

Conspecific brood parasitism as a flexible female reproductive tactic in American coots

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Abstract. Conspecific brood parasitism was a common component of reproduction in a population of American coots, *Fulica americana*, in central British Columbia, Canada. In a 4-year study, over 40% of nests were parasitized and 13% of all eggs were laid parasitically. Parasitism occurred in several ecological contexts, each involving different constraints and trade-offs. A quarter of the parasitic eggs were attributed to floater females without nests or territories of their own. The annual reproductive success of floaters was 16 times lower than that of territorial, nesting females, indicating that parasitism was a low-paying alternative to non-breeding rather than a specialized, equal-fitness alternative to nesting. Nest loss during laying accounted for few cases of parasitism. Most of the parasitism in the population was attributed to nesting females that laid additional eggs parasitically. One quarter of the nesting females were parasitic, and these females usually laid parasitically prior to laying full-sized clutches in their own nests. Brood reduction through starvation was prevalent in all years and on all wetlands, indicating that post-hatching parental care limits the number of offspring that pairs can raise in their own nests. By laying surplus eggs parasitically, females can bypass the constraints of parental care and increase their total production of offspring. As a flexible reproductive tactic used in several ecological contexts, parasitism permits a more finely tuned life-history strategy for dealing with reproductive and social constraints.

The repeated, independent evolution of parental care in a diversity of taxa attests to the benefits of providing care to offspring, but parental care also has associated costs like reduced fecundity or parental survival (Williams 1966; Trivers 1972). In some cases these costs may favour the evolution of brood parasitism because 'brood parasites' that lay their eggs in the nests of others gain the benefits of parental care without paying the costs. It is therefore not surprising that the evolution of parental care has been accompanied by the evolution of brood parasitism in several taxa; birds (Lack 1968; Payne 1977), insects (Eickwort 1975; Tallamy 1985) and fish (Tetsu 1986).

Brood parasitism has been most thoroughly studied in birds and two distinct forms are recognized. Some species do not provide parental care and are completely dependent on hosts of other species to rear their young. This obligate inter-specific brood parasitism has been the subject of

many detailed studies in a variety of species, and many of its characteristics are well understood (Hamilton & Orians 1965; Lack 1968; Payne 1977; Rothstein 1990). During the last decade it has become clear that conspecific brood parasitism also occurs. The difficulties in distinguishing among the eggs of conspecific females initially caused conspecific parasitism to be overlooked in many species (Yom Tov 1980). However, careful nest monitoring studies (e.g. Gibbons 1986; Møller 1987), detailed behavioural observations (e.g. Emlen & Wrege 1986; Brown & Brown 1989), and biochemical and molecular techniques (e.g. Manwell & Baker 1975; Quinn et al. 1987) are all helping to overcome these difficulties and it is now clear that conspecific parasitism is more common than previously thought.

Conspecific brood parasitism has been recorded in over 160 species, representing a diversity of taxa, social systems, and life histories. Despite this widespread occurrence, the adaptive basis of conspecific parasitism remains poorly understood. A clear demonstration of the benefits of parasitism requires

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not only the ability to identify which females in the population are the parasites, but also to document the ecological or social contexts in which parasitism occurs and the trade-offs involved. The identities of parasitic females have been determined for less than 10 species, and many of these studies were unable to fully explain why parasitism occurs. In particular, few studies have sought to understand how parental care constrains the number of young that a female or pair can raise in their own nest. This is surprising because parenting and parasitism are behavioural alternatives, and understanding the constraints of parental care may be essential to explain why females lay eggs parasitically rather than in their own nests.

In this paper I report the results of a 4-year study of conspecific brood parasitism and parental care in American coots, *Fulica americana*, a monogamous, marsh-nesting rail (family Rallidae). My main goal was to test alternative hypotheses about the adaptive basis of brood parasitism as a reproductive tactic. I have also placed special emphasis on understanding the constraints of parental care and interpreting the significance of parasitism in light of these constraints. I start by presenting information on the basic natural history of parasitism and demonstrate that parasites fall into two broad groups of females, floater females without territories and territorial, nesting females. I then outline and test hypotheses for each of these two classes of brood parasites separately.

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 at Riske Creek in 1987: 84 pairs on 12 lakes and ponds; (2) Jaimeson Meadow near Big Creek, 1988–1990: 52, 43 and 46 pairs, respectively, on one large wetland; and (3) Chilco West Marshes, 15 km southeast of Hanceville, in 1989 and 1990: 129 and 88 pairs, respectively, at Kloe Lake, Jones Lake and Pond S5. The ponds at Beecher Prairie were unsuitable for breeding after 1987 because of a drought. The other two study sites, Jaimeson Meadow and the Chilco West wetlands, were managed by Ducks Unlimited, Canada, and water levels were maintained at normal levels from 1988 to 1990. Hardstem bullrush, *Scirpus acutus*, was the dominant emergent plant

at all wetlands, and was limited to a strip along shore on most wetlands. However, sparse patches of bullrush grew in the middle of both Kloe Lake and Jaimeson Meadow, providing nesting cover for coots away from the shoreline.

In central British Columbia coots are migratory, and, because adult philopatry was rare (unpublished data), I usually studied different individuals each year. Coots are monogamous and males help in all aspects of reproduction including nest-building, incubating, feeding and brooding the chicks, and defending the territory (Gullion 1953; Ryan & Dinsmore 1979). Coots defend their all-purpose territories throughout the entire reproductive cycle, and fights with neighbours and non-breeding intruders are frequent (Gullion 1953). The chicks are precocial (Nice 1962) and are able to follow the parents around the territory within a day of hatching. They are dependent on the parents for food for at least 10 days (Ryan & Dinsmore 1979; Desrochers & Ankney 1986; this study), but some chicks are fed until they are 30 or 40 days old. Chicks remain on the parental territory until they are about 50 days old and are attacked if they stray onto the territories of neighbouring pairs. From 1987 to 1989 all pairs were single-brooded, but in 1990, six of the 134 pairs (4%) attempted second broods after successfully raising their first brood. Nest predation was frequent on some wetlands and some females laid up to three replacement clutches.

Censusing Nests and Detecting Parasitism

I checked the vegetation every 1–2 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. On each visit I also recorded the number of adults defending the nest or on the territory and, when possible, sexed them by their calls (Gullion 1950). 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 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 criteria will detect parasitism depends on reproductive attributes of the species and on logistic details of the study (Frederick & Shields 1986), I also provide the following 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 & Shields 1986). Female coots normally laid an egg a day in a continuous sequence and skips during laying were rare. The average clutch size for this population was 8.1 eggs, and 91% of the females laid between six and 13 eggs. 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 second day (210 nests) during the laying and incubation periods.

Because laying skips were so rare, new eggs laid 2 or more days after clutch completion also indicated that parasitism had taken place. In a population of coots in Washington, Hill (1986) found a few cases of clutch overlap, where nesting females laid second clutches in their nests before the first clutch hatched. I recorded no cases of clutch overlap and all eggs laid after clutch completion were distinguishable from the hosts' eggs (see below).

Egg features like shape, spot colour and pattern, and background colour varied considerably among clutches but little within females' clutches (Fig. 1), as has been reported for numerous other species (Craig 1980; Fleischer 1985; Gibbons 1986; Møller 1987). 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. Using eggs from known clutches to assemble artificially 'parasitized' clutches, he found that 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 egg features and the timing of new

eggs to detect parasitism, I probably 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 also affect the ability to detect parasitism because instances in which new parasitic eggs were rejected before the nest was next censused 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 being buried and in 90% of the cases where the timing of burial could be accurately determined ($N=135$), the egg was in the host nest for at least 2 days before burial. In addition, eggs remained buried in the nesting material for at least a week before falling through the bottom of the nest. I regularly checked down in the nesting material to ensure that eggs had not been buried before their presence in the nest had been 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 in which 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 & Wrege 1986).

Identifying Parasitic Females

The striking variation among features of eggs laid by females (Fig. 1) 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 I could not be certain. These females were excluded from any analyses based on parasitic status. This

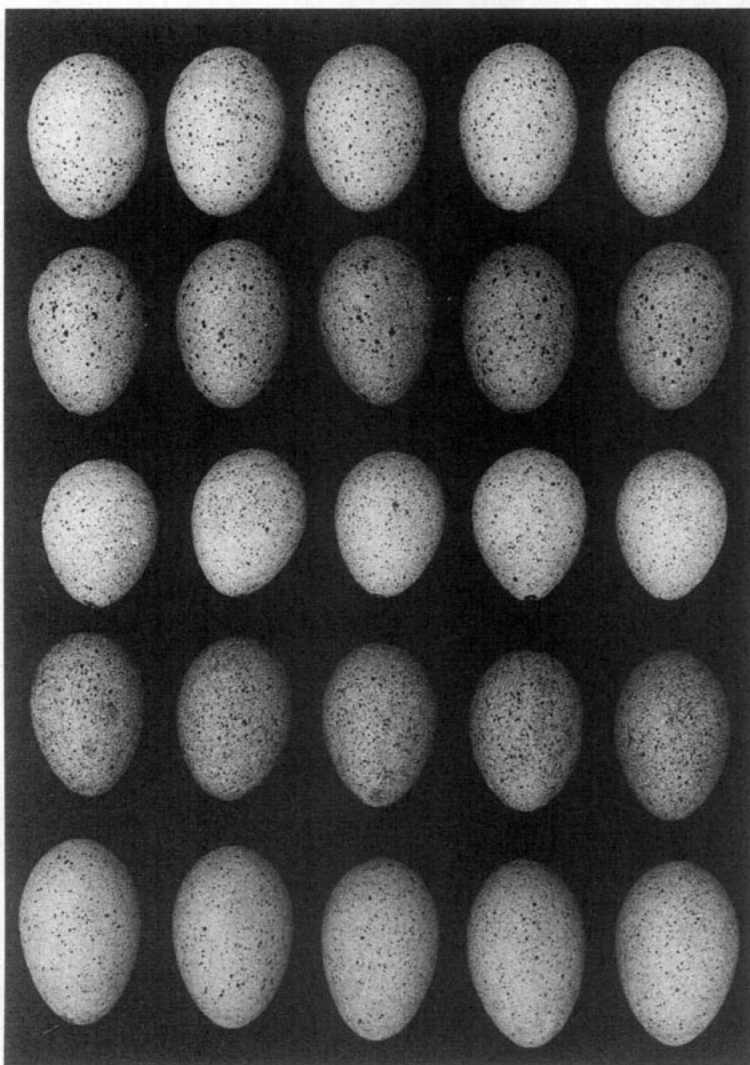


Figure 1. A photograph of eggs from five females, chosen from a pool of 20 females, illustrating the representative range of variation in egg features among females. Eggs in each row are from the same female.

may have resulted in a few parasitic females being excluded from the analysis but it also reduced the probability that non-parasites were mistakenly identified as parasites, a more serious problem given that there are fewer parasites than non-parasites (see below).

The ability to correctly identify parasitic females is central to this study. Elsewhere, I use discriminant function analysis to provide an objective, independent demonstration that the eggs of different females can be distinguished by their features (see Lyon, *in press*). When relevant biological restrictions are

applied to the analysis, the discriminant functions matched 32 of the 35 parasitic eggs (91.4%) in the sample to the 'correct' parasite (i.e. the female I had identified as the parasite in the field).

Estimating Components of Reproductive Success

Chicks in most host broods and in focal non-parasitized broods were marked at hatch with nape tags (Foley 1956) containing combinations of coloured seed beads, unique within each brood. Nests were normally checked once a day during the

Table I. Annual variation in the frequency of brood parasitism

Year	% Pairs parasitized	Range*	% Of all eggs parasitic	Number of pairs	Number of lakes
1987	23.1	0-42.9	5.1	65	8
1988	46.2	—	20.0	52	1
1989	45.6	41.8-58.8	11.5	160	4
1990	42.8	32.2-56.0	15.6	140	3
All years	41.2	23.1-58.8	12.7	417	16

*Range of percentages for individual wetlands.

hatch 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. Chicks were pip-marked by clipping the end of the middle claw on one foot and, at some nests, host chicks were marked, while at others, parasitic chicks were marked. I censused broods from mobile, floating blinds to determine which chicks survived, and at focal broods, the timing and causes of death. Chicks were considered independent, or 'fledged', if they were alive after 30 days because virtually no mortality occurred after 30 days. However, most broods were monitored well past this point. In a few cases parasitic eggs hatched but their subsequent fate could not be determined because the brood was not marked or because tags fell off. I assigned these chicks a fledging success equal to the proportion of hatched parasitic eggs that produced a fledged young on the same lake. This was preferable to omitting the eggs from the analysis because most parasitic eggs fail to hatch, and omitting these successfully hatched eggs would have underestimated the reproductive success accrued from parasitism.

Clutch sizes varied among sites and among years, so I compared the clutch sizes of parasites and non-parasites for each wetland within years separately. However, I pooled all the wetlands at Riske Creek because of their small populations. Clutch size declined with season at most sites and I used analysis of covariance to control for this source of variation where possible (i.e. when slopes for parasites and non-parasites did not differ), using the date females laid the first egg in their own nests as the covariate. For pairs that suffered nest predation before clutch completion, I used re-nest clutch size. In analyses where birds from among years were pooled, the day the first egg was laid in the

population each year was designated as day 0 and date is the number of days after day 0. There was considerable variation among sites in the reproductive success of nesting pairs and parasites and I did not obtain estimates for the success of parasitic eggs at all sites. Therefore, when comparing the success of floater parasites and nesting females, I included only nesting females from sites where I obtained estimates for the success of parasitic eggs. When comparing egg sizes, I used an index of egg volume; length (mm) times width² divided by 10⁴, and compared mean values for each female.

Adults were trapped and marked with neck collars at a single focal study site in each of 3 years: Jaimeson Meadow in 1988, and pond S5 in 1989 and 1990. The locations of territory borders and, therefore, the relative territory positions for each unique host-parasite combination, were also established at these focal study sites, but not at other sites. Statistical tests follow Siegel (1956) or Sokal & Rohlf (1981) and are two-tailed unless indicated otherwise. Wherever possible, I provide exact probabilities. Values presented with means are standard errors and William's correction was applied to all *G*-tests.

THE FREQUENCY AND CONTEXTS OF BROOD PARASITISM

Brood parasitism was common in all 4 years of the study (Table I). Overall, 41% of the 417 pairs observed received at least one parasitic egg, while frequencies for individual wetlands ranged from 0% to nearly 60% of pairs. In terms of eggs, 12.7% of all eggs during the study were laid parasitically, and values among years ranged from 5 to 20% of eggs (Table I). Host nests received from one to 17 parasitic eggs ($\bar{X} = 3.1 \pm 0.23$, $N = 166$) and were

Table II. The percentage of parasitic eggs laid by territorial nesting females and floater females at each wetland

Year	Lake/site	Total parasite eggs	% Parasite eggs by		
			Territorial females	Probably territorial females	Floater females
1987	Riske*	38	84.2	2.6	13.2
1988	Jaimeson	100	58.0	0	42.0
1989	Jaimeson	74	59.5	10.8	29.7
	S5	58	96.6	0	3.4
	Jones	50	72.0	0	28.0
	Kloe	37	70.3	5.4	24.3
1990	Jaimeson	107	57.9	5.6	36.5
	S5	66	75.8	13.6	10.6
	Kloe	61	49.2	13.1	37.7
All lakes/years		591	66.7	5.7	27.6

*Values for the eight wetlands were pooled because of low frequencies of parasitism.

parasitized by one to five parasites ($\bar{X} = 1.4 \pm 0.06$, $N = 161$). Ninety-three per cent of parasitic eggs ($N = 591$) were laid in active host nests; 19 of the remaining 39 eggs were laid by four females in a 'dump nest' on a muskrat mound and the other 20 eggs were laid in deserted nests, recently depredated nests, or on muskrat mounds.

I found no evidence that any nests where two or more females laid in the same nest were actually joint-nests. Like parasitism, joint-nests contain eggs from more than one female but, in contrast to parasitism, all of the females provide care for the eggs and young (Verencamp 1978; Brown 1987). Joint-nesting occurs in several Rallids (Garnett 1978; Craig 1980; Gibbons 1986), so it might be expected in coots. However, when checking nests or trapping and marking adults during incubation, or observing broods from floating blinds, I never encountered more than two resident adults on a territory, and pairs were invariably heterosexual pairs. Territories are small in this species (Lyon 1992) and the presence of more than two adults would have been immediately apparent. Moreover, 44% of the adults at the three focal study sites were trapped during incubation and marked with unique neck-collars and most of the remaining unmarked individuals could be distinguished by variation in their frontal shield markings (e.g. Gullion 1951). Thus, joint-nesting would have easily been detected

had it occurred. All nests with eggs from more than one female represent true cases of brood parasitism.

Two broad classes of parasites were identified; floater females without territories or nests of their own and nesting females that also laid eggs parasitically. Two-thirds of all parasitic eggs were attributed to paired, territorial females that had nests of their own (Table II). Another 6% of the eggs were suspected of having been laid by nesting females, based on egg characteristics, but I was not certain. In some of these cases visual confirmation of the parasite's identity was not possible because of nest destruction. The remaining 28% of parasitic eggs could not be attributed to any nesting female on the wetland, and I concluded that these were laid by floater females without nests or territories of their own during that season.

Although rates of parasitism were consistently high among years, there was considerable variation among lakes and ponds in the occurrence of parasitism by floater females (Table II). Some of this variation may be explained by the availability of roosting areas for floater females. Two of the wetlands, Jaimeson Meadow and Kloe Lake, contained small islands away from nesting territories and these were used as roosting sites by floaters. The proportion of parasitic eggs attributed to floaters on these lakes was significantly higher than at wetlands without such sites (Table II; each year

considered independent, Mann-Whitney $U=19$, $N=4,5$, one-tailed $P=0.025$).

WHY ARE FLOATER FEMALES PARASITIC?

Hypotheses

There are two hypotheses for the adaptive significance of parasitism by floater females.

Lifelong specialist parasites

Floater parasites could be specialist lifelong parasites that depend entirely on other females to raise their offspring, a within-species equivalent of a cuckoo (Yom Tov 1980; Andersson 1984). According to theory, specialist parasites would have a higher fitness than nesting females when specialists are rare in the population. However, because specialist parasites depend completely on nesting individuals to rear their offspring, negative frequency-dependent selection would stabilize the frequencies of nesting and parasitic females where both strategies yielded equal fitness (Andersson 1984). Assuming that a population is close to equilibrium, this hypothesis predicts that nesting females and parasites have equal fitness.

Parasitism as a conditional reproductive tactic

If a female were unable to establish a territory or nest of her own in a particular year, possibly due to her age, condition or fighting ability, then her only option for reproducing would be through parasitism. As a conditional 'best-of-a-bad-situation' type of tactic (Dawkins 1980), parasitism would be favoured, even though it yielded a lower payoff than nesting, because it permits fitness to be obtained that would otherwise not be possible. This hypothesis predicts that, within a breeding season, the reproductive success of floater parasites is lower than that of territorial nesting females. To distinguish between this hypothesis, and the previous one, I compare the annual reproductive success of floater parasites and nesting individuals, where nesting individuals include both parasitic and non-parasitic nesting females.

Reproductive Success of Floater Versus Parental Females

I used an indirect method to estimate the annual reproductive success of floaters because I was not

always certain which floater eggs were laid by the same females. I calculated the average number of eggs laid by floater females whose 'clutch sizes' were accurately known, due to their distinctive eggs, and multiplied this by the average success of all floater female eggs (Table III). The reproductive success of floater parasites was dramatically lower than that of territorial, nesting females in all 3 years for which estimates were available, and on average, was a mere 6% of the reproductive success of nesting females (Table III).

To obtain a statistical comparison of floater parasites and nesting female reproductive success, I used a second method to calculate the reproductive success of individual floater females. Simply calculating the reproductive success of floater females included in Table III would grossly underestimate the average reproductive success of floaters because four of the five successful floater parasites were not included in the clutch-size estimates in Table III. I therefore calculated the reproductive success of the individual females included in Table III, plus all other successful floaters (four females). This method provides a conservative test because it excludes an unknown number of females that were completely unsuccessful, and therefore slightly inflates the average reproductive success of floaters: 0.21 young per female ($N=22$) versus the estimated 0.17 young per female in Table III. None the less, the reproductive success of floaters differed significantly from the reproductive success of nesting females (Table III; Mann-Whitney U -test, $z=4.83$, $N=22, 185$, $P<0.001$). Tests done for each year separately were also significant. This finding clearly rejects the specialist parasite hypothesis and indicates that parasitism by floaters is a conditional, best-of-a-bad-situation reproductive tactic.

The difference in the reproductive success of floater and nesting females was partially due to floater females' lower fecundity, but was mainly due to the poor success of their eggs. Only 3.6% of floater eggs produced fledged young, which is only 12% the success of parental eggs (31% success; $N=1701$ eggs). Two mortality factors were responsible for this low success. First, egg rejection was a common anti-parasitic behaviour used by hosts and 38% of the 163 floater parasitic eggs were rejected. Second, most of the parasitic eggs from floaters were laid late in the host's laying sequence, or after clutch completion, and either failed to hatch or died shortly after hatch due to age-dependent brood reduction (see below).

Table III. The reproductive success (RS) of parasitic floater females and nesting, territorial females

Year	Floater parasites			Nesting female RS†	RS floater/ nesting female	Floater clutch size for equal fitness§
	Eggs/ female	Proportion eggs fledged*	Estimated RS†			
1988	5.4 (5)	0.024 (42)	0.12	1.79 ± 0.29 (43)	6.7%	75
1989	3.6 (9)	0.047 (47)	0.18	2.97 ± 0.21 (115)	6.1%	63
1990	6.0 (4)	0.034 (39)	0.20	3.74 ± 0.61 (27)	5.3%	110
All years	4.6 (18)	0.036 (128)	0.17	2.81 ± 0.18 (185)	6.0%	78

Sample sizes in parentheses denote number of eggs for floater female egg success and number of females for both floater female clutch size and nesting female reproductive success.

*The total number of chicks used in calculating proportion fledged was not always an integer because some individual eggs were assigned survival probabilities.

†Calculated as the product of the average clutch size of floaters and the proportion of all floater eggs that produced fledged young.

‡ $\bar{X} \pm \text{SE}$, includes both parasitic and non-parasitic nesting females.

§Clutch size required for floaters to have a reproductive success equal to nesting females, given the observed egg success of floaters.

Floater parasites differed from nesting females in two attributes that suggest that they were younger or in poorer condition than nesting females. Floater females laid their first eggs significantly later in the season than nesting females, including both parasitic and non-parasitic nesting females (first egg date for floater females 27.7 ± 2.59 versus 17.6 ± 0.49 for nesting females (Mann-Whitney *U*-test, $z = 3.87$, $N = 18, 401$, respectively, $P < 0.001$). The eggs laid by floater parasites were also smaller than those laid by nesting females (both parasitically and in their own nest); egg volume indices for floater females: 5.19 ± 0.10 ($N = 17$ females) versus 5.55 ± 0.04 ($N = 120$ females), $t = 3.08$, $df = 135$, $P = 0.003$.

WHY ARE NESTING FEMALES PARASITIC?

Hypotheses

Four hypotheses can explain the adaptive significance of parasitism by territorial, nesting females, and more specifically, why nesting females did not lay the parasitic eggs in their own nest. The first two hypotheses, nest loss and constraints on timing of breeding, assume a best-of-a-bad-situation

and that females would be better off nesting than laying parasitically, but are constrained from laying in their own nests. The last two hypotheses, spreading the risk of predation and mixed reproductive strategy, assume that females have a choice of whether to lay in their own nests or lay parasitically, but that they do better by laying parasitically.

Nest loss

Yom Tov (1980) suggested that parasites could be nesting females who lose their nests during laying and have eggs ready to lay but no nest to lay them in. Nest loss could force females to choose between wasting partially formed eggs or laying them in the nests of other females. If nest loss is the primary cause of parasitism by nesting females in a population, then most of the parasitism should be associated with specific cases of nest loss.

Constraints on nest initiation

Reproductive success declines with season in many species of birds (Klomp 1970) and females that delay their own nests to lay parasitically may incur a cost of delayed breeding. If the costs of delayed breeding exceed the benefits of parasitism, then parasitism would only be profitable for females that are unable to lay in their own nests

Table IV. The proportion of territorial, nesting females each year that also laid eggs parasitically

Year	Number of nesting females	Number of parasitic females	% Females parasitic	Number of wetlands	Range for individual wetlands
1987	66	13	19.7%	8	0-33%
1988	49	17	34.7%	1	—
1989	164	40	24.4%	4	15-30%
1990	134	38	28.4%	3	25-39%
All years	413	108	26.2%	16	0-39%

until later in the season due to some constraint like the condition of their mate or territory (Gibbons 1986). Since these females delay breeding for reasons other than parasitism, the costs of delayed nesting do not affect the net benefit they accrue from parasitism. Thus, parasitism allows females to obtain some reproductive success while they wait for conditions to improve, but without such constraints on nesting, nesting is superior to parasitism. This hypothesis predicts that the costs of delaying nesting are greater than the benefits accrued from parasitism.

Parasitism as a mixed reproductive strategy

Parasitism may allow females to bypass some of the constraints of parental care and increase their immediate or lifetime production of offspring (Yom Tov 1980; Møller 1987). If females lay more eggs than they can successfully rear in their own nests, due to parental care constraints, then laying these surplus eggs in the nests of other pairs would permit females to increase their total annual production of offspring. According to this hypothesis, parasitism should be associated with an increase in fecundity and/or other components of reproductive success. Furthermore, the brood size females raise in their own nest should be constrained by parental care rather than egg-laying capacity. Alternatively, laying parasitically may allow females to reduce their reproductive effort, live longer and thereby increase their lifetime reproductive success. This predicts that parasites have smaller clutch and brood sizes in their own nests, and that reducing brood size increases life span.

Spreading the risk of predation

Following Gillespie's (1977) demonstration that variance in the number of offspring produced can

have important fitness consequences, some authors suggested that parasitism could be favoured in the face of high nest predation because spreading eggs among several nests lowers the probability of complete reproductive failure for individual females (Payne 1977; Rubenstein 1982). Most studies of parasitism have not dealt with this hypothesis (but see Brown & Brown 1989), presumably because Bulmer (1984) demonstrated that the fitness benefits yielded by this type of risk-spreading are very small. It also has not been clear which predictions clearly distinguish this hypothesis from the previous one.

I suggest that if risk-spreading were the primary benefit to laying parasitically, then parasitism should be associated with a reduction in the variance of annual reproductive success, but not with an increase in the mean. Thus, parasites should lay the same number of eggs as non-parasites, but spread them among more than one nest. Finding that parasitism is associated with an increased mean reproductive success, or component of reproductive success, would reject the risk-spreading hypothesis. Additionally, because the benefits of risk-spreading are very small (Bulmer 1984), risk-spreading can be rejected if parasitic eggs do far worse than parental eggs. Otherwise, it would benefit females to lay the eggs in their own nests, all else being equal.

Parasitic Behaviour of Nesting Females

One quarter of all nesting females laid eggs parasitically (Table IV). Frequencies for individual wetlands ranged from 0% to nearly 40% of the nesting females (Table IV). On average these females laid 3.5 eggs parasitically ($N=98$ females), but extremes ranged from one to 20. Most females laid parasitically before initiating their own clutches. Of the 394 parasitic eggs laid by nesting females,

Table V. The frequency of nest loss during laying and its importance as a proximate cause of parasitism

Year	Total cases of parasitism	Parasitism after nest loss (% of total)	Total cases of nest loss	% Cases of nest loss leading to parasitism
1987	14	1 (7%)	3	33%
1988	17	0 (0%)	4	0%
1989	44	6 (14%)	35	17%
1990	40	0 (0%)	8	0%
All years	115	7 (6%)	50	14%

329 (84%) were laid before the parasite initiated her own clutch, 34 (9%) were laid at the same time the parasite laid her own clutch, and only three eggs (1%) were laid after the parasite completed the clutch in her own nest. An additional 28 eggs (7% of total) were laid after nest desertion or immediately following nest destruction. Thirty-seven of the 67 females (55%) whose exact dates of laying were known laid all of their parasitic eggs in a continuous sequence with their own eggs.

Nesting parasites were resident on their territories at least a week before they began to lay parasitically, and in some cases up to a month. In addition, the females that laid parasitically prior to laying eggs in their own nests were not forced to lay parasitically because they lacked their own nests. Many of the parasites had nest platforms of their own when they laid parasitically. Furthermore, observations of birds that re-nested immediately following nest predation indicate that most coots can build suitable nests in 1 day. Most females parasitized their immediate neighbours; 85% of 65 different host-parasite combinations (accounting for 83% of the parasitic eggs in these combinations) involved immediate neighbours. With respect to the hosts' breeding cycle, 55% of the parasitic eggs ($N=355$) laid by territorial parasites were laid during the hosts' laying periods.

Nest Loss and Reproductive Failure

I considered cases of parasitism to be a direct consequence of nest loss only if they occurred within 2 days of the nest loss. Because most coots can assemble new nests within a day of nest loss, females that were parasitic several days after losing their nest, but immediately prior to re-nesting, would have had plenty of time to build a new nest. For these females, parasitism was clearly associated

with re-nesting, not with nest loss. Six females laid parasitically in what were clearly two independent bouts (e.g. prior to first nests and re-nests); one bout of parasitism was associated with nest loss for three of these females. In the following analysis I counted each bout of parasitism by these six females as an independent case. Only 6% of the cases of parasitism were associated with nest loss (Table V). This result was not merely a consequence of the rarity of nest loss during laying. Overall, 50 females lost nests during laying but only 14% of these responded by laying parasitically (Table V). Clearly, nest loss does not play an important role in promoting brood parasitism in American coots.

Fecundity and Egg Success Trade-offs

The clutch size that parasites laid in their own nests did not differ from the clutch sizes of non-parasites at any of the wetlands (Fig. 2). However, parasites laid more total eggs than non-parasites, where total eggs is clutch size in own nest plus eggs laid parasitically. Mean total fecundity for parasites was significantly larger at all wetlands and the average increase in fecundity for parasites ranged from 2.1 to 4.7 eggs (Fig. 2). Taken together, these two comparisons show that parasites are not simply trading eggs among nests, but are producing extra eggs to lay parasitically. This observation is clearly inconsistent with the risk-spreading hypothesis.

The eggs that nesting females lay parasitically are, on average, only a quarter as successful as eggs they lay in their own nests (Table VI). As was the case with floaters, this difference is due mainly to mismatched timing by parasites and to egg rejection by hosts. I did not include the eggs of non-parasites in this comparison because only parasites are making the potential trade-off that parasitism

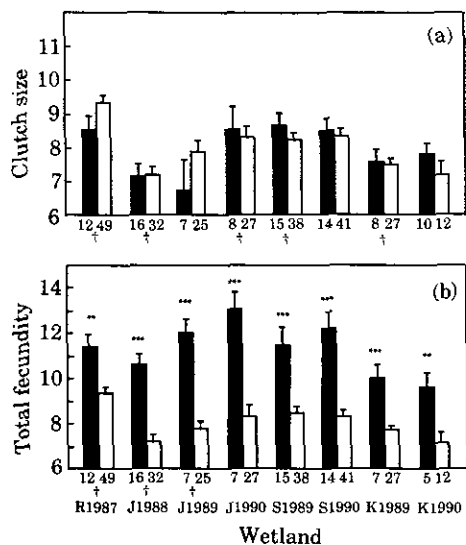


Figure 2. Fecundities of parasitic (■) and non-parasitic nesting females (□) for each wetland within years; (a) clutch size laid in own nest and (b) total fecundity of parasites (clutch size in own plus eggs laid parasitically) versus clutch sizes of non-parasites. Values are means \pm SE and significant differences are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Adjusted means are provided for comparisons using ANCOVA and are indicated with a †. Numbers below comparisons are sample sizes and wetland symbols are: R: Riske, J: Jaimeson, K: Kloe, S: S5.

entails, namely increased fecundity versus reduced egg success. However, non-parasites and parasites had very similar egg success in their own nests; 30% of non-parasitic eggs ($N = 1234$) produced independent offspring, whereas 33% of the egg parasites laid in their own nests produced independent offspring (Table VI; $G = 1.78$, $df = 1$, $P > 0.1$). Moreover, parasites and non-parasites did not differ in the number of chicks fledged from their own nests (excluding parasitic chicks from other females); 3.18 ± 0.29 chicks/pair for parasites ($N = 67$) versus 3.27 ± 0.20 chicks/pair for non-parasites ($N = 160$; $t = 0.25$, $P = 0.80$). Thus, parasitic females do not appear to be of poorer quality nor do they nest on poorer quality territories. In addition, parasitism is not associated with a reduced cost of reproduction, because parasites laid full-sized clutches in their own nests and subsequently fledged full-sized broods.

The four-fold reduction in the success of eggs laid parasitically provides additional evidence against risk-spreading as an explanation because the fitness costs associated with spreading eggs among nests

would far outweigh the small benefits that might be gained by reducing variance. However, the poor success of parasitic eggs does raise the question why do parasites not lay the extra eggs in their own nests, rather than parasitically? This can be answered only by understanding how parental care constrains the number of chicks a pair can raise in their own nest by focusing on the success of specific eggs rather than averages.

Constraints of Parental Care on Brood Size

Post-hatching parental care limits the number of young most pairs of coots can raise in their own nests. Chick mortality was pronounced in all years of the study, and most of the pairs that successfully hatched a clutch of eggs subsequently lost several young (Fig. 3). Only four of 156 pairs (2.6%) fledged all of the eggs in their clutch, and losses of 50% were common (Fig. 3). In nests that escaped predation and successfully hatched young, only 52% of the eggs produced independent young ($N = 1289$ eggs). Most of this mortality occurred after hatching, since only 7% of the eggs failed to hatch. Eggs that failed to hatch included eggs that disappeared, added eggs, or viable, late-laid eggs that were abandoned by their parents.

Several lines of evidence indicate that chick mortality was usually the result of brood loss through starvation rather than predation. Parent-offspring aggression over food allocation was common (unpublished data), suggesting that the food provided by parents was limited. Hatching asynchrony was extreme and the hatching spread at nests ranged from 3 to 9 days. The probability of a chick surviving to independence was correlated with its hatching position (Fig. 4; $r_s = 1.0$, $df = 4$, $P = 0.03$), as predicted by brood reduction theory (Lack 1947). The first five chicks to hatch in a brood were twice as likely to survive (62% of 178 chicks) as chicks that hatched sixth or later (31% of 90 chicks; $G = 22.8$, $df = 1$, $P < 0.001$).

Frequent censuses of 13 focal broods revealed that most chicks died in the first 10 days after hatching, the period when the chicks are most dependent on the adults for food. Seventy per cent of the chicks that died before independence died by the age of 10 days ($N = 34$ chicks whose age at death was known, excludes four chicks whose age at death was not accurately known). The bodies of 20 of the 38 chicks (53%) that died on focal territories were found intact, further ruling out predation, and

Table VI. The success of eggs that nesting females laid parasitically and in their own nests

Year	Success of parasitic eggs*	Success of eggs in own nest*	Relative success parasite/parental
1988	0.017 (58)	0.286 (77)	6.0%
1989	0.080 (157)	0.319 (260)	25.1%
1990	0.176 (53)	0.420 (81)	41.9%
All years	0.086 (268)	0.333 (418)	25.7%

Sample sizes in parentheses denote numbers of eggs.

*Success is measured as the proportion of eggs producing fledged young. For parasitic eggs, the total number of surviving chicks used to calculate success was not always an integer because some individual eggs were assigned survival probabilities.

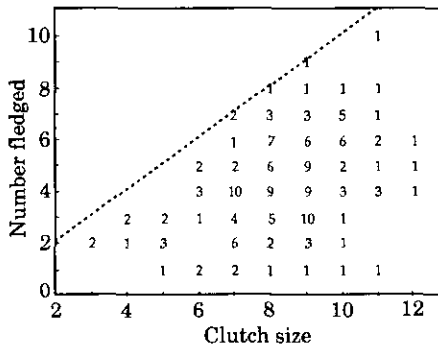


Figure 3. Fledging success as a function of clutch size. Numbers are the number of pairs with each clutch size–number fledged combination. The broken line indicates the number of chicks that would have fledged for each clutch size with no mortality.

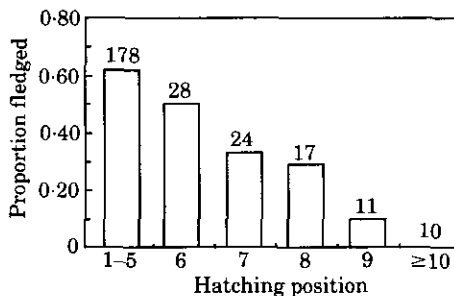


Figure 4. The probability that chicks survived to fledging as a function of their position in the hatching sequence. Numbers above bars are total numbers of chicks hatched.

even more would probably have been found with more frequent surveys. In addition, all 15 dead chicks that were weighed and could be accurately aged at death were lighter than the mass predicted from a regression of mass on age for live chicks (sign test, $P < 0.001$, predicted mass was based on 140 mass measurements of 35 live chicks). On average, chicks that died were only 56% of the mass predicted for their age (range = 29.4–95.1%, first quartile 38.0%, third quartile 77.2%).

Although parental aggression towards chicks was common, I never observed the direct infanticide that Horsfall (1984) observed in European coots, *Fulica atra*, despite several hundred hours of brood observations and surveys from blinds. However, observations at two focal broods showed how parental aggression could result indirectly in starvation. Three small chicks that were aggressively shaken and pecked by their parents until they feigned death, ceased begging for food after the aggression and were found dead on their territories the following day. Nest chicks at non-focal territories suggest that this 'indirect' infanticide (Hrdy & Hausfater 1984) may be fairly common. Chicks that hatched late in the hatch sequence were often found dead in the nest 2–3 days after hatching, and many had peck marks and bruises on the tops of their heads.

These observations all provide strong evidence that death by starvation is the primary cause of post-hatch mortality in this population of coots. The prevalence of brood reduction and poor success of late-hatched eggs explains why females lay surplus egg parasitically, rather than in their own nests. However, the question remains as to whether

the benefits of parasitism exceed the costs of delaying nest initiation and, thus, whether parasitism profits only females that are waiting for conditions to improve before initiating their own nests.

Costs of Delayed Nesting Relative to the Benefits of Parasitism

To compare the benefits of parasitism with the costs of delayed nesting, I determined the rate at which chicks were gained or lost per day from parasitism and from delayed nesting (Gibbons 1986). There was a significant decline in the number of young fledged with date of clutch initiation, which suggests that there is a cost of delaying nesting; (number fledged = $4.42 \text{ chicks} - 0.07 \text{ (chicks/day)} \times N \text{ days}$; $F = 16.7$, $N = 216$, $P < 0.001$). However, much of this decline could be due to differences in territory quality or individual quality, rather than the effects of season per se, because birds that nest late in the season may be poorer quality individuals or on poorer quality territories. Only decline due to season per se is relevant to the costs and benefits of parasitism.

To separate the effects of quality and season, the timing of breeding must be varied without altering the quality of the territory or individuals (Hochachka 1990). Nest predation provides a natural experiment to uncouple seasonal from quality effects because it forces birds to nest later than the date determined by territory and or bird quality (i.e. date of first nest initiation). To determine the gain or loss of chicks due to seasonal effects per se, I compared the observed number of young fledged by pairs that were forced to nest later in the season, due to nest predation, with the number of fledglings predicted for them had their first nesting attempt been successful. To predict the number of fledglings that these pairs would have had if their first nests had been successful, I used regressions of the number of chicks fledged on date of first nest initiation. I included only birds that did not suffer nest predation, and ran separate regressions for each wetland within years. Dividing the difference between the observed and predicted number of fledged chicks by the number of days between initiation of the first and second nests yields an estimate for the rate of gain or loss of chicks for each day nesting was delayed for each pair. The average rate at which chicks were gained or lost per day of delayed nesting did not differ significantly from zero (Fig. 5; $0.043 \pm 0.03 \text{ chicks/day}$,

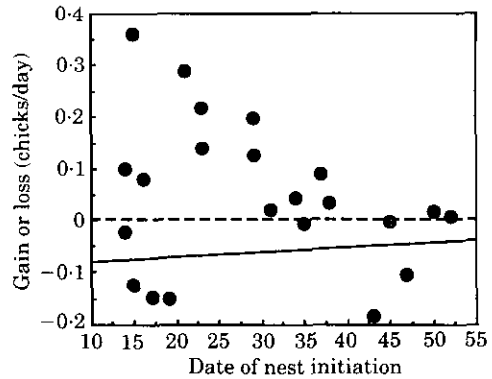


Figure 5. The costs of parasitism (●), i.e. delayed nesting costs, relative to the benefits of parasitism, both in terms of the rate of gain or loss of chicks per day. Multiplying the regression equation for the benefits of parasitism by -1 yields the threshold (solid line) below which the costs of delayed nesting exceed the benefits of parasitism. The broken line designates zero cost or benefit. Date is the date on which pairs initiated their replacement clutches.

one sample t -test, $t = 1.43$, $df = 21$, $P = 0.16$). In addition, there was no clear seasonal pattern to the rate of gain or loss of chicks (Fig. 5; $r_s = -0.21$, $df = 20$, $P = 0.33$), although early in the season most 'delays' yielded a gain in chicks rather than a loss.

To determine the benefits of parasitism, in terms of the rate at which chicks were produced per day, I multiplied the rate at which each female laid parasitic eggs times the overall average success of parasitic eggs laid by nesting females. The benefits of parasitism decreased with season because later nesting females laid parasitic eggs at a lower rate; chicks/day from parasitism = $0.091 - 0.001 \text{ date}$, $F = 11.27$, $N = 67$, $P = 0.001$. Multiplying this benefit regression by -1 indicates the threshold below which the costs of delaying nesting to lay parasitically would exceed the benefits accrued from parasitism (Fig. 5, solid line). Seventeen of the 22 'cost of delay' estimates lie above this threshold (Fig. 5; one-tailed binomial $P = 0.008$), indicating that the costs of delayed nesting do not exceed the benefits of parasitism. Thus, parasitism is not a best-of-a-bad-situation tactic adopted by females that are waiting for conditions to improve before they initiate their own nests.

DISCUSSION

Brood parasitism is an important component of reproduction for female American coots in central

British Columbia and it was common in all years and at all sites. Some of the parasitism was attributed to floater females without territories or nests of their own that resorted to parasitism as an alternative to not breeding at all. A few females laid parasitically after their own partially complete clutches were destroyed during laying. However, most parasitism was attributed to nesting females that used parasitism to bypass the constraints of parental care and increase their total production of offspring. Female coots thus parasitized in a variety of ecological contexts, each involving a different set of constraints and trade-offs. As an alternative reproductive behaviour, parasitism allows for flexibility in responding to ecological and social constraints, and thus yields additional reproductive success that would otherwise not be possible. Such adaptive plasticity in behavioural and physiological traits is usually associated with organisms that encounter extreme environmental variability (Herre 1987 and references therein), but it is clear from this study that reproductive and social constraints can also favour behavioural plasticity.

A few other studies have also documented that parasitism occurs in more than one ecological context in a population (Clawson et al. 1979; Heusmann et al. 1980; Eadie 1989; Sorenson 1991). However, none of these were able to distinguish between floater and nesting females as the source of parasitic eggs, and were forced to use fitness estimates for all forms of parasitism combined when testing hypotheses. One of the strengths of this study is that I was able to identify parasitic eggs laid in these two contexts and thereby test context-specific hypotheses with the appropriate fitness estimates. The importance of analysing the costs and benefits for each context separately is underscored by my observation that the benefit per egg for floaters (0.036 chicks/egg; Table III) was less than half that for parasitic nesting females (0.086 chicks/egg; Table VI). In some cases, differences in fitness estimates of this magnitude could potentially alter conclusions about the adaptive basis of parasitism, especially where the fitness costs and benefits of parasitism are almost equal (e.g. Gibbons 1986).

Parasitism by Floater Females

Roughly a quarter of the parasitic eggs were attributed to females without nests of their own in a season. I rejected the hypothesis that floater parasites are specialist lifelong parasites. Similarly, no

other study to date has found evidence that such specialists exist (Clawson et al. 1979; Heusmann et al. 1980; Gibbons 1986; Møller 1987; Eadie 1989; Sorenson 1991). My rejection of the specialist-parasite hypothesis was based on a somewhat crude test, a comparison of the annual reproductive success of floater parasites and nesting females. Ideally, one should compare the lifetime reproductive success of individuals because parasites might live longer by avoiding some of the costs of reproduction (Williams 1966; Yom Tov 1980). The experimental evidence for a survival cost of reproduction in birds is mixed (e.g. Askenmo 1979; Reid 1987; Gustafsson & Sutherland 1988; Nur 1988), but even if floater parasites gained a moderate survival advantage, this would not compensate for their 16-fold lower reproductive success.

Another factor that could have biased the comparison of floaters and nesting females was my estimate of the annual fecundity of floaters. I cannot rule out the possibility that floaters moved among wetlands and, as a result, that I underestimated their annual fecundity. Following Yom Tov (1980) I calculated the number of eggs a floater female would have to lay to obtain the same reproductive success as parental females (Table III). On average a floater would have to lay 78 eggs per season. However, host nests are available for successful parasitism for an average of only 59 days each season so even a phenomenally fecund parasite that laid an egg a day for the entire season would still not achieve a reproductive success equal to nesting females.

It is clear that parasitism by floater females is an inferior option to nesting, but it does permit females that are unable to establish their own nests to produce some offspring. Why would females be prevented from breeding, or choose not to breed? Nest-site limitation appears to be an important constraint in several species (Jones & Leopold 1967; Evans 1988; Eadie 1989; Lank et al. 1989; Gowaty & Bridges 1991). Alternatively, young birds or females in poor condition might actually choose not to breed, even though opportunities are available, because the prospects for success are outweighed by the costs of breeding (Curio 1983; Sorenson 1991).

Indirect evidence suggests that territory saturation played an important role in preventing many female coots from establishing territories and nests of their own. Fights between territorial owners

were intense and frequent throughout the breeding season. All suitable breeding sites were occupied, including ones in marginal habitats where the probability of success was low. Territory vacancies, created by predation on adults by northern harriers, *Circus cyaneus*, or desertion following egg destruction, demonstrated that many of the non-breeding females would breed if given the opportunity. Twelve of the 13 vacancies that occurred during the window of nest initiation in the population were quickly filled by replacement pairs and one was taken over by a neighbouring pair. This observation also indicates that there were also non-breeding males, ruling out the possibility that floater females were limited by a shortage of males. In fact, in a Manitoba population of coots, most floaters were males (Alisauskas 1987).

The observation that floater females began to lay eggs later in the season than nesting females, and laid smaller eggs, suggests that many floaters were young females because Crawford (1980) found that yearling female coots laid smaller eggs and began laying later in the season than older females. Moreover, most floater females in that population were 1-year-old birds (Crawford 1980). These observations are consistent with the idea that territory limitation prevents many birds from breeding because young birds are likely to be inferior competitors.

The Role of Nest Loss

Only a small fraction of the parasitism in this study was associated with nest loss. Traditionally, nest loss has been considered an important proximate cause of parasitism in avian populations (Yom Tov 1980), and Hamilton & Orians (1965) suggested that it may have been a critical factor in the evolution of interspecific brood parasitism. However, almost all studies that have been able to examine the proximate causes of parasitism have concluded that nest loss is unimportant (Brown 1984; Gibbons 1986; Møller 1987; Eadie 1989; Stouffer & Power 1991; Sorenson 1991). Emlen & Wrege (1986) found that nesting disruption was important but nest loss per se was not. These studies either indicate that nest loss itself is rare or that females have better options than parasitism to resort to when their nests are destroyed. For coots, the latter appears to apply. Nest loss during laying was common, but only 14% of cases led to parasitism. Most females responded to the destruction of their clutches by re-nesting, usually without

missing a day in their laying sequence. As indeterminate egg-layers, female coots are able to re-nest immediately without suffering a large decrease in clutch size (Arnold 1990; this study).

Parasitism as a Mixed Reproductive Strategy

Most of the parasitism in this study involved nesting females that also laid eggs parasitically. When I used the observed seasonal decline in reproductive success to estimate the costs of parasitism, in terms of delayed nesting, the costs of delay were similar in magnitude to the benefits derived from parasitism. However, once I controlled for the influence of territory and/or individual quality, the apparent costs of delay disappeared and the benefits of parasitism exceeded the costs. Thus, parasitism by nesting female coots is not a best-of-bad-situation tactic adopted by females that are waiting for breeding conditions to improve.

This difference in cost estimates from the observed seasonal pattern and from the 'natural experiment' based on nest predation underscores the importance of controlling for the influence of quality differences among individuals and territories when assessing the costs of parasitism by nesting females. For example, Gibbons (1986) used an observed seasonal decline in reproductive success to demonstrate that the cost of delaying nesting to lay parasitically exceeded the benefits of parasitism for female moorhens, *Gallinula chloropus*. Based on this, Gibbons suggested that parasites might have been females that were unable to lay in their own nests due to their mate's poor condition. However, quality differences among individuals or territories could have produced much of the observed seasonal decline in reproductive success. In fact, in a subsequent paper Gibbons (1989) showed that early nesting pairs had more breeding experience, larger territories and heavier males, indicating that variation in territory and bird quality probably does account for some of the seasonal decline in reproductive success. It is possible that once the effects of quality are properly controlled, that the benefits of parasitism will be found to exceed the costs, and that a different explanation will be required to account for parasitism in moorhens.

I also found no support for the idea that parasitism is primarily a risk-spreading behaviour in coots. Eggs laid parasitically suffered a four-fold reduction in success relative to parental eggs, a cost that

would far outweigh the meagre benefits derived from risk-spreading (Bulmer 1984). Most convincing was the observation that parasites were not simply spreading their eggs among more nests, but produced extra eggs to lay parasitically. However, increased fecundity provides only a partial explanation for parasitism because it does not explain why parasites do not lay the extra eggs in their own nests. A clear understanding of the factors that limit the number of young that a female can raise in her own nest is crucial for a complete understanding of brood parasitism.

Post-hatching parental care constrains the number of offspring that a pair of coots can raise in their own nest. Virtually all pairs were unable to raise all of their eggs through to fledging and many pairs lost a substantial proportion of their brood. Intensive observations of focal broods demonstrated that most post-hatching mortality was due to starvation, rather than predation. Given the limitations of post-hatching parental care it would have made little sense for females to lay additional eggs in their own nest. Laying eggs parasitically allows females to bypass the constraints of parental care and increase their total production of offspring.

The average number of young gained through parasitism can be estimated by multiplying the average number of eggs laid parasitically (3.5 eggs/female) by the average success of parasitic eggs (0.086 chicks/egg), 0.30 additional chicks per parasitic female. Since parasites raise an average of 3.18 chicks in their own nests, parasitism yields a 9.5% increase in reproductive success. The widespread starvation of chicks provides strong indirect evidence that these parasitic eggs would have been unsuccessful had the parasites laid them in their own nests. More direct evidence for this claim could be obtained by experimentally increasing the clutch sizes in parasites' own nests by the number of eggs they lay parasitically, and comparing the success of the experimental and parasitic eggs.

A reproductive strategy that combines opportunistic parasitism with regular nesting has been referred to as a mixed reproductive strategy (Møller 1987; Lank et al. 1989) by analogy with the mixed reproductive strategies of males (Trivers 1972). Although there are obvious differences between the mixed strategies of males and females, both permit individuals to increase their production of offspring by parasitizing the parental care of others. Females adopting mixed strategies have been reported for several other species as well

(Clawson et al. 1979; Heusmann et al. 1980; Gibbons 1986; Møller 1987; Eadie 1989; Brown & Brown 1991; Sorenson 1991), and interpretations of the adaptive basis of this form of parasitism have varied. Møller (1987) showed that parasitic female swallows, *Hirundo rustica*, fledged more total young than non-parasites. Presumably parental care constrains the number of young that can be raised in a female's own nest, but this was not investigated. For cliff swallows, *Hirundo pyrrhonota*, Brown & Brown (1989) concluded parasitism was favoured because it spread the risk of reproductive failure resulting from nest destruction and ectoparasite infestations. However, given the slight fitness benefits derived from this sort of spatial risk-spreading (Bulmer 1984), other explanations likely account for parasitism in this species (e.g. Davies 1988).

It is harder to understand why precocial birds like ducks employ a mixed strategy (Clawson et al. 1979; Heusmann et al. 1980; Eadie 1989; Sorenson 1991) because clutch sizes in waterfowl are thought to be limited by egg-laying capacity, rather than post-laying care (Lack 1968). Sorenson's findings provide one possible answer. He found that parasitic redhead ducks, *Aythya americana*, employed a 'dual' strategy of laying a first clutch of eggs parasitically, and following a lag, laying a second clutch in their own nest. However, red-head ducks are primarily interspecific parasites (Sorenson 1991) and it remains to be seen if dual strategies occur in species that parasitize mainly conspecifics. Another possibility is that clutch sizes in some species of waterfowl are not constrained by egg-laying capacity as formerly thought (Arnold & Rohwer 1991). This issue is still unresolved, but investigating the factors that limit clutch and brood sizes in species of waterfowl with mixed strategists would be worthwhile.

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