased with the number of parasitic eggs laid. However, the number of parasites responsible for host nests containing more than one parasitic egg is unknown. Parasites in other starling populations appear to lay one egg per host nest (Lombardo et al. 1989). Gibbons (1986) found that moorhens tend to lay several eggs per host nest but the consequences of multiple versus scatter laying were not examined.

For interspecific parasitism, Payne (1977b) studied the pattern of laying dispersion in several species of parasitic finches and found that multiple parasitism of nests was more common than expected by chance. The survival of parasitic chicks was independent of the number of parasitic chicks per nest, indicating little selection against multiple parasitism. Payne then concluded that since half the nests contained a single parasitic egg, despite a lack of penalty for multiple laying, that there must be an advantage to spreading eggs among host nests.

Payne (1977b) reasoned that spreading eggs among nests would minimize the risk that individual females loose an entire clutch to predation, a benefit that has more recently been applied to conspecific brood para-

sites as well (Rubenstein 1982; Brown and Brown 1989). However, the logic of this argument is flawed because it focuses on the reproductive consequences of spreading eggs for individual females, and does not consider the selective consequences of spreading eggs as a trait at the population level. Bulmer (1984) showed that at the population level there is virtually no selective advantage to spreading eggs among nests, at least with respect to minimizing the risk of complete reproductive failure. Thus, the most likely explanation for Payne's (1977b) observation is that parasites adjusted the number of eggs they laid according to the stage of the host's laying cycle, and that single eggs were instances where nests were first parasitized late in the host's laying cycle. Future studies should examine the pattern of egg dispersion in relation to the availability and timing of host nests.

Conclusions

The high mortality rate for parasitic eggs in this study was largely a consequence of two factors, mismatched timing of laying in the host's nesting cycle and egg rejection. Parasites could potentially improve the prospects of their eggs by decreasing the likelihood of rejection, by avoiding laying too many eggs in the same nest, or by laying eggs early in the host's laying cycle. Although parasites appear to lay more eggs per nest than would be predicted based solely on rates of egg-rejection and egg success, the fact that parasites avoid laying too many eggs per nest suggests that their laying tactics are optimized to some degree within the constraints imposed by host limitation. The observation that parasites adjusted their investment in a host nest according to how early in the host's cycle they began to lay suggests that parasites are capable of assessing the nesting stage at a host's nest. However, this ability to assess nests does not lead to a non-random pattern of host choice on the basis of nesting stage. As with the tactics of egg dispersion, host limitation appears to constrain the options for choosing hosts.

Two studies have found evidence for non-random host choice. Emlen and Wrege (1986) provided clear evidence that parasitic white-fronted bee-eaters (*Merops bullockoides*) choose hosts non-randomly on the basis of timing. Brown and Brown (1991) found that cliff swallows preferentially parasitized nests that ultimately had the lowest infestations of ectoparasites, an important source of mortality. In addition, birds that physically transferred their eggs to host nests by carrying the eggs in their bills parasitized nests that were more likely to be successful. The occurrence of non-random choice of hosts in these species probably reflect that fact that parasites have a much larger sphere of potential hosts to choose from than do parasitic coots, and this would reduce the constraints of host limitation. Both species nest in large dense colonies and for bee-eaters the sphere of potential hosts appears to be the entire colony (Emlen and Wrege 1986), while for cliff swallows the sphere of choice is a radius of five nests (Brown and Brown 1991).

In coots, parasitizing immediate neighbours appears to yield both a benefit and a cost. Limiting parasitism to immediate neighbours improves laying synchronization with the host's own laying cycle but it also imposes constraints associated with host limitation. It remains to be demonstrated which of these is more important. Nonetheless, another factor that may favour parasitism of neighbours is that birds on adjacent territories would well-informed about each other's fighting and defensive capabilities. Social interactions and fights between neighbours are frequent throughout the breeding season, whereas they occur rarely, if at all, between birds on non-contiguous territories (unpubl. data). Territorial fights can be vicious in this species, and can even result in death (Henshaw 1918), so attempts at parasitizing hosts of unknown fighting ability may be too costly for most females.

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Appendix

Following Fleischer (1985), I used discriminant function analysis to provide an objective, independent demonstration that the eggs of different females can be distinguished by their features. I photographed and measured 35 parasitic eggs that were attributed, through visual comparisons, to 11 parasitic, nesting females on one focal wetland (Pond S5, 1989). I also photographed and measured eggs that each of these 11 females laid in her own nest (five eggs at ten nests, four eggs at one nest). The following egg features were used in a stepwise discriminant function analysis using BMDP (Dixon 1985): spot densities for five size ranges of spots (counted on twice life size black and white photographs), egg length, width, width at 1/4 length from pointed end, width at 1/2 length, width at 3/4 length, egg sphericity (length/width) and egg pointedness (width 1/4 divided by width 3/4) and background colour darkness rank (a monochromatic scale from 1–10).

To determine the degree to which egg features can discriminate the eggs laid by different females, I first performed the analysis using only the eggs the females laid in their own nests, with each female (nest) representing an a priori group. This analysis provides a good indication of the precision of the technique, as long as we are reasonably sure that the females' own eggs were in fact their own eggs. Nests were checked daily at this wetland so virtually all cases of parasitism would have been detected based on a laying rate of more than one egg per day or the appearance of new eggs after the host ceased laying. In addition, egg features provide an independent method for identifying parasitic eggs and would have identified the rare cases of parasitism that would have been missed based on laying rate alone. In fact these criteria did detect two cases of parasitism at these 11 nests; one case (three parasitic eggs) was identified by a laying rate of two eggs per day and the other case (three parasitic eggs) was identified by egg appearance alone. These parasitic eggs were excluded from the nest owner's group.

Discriminate function analysis revealed that there were significant differences among these females in egg morphologies ($F=26.23$, $df=50,341$, $P<0.001$). Five variables entered the model; spot densities for two size ranges of spots, length, width, and background rank. Based on the discriminant function, 29 of 35 eggs (82.9%) were classified as belonging to the correct group (i.e. to the female whose nest the egg was in). Clearly, variation in egg features among females is sufficient to permit accurate grouping of eggs by the females that laid them.

I next used the discriminant functions derived from the eggs females laid in their own nests to match the parasitic eggs to the females that laid them. The discriminant functions matched 21 of the 35 parasitic eggs (60%) to the "correct" parasite (i.e. the female I had identified as the parasite in the field). However, this classification is based solely on egg features and I used additional criteria when identifying parasitic females in the field. For example, since females cannot lay more than one per day, all females that laid an egg in their own nests on a day a given parasitic egg was laid can be ruled out as the parasite. When this restriction is ap-

plied, and the smallest Mahalanobis distance (D) in the pool of remaining females is taken as the “correct” parasite, 28 of the 35 parasitic eggs (80%) were classified to the “correct” parasite. Finally, only 1% of all parasitic eggs laid by nesting females were laid after they completed their own clutches. If females that had completed their own clutches are also excluded as possible parasites when each parasitic egg was laid, then 32 of the 35 parasitic eggs (91.4%) were correctly classified. This success rate is very close to the value obtained for the eggs that the females laid in their own nests, when the same restrictions are applied (94.4% of 54 eggs; comparing the number of successes and failures in the two groups, $\chi^2 = 0.31$, $P = 0.58$, $df = 1$). The similar error rates for parasitic eggs and for eggs from clutches in females’ own nests suggests that the errors for parasites obtained here represent imprecision

in the accuracy of the method rather than cases that were misidentified in the field.

These analyses are not meant to provide an accurate assessment of my own accuracy in the field. I use them only as an objective demonstration that the variation among the eggs of females is sufficient to allow eggs to be matched to the females that laid them, with some degree of accuracy. These analyses probably underestimate the accuracy of visual comparisons because I used additional eggs features in the field to match eggs to females. These features, like spot and background colour, were not used in the present analysis because they were too difficult and time consuming to quantify in the field. However, it is clear that these features are very important in helping to distinguish the eggs of different females.