

**ALTERNATIVE REPRODUCTIVE TACTICS IN A PRECOICIAL BIRD: THE
ECOLOGY AND EVOLUTION OF BROOD PARASITISM IN GOLDENEYES**

By

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ABSTRACT

Facultative brood parasitism is common among waterfowl (Anatidae), but we have limited understanding of the ecological or evolutionary basis for this behaviour. I studied facultative brood parasitism in two species of cavity-nesting ducks, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). During a four year study in central British Columbia, I used field experiments, observational studies of marked individuals, and simulation models to (i) examine the consequences of brood parasitism to hosts, and (ii) identify the factors that promote and maintain parasitic behaviour.

In order to assess the costs and benefits of brood parasitic behaviour, I first examined proximate influences on reproductive performance of goldeneye females. Variance in reproductive success among females was substantial and some females were consistently more successful than others. Reproductive success was also influenced by breeding experience, time of breeding, and by the availability and quality of nest-sites. Circumstantial evidence suggests that females compete exploitatively and aggressively for nest-sites and brood territories. I argue that such conditions favour the evolution of parasitic reproductive behaviours.

Parasitic egg-laying occurred frequently during the four years of this study; 35% of all nests were parasitized, while 17% of all eggs were parasitic. Parasitism had few deleterious effects on the reproductive success of hosts. On average, parasitized females produced as many of their own young as non-parasitized females, and there was no effect of parasitism on female survival or on the growth and survival of host young. Hatch success was reduced in some host nests when the frequency of parasitism was high, but such levels of parasitism were uncommon. These results suggest that the costs of brood parasitism to precocial hosts are low. My findings do not support recent speculations that hosts benefit from being parasitized.

Goldeneye females exhibited few defences against parasitic intrusions. Females were more likely to desert their nests when clutch sizes were extreme (i.e., > 16 eggs), but desertion rates did not differ significantly between parasitized and non-parasitized nests. I found no evidence

that hosts reduce the size of their own clutch when parasitized, contrary to Andersson & Eriksson's (1982) findings for common goldeneyes in Sweden. On some occasions, hosts removed eggs from their nests, but this appeared to be a response to damaged eggs, rather than a defence against parasitism. Finally, females with territories adjacent to their nest sites were parasitized as often as females with non-adjacent territories, indicating that site-specific territoriality in goldeneyes does not serve to guard nests from parasites.

I tested three hypotheses that have been proposed to explain parasitic behaviour. Brood parasites did not attempt to incubate clutches to which they had contributed, even when host females were experimentally removed from those nests. I therefore reject the hypothesis that brood parasitism is an inadvertent consequence of contests among females for the same nest site. In contrast, parasitic behaviour was more frequent in young females, and was strongly related to the availability of nest-sites. These results support the hypothesis that parasitic laying is a conditional strategy pursued by young females when nest-sites are limited. However, other evidence was consistent with the hypothesis that 'parasitic' and 'parental' behaviours are alternative tactics in a mixed strategy. Estimated lifetime reproductive success was nearly identical for the two groups of females, and the relative reproductive success of parasites was negatively frequency-dependent.

A simulation model incorporating the effects of both density-dependence and frequency-dependence resolved this paradox. The model revealed a density threshold below which frequency-dependence effects were negligible, but above which frequency-dependence played a prominent role. I show that results consistent with both hypotheses are possible when the effects of population density are included. Current theories for the evolution of alternative reproductive tactics focus primarily on the frequency-dependent components of fitness and ignore the effects of population density. My results indicate that density-dependence and frequency-dependence can interact in an unanticipated way to maintain alternative nesting tactics in goldeneyes.

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CHAPTER 1

GENERAL INTRODUCTION

Life history theory attempts to predict how individuals should allocate resources to the conflicting demands of growth, survival, and reproduction (Stearns 1976, 1977). Early life history models were based on the assumption that there is a single optimal reproductive strategy that all individuals in a population should pursue (e.g. Schaffer 1974, and review in Rubenstein 1980). Deviations from these presumed optima were regarded as chance anomalies, inevitable variability, or maladaptive aberrations of little evolutionary interest (Dunbar 1982). More recently, it has become apparent that individuals in the same population do not always follow the same reproductive strategy. For example, alternative reproductive behaviours have now been reported for a wide variety of organisms, including insects (Alcock et al. 1977, Brockmann et al. 1979, Eberhard 1982, O'Neill & Evans 1983), fishes (Constanz 1975, Gross & Charnov 1980, Gross 1982, 1985), amphibians (Emlen 1976, Perill et al. 1978, Howard 1984, Arak 1988), birds (van Rhijn 1983, Smith & Arcese 1989), and mammals (Clutton-Brock et al. 1979).

A central question that has arisen from these studies is: how are alternative strategies maintained in the same population? Gadgil (1972; Gadgil & Taylor 1975) provided the first explanation for the evolution of alternative mating behaviours. He suggested that alternative tactics are favoured when the investment in traits associated with competition for mates becomes so extreme that some individuals do equally well by pursuing alternative low-cost, low-benefit behaviours (e.g. sneaking). Gadgil's (1972) idea was based on the notion of frequency-dependence such that the relative fitness of a tactic declines as its frequency in the population increases. This was an important contribution because it emphasized that the success of an individual depends on the actions of other individuals in the population. Maynard Smith's (1976, 1982) concept of the evolutionarily stable strategy (ESS) embodied this idea explicitly, and the subsequent application of ESS theory to the study of alternative tactics led to a proliferation of both theoretical and empirical analyses (reviews in Davies 1982, Dunbar 1982, Austad 1984).

ESS theory has now become established as the central theoretical framework for research on alternative reproductive behaviours. However, there has been increasing debate over the utility of this approach (reviews in Austad 1984, Dominey 1984). It has proven extremely difficult, for example, to test the hypotheses posed by ESS theory for natural populations in the field. Most researchers have obtained only crude approximations of the fitness of alternative tactics, and little information is available on the flexibility of tactics within individuals. Few studies have experimentally modified environmental variables that might influence the frequency of alternative behaviours. Moreover, analyses of alternative reproductive behaviours have dealt almost exclusively with mating tactics of males on the grounds that selection for alternative tactics in females will be weak, given that the variance in reproductive success among females is generally low (Payne 1979, Hafernik & Garrison 1986). However, females of several species do vary in their ability to obtain resources necessary for reproduction, and this variation could lead to the evolution of alternative reproductive behaviours in females (Dunbar 1982, Wasser and Waterhouse 1983).

This thesis, then, has two goals: (1) to test rigorously the hypotheses posed by ESS theory to explain the occurrence and maintenance of alternative reproductive behaviours, and (2) to examine an alternative female reproductive behaviour, and thereby assess the generality of theories that have, until recently, been considered only for males. My research was conducted on two species of cavity-nesting ducks, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). Goldeneye females pursue two nesting tactics: parental females establish their own nests, incubate the clutch, and tend their young for up to two months after hatch; parasitic females lay eggs in the nests of other females and thereby abandon all subsequent care of those eggs and resulting offspring to the parasitized host. Brood parasitism occurs in several species of birds (Payne 1977a and see below), insects (Wilson 1975, Eberhard 1986, Tallamy 1985, 1986) and fishes (Sato 1986), but few studies have systematically quantified the costs and benefits of parasitism to both parasites and hosts.

Brood Parasitism in Birds

Approximately 200 species of birds are known to lay eggs in the nests of other birds (Payne 1977a, Yom-Tov 1980a, Eadie et al. 1988, Rohwer & Freeman 1989). Nearly half (87) of these species are obligate brood parasites that depend entirely on another species to rear their young. The remainder are facultative brood parasites, in which females breed by both parasitic and parental nesting. Obligate brood parasitism has evolved independently in four families of altricial birds, the Indicatoridae, Cuculidae, Ploceidae, and Emberizidae, whereas only a single precocial species, the black-headed duck (*Heteronetta atricapilla*), is an obligate brood parasite (Weller 1959, Payne 1977a). The pattern of facultative brood parasitism is the opposite. Facultative parasitism is rare in altricial birds (Payne 1977a), although intraspecific parasitism may be more common than previously suspected (Gowaty & Karlin 1984, Brown 1984, Moller 1987, Evans 1988). In contrast, facultative brood parasitism (within and between species) occurs frequently in precocial birds and has been recorded in 71 species of Anseriformes, 20 species of Galliformes, 6 species of Gruiformes, as well as several Charadriiformes (Weller 1959, Yom-Tov 1980a, Eadie et al. 1988, Rohwer & Freeman 1989). In at least 10 species of waterfowl, more than half of the nests in a single population may be parasitized (Jones & Leopold 1967, Joyner 1976, Clawson et al. 1979, Semel & Sherman 1986, Rohwer & Freeman 1989).

This pattern may reflect differences in the costs and benefits of parasitism to altricial and precocial birds. Altricial birds invest a large part of their reproductive effort into the care and feeding of dependent offspring (Lack 1968, Ricklefs 1974), and there would be considerable advantages to individuals that were able to parasitize the parental care of other individuals. The time and energy that would otherwise be expended in brood care could instead be channelled into increased fecundity or longevity. For example, parasitic cowbirds, cuckoos, and finches lay up to 7 times the number of eggs produced by non-parasitic relatives (Payne 1973, 1976, 1977b; Scott and Ankney 1980). Precocial birds, on the other hand, invest relatively more of their reproductive effort into eggs, and less into post-hatch care of young (Ar & Yom-Tov 1978). In some species of ducks, the young become independent soon after hatching (Andersson 1984). The advantages to avoiding brood rearing, via brood parasitism, would therefore be reduced.

Females might be better off caring for their own eggs and offspring, rather than risking this investment on another female.

Why, then, is facultative brood parasitism so common in precocial birds, and the Anseriformes in particular? I examined the phylogenetic distribution of parasitism in the North American Anatidae by mapping the frequency of facultative parasitism (from Eadie et al. 1988) on the phylogeny of the Anseriformes derived by Livezey (1986; Figure 1.1). This analysis suggests that parasitic behaviour is a primitive trait. Parasitism occurs throughout the Order and the behaviour is not constrained to any particular tribe or genus. Moreover, facultative parasitism has been recorded in all three of the sister groups of the Anseriformes; viz. Galliformes, Charadriiformes, and Ciconiformes (Rohwer & Freeman 1989). Parasitic behaviour probably arose in an ancestor of the Anseriformes and it is likely that all species in the Order are capable of laying eggs parasitically. Parasitic behaviour is not, however, equally common in all species of modern Anseriformes. For example, brood parasitism has not been reported in any of the North American swans (*Cygnus*), yet it is extremely common in the perching ducks (*Dendrocygna*), some of the diving ducks (*Aythya*), and some of the sea ducks (*Bucephala*, *Mergus*, and *Lophodytes*). There is considerable variation even within members of the same genus (e.g. *Anser*, *Anas*, *Aythya*). The Anseriformes are therefore well suited to a study of the social, ecological, and life history factors that influence the frequency of brood parasitic behaviour.

Although there have been several studies of facultative brood parasitism in waterfowl (reviews in Andersson 1984, Eadie et al. 1988), most share three shortcomings. (1) Research has focused almost exclusively on the consequences of parasitism to the host. Minimal information is available on the costs and benefits to the parasite, and even less is known about the identity of parasites or the flexibility of parasitic behaviour within and among individuals. (2) Because of the economic importance of waterfowl, studies of parasitism have been management-oriented. Researchers have been more concerned with the effects of parasitism on the net productivity of a local population, than with its effects on individual reproductive success. Such an approach offers little insight into the evolutionary basis for parasitic behaviour. (3) Most studies are

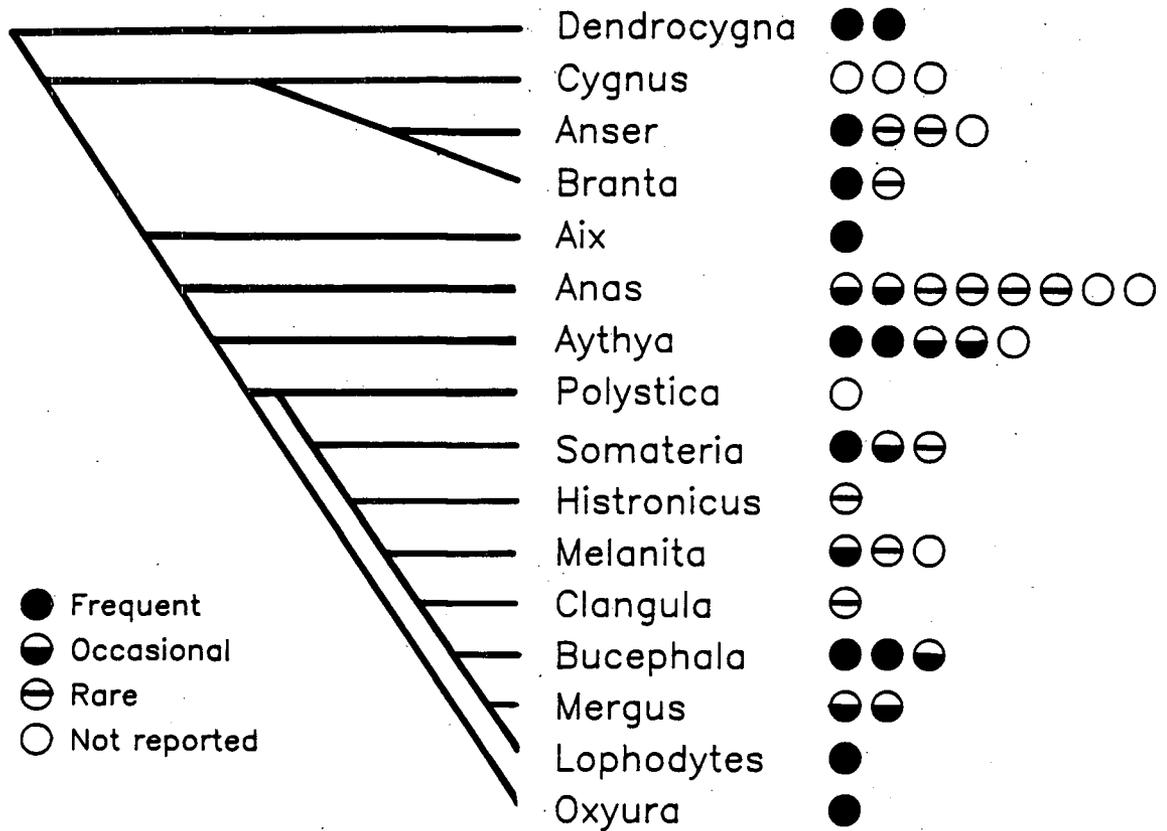


Figure 1.1. The phylogenetic distribution of brood parasitism in the North American Anseriformes. Each circle represents a species and the degree of shading indicates the frequency of brood parasitism. The phylogeny is based on Livezey's (1986) cladistic analysis, while the frequency of parasitism is determined from Eadie et al. (1988).

observational, rather than experimental. It is therefore difficult to reliably assess the costs and benefits of brood parasitism, particularly in cases of intraspecific parasitism where one cannot easily distinguish host and parasite eggs or offspring (see Andersson 1984 and Amat 1987).

Goals of the Thesis

This thesis investigates the adaptive significance of brood parasitic behaviour in goldeneyes with three specific objectives:

- (1) To determine the effects of brood parasitism on the reproductive success of host females;
- (2) To determine if hosts respond in an adaptive fashion to being parasitized; and
- (3) To determine the factors that promote parasitic egg-laying; specifically to test the hypotheses posed by ESS theory for the maintenance of alternative reproductive behaviours.

In Chapter 2, I provide an overview of the study system and describe the general research methods that apply to all following chapters. Several aspects of this study depend on the correct identification of parasitized nests and parasitic eggs. I therefore conducted an extensive evaluation of the criteria used to assess the frequency parasitism, and I present the results of that analysis in Appendix 1. Chapter 3 examines the factors that most influence reproductive success of goldeneye females. This chapter is largely descriptive, but it provides an important baseline for the studies that follow. For example, alternative reproductive behaviours are thought to be favoured under conditions of intense intrasexual competition and highly variable reproductive success (see above). In Chapter 3, I show that there is substantial individual variation in reproductive success of goldeneye females, and I discuss the potential role of intrasexual competition in generating this variance.

Chapter 4 focuses specifically on the effects of brood parasitism on the reproductive success of hosts. There is currently some debate over whether brood parasitism has a deleterious effect on the reproductive success of precocial hosts. I evaluate this directly by monitoring the success of naturally parasitized nests and by experimentally parasitizing goldeneye females. This chapter also provides insight into the factors that influence the success of parasitic eggs. Chapter 5 addresses the question of whether hosts respond in an adaptive fashion to being parasitized. I test

two hypotheses proposed by Andersson & Eriksson (1982) regarding nest desertion and clutch size adjustments, I test Gauthier's (1987) hypothesis on territoriality as a defence against parasitism, and I consider the possibility that hosts manipulate the number or position of parasitic eggs in their nests.

In Chapter 6, I test three hypotheses proposed to explain brood parasitism in waterfowl. I consider the reproductive success of both parasites and hosts, and I determine the influence of several ecological factors that might influence the frequency of brood parasitism. This chapter deals directly with the issue of the utility of ESS theory in studying alternative reproductive behaviours. In Chapter 7, I construct a simple simulation model to explore the interaction between density-dependent and frequency-dependent processes in maintaining parasitic egg-laying in a population. Finally, Chapter 8 provides a synthesis and general discussion of the main findings of this thesis, while Appendix 2 explores some ideas on the evolution of obligate brood parasitism.

CHAPTER 2

GENERAL METHODS

The Study Species

Barrow's goldeneyes and common goldeneyes are medium-sized sea ducks (Anatidae, Tribe Mergini). Common goldeneyes are abundant throughout much of the Palearctic and Nearctic region (Palmer 1976) whereas Barrow's goldeneyes are restricted to two discontinuous breeding populations: a small Atlantic population breeding in Iceland and Quebec, and a larger Pacific population, breeding primarily in B.C. and Alaska. Over 60% of the world's population of Barrow's goldeneyes breeds and winters in British Columbia (Savard 1987).

Goldeneyes winter on the coast or on large lakes in the interior. Pair formation takes place during the late winter or early spring and males follow the female back to her nesting area. Goldeneyes are secondary cavity-nesting birds, requiring large cavities such as those excavated by pileated woodpeckers. Females readily use nest boxes and most of the birds in this study nested in wooden nest boxes. Pairs arrive on the breeding area in early or mid-April and nesting begins within a week of their arrival, continuing until the beginning of June. Males in both species are territorial and defend a site-specific territory during the egg-laying period. Pairs spend most of their time on these territories. Females lay clutches of 7-9 eggs over a 2 week period, and then incubate the clutch for approximately 30 days. The male plays no role in incubation and brood care and generally deserts the hen during the first week of incubation. After hatching, the young leave the nest within 24-48 hours. The young are precocial and can feed and swim on their own as soon as they leave the nest. The female guards the brood for up to 4-8 weeks and in both species, females aggressively defend site-specific brood territories. Ducklings fledge at approximately 60 days of age.

I chose goldeneyes as a study species for two reasons. First, numerous anecdotal reports indicate that brood parasitism occurs frequently in goldeneyes (Erskine 1972, Bellrose 1976, Palmer 1976, Eriksson & Andersson 1982), making these birds a good candidate to study the

consequences and adaptive significance of this behaviour. Most previous studies of brood parasitism in precocial birds have focused on either the wood duck (*Aix sponsa*) or the redhead (*Aythya americana*). An attempt to examine the generality of the explanations proposed for facultative brood parasitism requires that we test these hypotheses for a variety of species. Second, goldeneyes are particularly well suited for field studies. Because females will use nest boxes, it is possible to conduct detailed studies on reproductive ecology with only minimal disturbance and with much reduced searching effort. This also permits experimental manipulation of factors such as nest site availability and population density. Females and broods are easy to capture and mark, individuals tolerate handling well, and the birds can be followed over the course of the full breeding season. Emergent vegetation was limited or absent on my study lakes and it was possible to accurately and repeatedly census and observe pairs, females and broods.

The Study Area

The study was conducted from 1984 to 1987 in the Cariboo parklands of British Columbia. The study area encompassed 28 ponds and lakes on two main sites: the 108 Mile area, near the village of 100 Mile House, and the 148 Mile area, near the town of Williams lake (Figure 2.1). The habitat in this area is parkland, comprised of open rangeland interspersed with stands of Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus cornuta*). The 108 Mile site consisted of 4 lakes (40-120 ha) and 7 large ponds (7-25 ha) while the 148 Mile area comprised 17 small to large ponds (1-30 ha). All of the lakes and ponds were permanent, although most were relatively shallow (usually less than 3 m). The lakes were alkaline with little emergent vegetation other than bulrush (*Scirpus acutus*) and cattail (*Typha latifolia*). Several of the smaller ponds had been created by Ducks Unlimited in the early 1970's.

Nest boxes were installed on the 108 Mile area in the early 1970's and a well established population was present when this research was initiated. Nest boxes were present on only one lake (Red Lake) on the 148 Mile area at the start of this study. I installed 100 additional nest boxes in 1984, although use of these boxes was limited until 1985 and 1986. The location of all nest boxes in the study area is shown in Figure 2.1.

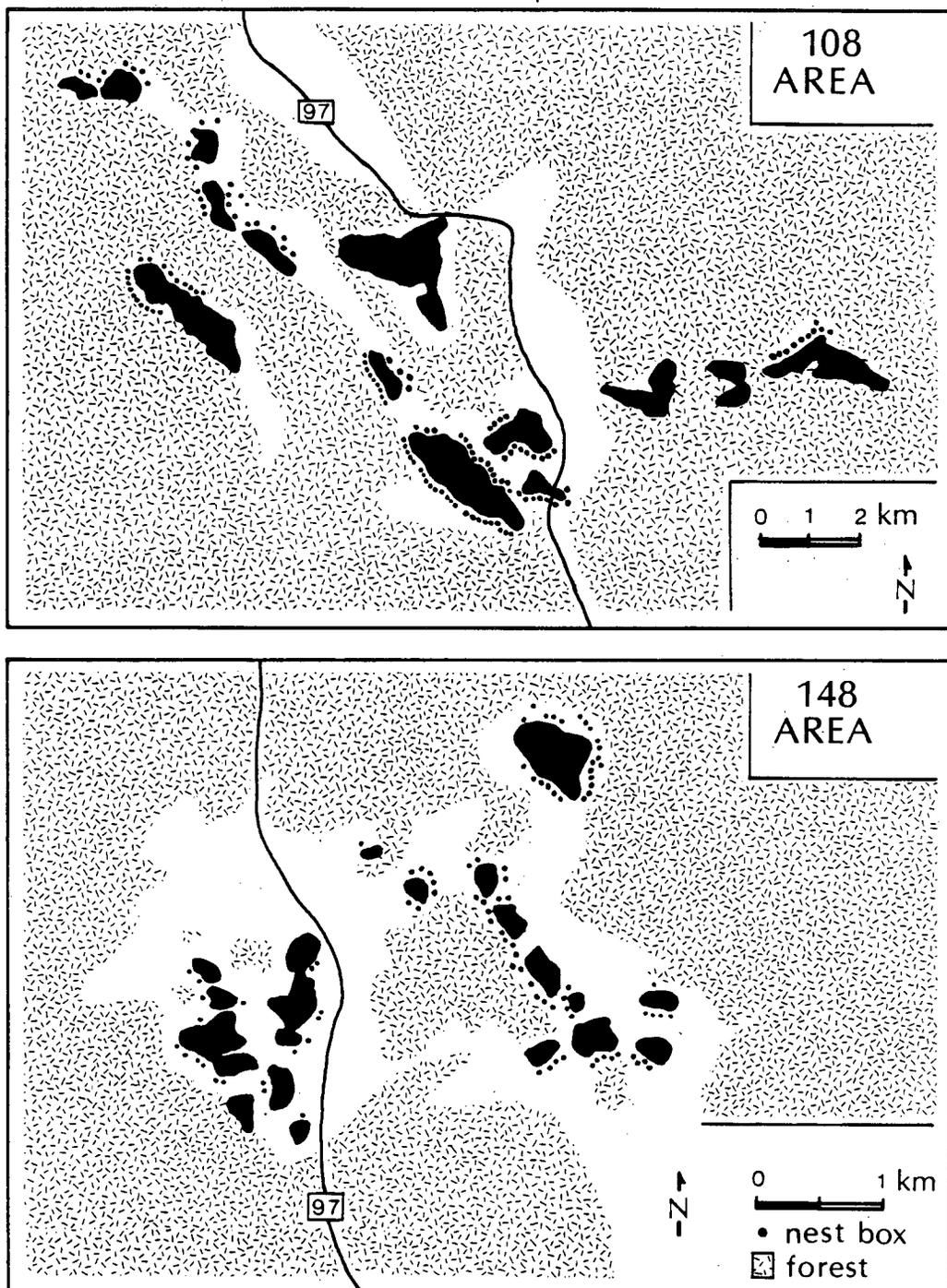


Figure 2.1. The 108 Mile and the 148 Mile study areas. Study lakes, nest boxes, major roads, and forested areas are indicated.

Both Barrow's goldeneyes and common goldeneyes nested on the 108 Mile area, whereas only Barrow's goldeneyes bred on the 148 Mile site. I studied both species, although Barrow's goldeneyes comprised the majority of all goldeneyes found nesting on the study area. All analyses were conducted separately for each species. It was occasionally difficult to identify the species since the females are very similar. I documented at least four cases of hybridization between the two species on the 108 study area and other instances were suspected. In most cases, females could be separated by weight, culmen length and the number of white secondary flight feathers (Eadie, in prep). It was more difficult to identify the eggs of each species although common goldeneye eggs are slightly smaller. I show in several of the following chapters that all aspects of reproductive success were nearly identical for both species. In some analyses, therefore, I pooled the results for the two species in the interest of brevity and to maximize sample sizes. Further rationalization for this pooling is presented in the relevant chapters.

Field Procedures

General Methods - Nest boxes and suitable natural cavities were censused every 4-7 days to locate active nests. Once located, nests were visited every day or every other day on most lakes in the 108 area, although 2 isolated lakes (Simon Lake and Lily Pad Lake) were followed less intensively. In 1984 and 1985, there were few nests on the 148 area, and I monitored those nests only 2-3 times to establish clutch size and hatch success. Eggs were individually numbered using permanent ink felt pens on or about the day they were laid. All eggs were measured (length and width) and weighed, and I noted the general colour and appearance of each egg. Clutches in a sample of nests were photographed against a standard background in 1986.

Females were trapped on the nest using an automatic nest trap or by blocking the entrance when the female was on the nest. Upon capture, all females were weighed, measured (culmen, wing, and tarsus length), and banded with Canadian Wildlife Service (CWS) metal leg bands and colour-coded leg bands. Most females were also fitted with colour-coded nasal saddles (Doty and Greenwood 1974) to permit identification of individuals from a distance.

Upon hatching, all young were weighed, measured, and web-tagged using monel fingerling tags (Haramis & Nice 1980). In 1985 and 1986, young in most nests were web-tagged in the egg at pipping (Alliston 1975) so that the fate of young from each egg was known. All ducklings were marked temporarily on one or both cheek patches with coloured waterproof felt pens so that the fate of the young could be followed after they left the nest. Ducklings in the same brood were marked with the same colour. Goldeneye broods leave the nest 24-48 hours after hatching and remain on the water, usually with the female, until fledging at 50-60 days. Broods often amalgamate after hatching (Eadie, in prep) and colour marking was necessary to identify and follow the fate of young from different nests. The colour marks were visible for 3-4 weeks, the period when most brood mixing occurs. Colour marking did not appear to affect the survival of the young or the behaviour of the female. I used colours that were muted or dark (dark red, blue, green, black) although even yellow marks did not seem to disturb the birds.

Most mortality of young occurs within the first two weeks after hatching, and young that survive past 21 days generally fledge (Savard 1986, pers. obs.). I conducted repeated surveys of broods on each lake to monitor survival of young (I did not survey Simon lake and Lily Pad lake on the 108 area and lakes on the 148 area were surveyed only in 1986). Ducklings were considered to have fledged if they survived for over 21 days, although I usually followed broods for much longer periods. When ducklings were 4-5 weeks old, I rounded up young by herding the brood with canoes into a floating trap. Upon capture, the webtag of each duckling was noted and I weighed, measured, and banded each young with numbered metal leg bands and coloured plastic bands. It was not always possible to capture all of the young in a brood and the identity of some of the surviving ducklings remained unknown. In all cases, however, the total number of survivors was known.

Measuring the Growth of Young - I measured the growth of young as the net gain in weight from hatching to the date of capture in brood drives (at 20-60 days of age). Growth of ducklings was linear over this range. Ducklings were sexed by the presence or absence of a phallus (Larson & Taber 1980) and I calculated linear regressions of weight on age for each sex separately. Residuals from these regressions were then calculated for each duckling. Because broods were

caught at different ages, all further analyses were based on these residuals. This analysis also effectively removes any effect of sex. There was no difference in residuals between the two species of goldeneyes over this period (Mann-Whitney U-test, $P > .20$, $N = 133$ Barrows goldeneye; 43 common goldeneyes), so data for both species were pooled.

Measuring Reproductive Success - I partitioned the reproductive success of females into 5 components:

- (1) clutch size (CS) - the number of egg laid,
- (2) hatch size (HS) - the number of young that hatched,
- (3) hatch success (pH) - the proportion of eggs that hatched,
- (4) fledge size (FS) - the number of young that survived to 21+ days, and
- (5) fledge or success (pF) - the proportion of hatched young that survived to 21+ days.

I also monitored the initiation date, hatch date, and the length of the incubation period for each nest and I tallied the proportion of nests in which at least one duckling left the nest (nest success). By partitioning reproductive success in this manner, it is possible to determine the stages of the nesting effort that are most influenced by brood parasitism or other social or ecological factors (see Howard 1979, Cooke and Rockwell 1988).

A large number of nests were deserted, many with only a single egg. Because I could not be sure that these nests represented true nest starts, I considered only nests with 3 or more eggs in estimating desertion rates. I analyzed clutch size only for nests where the clutch was incubated or hatched. Inclusion of all nests would bias clutch sizes since many nests with fewer than 5 eggs are deserted and it is not certain that these represent complete clutches. Hatch success and fledge success were analyzed only for successful nests (i.e. hatched) to avoid confounding desertion rates with hatching and fledging rates.

Sample sizes differ for each component of reproductive success for two reasons. First, different conditions were set for each component as outlined above (e.g. incubation rates were calculated for all true nest starts, clutch size was analyzed only for complete nests, and hatch success and fledge success were analyzed only for successful nests). Second, nests on more

isolated lakes were followed less intensively and I did not measure every component of reproductive success for each nest. This could bias my results if reproductive success differed on these isolated lakes, or if nests that were followed less intensively were a non-random sample of all nests. To control for such effects, I repeated all comparisons using only those lakes and nests where I had measured every component of reproductive success. The patterns were virtually identical to those based on the full sample of lakes and nests. Because sample sizes were considerably reduced in this second analysis, I present the results of the first analysis using all nests on all lakes.

Detailed analyses of reproductive success were conducted in the first 3 years of this study (1984 - 1986). In 1987, only limited field work was conducted, primarily to monitor rates of parasitism and return rates of females. Nests were simply scored as successful if some young hatched, or unsuccessful if young did not successfully leave the nest. Parasitized nests were identified by clutch size criteria and egg morphology since egg-laying rates were not monitored in detail (see below).

Identifying Parasitized Nests - I identified parasitized nests using 6 criteria: (1) more than one egg laid per day, (2) clutch size greater than 13 eggs, (3) evidence of 2 or more females laying eggs in the same nest, (4) eggs laid 2 or more days after the start of incubation, (5) distinct differences in the morphology or appearance of eggs, and (6) skips in egg-laying greater than 6 days, or more than 2 skips of 4+ days. These criteria have been used by several other authors (Clawson et al. 1979, Yom-Tov 1980a,b, Eriksson & Andersson 1982, Moller 1987) and I provide a detailed analysis of these criteria in Appendix 1 (see also Chapter 4).

Identifying Parasitic Females - Detailed nest observations were made on a number of parasitized nests to identify females involved in brood parasitism. I also used nest traps, automatic cameras and an automatic banding procedure to mark and/or identify females associated with a given nest. These procedures are described in Chapter 4.

Identifying Parasitic Eggs - I attempted to identify the eggs of the host and parasitic females using several methods (following Bertram 1979, Fleischer 1985, Gibbons 1986, Moller 1987).

First, I was often able to determine which female laid a given egg by nest trapping females during laying, or by direct observation of a female on the nest. Second, I inferred the identity of laying females by egg-laying patterns. Females are regular in their laying patterns, such that 1 egg is added approximately every other day. Eggs that were laid out of schedule were inferred to be laid by other females. Finally, it was often possible to separate eggs by differences in size, shape and/or colour (see Fetterolf & Blokpoel 1984, Fleischer 1985, Gibbons 1986, Moller 1987, Freeman 1988). To separate host and parasite eggs in parasitized nests, I conducted cluster analyses on all eggs in each nest (using complete linkage clustering on standardized values (z-scores) of egg length, width and weight). These procedures are described in Appendix 1.

Experimental Methods - I conducted several experiments to more fully document the consequences of brood parasitism to goldeneyes. Details of these experiments are given in the relevant chapters and I simply list the experiments here for completeness.

(1) Experimental parasitism - I experimentally parasitized goldeneye nests during the host's laying period to determine the effects of parasitism on the reproductive success of the host.

(2) Decoy egg nests - I constructed simulated nests containing goldeneye eggs or chicken eggs to determine whether females were attracted to nests containing eggs and to determine whether "deserted" nests were more likely to be parasitized.

(3) Nest box manipulations - The availability of nest sites was manipulated in two separate experiments. In the first experiment, I varied the number of nest boxes over time (4 years) on four large lakes in the 108 area. In the second experiment, I varied the number of nest boxes spatially on the 148 area according to two treatments: a high nest density treatment and a low nest density treatment.

(4) Female removal experiments - To determine whether putative parasitic females would incubate a nest into which they had laid eggs if given the opportunity to do so, I removed the host female at the end of egg-laying and monitored the response of the parasitic females. To control for disturbance effects, I conducted the reciprocal experiment in a second group of nests

by removing the parasitic female. The ovaries of all females removed were dissected and the number of post-ovulatory follicles and large developing follicles were counted (Payne 1966, Hannon 1981) to estimate the clutch size of parasitic and non-parasitic females.

(5) Nest predation experiments - This experiment tested the hypothesis that females lay eggs parasitically after their own nest is destroyed. Laying females were caught on the nest, injected with tetracycline, and released. I removed some or all of the eggs from the nest and followed any subsequent egg-laying by that female using a portable UV light to detect the characteristic fluorescence of tetracycline in newly laid eggs (Haramis et al. 1983, Eadie et al. 1987).

(6) Decoy female nests - To determine the response of goldeneye hens to the presence of another female, I placed a stuffed female goldeneye on or in a nest during egg-laying.

All statistical analyses follow Zar (1984), Sokal & Rohlf (1981) or Siegel (1956). Data were analysed using SPSSx, S, and SYSTAT programs. Probabilities are two-tailed unless otherwise indicated. Means \pm 1 standard error (SE) are presented throughout. In a few analyses, I considered the same lakes in different years as independent samples. I justify this approach by noting that, in the analyses concerned, the variation within lakes between years was equal to or greater than that between lakes. Nonetheless, I recognize that statistical inferences based on these samples are questionable, and I note in the text any analysis based on the pooled sample for all years. Where possible, I analyse each year separately.

CHAPTER 3

DETERMINANTS OF FEMALE REPRODUCTIVE SUCCESS IN GOLDENEYES

One goal of evolutionary ecology is to understand the form and intensity of natural selection operating on organisms in the wild. To address this goal, we need to (i) measure the survival and reproductive success of individuals under different environmental and social circumstances, (ii) determine whether variation in reproductive success and survival is due to phenotypic differences, or to stochastic or environmental variation, and (iii) determine the extent to which phenotypic differences are heritable (Clutton-Brock 1988). Because selection operates differently on each sex (Payne 1979, Howard 1983), it is important to separate male and female contributions to reproductive success. To do so, we ideally need to study organisms in which one sex provides little other than gametes. Many species of waterfowl (Anatidae) meet this criterion. In most ducks, females alone choose the nest site, incubate the eggs, and tend the young until they fledge. Males rarely defend resources needed by the female, and they provide little material investment other than sperm. In some species of Anatids, males guard females during the laying period. However, this behaviour may function only to protect the paternity of the male and little benefit may accrue to the female (Gauthier 1987). We can therefore assess the factors that limit reproductive success of females while minimizing the confounding contributions of males.

In this Chapter, I analyse reproductive success of females in two species of cavity-nesting ducks, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). I first quantify the variation in annual reproductive success among females, and estimate total reproductive success for females followed over the four years of this study. I then determine the factors that most influence female success. Previous studies have identified four factors with an almost ubiquitous influence on reproductive success in birds: (1) older birds tend to be more successful than young birds (Rockwell et al. 1983, Nol & Smith 1987); (2) birds that nest early in the season frequently have larger clutches, and fledge more young than birds that nest late (Birkhead et al. 1983, Cooke et al. 1984, Dow & Fredga 1984); (3) reproductive success is usually influenced by the quality of the nest site or breeding territory (Bengston 1972, Dow &

Fredga 1985); and (4) the ability to breed successfully often differs consistently among individuals, irrespective of other phenotypic or ecological factors (Raveling 1981, Dow & Fredga 1984). I investigate the influence of each of these factors on the reproductive success of female goldeneyes. Finally, I consider the role of intrasexual competition among females in contributing to the variance in reproductive success.

METHODS

Detailed descriptions of the study site and field methods are given in Chapter 2. I monitored the reproductive success of all females nesting on the study area in 1984-1986. Limited field work was carried out in 1987 and nests were simply scored as successful, if some young hatched and left the nest, or unsuccessful, if young did not successfully leave the nest.

I followed the success of 76 marked females over the four years of this study and so could estimate the total reproductive success of these individuals. These measures underestimate lifetime reproductive success to an unknown degree for several reasons. First, 12 females were still alive at the end of this study, and others may have bred in the year prior to the start of this study. Second, I had incomplete records on the number of young produced for six females, and so I use these females only in calculating average breeding lifespan. Third, I did not assess fledge success in 1987 and therefore use information from that year only to estimate average breeding lifespan.

Most goldeneyes do not breed until their second or third year (Bellrose 1976, Palmer 1976) and only a small number of young of known age had recruited by the end of the present study. To examine the influence of female age on reproductive success, I followed Dow & Fredga (1984) in computing breeding age as the number of years each female had bred. Females that had not been observed nesting in a previous year were assumed to be breeding for the first time. This assumption is reasonable because of the strong breeding philopatry shown by females (see below).

Facultative brood parasitism occurred frequently in the study population (Chapter 4). I identified the eggs of the host and parasitic females using methods described in detail in Appendix 1 (and see Chapter 4). I report values for each component of female reproductive success for both total clutch size and clutch size less parasitic eggs.

To determine whether some females were more successful than expected by chance, I compared the distribution of the number of offspring produced per female to a Poisson distribution. This analysis simply asks whether offspring are distributed among females in a random or clumped manner. The probability of a female producing X fledglings by chance is calculated as:

$$P(X) = \frac{e^{-\mu} \cdot \mu^x}{X!}$$

where μ is the mean number of fledglings per female in the study population. I also analysed breeding lifespan for each female using a similar procedure, although expected values were generated from a truncated Poisson distribution since I did not know the number of females that died before breeding (i.e. 0 years breeding).

I monitored the use of all nest boxes by goldeneyes between 1984-87, and tallied the number of nests that were successful. To determine if some nest sites were more likely to be consistently used or successful over the four years of the study, I compared the observed distributions of nest use and success to a binomial distribution (see also Dow & Fredga 1985). The probability that a nest is used or successful in X years (i.e. 0, 1, 2, 3, or 4) is calculated as:

$$P(X) = \frac{N!}{X! N-X!} \cdot p^X \cdot q^{N-X}$$

where N = the number of trials (= 4 years), p = the proportion of nest sites that are used or successful per year, and $q = 1 - p$.

To determine the influence of habitat on nest site use by goldeneyes, I measured the following variables at each nest site: nest height, vegetation cover (%) at 3 heights (ground, entrance height and 5 m), nest visibility (%), distance and direction to water, direction the box was facing, distance to nearest tree in each quadrant (0, 90, 180, and 270 °), stand size, stand

density, and stand type (dominant species), nest box type, and the tree species on which the box was erected. A principal components analysis did not substantially simplify the associations among these variables, so I consider only the original habitat variables.

RESULTS

Variation in Female Reproductive Success

There was considerable variation in the reproductive success (RS) of goldeneye females (Table 3.1). Analyses using each nest attempt as an independent sample revealed coefficients of variation of 9-153% for different components of reproductive success (Table 3.1). Standardized variances ($I = s^2/x^2$), ranged from 0.01 to 2.33. Much of the variation in RS was the result of nest failure. When I restricted the analysis to successful nests (those in which at least one young hatched), the variation was reduced considerably (Table 3.1). Still, substantial variation remained in the number and proportion of young that fledged.

Goldeneye females bred for an average of $1.8 \text{ years} \pm 0.1 \text{ SE}$ ($I = 0.22$), produced an average of 3.3 ± 0.3 young per year ($I = 0.71$), and produced a total of 5.4 ± 0.7 young over their lifetime ($I = 1.04$). Some females fledged no young while others produced 12 or more offspring. One particularly successful female fledged 29 young over a three year breeding lifespan.

Are Some Females Consistently More Successful?

There were insufficient numbers of mother-daughter pairs to estimate heritabilities for any component of reproductive success (*sensu* van Noordwijk et al. 1981, Gustafsson 1986). However, it was possible to determine repeatabilities for 26 females that bred in two or more years (following Lessells & Boag 1987). Repeatability estimates the upper limit of heritability (Falconer 1981). There were significant repeatabilities for three variables: laying date, clutch size, and the number of young that hatched (Table 3.2). Repeatabilities were low and not significant for the proportion of eggs that hatched, or the number and proportion of young that fledged.

Table 3.1. Components of reproductive success of female goldeneyes. For each variable, the mean, standard error, standardized variance (I), coefficient of variation, and range are shown.

		(N)	\bar{x}	SE	I	CV	Range
a) <u>All nests</u>							
Laying Date ^a		127	124.1	0.99	.008	9.0	96-152
		127	28.1	0.99	.138	32.7	0-56
Clutch Size:	Total	159	9.0	0.34	.235	48.5	1-28
	Own	151	6.7	0.23	.171	41.4	1-11
No. Hatch:	Total	159	5.6	0.41	.855	92.4	0-18
	Own	151	4.2	0.32	.858	91.9	0-11
No. Fledge:	Total	137	2.4	0.33	1.927	138.8	0-16
	Own	131	1.6	0.23	2.330	152.7	0-8
b) <u>Successful Nests</u>							
Laying Date ^a		80	121.1	1.18	.008	8.7	96-150
		80	25.1	1.18	.177	42.1	0-54
Clutch Size:	Total	95	10.6	0.32	.088	29.7	4-20
	Own	88	7.9	0.17	.038	19.5	4-11
No. Hatch:	Total	95	9.3	0.31	.106	32.6	2-18
	Own	88	7.2	0.22	.080	28.3	2-11
No. Fledge:	Total	73	4.5	0.43	.645	80.3	0-16
	Own	67	3.2	0.31	.624	79.0	0-8

^a The upper value is the observed laying date; the lower value is scaled so that the first nest date = 0.

Table 3.2. Repeatabilities of reproductive traits of goldeneye females. The table shows the mean squares among (MS_A) and within (MS_W) females, the repeatability (r), and the F-ratio (F) from analysis of variance.

	MS_A	MS_W	r^a	F^b
Laying Date	181.609	92.884	.341	1.96 *
Clutch Size	3.176	1.667	.329	1.91 *
No. Hatch	11.234	5.707	.344	1.97 *
Pn Hatch ^c	0.286	0.231	.114	1.24
No. Fledge	8.182	6.813	.098	1.20
Pn Fledge ^c	0.244	0.276	-.067	0.89

^a calculated using formulae in Lessells & Boag (1987); $n_o = 1.847$ in all cases

^b $df = 25, 23$ for all cases, * $P < .05$

^c arcsin square-root transformed

This analysis is restrictive since it includes only those females that live and breed for at least two years. Low quality females might survive poorly and would thus be missing from the sample. I therefore compared, for all females, the distribution of (i) breeding lifespan, (ii) number of young produced per year, and (iii) total number of young produced to that expected if reproductive success was distributed randomly among females (Figure 3.1). In this analysis, the distribution of breeding lifespan did not differ from random ($G_w = 3.8$, $df = 3$, $P > .30$; Figure 3.1a). However, the distributions of the number of young produced per year and the total number of young produced were different from random ($G_w = 21.4$, $df = 3$, $P < .001$; $G_w = 30.7$, $df = 3$, $P < .001$; Figure 3.1b and 3.1c, respectively). In both cases, some females were more successful and others less successful than expected by chance.

Total lifetime reproductive success was positively correlated with breeding lifespan ($r_s = .39$, $N = 70$, $P < .01$) and annual reproductive success ($r_s = .91$, $N = 70$, $P < .001$), but there was no relationship between these latter two variables ($r_s = .10$, $N = 70$, $P > .10$).

Comparisons Between Species

A potential confounding factor in the above analyses is that I consider two species simultaneously. This was necessary because I could not reliably distinguish between the eggs and offspring of Barrow's and common goldeneyes, nor I did not know the identity of the female for every nest (e.g. some deserted or failed nests). To determine if my analyses were influenced by this factor, I analysed RS separately for those nests in which the taxonomic status of the female was certain. The means for all measures of RS were very similar for the two species of goldeneyes (Mann-Whitney U-tests, all $P > .10$; Table 3.3). The same results were obtained when I excluded parasitic eggs (Table 3.3). Elsewhere, I show that the RS of each species was also similar when parasitized nests were compared to non-parasitized nests (Chapter 4).

Most other aspects of the reproductive ecology of the two species of goldeneye were similar and I was unable to find any differences save for male courtship behaviour, and body size (common goldeneyes are slightly smaller than Barrow's goldeneyes). I observed four cases of

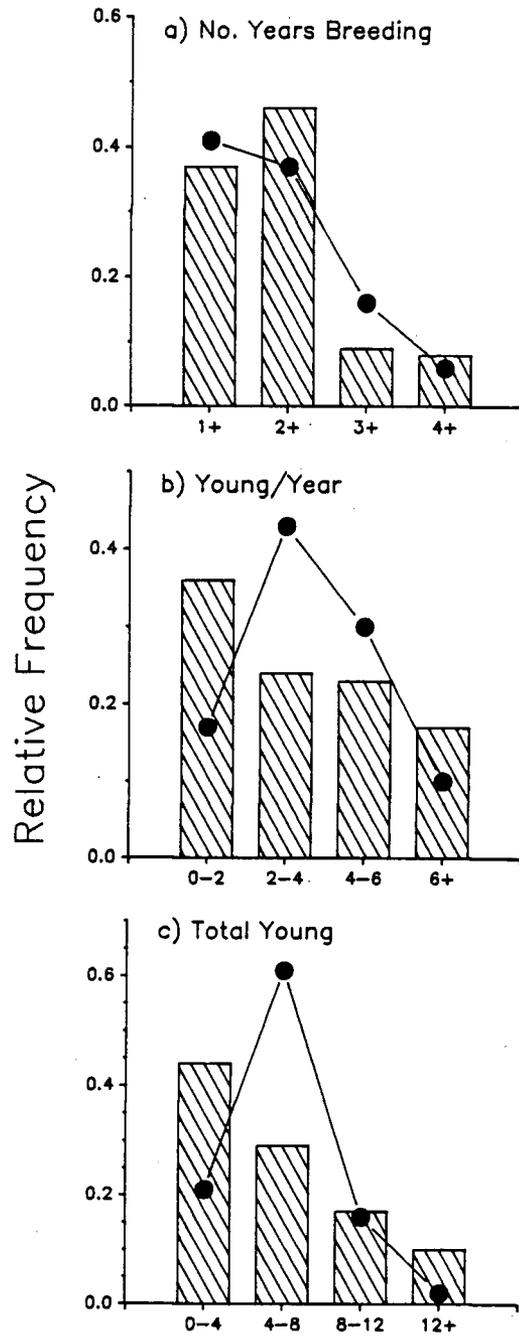


Figure 3.1. Frequency distributions of (a) breeding lifespan, (b) annual reproductive success, and (c) lifetime reproductive success for goldeneye females. Bars represent observed frequencies and circles represent expected frequencies based on a Poisson distribution.

Table 3.3. Comparison of the reproductive success of Barrow's and common goldeneye females. Means \pm 1 SE. Sample size in parentheses.

		Barrows	Common ^a
Laying Date		123.3 \pm 1.3 (45)	118.3 \pm 2.0 (35)
Nest Success		0.70 \pm .05 (94)	0.77 \pm .05 (61)
Clutch Size:	Total ^b	10.7 \pm 0.5 (57)	10.3 \pm 0.5 (38)
	Own	7.9 \pm 0.2 (53)	7.9 \pm 0.3 (35)
No. Hatch:	Total	9.6 \pm 0.4 (57)	8.9 \pm 0.5 (38)
	Own	7.4 \pm 0.3 (53)	7.0 \pm 0.4 (35)
Pn Hatch:	Total	0.90 \pm .02 (57)	0.87 \pm .03 (38)
	Own	0.92 \pm .02 (53)	0.89 \pm .03 (35)
No. Fledge:	Total	4.9 \pm 0.6 (39)	4.2 \pm 0.6 (34)
	Own	3.3 \pm 0.4 (36)	3.0 \pm 0.5 (31)
Pn Fledge:	Total	0.47 \pm .05 (39)	0.44 \pm .06 (34)
	Own	0.45 \pm .05 (36)	0.43 \pm .06 (31)

^a All differences between species are not significant at $P < .05$

^b TOTAL includes parasitic eggs; OWN includes only host eggs

interspecific hybridization between the two species, and three other cases were suspected. Thus, on my study area, Barrow's goldeneyes and common goldeneyes appear to function as a single ecological species. I therefore combined data for both species in the following analyses to (a) maximize sample size and (b) to permit use of nests in which species identity was uncertain.

The Effects of Breeding Experience and Laying Date

Breeding age had a significant effect on laying date ($H = 10.0$, $df = 2$, $P < .05$) and fledge success ($H = 7.1$, $P < .05$), with trends apparent for total clutch size and total hatch success ($H = 4.6$ and 5.1 respectively, both $P < .10$). As observed in other studies, older and more experienced females initiated nests earlier, laid larger clutches and fledged more young (Figure 3.2). Laying date also affected all components of reproductive success (Figure 3.3). Females that nested earlier laid larger clutches ($r_s = -.45$, $N = 81$, $P < .001$), hatched more eggs ($r_s = -.38$, $N = 81$, $P < .001$), and fledged more young ($r_s = -.31$, $N = 70$, $P < .05$).

Because age, laying date and RS are correlated, I repeated the analyses of the effects of breeding experience using laying date as a covariate in an ANCOVA. There were no significant interactions between laying date and breeding age (all $P > .25$) for any measure of RS, thus meeting the assumption of homogeneity of slopes. When the influence of laying date was removed, clutch size and hatch success no longer varied with breeding age (both $F < 1.0$, $P > .10$), whereas the effects of breeding experience on fledge success remained ($F = 4.7$, $df = 2,48$, $P < .05$).

The Influence of Population Density and Brood Parasitism

Studies of other cavity nesting ducks have shown that reproductive success of females is reduced under conditions of high population density and/or frequent brood parasitism (Jones & Leopold 1967, Haramis & Thompson 1985, Gauthier & Smith 1987). I found similar effects for goldeneyes. Fledge success was negatively correlated with the number of breeding pairs per lake ($r_s = -.43$, $P < .05$, $N = 30$ lake-years, pooling data for all lakes for 3 years). Average clutch size

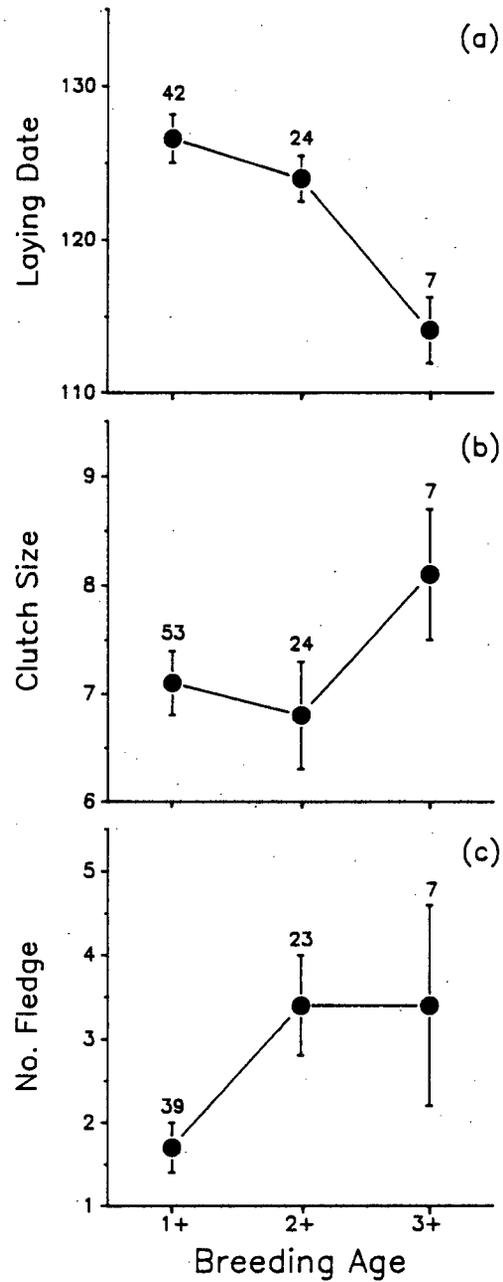


Figure 3.2. The effect of breeding age on (a) laying date, (b) clutch size, and (c) number of fledglings. Means \pm 1 SE. Sample sizes are shown above error bars.

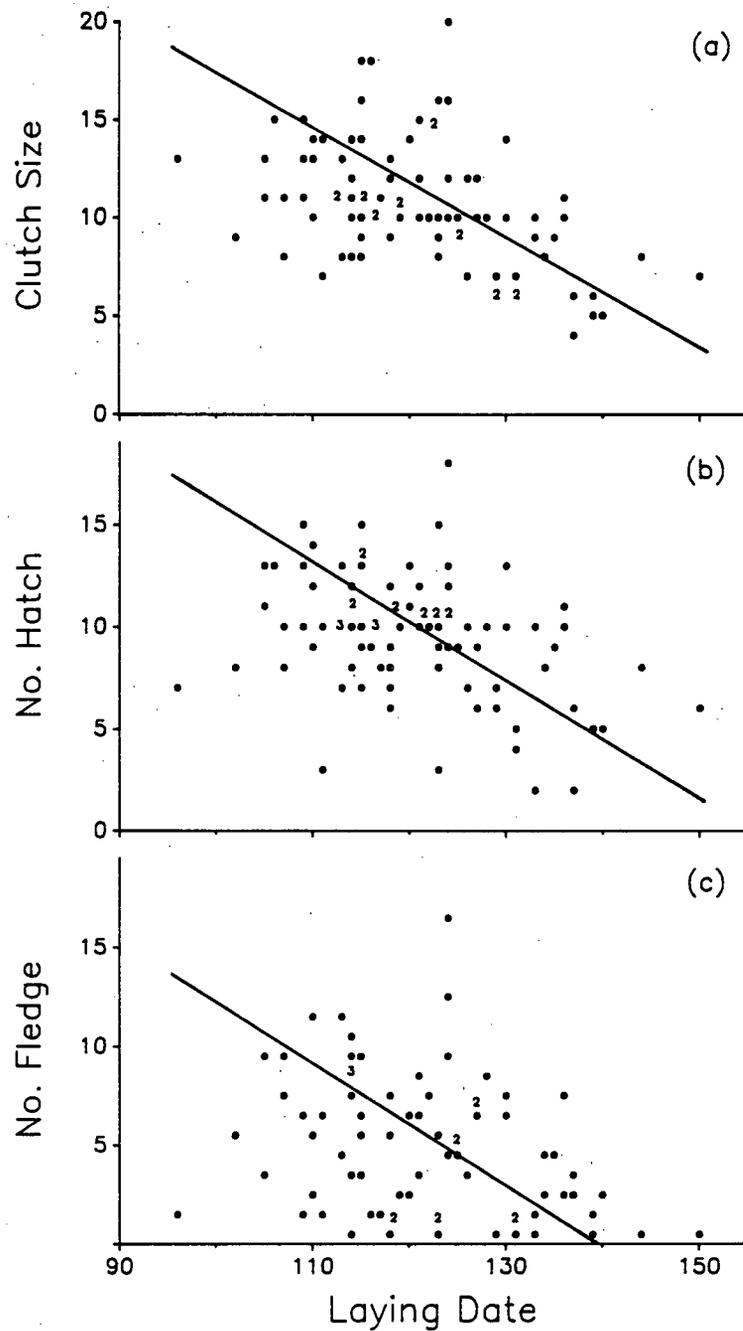


Figure 3.3. The effect of laying date (LD) on (a) clutch size (CS), (b) number of eggs hatching (HS), and (c) number of fledglings (FS). Lines are geometric mean regressions:

$$CS = 47.3 - .30 LD; \quad HS = 45.3 - .30 LD; \quad FS = 44.7 - .33 LD.$$

was positively correlated with the proportion of parasitized nests on each lake ($r_s = .86$, $P < .001$) while nest success was negatively correlated with the frequency of parasitism ($r_s = -.52$, $P < .01$).

The Role of Nest Site Selection

Goldeneye females are highly philopatric; 70% of the 66 females that returned to the study area used the same nest site in consecutive years. Hence, it is difficult to separate the effects of female quality from the effects of nest site quality. A female might have consistently high reproductive success, not because she is a better parent, but because she chose a good nest site and returned to that site in subsequent years. To separate these influences, we need to know if the quality of nest sites varies and if females respond to this variation.

(i) Patterns of nest use and success - The pattern of nest-box use was different from that expected if females used boxes at random ($G_w = 24.0$, $df = 4$, $P < .001$; Figure 3.4a). Some nest sites were used more frequently than expected, while others were used less often than expected. The same pattern was observed when I considered only nests that were used by a new female ($G_w = 27.6$, $P < .001$; Figure 3.4b).

Nest success also varied among nest sites. Nests in some boxes were consistently more successful or less successful than expected by chance (Figure 3.5). The pattern was not different from random when analyses were based on boxes that were used at least once in 4 years ($G_w = 4.5$, $P > .10$; Figure 3.5a). However, that analysis confounds patterns of nest use and nest success, since sites that were unsuccessful may be less likely to be used. I therefore repeated the analysis for only boxes that were used in all 4 years (Figure 3.5b). In this sample, the pattern of nest success differed significantly from random ($G_w = 6.8$, $df = 2$, $P < .05$; 0 and 1 classes and 3 and 4 classes pooled).

(ii) Nest Habitat - In all 3 years, nest boxes that were (a) closer to the water and (b) in open stands of trees were more likely to be used (Mann-Whitney U-tests, all $P < .05$). In contrast, habitat had little effect on nest success. I did not find differences between successful and failed nests for any habitat variable (all comparisons, $P > .05$).

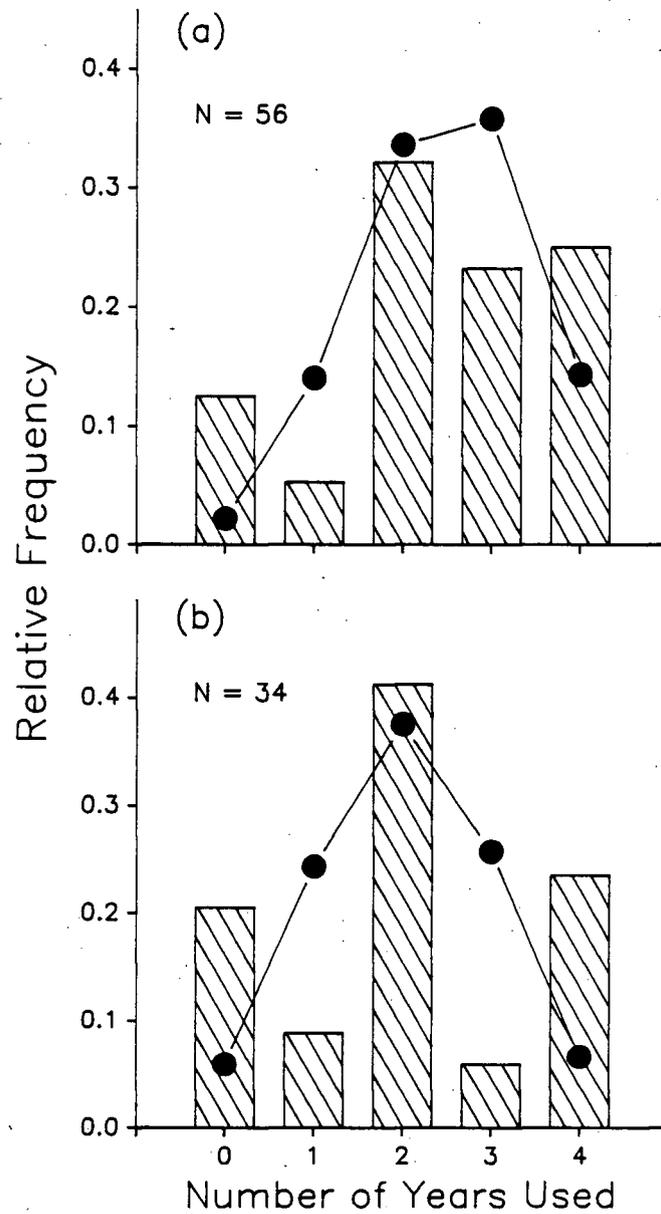


Figure 3.4. Patterns of nest site use by goldeneye females. Bars represent observed frequencies and circles represent expected frequencies if females used nest sites at random (based on a binomial distribution). The upper graph includes females that returned to their previous nest site, while the lower graph excludes these females.

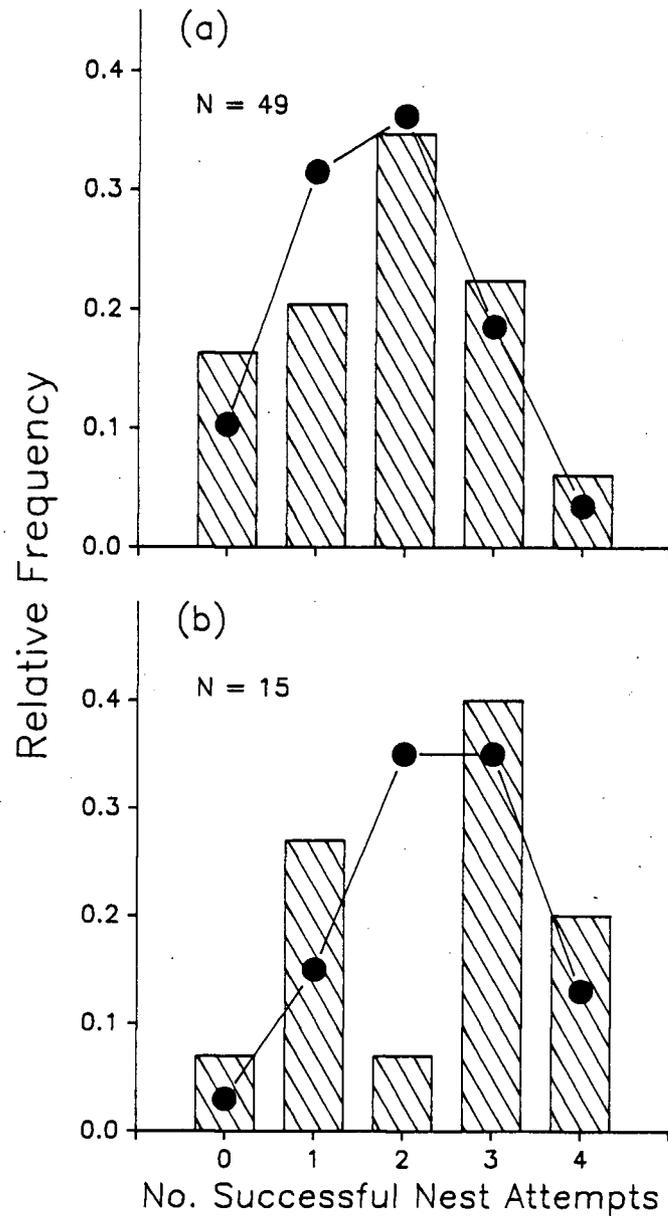


Figure 3.5. The distribution of nest success among nest sites. Bars represent observed frequencies and circles represent expected frequencies if nest success was distributed randomly among sites (based on a binomial distribution). The upper graph includes sites that were available for all 4 years of the study and were used at least once; the lower graph includes only boxes that were used in all 4 years.

(iii) Previous History - Goldeneye females were more likely to use nest sites that had been occupied in the previous year ($G_w = 41.4$, $P < .001$; Table 3.4). This pattern was not simply due to female philopatry since the result was the same when I excluded returning females ($G_w = 19.1$, $P < .01$; Table 3.4). Breeding success was also influenced by the previous history of a nest site. Females that used previously-successful or previously-empty nest boxes were more likely to be successful themselves ($G_w = 16.8$, $P < .001$; Table 3.5). Again, this remained true when I excluded returning females ($G_w = 13.5$, $P < .01$).

These results suggest that nest site quality varies and that females respond to this variation. Patterns of breeding dispersal substantiate this notion. Females that were unsuccessful in a nest site were more likely to change nests in the following year (7 of 10 unsuccessful females changed sites compared to 13 of 56 successful females; $G_w = 7.6$, $P < .01$). To separate the effects of nest site quality from the effects of female quality, I compared the success of females that changed nest sites between breeding attempts. If female quality is important, individuals that were successful previously should be more likely to be successful in a new site. However, only 20 goldeneye females changed nests and almost all (16) were successful in their new site, regardless of their previous history. Of the four unsuccessful females, two had been previously successful while the other two had failed.

Are Nest Sites Limited?

Female reproductive success might be influenced by the quantity as well as the quality of nest sites. I found that the number of breeding pairs was strongly correlated with the number of nest sites ($r_s = .55$, $N = 31$ lake-years, $P < .001$) and the size of the lake ($r_s = .78$, $P < .001$). Because lake area and the number of nest sites were also correlated ($r_s = .58$), I used partial correlation analyses to examine the effect of each variable on pair density while holding the other variable constant. Partial correlations were significant and of similar magnitude when I controlled either the number of nest sites ($r_p = .54$, $P < .01$) or lake size ($r_p = .51$, $P < .02$). Thus, both nest site availability and lake area appear to influence the number of breeding pairs.

Table 3.4. Nest box use by goldeneye females according to the fate of the nest at that site in the previous year. Values in parentheses are proportions.

<u>Previous Fate</u>	<u>All Nests ^a</u>		<u>Nests with New Females</u>	
	<u>Used</u>	<u>Not Used</u>	<u>Used</u>	<u>Not Used</u>
Successful Last Year	59 (.78)	17 (.22)	26 (.60)	17 (.40)
Failed Last Year	33 (.62)	20 (.38)	31 (.61)	20 (.39)
Empty Last Year	20 (.27)	54 (.73)	20 (.27)	54 (.73)

^a ALL NESTS includes nest sites used by females returning to their previous nest site; NESTS WITH NEW FEMALES considers only those boxes used by a new female

Table 3.5. Breeding success of goldeneye females according to the fate of the nest at that site in the previous year. Values in parentheses are proportions.

<u>Previous Fate</u>	<u>All Nests ^a</u>		<u>Nests with New Females</u>	
	<u>Success</u>	<u>Fail</u>	<u>Success</u>	<u>Fail</u>
Successful Last Year	43 (.73)	16 (.27)	15 (.58)	11 (.42)
Failed Last Year	11 (.33)	22 (.67)	9 (.29)	22 (.71)
Empty Last Year	16 (.80)	4 (.20)	16 (.80)	4 (.20)

^a ALL NESTS includes nest sites used by females returning to their previous nest site; NESTS WITH NEW FEMALES considers only those boxes used by a new female

DISCUSSION

In goldeneyes, females alone select the nest site, incubate the clutch and provide all post-hatch care of offspring. It is therefore possible to assess some of the factors that influence female reproductive success without confounding the effects of male care or male quality. There was considerable variance in reproductive success among goldeneye females. Standardized variances (I) for measures of RS were higher than those reported for females of several other species. For example, Clutton-Brock (1988) reported a median value of I near 0.70 for lifetime reproductive success of females in 12 species of birds and mammals. In contrast, I observed values of 1.04 and 2.33 for total and annual reproductive success of goldeneyes, respectively. Why is reproductive success so variable among goldeneyes? I found three primary sources of variation: (1) differences in female quality, (2) variation in nest site quality, and (3) timing of breeding.

Female Quality

There were marked differences among individual females in their ability to breed successfully. Some females were consistently more successful than others (Figure 3.1), and there were significant repeatabilities for clutch size, number of hatchlings, and the timing of nest initiation (Table 3.2). These results suggest that there may be heritable differences among females in at least some components of RS, as has been reported for other birds (van Noordwijk and van Balen 1988, Gustafsson 1986, review in Boag & van Noordwijk 1987). There was also evidence for an effect of female age and breeding experience. Older females laid more eggs and fledged more young than less experienced females (Figure 3.2). Breeding experience might be particularly important in goldeneyes for two reasons. First, the large nest cavities required for breeding are generally scarce (Savard 1986, Gauthier & Smith 1987) and increased familiarity with an area could enhance a female's ability to locate a suitable nest site. Goldeneyes are among the few species of North American ducks that do not breed until 2 or 3 years of age, and Eadie & Gauthier (1985) showed that non-breeding females spend their first summer prospecting for nest sites. Second, age and experience might influence a female's ability to locate and defend a high quality brood territory. Goldeneye females with broods are extremely territorial, and

aggressive interactions among females may be a major source of duckling mortality (Savard 1986). Young females often fail to establish a brood territory and frequently suffer total brood loss.

Lifetime reproductive success of goldeneyes was also positively correlated with breeding lifespan, as was found by Dow & Fredga (1984; see also Smith 1981 and Newton 1985 for other species). This relationship could also be a result of female quality if high quality females both laid larger clutches and were more likely to survive. However, survivorship did not differ consistently among goldeneye females (Figure 3.1a) and there was no relationship between longevity and the number of young produced per year. Instead, lifetime fledge success was correlated only with annual success. Thus, females that are more successful in any given year will tend to produce more young in total. Annual reproductive success provides a reasonable index of lifetime success.

Nest Site Quality

The quality of the nest site had a large influence on female RS. Nests in certain sites were more likely to be consistently successful. This was not simply the result of successful females returning to their previous nest since the pattern remained when returning females were excluded from the analysis. Nest success did not vary significantly with any habitat factor but, rather, was related to the success of the nest at that site in the previous year. Dow & Fredga (1985) observed a similar result for common goldeneyes in Sweden. In their study, nest predation was the major cause of nest failure and they suggested that nests within the home range of an individual predator (the pine marten) were more likely to be preyed upon in consecutive years. Certain sites would therefore fail consistently. This hypothesis cannot explain my results since nest predation was infrequent on my study area (3% of nests over four years), and the major cause of nest failure was desertion. Patterns of consistent nest failure might instead reflect the effects of interference among females (Grenquist 1963, Jones & Leopold 1967, Eriksson & Andersson 1982, Gauthier 1987). Certain nest sites might attract more females, and if interference is extreme,

those sites might be deserted consistently from one year to the next (Semel & Sherman 1986, Semel et al. 1988).

Goldeneye females were, in fact, attracted to certain nest sites. Nest boxes that were close to water in open stands of trees were used more frequently. Further, sites that had been used in one year were more likely to be used in the following year; even when returning females were excluded from the analysis. These results again mirror those of Dow & Fredga (1985). They suggested that females might use information on the prior use of a nest site as an indication of the quality of the site. Successful occupancy in the preceding year would indicate that a nest site was safe and suitable. However, in contrast to Dow & Fredga's (1985) findings, goldeneyes in B.C. did not distinguish between previously-successful and previously-unsuccessful nest sites (Table 3.4), even though it would have paid them to do so (Table 3.5). In fact, females would have been better off to choose a site that was previously empty over a site in which the nest had previously failed (Table 3.5). Evidence of prior use of a nest site, then, does not necessarily predict the success of a future nest at that site. An alternative explanation is that females "choose" previously-used nest sites simply because all females respond to the same nest characteristics. For example, nest sites that are closer to water may be more attractive and therefore would be more likely to be used repeatedly, regardless of the success of the previous nest at that site.

Because of the high degree of philopatry of females to their nest site, it is difficult to separate the effects of nest quality from the effects of individual quality in accounting for consistent differences among females in RS. Ideally, we need to examine the success of females that change nest sites between breeding attempts. My data were insufficient to discriminate between these alternatives, primarily because few females failed after changing nest sites. This is not just a problem with small sample size. If females change nests to obtain a higher quality nest site, then we might not detect any consistent pattern of success among individuals since even low quality individuals could benefit by moving to a better nest. Moreover, if female quality influences the ability to compete for nest sites, then high quality females might also obtain the best sites. It may be impossible to separate these effects.

Timing of Breeding

Timing of breeding had a strong influence on all aspects of the reproductive success of goldeneye females. Moreover, some of the effects of breeding experience disappeared when laying date was controlled, indicating an over-riding influence of time of breeding. Reproductive success is strongly correlated with laying date in several other birds (Batt & Prince 1979, Birkhead et al. 1983, Cooke et al. 1984, Dow & Fredga 1984, Toft et al. 1984), although there appears to be no single explanation for this pattern (see Toft et al. 1984). Three possibilities have been suggested for goldeneyes: (1) food abundance is highest early in the season and early-nesting females are therefore able to produce more eggs and/or rear larger broods (Eriksson 1978); (2) delays in nesting in late years cause females to use nutrient or energy reserves that would otherwise have gone into reproduction (Bengston 1972, Fredga & Dow 1983); (3) early nesting females obtain access to the best nest sites and brood territories (Savard 1986). These mechanisms are not mutually exclusive. In fact, all three suggest that the effects of laying date are related in some manner to resource availability and/or resource acquisition.

Intrasexual Competition & Variance in Female RS

In many vertebrates, variation in reproductive success among females is low relative to males, and competition among females is thought to be weak (Trivers 1972, Payne 1979, Clutton-Brock 1988). My results, along with those of several other recent studies (Howard 1983, Hafernik & Garrison 1986, and see reviews in Wasser 1983, Clutton-Brock 1988), suggest otherwise. Variance in female RS can be substantial, even in strongly sexually-selected species (Howard 1983, Hafernik & Garrison 1986). The importance of intrasexual competition in generating this variance remains to be demonstrated, but there is increasing evidence that females in a variety of species compete for resources that are critical to successful reproduction (Hannon 1984, Davies & Houston 1986, Arcese 1988, van den Berghe & Gross 1989, and reviews in Wasser 1983).

Reproductive success in goldeneye females is closely tied to access to resources that are essential for reproduction; notably nest sites, brood territories, and food resources (Eriksson

1979, Dow & Fredga 1984, 1985, Savard 1986, this study). Moreover, several lines of evidence indicate that females compete with each other for these resources.

(1) The number of breeding pairs on a lake was strongly correlated with the number of nest sites and with lake size, indicating that nest sites and suitable territory locations may have been limited (see also Savard 1986).

(2) Nest site quality varied, and females preferred certain sites. Competition among females for preferred nest sites could account for the consistent pattern of nest failure among nests (above).

(3) RS was reduced on lakes where the frequency of brood parasitism was high. I show in Chapter 6 that the frequency of parasitism is positively correlated with population density and negatively related to the availability of nest sites. I also demonstrate that nest desertion is a function of the intensity of parasitism (Chapter 5).

(4) There was a negative relationship between density and brood survival, which would be expected if females compete exploitatively or via interference competition for brood territories. Mortality could occur as a direct result of female aggression (Savard 1986) or as a consequence of brood movements overland in search of suitable territory locations (Eriksson 1979).

(5) Finally, the strong correlation of laying date with several components of RS could be explained if early nesting allowed females first access to the highest quality food resources, nest sites or brood territories (see above, and Savard 1986).

This evidence is admittedly circumstantial. However, the two most variable components of female RS were nest success and viability of young (Table 3.1), and these were also the components that were influenced most by laying date, nest site quality, population density, and brood parasitism. Thus, much of the variation in female RS derives from factors that relate to the availability of resources, and to social interactions among individuals that might constrain access to these resources. Intrasexual competition among females may therefore be an important force in generating the high variance in RS observed in goldeneyes.

If this interpretation is correct, it could explain why some females act as brood parasites, rather than establishing their own nest. High population densities leading to increased competition for nest sites or brood territories could limit breeding opportunities for young or competi-

tively inferior females. Parasitic egg-laying would provide a means by which these females could salvage some reproductive success. Moreover, since fledge success of young increases with age of the female, a young bird might obtain better care for her offspring by parasitizing an older female. Alternative reproductive behaviours are typically found in species in which the variance in RS is high and intrasexual competition is considerable (reviews in Davies 1982, Dunbar 1982). My results suggest that such conditions obtain for goldeneyes and that parasitic behaviour may be an alternative tactic of females. The remainder of this thesis is devoted to exploring this possibility.

CHAPTER 4

BROOD PARASITISM IN A PRECOICIAL BIRD: I. EFFECTS ON THE REPRODUCTIVE SUCCESS OF THE HOST

Parental care in many vertebrates entails considerable expenditures of time and energy. It is therefore not surprising that parasitic reproductive behaviours have evolved in several species of birds (Weller 1959, Yom-Tov 1980a, Gowaty & Karlin 1984, Moller 1987, Evans 1988), insects (Wilson 1975, Tallamy 1985, 1986, Eberhard 1986), and fishes (McKay 1985, Sato 1986). Avian brood parasites, for example, lay their eggs in the nests of other birds, and the recipients provide all subsequent care for the parasitic eggs and offspring. While parasitic egg-laying is obviously beneficial to the parasite, it can severely reduce the reproductive success of the host. Costs to the host range from those involved in providing care for additional, unrelated offspring to the outright destruction of the host's eggs or young (review in Payne 1977a). In some species, hosts fail to produce any young of their own (Davies and Brooke 1988).

Most research on avian brood parasitism has focused on altricial birds (review in Payne 1977a). However, facultative brood parasitism occurs frequently in several species of precocial birds and conclusions about the effects of parasitism on host fitness, derived from studies of altricial birds, may not apply. Unlike altricial birds, precocial birds invest little into the post-hatch care of offspring and the young are relatively independent soon after hatching (Ricklefs 1977, Andersson 1984). The cost of accepting additional parasitic offspring may therefore be small (Nudds 1980, Andersson 1984, Eadie & Lumsden 1985). Some researchers have even suggested that precocial hosts might benefit from being "parasitized" through reduced mortality of host young in parasitized broods (Nudds 1980, Andersson 1984, Eadie & Lumsden 1985).

Attempts to determine the consequences of parasitism to precocial hosts have been hampered by the fact that researchers have relied primarily on an observational approach (e.g. Weller 1959, Joyner 1976, Eriksson & Andersson 1982, Amat 1985). Observational studies of intraspecific brood parasitism are particularly difficult to interpret since parasitic eggs cannot easily be distinguished from host eggs, and one cannot reliably assess the effects of parasitism on

host fitness. Differences in the age, ability, or time of breeding of parasitized and non-parasitized females can further complicate interpretation (Rohwer 1985, Amat 1987). Experimental parasitism of host nests provides an alternative and effective way to directly assess costs or benefits to the host, but surprisingly few studies have used such an approach for precocial birds (see Heusmann et al. 1980 and Andersson & Eriksson 1982 for notable exceptions).

In this Chapter, I combine field experiments and observational studies to investigate directly the effects of brood parasitism on the reproductive success of hosts in two species of precocial birds, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). I assess several potential costs to hosts, and I consider the possibility that hosts might benefit through being parasitized. In a companion paper (Chapter 5), I examine the behavioural responses of hosts to parasitism.

METHODS

Descriptions of the study area and the general field methods are provided in Chapter 2.

Identifying Parasitized Nests - I identified parasitized nests using 6 criteria:

- (1) More than one egg laid per day;
- (2) Clutch size greater than 13 eggs;
- (3) Direct observation of 2 or more females laying eggs in the same nest;
- (4) Eggs laid 2 or more days after the start of incubation;
- (5) Distinct differences in the morphology or appearance of eggs;
- (6) Skips in egg-laying greater than 6 days, or more than 2 skips of 4+ days (Clawson et al. 1979, Yom-Tov 1980, Eriksson & Andersson 1982, Moller 1987).

A detailed evaluation of these criteria is provided in Appendix 1.

Identifying Parasitic Eggs - I determined the ownership of eggs using 4 methods: (1) by trapping females on the nest; (2) by direct observation of females during egg-laying; (3) by abnormal egg-laying patterns (e.g. eggs laid out of schedule); and (4) by differences in size, shape and/or colour (see Fetterolf & Blokpoel 1984, Fleischer 1985, Gibbons 1986, Moller 1987, Freeman

1988). I performed cluster analyses on size and shape measures for all eggs in each parasitized nest and considered eggs that differed by a Euclidean Distance greater than 2.5 to belong to different females (see Appendix 1). It was not possible to assign eggs to individual brood parasites, although it was possible to estimate the number of different parasites per nest. In the analyses presented here, I simply group all parasitic eggs in each nest.

Some nests were followed infrequently, and I did not observe females on the nests nor did I have detailed information on egg-laying patterns. In cases in which only a few eggs differed from the majority of the clutch, I assumed that the few unusual eggs were parasitic eggs, while the majority belonged to the host. This appeared to be valid based on nests for which more detailed information was available. In cases in which the number of eggs in each egg cluster was similar, I assigned the clusters randomly to the host and to parasites.

Growth of Young - I measured the growth of young as the net gain in weight from hatching to the date of capture in brood drives (at 20-60 days of age). Linear regressions of weight on age were calculated for each sex, and residuals from these regressions were then calculated for each duckling. To compare the growth of young in parasitized and non-parasitized broods, I determined the mean residual and the maximum residual for all ducklings in each brood. Each brood was considered to be an independent sample. Further details are provided in Chapter 2.

Experimental Parasitism - To determine the effects of parasitism on hosts, I added goldeneye eggs to nests during the host's laying period. Four treatment groups were established: 2-3 eggs added, 4-5 eggs added, 6-7 eggs added, and 8-12 eggs added. Eggs were added to nests 2 at a time, usually every other day. In the 8-12 addition nests, I added some eggs on consecutive days to ensure that all eggs were placed in the nest before the host began incubation. Goldeneye eggs were obtained from other nests on the study area, with the exception of the +3 egg treatment. In this treatment, I used fresh chicken eggs painted to resemble goldeneye eggs. Large chicken eggs are similar in size and shape to goldeneye eggs.

Control nests were established and matched with experimental nests for initiation date, nest box type, and pond/lake location and size. Experimental and control nests received the same

number of nest visits and the same degree of nest disturbance, and eggs in control nests were handled in the same manner as host eggs in experimental nests. Nests that were parasitized naturally were removed from the analysis, except for a few cases in which the identity of the parasitic eggs was clear. In those cases, I added the parasitic eggs to the total number of experimental eggs. The results did not change when those nests were removed from the analysis.

Reproductive Success - I measured six components of reproductive success: (i) nest success (the proportion of nests in which at least one young hatched), (ii) clutch size, (iii) the number of eggs that hatched, (iv) the proportion of eggs that hatched (hatch success), (v) the number of young that fledged, and (vi) the proportion of young that fledged (fledge success). I estimated the net reproductive success of females as the number of young that fledged from each nest attempt, averaged over all nests (including deserted or incomplete nests). This estimate is restricted to nests that were followed in detail on lakes where brood survival was monitored (see Chapter 2). Several components of reproductive success (RS) varied between years. I therefore standardized each component of RS by subtracting the yearly mean from the raw data. All statistical analyses were based on the standardized data.

Nests that were initiated early in the season were more likely to be parasitized (see below). I controlled for the effects of laying date using partial correlation and analysis of covariance (ANCOVA). I assessed departures from normality using Kolmogorov-Smirnov tests (Lilliefors test, Wilkinson 1988) and by visually examining normal probability plots. Variables that were not distributed normally were log-transformed, or in the case of proportions, arcsin square-root transformed. In analysis of covariance, I tested for homogeneity of slopes by examining the interaction between the covariate (laying date) and the treatment (parasitized versus non-parasitized). In all analyses, interaction terms were small and not significant (all $P > .20$), thereby validating tests for treatment effects after the effects of the covariate were removed.

Nest desertion and reduced clutch size (via depressed ovulation) are traditionally viewed as "costs" to the host (e.g. Weller 1959, Jones & Leopold 1967). However, these costs are the direct result of some action by the host, and Andersson (1984) argued that desertion and clutch size

adjustments are better viewed as potentially adaptive host responses. I therefore defer a detailed analysis of host clutch sizes and nest desertion to Chapter 5.

RESULTS

Brood parasitism occurred frequently on the study area. An average of 35% of all nests were parasitized while approximately 17% of all eggs were laid parasitically. Nests that were initiated earlier in the season were more likely to be parasitized. The mean Julian date for 62 parasitized nests was 119 ± 1 SE whereas that for 30 non-parasitized nests was 125 ± 2 (Mann-Whitney U-test, $P < .05$). Clutch sizes were consistently larger in parasitized nests and averaged 3-5 eggs more than clutches in non-parasitized nests (Table 4.1). It was not uncommon to find 15 or more eggs in a nest, while the largest parasitized clutch contained 28 eggs (Figure 4.1). More eggs hatched and more young fledged from parasitized nests than from non-parasitized nests. However, the proportion of eggs that hatched was significantly lower in parasitized nests, while there was no effect on the proportion of young that fledged (Table 4.1).

I found similar results when I considered nests of Barrow's goldeneyes and common goldeneyes separately (Table 4.1). Clutch sizes, the number of young that hatched, and the number of young that fledged were significantly larger in parasitized nests for both species. The proportion of eggs that hatched was lower in parasitized nests for Barrow's goldeneyes but not for common goldeneyes, although sample sizes were small in the latter case. The frequency of brood parasitism was also very similar in both species. Thirty-nine percent of Barrow's goldeneye nests were parasitized, compared to 36% of common goldeneye nests. Barrow's goldeneye nests were parasitized equally by conspecifics (52%) and by common goldeneyes (48%); and vice versa for common goldeneyes (47% by conspecifics and 53% by Barrow's goldeneyes). Because the effects of parasitism were nearly identical for both species of goldeneyes, I pooled results for the two species in all following analyses.

Table 4.1. Components of reproductive success in non-parasitized and parasitized goldeneye nests. Means \pm 1 S.E. Sample sizes are in parentheses.

	Non-parasitized			Parasitized	
Clutch Size ^a					
Barrows	7.9 \pm 0.3	(31)	***	12.6 \pm 0.5	(42)
Common	8.3 \pm 0.4	(16)	***	11.3 \pm 0.5	(32)
Both ^b	8.1 \pm 0.2	(50)	***	12.0 \pm 0.3	(76)
No. Egg Hatch ^c					
Barrows	7.6 \pm 0.4	(25)	***	10.7 \pm 0.5	(39)
Common	7.3 \pm 0.6	(14)	**	9.6 \pm 0.6	(27)
Both	7.6 \pm 0.3	(40)	***	10.3 \pm 0.4	(68)
Pn Eggs Hatch					
Barrows	0.94 \pm .03	(25)	*	0.86 \pm .03	(39)
Common	0.87 \pm .05	(14)		0.86 \pm .03	(27)
Both	0.92 \pm .03	(40)	*	0.86 \pm .02	(68)
No. Young Fledge					
Barrows	2.9 \pm 0.6	(15)	**	5.9 \pm 0.8	(29)
Common	3.3 \pm 0.8	(12)		4.4 \pm 0.7	(25)
Both	3.1 \pm .05	(27)	**	5.2 \pm 0.5	(54)
Pn Young Fledge					
Barrows	0.43 \pm .08	(15)		0.52 \pm .06	(29)
Common	0.41 \pm .19	(12)		0.45 \pm .07	(25)
Both	0.42 \pm .06	(27)		0.49 \pm .04	(54)

^a Includes only nests that were incubated or hatched (complete clutches)

^b Includes nests in which species identity was uncertain

^c Only successful nests (hatched) are included for all measures other than clutch size

*** P < .001, ** P < .01, * P < .05

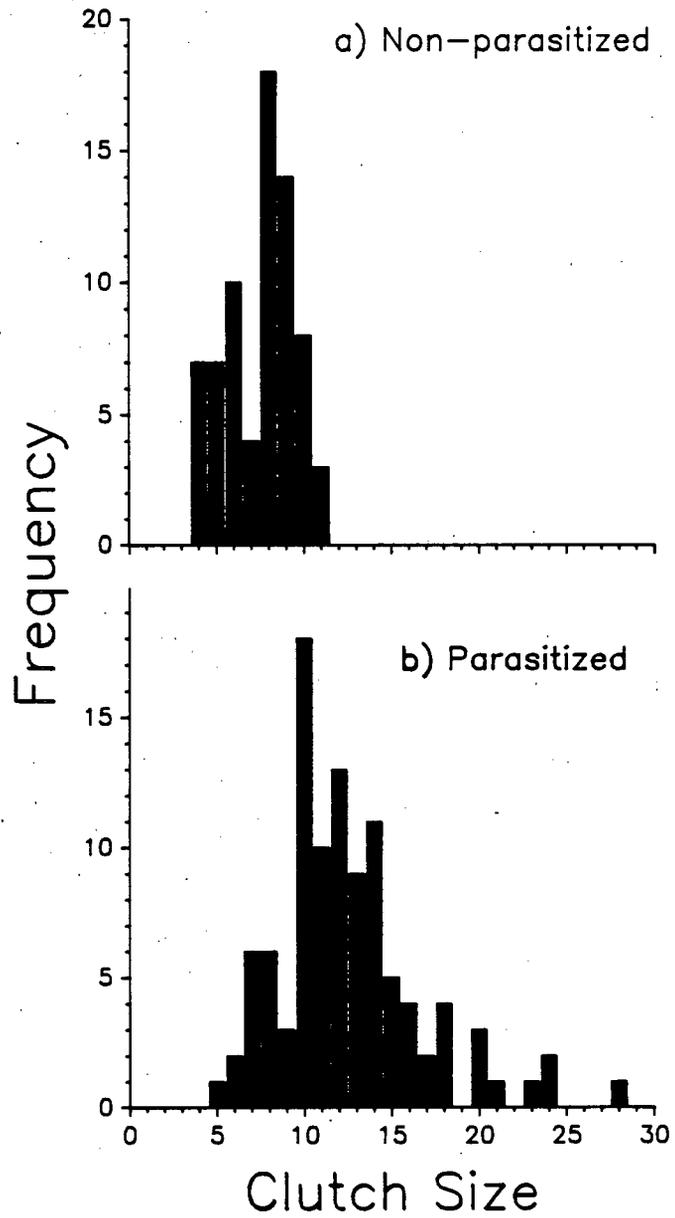


Figure 4.1. The distribution of clutch sizes in (a) non-parasitized and (b) parasitized nests.

The above comparisons consider only naturally parasitized nests, and do not distinguish between the success of host and parasite eggs. In the following analyses, I examine each component of reproductive success for both naturally and experimentally parasitized nests, and I analyse separately the success of host and parasite eggs, where appropriate.

Nest Success

Unmanipulated nests - Parasitism did not reduce the proportion of host nests in which at least one young hatched and left the nest. Sixty-eight of 102 parasitized nests (67%) were successful compared to 41 of 71 non-parasitized nests (57%) (G-test with Williams' correction, $G_w = 1.59$, $P > .20$). However, nest success did vary with the total number of eggs in the nest ($G_w = 57.5$, $df = 4$, $P < .001$; Table 4.2). Nests with fewer than five eggs were rarely incubated and were probably incomplete, whereas none of the nests with more than 20 eggs were successful. Nest desertion was the major reason for nest failure, although some nests were depredated or destroyed by other agents. I consider nest desertion in more detail in the following chapter.

Experimental nests - There was no effect of experimental parasitism on nest success. Twenty of 37 control nests (54%) were successful compared to 23 of 39 (59%) experimental nests ($G_w = 0.18$, $P > .20$). Nest success also did not vary significantly with the number of experimental eggs added ($G_w = 0.57$, $df = 3$, $P > .20$; 6-7 and 8-12 treatments pooled), although only one of the five nests with 8-12 eggs added was successful (Table 4.2).

Clutch Size

Unmanipulated nests - Clutch sizes of hosts were not affected by brood parasitism (Table 4.3 and see Chapter 5 for analyses). Joyner (1976) argued that egg displacement was a primary cause of host clutch reduction in ground-nesting ducks, but I found no evidence that eggs were inadvertently displaced from goldeneye nests. Parasitized nests contained an average of 3.8 parasitic eggs, approximately half the number of host eggs (Table 4.3).

Table 4.2. Nest success of goldeneyes as a function of (a) clutch size in unmanipulated nests and (b) number of eggs added (treatment) in experimental nests.

	<u>No. Hatch</u>	<u>No. Fail</u>	<u>Success (%)</u>
(a) Unmanipulated Nests			
<u>Clutch Size</u>			
1 - 5	4	38	9.5
6 - 10	58	30	65.9
11 - 15	39	13	74.5
16 - 20	8	5	61.5
> 20	0	5	0
(b) Experimental Nests			
<u>Treatment</u>			
Control	20	17	54.1
2 - 3	6	5	54.5
4 - 5	11	6	64.7
6 - 7	5	1	83.3
8 - 12	1	4	20.0

Table 4.3. Reproductive success of goldeneye hosts in naturally parasitized nests. Means \pm 1 SE. Comparisons between hosts in parasitized nests and females in non-parasitized nests are by Mann-Whitney U-tests; comparisons between hosts and parasites within parasitized nests are by Wilcoxon Signed-ranks tests.

	<u>Non-Parasitized</u>		<u>Parasitized</u>		
			<u>Host</u>		<u>Parasite</u>
Clutch Size ^a	8.1 \pm 0.2 (50)	ns	7.8 \pm 0.2 (66)	***	3.8 \pm 0.4 (66)
No. Eggs Hatch ^b	7.6 \pm 0.3 (40)	ns	7.0 \pm 0.3 (59)	***	2.9 \pm 0.3 (59)
Pn Eggs Hatch	0.92 \pm .03 (40)	ns	0.89 \pm .02 (59)	***	0.74 \pm .04 (59)
No. Young Fledge	3.1 \pm 0.5 (27)	ns	3.1 \pm 0.4 (48)	***	1.5 \pm 0.3 (48)
Pn Young Fledge	0.42 \pm .06 (27)	ns	0.46 \pm .05 (48)	c	0.46 \pm .05 (48)

^a Includes only nests that were incubated or hatched (complete)

^b Only successful nests (hatched) are included for all measures other than clutch size

^c Not tested

*** P < .001, ** P < .01, * P < .05, ns P > .10

Experimental nests - Host clutch sizes were not affected when eggs were added experimentally to their nests (Kruskal-Wallis One-way ANOVA; $H = 4.98$, $P > .20$; Table 4.4). Additional details are provided in Chapter 5.

Hatch Success

Unmanipulated nests - Although average hatch success was reduced in parasitized nests (above), the number and proportion of host eggs that hatched did not differ between parasitized and non-parasitized nests (Mann-Whitney U-tests, $P > .10$; Table 4.3). In contrast, hatch success of parasitic eggs was significantly lower than that of host eggs within parasitized nests (Wilcoxon Signed-ranks test, Table 4.3). This may be due to the fact that 23 of 166 parasitic eggs were laid after the host had started to incubate the clutch. Only 10 (57%) of these late eggs hatched compared to 119 of 143 parasitic eggs (83%) laid before the start of incubation ($G_w = 7.17$, $P < .01$).

Hatch success did not vary with total clutch size when data for all years were combined ($r_s = -.13$, $N = 108$, $P > .10$; Figure 4.2). The relationship was the same when laying date was controlled via partial correlation ($r_p = -.14$, $N = 88$, $P > .10$).

Experimental nests - Results from nests that were parasitized experimentally mirrored those from naturally parasitized nests. Average hatch success (host plus parasitic eggs) was lower in experimental nests ($.81 \pm .03$, $N = 19$) than in control nests ($.88 \pm .04$, $N = 20$; Mann-Whitney U-Test, $P < .03$). However, hatch success of host eggs did not differ among any of the treatments (Table 4.4). Rather, fewer experimental eggs than host eggs hatched in all treatments, significantly so when sample sizes were large enough for statistical analysis (Wilcoxon Signed-ranks tests, $P < .05$; Table 4.4).

Experimental eggs were often older than host eggs, and viability may have been compromised. Accordingly, I divided experimental eggs into those that were older ($N = 33$) or the same age ($N = 41$) as host eggs. Hatch success was only slightly lower for older eggs (64% versus 73%; $G_w = 0.76$, $P > .10$) and there was no decline in hatch success of eggs that were up to

Table 4.4. Reproductive success of goldeneye hosts in experimentally parasitized nests. Results are shown separately for each treatment group (number of eggs added) and for all treatments combined. Means \pm 1 SE. Sample sizes in parentheses.

	<u>Control</u>		<u>Experimental</u>			
			<u>Host</u>		<u>Added</u>	
Clutch Size						
All	7.6 \pm 0.3 ^a	(26)	7.1 \pm 0.2	b	5.0 \pm 0.4	(27)
2 - 3			6.8 \pm 0.7		2.7 \pm 0.2	(6)
4 - 5			7.5 \pm 0.7		4.1 \pm 0.1	(12)
6 - 7			6.6 \pm 0.4		6.4 \pm 0.3	(5)
8 - 12			7.0 \pm 0.6		9.3 \pm 1.0	(4)
No. Eggs Hatch						
All	6.8 \pm 0.5 ^a	(20)	6.4 \pm 0.3	b	3.2 \pm 0.3	(23)
2 - 3			6.5 \pm 0.8		1.5 \pm 0.5 ^c	(6)
4 - 5			6.6 \pm 0.4		2.9 \pm 0.4	(11)
6 - 7			6.4 \pm 0.3		4.0 \pm 0.3	(5)
8 - 12			6.0		6.0	(1)
Pn Eggs Hatch						
All	0.88 \pm .04 ^a	(20)	0.89 \pm .02	**d	0.69 \pm .06	(19)
2 - 3			1.00 \pm .07	c	0.75 \pm .25 ^c	(2)
4 - 5			0.88 \pm .07	*	0.71 \pm .09	(11)
6 - 7			0.90 \pm .04	*	0.63 \pm .07	(5)
8 - 12			0.75		0.67	(1)
No. Young Fledge						
All	2.2 \pm 0.5 ^a	(18)	2.2 \pm 0.7	b	1.0 \pm 0.7	(17)
2 - 3			2.8 \pm 0.9		1.0 \pm 0.9 ^c	(5)
4 - 5			2.0 \pm 0.9		0.8 \pm 0.9	(6)
6 - 7			2.2 \pm 2.0		1.4 \pm 2.0	(5)
8 - 12			0		0	(1)
Pn Young Fledge						
All	0.33 \pm .07 ^a	(18)	0.35 \pm .07		0.33 \pm .10	(17)
2 - 3 ^c			0.47 \pm .15		1.00 ^c	(5)
4 - 5			0.33 \pm .10		0.24 \pm .01	(6)
6 - 7			0.31 \pm .16		0.37 \pm .03	(5)
8 - 12			0		0	(1)

^a Differences between control and treatment nests are not significant ($P > .10$); Kruskal-Wallis Oneway ANOVA

^b Statistical differences between host and added eggs were not tested

^c Nests with painted chicken eggs are excluded

^d Wilcoxon Signed-ranks test; ** $P < .01$, * $P < .05$

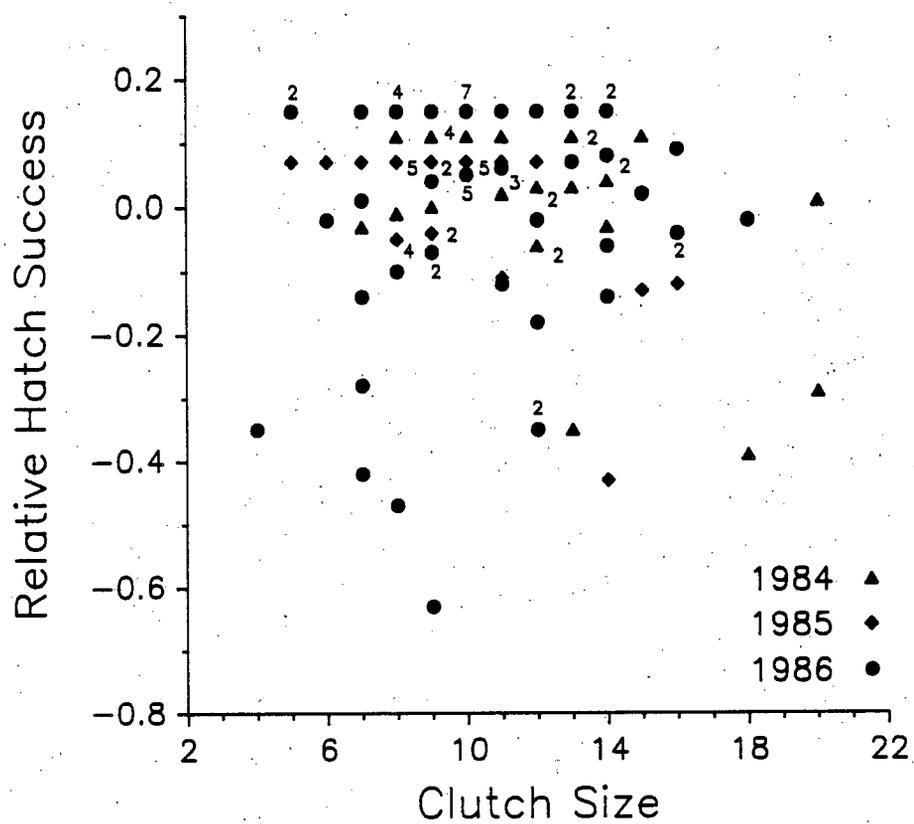


Figure 4.2. The relationship between clutch size and hatch success (standardized for differences among years). Numbers indicate multiple observations for that pair of values.

30 days old before being incubated ($G_w = 3.37$, $df = 5$, $P > .10$; eggs grouped into six periods of 5 days each).

Fledge Success

Unmanipulated nests - Fledge success of young was the same for broods from parasitized nests and non-parasitized nests (Table 4.3). Host and parasite young also survived equally well within parasitized broods ($G_w = 0.05$, $P > .20$; Table 4.5). There was some suggestion, however, that fledge success was greater in larger broods. The proportion of young that fledged per brood was significantly correlated with brood size ($r_s = .36$, $N = 68$, $P < .01$; Figure 4.3), even after I controlled for the effects of laying date ($r_p = .31$, $df = 64$, $P < .01$).

Experimental nests - Fledge success did not differ significantly between experimentally parasitized nests and control nests, nor did it vary with the number of eggs added (Table 4.4) or the total brood size in experimental nests ($r_s = .03$, $P > .10$). Survival of host and added young was also similar in all treatments ($G_w = 2.42$, $P > .10$; Table 4.5). Controlling for laying date or for differences among years did not change any of these conclusions; fledge success in experimentally parasitized broods did not differ from control broods, and there was no effect of the number of eggs added on the survival of young (all $P > .10$).

Differences Among Years

The above analyses consider the effects of brood parasitism for all years combined (after standardizing for year differences). However, some patterns differed when each year was considered separately. For example, nest success was lower in parasitized nests than in non-parasitized nests in 1984, but not in 1985 and 1986 (Figure 4.4; the only significant difference occurred in 1986; $G_w = 6.35$, $P < .05$). Hatch success was also reduced in parasitized nests in 1984, and this remained true when only hosts' eggs were considered (Mann-Whitney U-Test, $P < .02$; Figure 4.4). In 1985, hatch success was lower in parasitized nests, but not significantly so ($P > .10$), and there was no difference in 1986. Hatch success was negatively correlated with

Table 4.5. Recaptures of host and parasite young in broods from (a) naturally parasitized nests and (b) experimentally parasitized nests. Values in parentheses are proportions.

	Host	Parasite	Total
(a) Unmanipulated broods (N = 19)			
No. Hatched	137 (.70)	64 (.30)	201
No. Recaptured	57 (.68)	24 (.32)	82
(b) Experimental broods (N = 8)			
No. Hatched	46 (.73)	17 (.27)	63
No. Recaptured	17 (.89)	2 (.11)	19

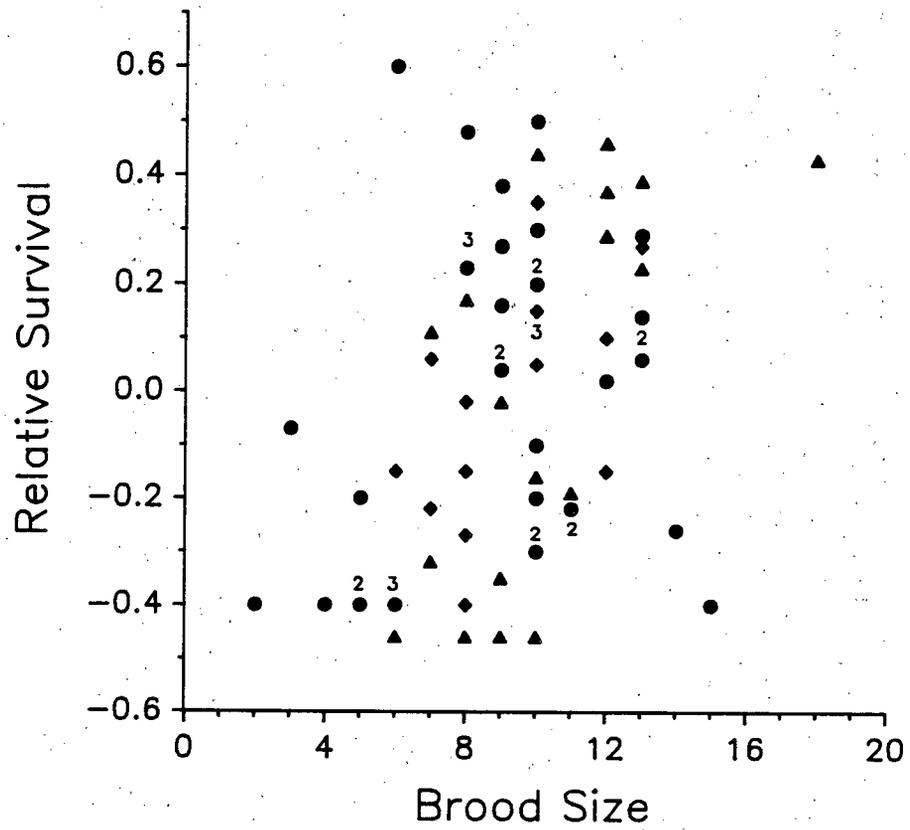


Figure 4.3. The relationship between brood size at hatch and duckling survival (standardized for differences among years). Symbols as in Figure 4.2.

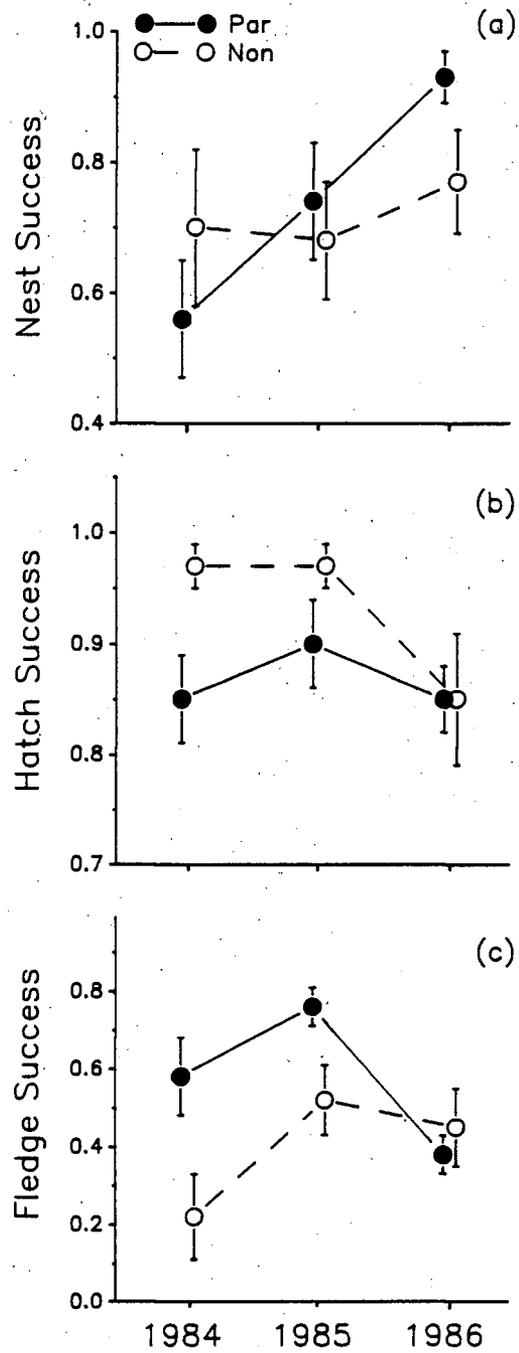


Figure 4.4. Variation in (a) nest success, (b) hatch success, and (c) fledge success among years. Parasitized and non-parasitized nests are shown separately. Means \pm 1 SE.

clutch size in 1984 ($r_p = -.46$, $df = 22$, $P < .05$) and 1985 ($r_p = -.64$, $df = 14$, $P < .01$), but not in 1986 ($r_p = .00$, $df = 47$, $P > .10$; partial correlations controlling for laying date).

These differences correspond to changes in the frequency of brood parasitism among years. For example, parasitism was frequent in 1984 relative to 1985 and 1986. Thirty-one percent of all eggs were parasitic in 1984 compared to 8 percent in 1985 and 18 percent in 1986. In 1984, clutch sizes in parasitized nests averaged 15.2 eggs ($N = 32$) compared to 11.3 eggs in 1985 ($N = 27$) and also in 1986 ($N = 43$). The lower hatch success and nest success in 1984 may therefore have been the result of frequent parasitism and large clutch sizes. This idea is substantiated by the negative correlations between hatch success and clutch size in 1984 and 1985.

Patterns of fledge success also varied among years (Figure 4.4). Fledge success was higher in parasitized broods in 1984 and 1985, although the differences were marginal after controlling for the effects of laying date (both $.10 > P > .05$). Fledge success was significantly correlated with brood size in 1984 ($r_p = .65$, $df = 15$, $P < .05$), but not in 1985 ($r_p = .40$, $df = 12$, $P > .10$) or 1986 ($r_p = .15$, $df = 31$, $P > .10$; partial correlations controlling for laying date).

Net Reproductive Success

Considering all components of reproductive success for all nests (including failed nests), I found no difference between the total number of young fledged from parasitized nests and non-parasitized nests in any of the three years (Mann-Whitney U-tests, all $P > .10$; Table 4.6). In fact, in two years, slightly more host young fledged from parasitized nests. Similarly, the number of host young that fledged from experimentally parasitized nests was equal to the number of young that fledged from control nests (Kruskal-Wallis One-way ANOVA, $H = 3.85$, $df = 4$, $P > .10$; Table 4.6). The only exception to this pattern occurred when 8-12 eggs were added experimentally. In all five of those nests, hosts failed to fledge any young.

Growth of Young

When year effects were removed, there was no difference between parasitized and non-parasitized broods in either mean growth of young ($F = 1.68$, $df = 1,41$, $P > .20$) or maximum

Table 4.6. Net reproductive success (number of fledged young) of goldeneye females in non-parasitized and parasitized nests (hosts only). Means \pm 1 SE. Sample size in parentheses.

	<u>Non-Parasitized</u>		<u>Parasitized</u>	
(a) Unmanipulated Nests ^a				
All	2.05 \pm 0.4	(41)	2.29 \pm 0.3	(70)
1984	1.71 \pm 0.8	(7)	1.52 \pm 0.6	(21)
1985	2.46 \pm 0.7	(11)	3.07 \pm 0.7	(14)
1986	1.96 \pm 0.6	(23)	2.43 \pm 0.4	(35)
(b) Experimental Nests ^b				
All	1.54 \pm 0.4	(26)	1.27 \pm 0.4	(34)
2 - 3			1.40 \pm 0.6	(10)
4 - 5			1.39 \pm 0.5	(13)
6 - 7			1.83 \pm 1.1	(6)
8 - 12			0 \pm 0	(5)

^a None of the comparisons between parasitized and non-parasitized nests are significantly different; $P > .10$; Mann-Whitney U-tests

^b The comparison between control (non-parasitized) and parasitized (experimental) nests was not significant; $P > .10$; Kruskal-Wallis Oneway ANOVA

growth of young ($F = 2.36$, $P > .10$). The same results were obtained when each year was analysed separately (all $P > .10$).

Survival of Females

Thirty-three of 61 parasitized females (54%) returned to the study area in the following year compared to 33 of 53 non-parasitized females (62%; $G_w = 0.77$, $P > .20$). Similarly, 19 of 30 experimental hosts (63%) and 13 of 21 control females (62%) returned in the following year ($G_w = 0.10$, $P > .20$). Since female goldeneyes are highly philopatric and return rates closely approximate survival rates (Savard and Eadie 1989), I conclude that parasitism did not affect the survival of host females.

DISCUSSION

Costs to the Host?

Several researchers have argued that brood parasitism is detrimental to the precocial host (Weller 1959, Jones & Leopold 1967, Joyner 1976, Giroux 1981). I found little evidence to support such a claim for goldeneyes. Parasitized females produced, on average, the same number of young as non-parasitized females (Table 4.6), growth of young was not compromised in parasitized broods, and there was no effect of parasitism on female survival. This was true for both naturally and experimentally parasitized nests. The only indication of any deleterious effect of parasitism on hosts occurred when the frequency of parasitism was high and clutch sizes were extremely large. In 1984, the average clutch size in parasitized nests was almost double the size of non-parasitized clutches. In that year, there was a negative correlation between hatch success and clutch size, and hatch success of host eggs was significantly reduced in parasitized nests (Figure 4.4). In contrast, the frequency of parasitism was low to moderate in 1985 and 1986 and I did not detect any effects of parasitism on host success. Thus, there may be a limit to the number of parasitic eggs that can be added to a host nest without affecting the success of the host. This idea is supported by the observation that nests with more than 20 eggs failed to

produce any young (Table 4.2). A similar result was obtained when large numbers of eggs (8-12) were added experimentally to host nests (Table 4.4).

If this pattern is typical of other species, it could account for conflicting evidence on the effects of brood parasitism on precocial hosts. Studies on the same species have often yielded entirely different conclusions (e.g. Jones and Leopold 1967, Morse and Wight 1969 versus Clawson et al. 1979, Heusmann and Belville 1982). However, most studies have been short-term or have been conducted in a single location. The effects of brood parasitism on hosts will undoubtedly vary with the frequency of parasitism among years and/or among areas. Two long-term studies on wood ducks (Haramis & Thompson 1985, Semel et al. 1988) demonstrate this convincingly. Haramis & Thompson (1985) found that proportion of parasitized wood duck nests ranged between 14% and 73% over the seven years of their study. Nesting success of hosts was affected only when more than 50% of the nests were parasitized and clutch sizes were 2-3 times larger than in non-parasitized nests. Semel et al. (1988) found similar results, and showed that hatch success declined significantly when clutch sizes exceeded 16-20 eggs. In both of these studies, population density was an important factor - high densities led to frequent brood parasitism and, correspondingly, low success of hosts.

My results parallel these observations. Further, I show in Chapter 6 that the frequency of parasitism is related to the density of breeding females. Taken together, all three studies indicate that demographic and social factors influence the extent to which host reproductive success is affected. For goldeneyes, I conclude that the effects of parasitism on hosts are minimal in most years, but that the reproductive success of hosts may be reduced when the frequency of parasitism is high.

Benefits to the Host?

Nudds (1980), Andersson (1984) and Eadie & Lumsden (1985) recently suggested that hosts might benefit from being "parasitized" through a reduction in mortality of host young in parasitized broods. I found no convincing evidence for such an effect, although there was some disagreement between the results of the observational and experimental studies. There was a

trend for increased survival in naturally parasitized broods in two of three years (Figure 4.4), and fledge success and brood size were positively correlated in 1984 and for all years combined. However, survival was not higher in broods from experimentally parasitized nests, and there was no relationship between brood size and fledge success in experimental broods.

The results from the naturally parasitized broods were potentially confounded by two factors. First, nests that were initiated early in the breeding season were more likely to be parasitized, and the higher survival of young in naturally parasitized nests might simply reflect the seasonal decline in fledge success (Chapter 3). When I controlled for the effects of laying date, fledge success was not significantly higher in parasitized broods, although the relationship between brood size and survival remained. Second, parasitic females might choose better hosts such that the higher survival of parasitized broods is a consequence of female quality, rather than a direct effect of brood parasitism. For example, older females were more likely to be parasitized (Eadie, in prep), and fledge success improves significantly with age of the female (Chapter 3). The results of the observational studies are therefore inconclusive. Experimental manipulations provide the only method to control for such effects. Since I found no effect on brood survival when I parasitized goldeneye nests experimentally, I conclude that hosts do not benefit by being "parasitized".

In an earlier study, Eadie & Lumsden (1985) found that the survival of common goldeneye young was higher in broods parasitized by hooded mergansers (*Lophodytes cucullatus*). Survival of host young was also superior to that of the parasite young within parasitized broods. We suggested that mortality of host young may have been reduced through a selfish herd effect, such that the risk of predation was displaced to the parasitic offspring. Amat (1987) countered that our study failed to control for the effects of initiation date or for differences in habitat requirements of the parasitic ducklings. Although a reanalysis of the data did not change our original conclusions (Eadie & Lumsden, in prep), the results of the present study support Amat's (1987) criticisms. Factors such as laying date or female quality can confound interpretations based on observational studies.

The benefit hypothesis assumes that mortality of young is due largely to predation. While there is circumstantial evidence to suggest that this assumption is often valid (Safriel 1975, Bellrose 1976), exposure and starvation are important additional sources of mortality. Amat (1987) argued that, in cases of interspecific parasitism, differential mortality of parasite young could be due simply to inappropriate habitat use or parental care patterns of the host. However, predation could still fall disproportionately on parasite young if, by virtue of being starved or in poorer condition, parasitic offspring react more slowly to a predator.

The benefit hypothesis also proposes that survival of precocial young is improved in larger broods because of increased vigilance, predator swamping, and/or a dilution effect (review in Eadie et al. 1988). There have been relatively few tests of the relationship between brood size and offspring survival in birds with precocial offspring, and the majority of these have been based on observational data. Of ten observational studies, 3 found that survival was greater in smaller broods (Andersson and Eriksson 1982, Rockwell et al 1987, Erikstad and Andersen 1983), 3 found no effect of brood size (Clawson et al 1979, Heusmann et al 1980, Dow and Fredga 1984), and 4 found that survival was greater in larger broods (Eltringham 1974, Munro and Bedard 1977, Eadie and Lumsden 1985, Kehoe 1986). Only four studies manipulated brood size or clutch size experimentally; three of these found no effect of brood size on offspring survival (Rohwer 1985, Lessells 1986, present study) while one found that survival was reduced in large broods (Safriel 1976). Clearly, no single pattern emerges from these studies and support for the benefit hypothesis remains weak and unsubstantiated.

Costs to the Parasite?

The hatch success of parasite eggs was significantly lower than that of host eggs in the same nest. One reason for this pattern is that parasites occasionally laid eggs after the host had started to incubate the clutch. In waterfowl, eggs laid during incubation either fail to hatch, or the hatchlings are abandoned in the nest. Observations of large numbers of non-term eggs or deserted newly-hatched ducklings are common in parasitized nests of wood ducks and black-bellied tree ducks (Morse and Wight 1969, McCamant and Bolen 1979, Haramis and Thompson

1985). However, only 14% of all parasitic goldeneye eggs were laid during the incubation period of the host and many of these eggs hatched, indicating that they were laid soon after the host started incubation. Thus, parasitic goldeneyes appear to be relatively efficient at parasitizing hosts during the period when eggs have the greatest chance of being successful.

Hatch success of eggs added experimentally to nests was also lower than that of host eggs. These results cannot be explained by "late" laying since, in all cases, I added the eggs to the nest before the host began to incubate the clutch. The experimental eggs were often older than those of the host, but this did not significantly affect egg viability. Hatch success remained high for eggs that were up to 30 days old before being incubated. There are two other possibilities: First, the reduced success of the experimental eggs may be an artifact of handling and transportation. I handled host eggs in control and experimental nests in an identical manner, but experimental eggs were, of necessity, collected elsewhere and subsequently transported to the host nest. I did not control for this effect. Second, hosts might displace parasitic eggs to the periphery of the clutch where incubation is less efficient. Such displacement occurs in multiple-female nests of ostriches (*Struthio camelus*; Bertram 1979) and has been suggested for shelducks (*Tadorna tadorna*; Pienkowski & Evans 1982). I examine this possibility in the following chapter.

Comparisons to Other Species

My results contrast with studies of altricial birds in which the effects of brood parasitism can be so severe that hosts fail to produce any young of their own (Payne 1977a, Davies & Brooke 1988). In altricial birds, the demands of providing for young after hatch are substantial, and caring for additional parasitic young could exceed the capabilities of the parents. In contrast, the young of precocial birds require little parental care and the costs of providing for parasitic young may be small. To test this idea more thoroughly, I surveyed the literature for studies that have measured the effects of facultative brood parasitism on the reproductive success of altricial and precocial hosts (Table 4.7). Most of the 31 studies demonstrate some effect of parasitism.

Table 4.7. The effects of facultative brood parasitism on nest success (NS), clutch size (CS), hatch success (HS), and fledge success (FS) of altricial and precocial hosts.

	Effect on:				Source ^a
	NS	CS	HS	FS	
Altricial Birds					
Cliff Swallow (<i>Hirundo pyrrhonata</i>)		X ^b		X	1
Barn Swallow (<i>H. rustica</i>)		X		X	2
Starling (<i>Sturnus vulgaris</i>)		X	X	X	3
House Sparrow (<i>Passer domesticus</i>)		X		- ^c	4
Dead Sea Sparrow (<i>P. moabiticus</i>)	X		X	X	5
Semi-Precocial Birds					
Moorhen (<i>Gallinula chloropus</i>)				X	6
American Coot (<i>Fulica americana</i>)	(+)			(X)	7,8
Precocial Birds					
a) Intraspecific Parasitism					
Wood Duck (<i>Aix sponsa</i>)	(X) ^c	-	(X) ^c	-	9
" "	(X) ^c		(X) ^c		10
" "			X	-	11
" "	X			-	12
" "			X		13
" "					14
Common Goldeneye (<i>B. clangula</i>)	X			-	15
" "	?			-	16
" "	(X) ^c	X		X	17
" "	(X) ^c			(+)	18
Barrow's Goldeneye (<i>B. islandica</i>)	(X) ^c			(+)	18
Bufflehead (<i>B. albeola</i>)	X				19
Shelduck (<i>Tadorna tadorna</i>)	X		X	-	20
Gadwall (<i>Anas strepera</i>)	X		X	-	21
Snow Goose (<i>Chen caerulescens</i>)		-	(X)	-	22
Black-bellied Whistling Duck (<i>Dendrocygna autumnalis</i>)	X		X	-	23
b) Interspecific Parasitism					
Canvasback (<i>Aythya valisineria</i>)		X		-	24
" "		X	X	-	25
" "	?	X	X	-	26
Redhead (<i>A. americana</i>)	X	X		-	27
Pochard (<i>A. ferina</i>)			?	-	28
Ruddy Duck (<i>Oxyura jamaicensis</i>)	?	X		-	27

Continued next page ...

Table 4.7. Continued.

	Effect on:				Source ^a
	<u>NS</u>	<u>CS</u>	<u>HS</u>	<u>FS</u>	
Mallard (<i>Anas platyrhynchos</i>)				-	27
" "		X	X	-	29
" "		?		-	26
Cinnamon Teal (<i>A. cyanoptera</i>)		X	X	-	27
" "	X	X		-	26
Pintail (<i>A. acuta</i>)				-	27
Gadwall (<i>A. strepera</i>)			?	-	21
Common goldeneye (<i>B. Clangula</i>)				(+)	30
" "	(X) ^c			(+)	18
Barrow's Goldeneye (<i>B. islandica</i>)	(X) ^c			(+)	18
Hooded Merganser (<i>Lophodytes cucullatus</i>)				-	31

^a Sources: (1) Brown 1984; (2) Moller 1987; (3) Evans 1988; (4) Yom-tov 1980b; (5) Kendra et al. 1988; (6) Gibbons 1986; (7) Weller 1971; (8) Fredrickson 1969; (9) Semel et al. 1988; (10) Haramis & Thompson 1985; (11) Morse & Wight 1969; (12) Jones & Leopold 1967; (13) Clawson et al. 1979; (14) Heusmann & Bellville 1982; (15) Grenquist 1963; (16) Eriksson & Andersson 1982; (17) Andersson & Eriksson 1982; (18) This study; (19) Pienkowski & Evans 1982; (21) Hines & Mitchell 1984; (22) Lank et al. 1988; (23) McCamant & Bolen 1979; (24) Sugden 1980; (25) Bouffard 1983; (26) Weller 1959; (27) Joyner 1976; (28) Amat 1985; (29) Joyner 1976; (30) Eadie & Lumsden 1985; (31) Bouvier 1974

^b "X" negative effect; "+" positive effect; " " no effect; "()" uncertain effect; "-" not measured;

^c Negative effects on the host were apparent only at high levels of parasitism

In altricial birds, parasitism frequently caused a reduction in clutch size and a reduction in fledge success of the host (Table 4.7). Reduced nest success (mostly due to nest desertion) and reduced hatch success were more often observed for precocial hosts. These results are consistent with expectations based on the patterns of parental care in the two groups of birds. Altricial birds lay small clutches and invest considerable time and energy into feeding and caring for offspring after hatch. The effects of parasitism would therefore be manifest in a reduction of fledging success. Clutch size reductions might result through either depressed ovulation or egg removal by parasitic females (e.g. Brown and Brown 1987). Precocial birds, on the other hand, lay large clutches and hatch success can be compromised when clutch sizes become extreme (Jones and Leopold 1967, Hines and Mitchell 1984). Parasitism in precocial birds should therefore have a greater influence on nest success and hatch success, as observed.

There was some suggestion that the effects of parasitism on precocial hosts differed when parasitism was between, rather than within, species. Specifically, host clutch sizes were more often affected in cases of interspecific brood parasitism, while nest success was more frequently affected in cases of intraspecific parasitism (Table 4.7). However, these patterns are confounded by differences in nesting habits of hosts. All but one of the studies of interspecific parasitism dealt with ground nesting ducks, whereas all but two of the studies of intraspecific parasitism dealt with cavity or burrow nesting ducks. We would expect clutch reductions to be more frequent in ground nesting hosts simply because eggs are more likely to be displaced from a ground nest than from a burrow or cavity nest (see also Joyner 1976). Conversely, increased competition among cavity-nesting females for limited nest sites might lead to increased interference and ultimately nest desertion at high frequencies of parasitism (Jones & Leopold 1967, Haramis & Thompson 1985, Chapter 3). The consequences of parasitism therefore appear to be influenced more by the nesting habits of the host than by the species of the parasite.

One difficulty in interpreting this survey is that so few of the studies were experimental. My own results for goldeneyes show that inferences based on observational analyses alone can be misleading. This was particularly true in assessing the effects of parasitism on hatch success and brood survival of hosts (above). Nonetheless, numerous authors have drawn conclusions about

the consequences of brood parasitism to precocial hosts based only on observational comparisons of the average success of parasitized and non-parasitized nests (Jones and Leopold 1967, Morse and Wight 1969, Yom-Tov et al. 1974, Clawson et al. 1979, Yom-Tov 1980b, Pienkowski and Evans 1982, Hines & Mitchell 1984). Until further experimental studies are completed, such conclusions should be viewed with caution.

CHAPTER 5

BROOD PARASITISM IN A PRECOICIAL BIRD:

II. HOST RESPONSES

Avian brood parasites typically reduce the reproductive success of their hosts (Rothstein 1975a, Payne 1977a). In extreme cases, parasitic adults or nestlings kill all of the host's own young (Rothstein 1975a, Payne 1977a). More commonly, host offspring suffer increased competition with parasitic young for food and essential care. Traits that enabled hosts to avoid or reduce the impact of parasitism should therefore be at a selective premium. Indeed, numerous anti-parasite defences have been reported for hosts of obligate brood parasites (review in Payne 1977a).

Fewer studies have examined host defences in cases of facultative parasitism, and most of these have focused on altricial birds (Brown 1984, Emlen & Wrege 1986, Moller 1987). Studies of precocial hosts have generally failed to reveal evidence of anti-parasite defences (e.g. Weller 1959, Joyner 1976, Saylor 1985, but see Andersson & Eriksson 1982 and below). In some ducks, hosts readily "accept" parasitic eggs and even tolerate egg-laying by parasites while remaining on or near the nest (Nudds 1980, Saylor 1985). This has led to some debate over the adaptive significance of such host tolerance (Nudds 1980, Giroux 1981, Saylor 1985). However, there are three reasons why a precocial host might not defend against parasites: (1) parasitism occurs infrequently and the selective value of host defence is low; (2) genetic or life-history constraints prevent the development of host defences; or (3) parasitism does not reduce the success of the host and anti-parasite behaviours are superfluous.

In the previous chapter, I showed that facultative parasitism in goldeneyes had little effect on the reproductive success of hosts. Accordingly, we would expect few host defences (hypothesis 3). However, Andersson and Eriksson (1982) demonstrated that common goldeneyes (*Bucephala clangula*) in Sweden do respond to parasitism by: (i) adjusting their clutch size and (ii) deserting the nest. In addition, Gauthier (1987) argued that territoriality in buffleheads (*B.*

albeola) functioned, in part, to defend the nest site from parasitism by conspecifics. In this study, I repeat and extend Andersson & Eriksson's (1982) experiments and test Gauthier's (1987) hypothesis for common and Barrow's goldeneyes (*B. islandica*). I consider further the possibility that hosts manipulate or remove parasitic eggs, and I assess the effects of parasitism on host fidelity to their nest site.

HOST RESPONSES TO PARASITISM: PREDICTIONS

Nest Desertion

If parasitism severely reduces either the reproductive success or the survival of females, hosts might benefit by abandoning their nests. They could then either start new nests, or defer breeding to the following year (Andersson 1984). Although desertion is often related to brood parasitism in ducks (Weller 1959, Jones and Leopold 1967), cause and effect are rarely demonstrated. Nests that are deserted for other reasons may be more likely to be subsequently parasitized, particularly if there is no host present to deter parasitic females (Andersson 1984). Desertion might also be a generalized response to any disturbance at the nest, including interference by other females (Hamilton and Orians 1965, Andersson 1984). I tested the prediction that desertion rates would be higher in parasitized nests and determined whether desertion was a direct response to parasitism.

Host Clutch Size

Hosts might respond to parasitism by adjusting their own clutch size (Weller 1959, Andersson & Eriksson 1982, Brown 1984). Andersson and Eriksson (1982) proposed 3 hypotheses:

- (1) Hosts are determinate layers and do not adjust their own clutch size when parasitized.
- (2) Hosts reduce their clutch size by the number of parasitic eggs added. According to this hypothesis, hosts accept parasitic eggs because they cannot distinguish their own eggs from those of another female. When parasite eggs differ in size, shape and/or colour (e.g. interspecific parasitism), hosts will not mistake parasite eggs for their own and so will not reduce their clutch size (Eadie and Lumsden 1985).

(3) Hosts recognize parasitic eggs, and alter their clutch size to maximize the production of their own young. An optimality model developed by Andersson and Eriksson (1982) predicts that hosts should reduce their own clutch by half as many eggs as the parasite has added. However, this prediction holds only if duckling survival is negatively related to brood size. Otherwise, hosts should not reduce their clutch size when parasitized.

These hypotheses give contrasting predictions which depend on (i) the similarity of host eggs to parasite eggs, and (ii) the relationship between brood size and survival (Table 5.1). I tested these predictions by quantifying the relationship between brood size and survival, and by adding either goldeneye eggs (similar) or bufflehead/chicken eggs (different) to host nests.

Nest Guarding

Territoriality is absent or reduced in most ducks, but it is prominent in all three species of *Bucephala*. Gauthier (1987) proposed that site-specific territories prevented intraspecific brood parasitism in buffleheads. I tested three predictions of this hypothesis: (1) most territories will be adjacent to the nest site; (2) females with territories that are not adjacent to their nest will be more likely to be parasitized; and (3) females that change nest sites between years will change their territory location to correspond, and vice versa (Gauthier 1987).

Egg Tossing

Hosts might reduce the impact of parasitism by removing parasitic eggs, or by displacing them to the edge of the nest (e.g. Brown 1984, Moller 1987, Arnold 1987). This requires that hosts can distinguish parasitic eggs of conspecifics. I looked for evidence of egg tossing or egg displacement in naturally and experimentally parasitized nests.

Change of Nest Sites

Breeding dispersal in birds and other vertebrates often occurs in response to nest failure or low reproductive success (Newton & Marquiss 1982, Dow and Fredga 1983, Sonerud 1985). Parasitized females might change nest locations in the following year to avoid being parasitized

Table 5.1. Predicted clutch size adjustments by hosts according to the Determinate Layer hypothesis, the Egg Recognition hypothesis and the Optimal Adjustment hypothesis.

Survival vs. Brood Size:	Negative		Not Negative	
	Similar	Different	Similar	Different
Determinate Layer Hypothesis	No Change	No Change	No Change	No Change
Egg Recognition Hypothesis	Reduce	No Change	Reduce	No Change
Optimal Adjustment Hypothesis	Reduce by 1/2	Reduce by 1/2	No Change	No Change

repeatedly. This would be particularly effective if certain nest boxes were more attractive to parasites. I tested this prediction by comparing the fidelity of parasitized and non-parasitized females to their previous nest sites.

METHODS

Methods follow the procedures outlined in Chapters 2 and 3. Parasitized nests and parasitic eggs were identified as described in Appendix 1.

Nest Desertion - I considered any nest that contained unincubated eggs to be deserted. Some nests were incubated for several weeks and then abandoned near the end of incubation. I did not include these nests in the present analysis since desertion may have occurred for reasons unrelated to brood parasitism. I also excluded nests containing less than 3 eggs. These nests were never incubated and were probably incomplete. Moreover, I could rarely determine whether these nests were parasitized. Finally, I excluded nests that were deserted in response to nest predation.

To determine whether females were attracted to nests containing eggs and to assess whether "deserted" nests were more likely to be parasitized, I constructed simulated nests containing three goldeneye eggs, or three chicken eggs painted to resemble goldeneye eggs. Pairs of nest boxes were erected within 100 m of each other in 1984. In 1985 and 1986, one member of each pair was randomly assigned to the treatment group (3 eggs placed in the nest) while the other box was designated as the control nest (only wood shavings in the box). Decoy eggs were placed in the treatment nest at the beginning of the nesting season. In 1986, I established a second group of control nests by adding down and eggs shells to simulate a previously used nest site. These nests were constructed in unused boxes (erected in 1984) and were located adjacent to treatment and control nests. Females did not respond differently to the two types of control nests and I pool them in this analysis.

Experimental Parasitism - I conducted two egg addition experiments. In the first, I added eggs that were either similar to those of the host (goldeneye eggs or large chicken eggs painted to

resemble goldeneye eggs) or different from the host (bufflehead eggs or small, unpainted chicken eggs). Four eggs were added to each host nest. In the second experiment, I added different numbers of goldeneye eggs in the following treatments: 2-3 eggs, 4-5 eggs, 6-7 eggs, 8-12 eggs. Details of the protocol for all of the egg addition experiments are given in Chapter 3.

I also monitored the number of eggs laid by hosts in naturally parasitized nests (see Chapter 3 for details). I standardized for differences in host clutch sizes among years by subtracting the yearly mean from the raw data. I used ANCOVA to control for the effects of laying date on clutch size (Chapter 3).

Territories - Territory locations of all nesting females were determined by repeated surveys of the study lakes, and by extended observations at particular locations. I defined a territory as being adjacent to a nest site if the female of the closest territorial pair was the owner of that nest (after Gauthier 1987). The distance from the closest edge of the territory to the nest site was measured on scale maps.

Egg removal and displacement - All eggs in nests were numbered with a permanent ink felt pen marker on or near the day they were laid. I recorded any instance in which numbered eggs went missing. I include here only nests that were incubated since the disappearance of eggs from deserted nests was probably the result of predation. I also exclude cases in which an egg was discovered missing from a nest during incubation and the nest was deserted immediately after; again, predation or nest disturbance could have been the cause.

I monitored the position of all eggs in thirty-three nests in 1986. An egg was classified as being in the center of a clutch (IN) if it was surrounded on all sides by other eggs. An egg was classified as being on the outside of a clutch (OUT) if it was on the perimeter of the clutch, and was adjacent to only 1 or 2 other eggs. I revisited nests up to 8 times during the incubation period (mean = 3.6 visits/nest), and noted the number and identity of the eggs that were in the IN or the OUT position.

RESULTS

Nest Desertion

Unmanipulated nests - Nest desertion was not significantly higher in parasitized nests compared to non-parasitized nests in any year (G-tests with Williams' correction, all $P > .05$; Figure 5.1), although more parasitized nests were deserted in 1984 when brood parasitism was frequent. Desertion did, however, vary with clutch size (Figure 5.2). The frequency of desertion increased rapidly in nests with more than 16 eggs, and clutches greater than 20 eggs were never incubated (Figure 5.2). These results suggest that parasitized nests were more likely to be deserted when clutch sizes were extreme.

Experimental nests - Addition of goldeneye eggs or bufflehead/chicken eggs did not increase nest desertion in experimental nests relative to control nests (Figure 5.3a; $G_w = 0.19$, $P > .20$). There was also no effect of the number of experimental eggs added (Figure 5.3b; $G_w = 1.99$, $P > .20$).

Decoy nests - Goldeneyes used decoy nests and control nests equally in the two years of the experiment; 8 of 20 (40%) decoy nests were used compared to 9 of 28 (32%) control nests (Fisher's Exact Test, $P > .30$). Only 4 of the 8 decoy nests were incubated compared to 8 of the 9 control nests (Fisher's Exact test, $P = .11$). Thus, in 4 cases, nests were "parasitized" after being "deserted".

I placed a stuffed female goldeneye on 4 nests to examine the response of goldeneye hens to the presence of another female. Three of these nests were deserted 2-7 days later. In two cases, the decoy was wet with ruffled and pulled feathers when I removed it from the nest. However, I did not witness any interactions of the host with the decoy female in 8 h of observation at each nest.

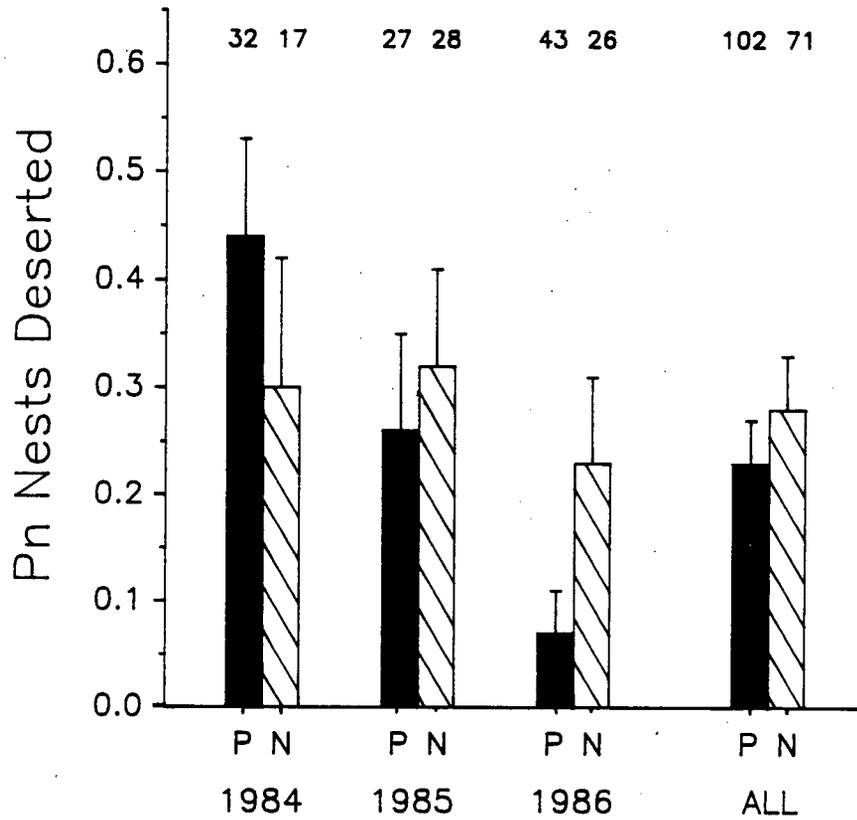


Figure 5.1. The frequency of nest desertion for naturally parasitized nests (solid) and non-parasitized nests (open). Numbers above bars are sample sizes; error terms are 1 SE.

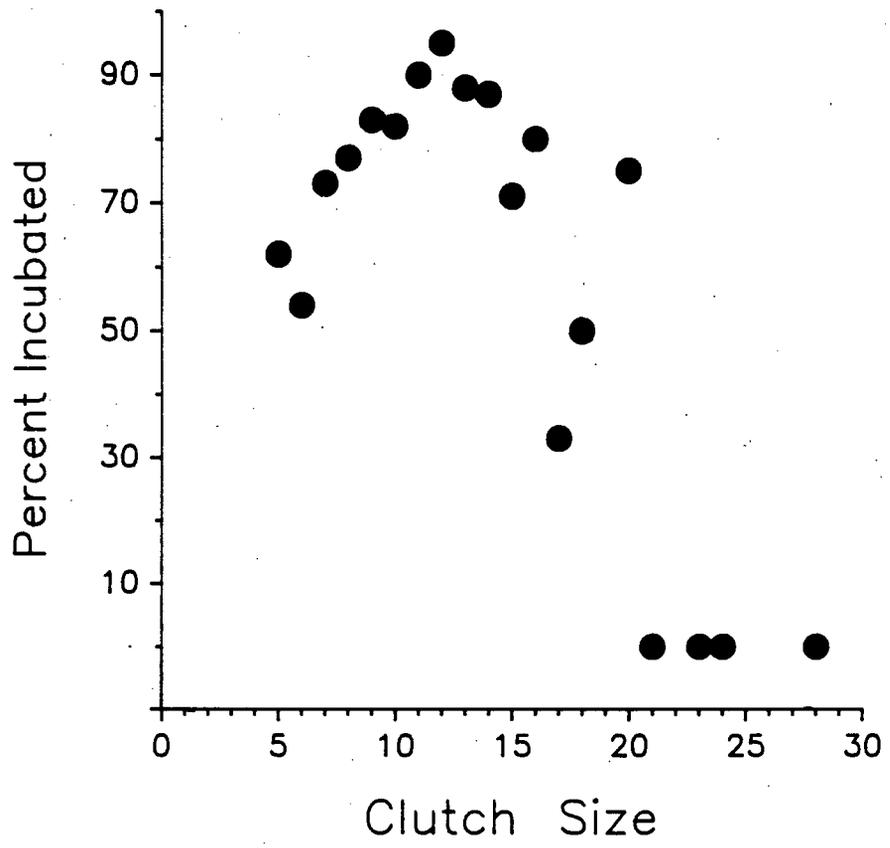


Figure 5.2. The relationship between clutch size and the proportion of nests incubated. Incomplete clutches (nests with fewer than 5 eggs) are not shown.

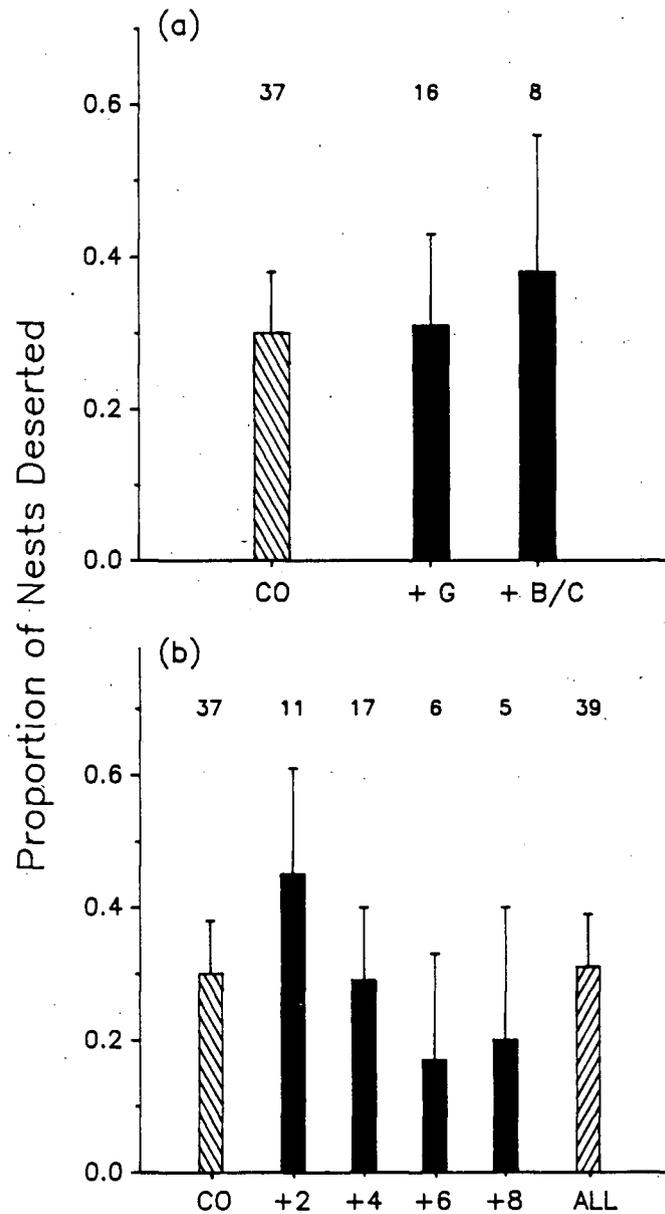


Figure 5.3. The frequency of nest desertion in experimentally parasitized nests. (a) Desertion rates in nests with 4 goldeneye eggs (G) or 4 bufflehead / chicken eggs (B/C) added compared to control nests (CO); (b) Desertion rates in nests with different numbers of goldeneye eggs added. Numbers above bars are sample sizes; error terms are 1 SE.

Host Clutch Size:

Unmanipulated nests - Hosts did not reduce their own clutch size when parasitized (Figure 5.4). Clutch sizes of females in parasitized and non-parasitized nests did not differ in any year, nor when all years were combined (Mann-Whitney U-tests, all $P > .10$). The results were unchanged when I controlled for laying date (ANCOVA; all $P > .10$), and when I considered each species separately (Means \pm 1 SE: **Barrow's** - parasitized host: 7.9 ± 0.3 eggs, $N = 39$ nests; non-parasitized: 7.9 ± 0.3 , $N = 31$; **common** - parasitized host: 7.5 ± 0.3 , $N = 28$; non-parasitized: 8.3 ± 0.3 , $N = 16$; both $P > .15$, Mann-Whitney U-tests).

I collected a small number of females to determine clutch sizes directly by counting the number of post-ovulatory follicles (POF's; Payne 1973, Scott and Ankney 1980). The average number POF's for 7 parasitized females (hosts) was 8.3 ± 0.4 SE compared to an average of 8.0 ± 0 for 2 females that were not parasitized. These values are in direct agreement with the observational analyses.

Experimental nests - Hosts did not reduce their own clutch size when either 4 goldeneye eggs or 4 bufflehead/chicken eggs were added experimentally to their nests (Kruskal-Wallis One-way ANOVA, $H = 0.10$, $P > .50$; Figure 5.5a). Clutch sizes of hosts did also not vary with the number of experimental eggs added ($H = 3.6$, $df = 4$, $P > .10$; Figure 5.5b).

Andersson and Eriksson (1982) found that goldeneyes reduced their clutch only if eggs were added early in the host's laying period. Accordingly, I divided the 27 goldeneye addition nests into those to which I added the eggs early in the host's laying period (less than 4 eggs laid), and those to which I added the eggs late (4 or more eggs present in the nest). Host clutch sizes averaged 7.0 ± 0.3 in early addition nests ($N = 17$), 7.4 ± 0.4 in late addition nests ($N = 10$), and 7.5 ± 0.3 in the control nests ($N = 26$). These differences were not significant (Kruskal-Wallis One-way ANOVA, $H = 2.45$, $P > .25$).

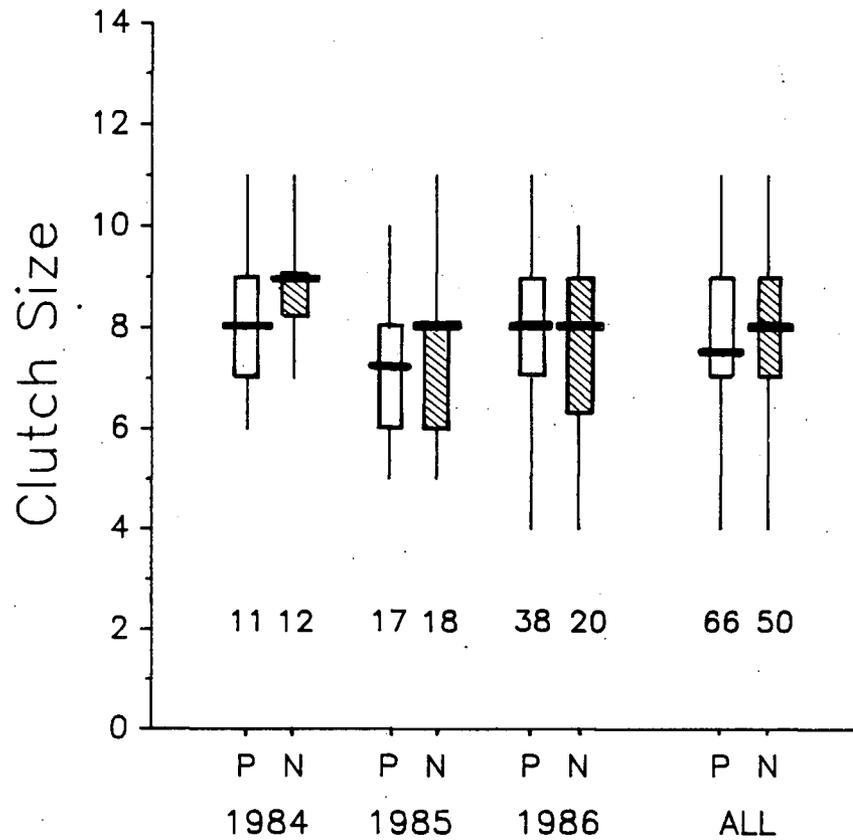


Figure 5.4. Clutch sizes of females (hosts) in naturally parasitized nests (P) and non-parasitized nests (N). The median (horizontal line), interquartile interval (box), and range (vertical line) are shown. Numbers below plots are sample sizes.

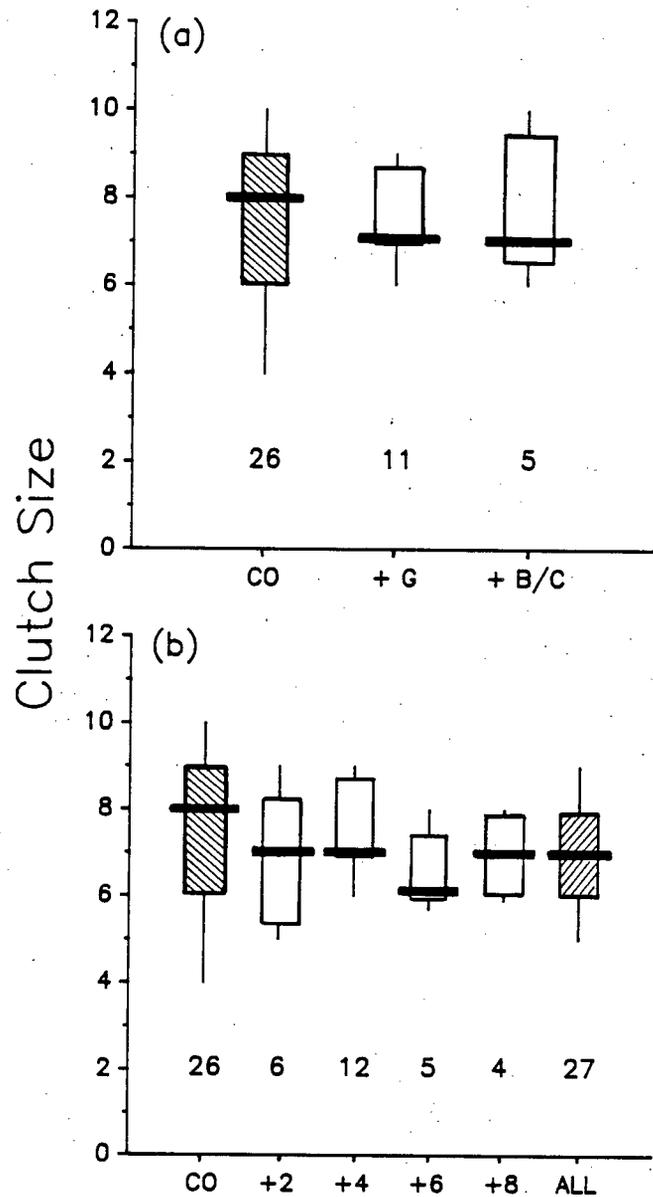


Figure 5.5. Clutch sizes of females in experimentally parasitized nests. (a) Clutch sizes in nests with 4 goldeneye eggs (G) or 4 bufflehead / chicken eggs (B/C) added, compared to control nests (CO); (b) Clutch sizes in nests with different numbers of goldeneye eggs added.

Nest Guarding

I found no relationship between territory location and the probability that a host would be parasitized. Only half of all pair territories were adjacent to the nest site used by the female (31 of 63 territories). Females with territories adjacent to their nest sites were parasitized as frequently as females with non-adjacent territories (20 of 31 females with adjacent territories compared to 21 of 32 females with non-adjacent territories; $G_w = .01$, $P > .50$). The average distance from the territory to the nest site was greater for parasitized than for non-parasitized females ($216 \pm 53\text{m}$, $N = 38$ and $154 \pm 66\text{m}$, $N = 20$, respectively), but the difference was not statistically significant (Mann-Whitney U-test, $U = 388.5$, $P > .5$).

I also found no evidence that females moved to a closer territory location when they changed nest sites. Of the seventeen females with known nest and territory locations in two consecutive years, most females (12) returned to the same nest site and the same pair territory. Two of the three females that changed nest sites also changed territories, but only one moved closer to her nest. Conversely, all of the four females that changed territory locations moved further, on average, from their nest (distance before: $179 + 97\text{m}$; distance after: $349 + 133\text{m}$). This pattern is opposite to that predicted if territoriality functioned to protect the nest from brood parasites.

Egg Tossing and Egg Displacement

(a) Egg Tossing:

Unmanipulated nests - I observed 36 cases (in 28 nests) in which eggs disappeared from nests. The eggs had been marked with a permanent ink marker on the day they were laid and were discovered missing several days to weeks later. Egg tossing occurred significantly more often in parasitized nests (Table 5.2a; $G_w = 11.7$, $P < .001$), although host and parasite eggs were equally likely to disappear from these nests ($G_w = 1.2$, $P > .20$; Table 5.3a).

Table 5.2. Disappearance of eggs from parasitized nests (Para) and non-parasitized nests (Non). Values in parentheses are proportions.

	Non	Para	Total
(a) Unmanipulated nests			
No. Nests In Which	5	14	19
Eggs Disappeared	(.30)	(.70)	
No. Expected ^a	12.4	6.6	
	(.65)	(.35)	
(b) Experimental nests			
No. Nests In Which	1	8	9
Eggs Disappeared	(.11)	(.89)	
No. Expected ^b	4	5	
	(.45)	(.55)	

^a Based on the observation that 35% of nests are parasitized

^b Based on the numbers of control (N=27) and experimental (N=32) nests

Table 5.3. Disappearance of host eggs and parasite eggs from within parasitized nests. Values in parentheses are proportions. Eggs that could not reliably be assigned to the host or the parasite are excluded.

	Host	Parasite	Total
(a) Unmanipulated nests			
No. Eggs	6	8	14
Disappeared	(.43)	(.57)	
No. Expected ^a	8.1	5.9	
	(.58)	(.42)	
(b) Experimental nests			
No. Eggs	1	10	11
Disappeared	(.09)	(.91)	
No. Expected ^b	7.6	3.4	
	(.69)	(.31)	

^a Calculated on the basis that 88 of 152 eggs (58%) were host eggs while 64 (42%) were parasitic

^b Calculated on the basis that 63 of 91 eggs (69%) were host eggs while 28 (31%) were added experimentally

Experimental nests - Eggs disappeared more frequently from experimental nests than from control nests (Table 5.2b; $G_w = 4.5$, $P < .05$). Within experimental nests, experimental eggs were more likely to disappear than host eggs ($G_w = 16.8$, $P < .001$; Table 5.3b). In all but 2 cases, the experimental eggs that were tossed were either bufflehead eggs (1) or chicken eggs (7).

(b) Egg displacement:

Unmanipulated nests - Contrary to the prediction that hosts would exclude parasitic eggs to the periphery of the clutch, parasite eggs were located slightly more often in the middle of the clutch (Table 5.4a). The same pattern held when each nest, rather than each egg, was considered as an independent sample. In 21 of 33 parasitized nests, parasite eggs occurred more often than expected in the IN position. In the 19 nests in which eggs were recorded in the OUT position, parasite eggs were OUT more often than expected in only 4 nests.

Experimental nests - Experimental eggs were not more likely to be excluded to the periphery of the clutch than host eggs (Table 5.4b). Host eggs occurred in the IN position slightly more often than expected, while added eggs occurred in the OUT position slightly more often than expected (Table 5.4b).

Nest Change

Unmanipulated nests - Females that failed to hatch young in a nest were more likely to change sites in the following year than females that were successful (Chapter 3). However, parasitism did not influence breeding dispersal since the same proportion of parasitized females changed nest sites (11 of 33) relative to non-parasitized females (9 of 33; $G_w = 0.28$, $P > .5$).

Experimental nests - Goldeneyes did not change nest sites in response to experimental parasitism. Six of 19 experimental females and 5 of 13 control females moved to a new nest site in the following year ($G_w = 0.15$, $P > .50$).

Table 5.4. The position of host eggs (Host) and parasite eggs (Para) within parasitized nests. Values in parentheses are proportions.

	Inside		Outside	
	Host	Para	Host	Para
(a) Unmanipulated nests				
Observed No.	190	118	46	19
Eggs	(.62)	(.38)	(.70)	(.30)
Expected	211.9	96.1	44.7	20.3
No. Eggs ^a	(.69)	(.31)	(.69)	(.31)
(b) Experimental nests				
Observed No.	20	4	2	4
Eggs	(.83)	(.17)	(.33)	(.67)
Expected	16.5	7.5	4.1	1.9
No. Eggs ^b	(.69)	(.31)	(.69)	(.31)

^a Calculated on the basis that 256 of 372 eggs in these nests (69%) were host eggs while 116 (31%) were parasitic eggs

^b Calculated on the basis that 24 of 36 eggs in these nests (69%) were host eggs while 11 (31%) were added experimentally

DISCUSSION

My results show that goldeneye females do not, on the whole, defend against parasitic intrusions. Contrary to previous studies, I found little evidence that hosts desert their nest, adjust their clutch size, defend their nest, or change their nest site or territory location in response to brood parasitism. Egg tossing was more frequent in parasitized nests, but it is not clear that even this was a direct response to parasitism.

Nest Desertion as a Response to Parasitism

Although several researchers have claimed an association between brood parasitism and nest desertion (e.g. Grenquist 1963, and Jones & Leopold 1967), cause and effect are rarely established. For example, parasitism might occur after the nest has already been deserted. The results of the decoy nest experiment support this idea. Goldeneyes laid eggs in several of the decoy egg nests, and only half of these nests were incubated. In a field situation, the abandoned nests would be classified as parasitized and deserted, yet parasitism was clearly not the cause of desertion. It is also possible that nest abandonment is a generalized response to any form of nest disturbance. Predation on female cavity-nesting ducks can be high (Erskine 1972, Dow & Fredga 1985, Semel et al. 1988), and could select for low tolerance to nest disruption. Females that are disturbed early in the laying period will often desert their nest (pers. obs.). Moreover, three of four nests were abandoned when I placed a stuffed goldeneye female on the nest. These results indicate that nest desertion is not necessarily a response to parasitism, *per se*.

However, nest desertion did vary with the number of eggs in the nest (Figure 5.2) and circumstantial evidence suggests a link between hatch success and nest desertion. Hatch success declined when clutch sizes became extreme (Chapter 4, Semel et al. 1988), and nest desertion rates increased dramatically when more than 16-20 eggs had accumulated in a nest (Figure 5.2 and see Haramis & Thompson 1985). Desertion may be the best option if hatch success of host eggs is severely compromised in large clutches (Andersson & Eriksson 1982, Haramis & Thompson 1985). Females could then initiate a new nest, lay the remainder of their clutch

parasitically, or defer breeding to the following year. This last option would be profitable only if female survival was compromised by incubating a large clutch.

Nest desertion is often viewed as a last resort for females that would otherwise have incubated the clutch, but there is one other possibility. Parasitic interactions might involve contests among females, each attempting to parasitize the other. If females are unaware of the "intentions" of other females, a large number of eggs could accumulate in a nest that would eventually be abandoned. This could account for the large "dump" nests observed for several species of waterfowl (e.g. Weller 1959, McCamant & Bolen 1979, Semel & Sherman 1986).

Do Hosts Reduce Their Own Clutch Size?

Contrary to the predictions of the egg recognition hypothesis (Table 5.1), I found no evidence that goldeneyes reduced their own clutch size when parasitized, either in unmanipulated nests or in experimental nests. Both species of goldeneyes responded in the same manner, and there was no effect of either egg similarity or the number of eggs added. Consequently, I reject the egg recognition hypothesis (Table 5.1).

The relationship between brood size and duckling survival was not negative (Chapter 4) and the optimal adjustment hypothesis therefore predicts that hosts should not reduce their own clutch size, regardless of the similarity of parasitic eggs (Table 5.1). My results are consistent with this prediction. Unfortunately, this is a weak test since, in effect, the hypothesis predicts no response at all. Simpler hypotheses, such as the determinate layer hypothesis (Table 5.1), predict the same outcome. While it is generally believed that waterfowl lay indeterminately, there is evidence that some anatids lay a fixed number of eggs. Rohwer (1984) found that wild blue-winged teal (*Anas discors*) and mallards (*A. platyrhynchos*) did not adjust their clutch size when eggs were added or removed from the nest. Likewise, wood ducks did not significantly reduce their own clutch size when eggs were experimentally added (Heusmann et al. 1980).

The strongest test of the optimal adjustment hypothesis would be to examine host clutch sizes in areas where the relationship between brood size and duckling survival was negative.

Andersson and Eriksson's (1982) study in Sweden provides the only example where such conditions obtain. There, goldeneye hosts did reduce their own clutch size when eggs were added experimentally to their nests. The relationship between brood size and survival was negative in Sweden, and the optimal adjustment hypothesis predicts that hosts should reduce their own clutch size. Although qualitatively consistent with the optimal adjustment hypothesis, Andersson and Eriksson's (1982) results are open to other interpretations. For example, they found a significant reduction in host clutch sizes only for nests in which eggs were added early in the host's laying period. However, the average host clutch size in those nests (8 eggs) did not differ from the average clutch size reported for non-parasitized nests in the same area (7.6 - 8.4 eggs; Eriksson and Andersson 1982; see also Dow and Fredga 1984). Thus, the apparent reduction of host clutch size in experimental nests may not be a reduction at all.

In contrast, the average clutch size in control nests (11.0 eggs) was substantially larger than that of non-parasitized nests, and was similar to the clutch sizes of parasitized nests (9.6 - 12.5 eggs; Eriksson and Andersson 1982). This suggests that some of the control nests were parasitized naturally. Control nests may have been more likely to be parasitized if parasitic females avoid nests in which larger numbers of eggs have accumulated (i.e. experimental nests). Such a tactic would maximize the chance that a parasitic egg would be successful, given the relationships between clutch size, hatch success, and brood survival (see above). The difference in clutch size between control and experimental nests would therefore result because of an adaptive response of parasitic females, rather than through an adaptive response of hosts.

A second explanation for Andersson & Eriksson's (1982) result is that goldeneyes respond in a simple but robust manner by laying 1 or 2 eggs less if parasitized early in the laying period (Andersson 1984). This would require little in the way of "strategic" manipulation by the host since it requires only that hosts (i) can detect when they are parasitized, (ii) do not or cannot discriminate against eggs laid by other females, and (iii) cannot cease laying immediately if a normal clutch size is reached suddenly by the addition of parasitic eggs late in the host's laying cycle (Andersson and Eriksson 1982). Conditions 2 and 3 probably hold for most species with

indeterminate laying, and Andersson and Eriksson (1982) favoured such an explanation for host responses in their study.

Small reductions in the clutch size of hosts would be difficult to detect statistically. I calculated the minimum difference that could be detected between host and control clutch sizes in my study, given the observed variances and sample sizes and setting $\alpha = .05$ and $\beta = .10$ (Zar 1974: 136). In unmanipulated nests, the minimum difference was: 1.74 eggs (1984), 2.21 eggs (1985), 1.39 eggs (1986), and 1.12 eggs (all years). The corresponding value for experimental nests was 1.27 eggs (all experimental nests lumped versus control nests). Thus, I could detect a reduction of 2 eggs in all but one case, but I could not detect a difference of only a single egg in any comparison. Interestingly, the median clutch size in both naturally and experimentally parasitized nests was about 1 egg less than that of non-parasitized nests (Figures 5.4 and 5.5). Clawson et al. (1979) and Heusmann et al. (1980) report similar results for wood ducks.

There is one other option open to parasitized hosts. Rather than reduce their own clutch size when parasitized, hosts could instead lay 1 or 2 eggs in another female's nest. By doing so, females would not forfeit those eggs. Once established, this behaviour could lead rapidly to widespread egg "dumping" via a domino effect (see also Semel et al. 1988). A balance between parasitic and non-parasitic egg-laying would then depend on the relationship between clutch size, the frequency of parasitism and offspring survival. I explore some of these ideas further in the next chapter.

Nest Guarding and Territoriality

In several species of altricial birds, hosts prevent parasitism by guarding their nests during egg laying (Emlen & Wrege 1986, Moller 1987). White-fronted bee-eater females, for example, spend up to 64% of daylight hours in their nest chamber (Emlen & Wrege 1986). In barn swallows, nest guarding rates were lower for parasitized than for non-parasitized females, indicating that guarding is an effective way to avoid parasitism (Moller 1987). Saylor (1985) and Semel & Sherman (1986) report that canvasback (*Aythya valisineria*) and wood duck females, respectively, attempt to aggressively exclude intruders from their nests. I did not observe such

interactions between goldeneyes. However, on two occasions when I placed a stuffed female on the nest, the decoy was wet and dishevelled when I removed it on the following day, suggesting that hosts might act aggressively to nest intruders.

An alternative form of nest guarding is to defend a territory around the nest site (Moller 1987). Gauthier (1987) suggested that territoriality in *Bucephala* could reduce parasitic intrusions by conspecifics. However, my results were inconsistent with all three predictions of the nest guarding hypothesis: (1) only half of all territories were adjacent to the nest site, (2) females with territories adjacent to their nests were not less likely to be parasitized, and (3) females that moved nest sites did not necessarily move to a closer territory, and vice versa. Thus, site-specific territoriality in goldeneyes does not function as a defence against parasitism, in contrast to Gauthier's (1987) conclusions for buffleheads.

Territorial behaviour could, however, indirectly limit the rate of parasitism. The frequency of parasitism on my study area was positively related to the density of breeding females (see Chapter 6). If territoriality limits breeding density (see Gauthier & Smith 1987), then it might also restrict the frequency of brood parasitism. In this case, reduced parasitism would be a secondary consequence of the spacing system of goldeneyes, and territorial behaviour would not represent an adaptive host defence, per se.

Egg Tossing and Egg Displacement

A final defence of parasitized hosts is to eject parasitic eggs from the nest. Egg tossing has been observed in several passerine hosts (white-fronted bee-eater, Emlen & Wrege 1986; barn swallow, Moller 1987; starling, Stouffer et al. 1987; house sparrow, Kendra et al. 1988). In most of these cases, eggs were ejected only if added to the nest before the host started to lay her own eggs. However, in a few species, females distinguish and selectively eject eggs of other females after laying some eggs of their own (Bertram 1979, Arnold 1987, Kendra et al. 1988). I found that eggs were more likely to disappear from naturally and experimentally parasitized goldeneye nests. There was no difference in the disappearance rates of host and parasite eggs in unmanipulated nests, but "parasitic" eggs were far more likely to go missing from experimental nests.

Most of these eggs were either painted or unpainted chicken eggs. Although I cannot be sure that all eggs were removed directly by the host, I have documented several cases of egg removal by hosts from nests on which automatic cameras were set up.

It is tempting to interpret these results as indicating that hosts selectively remove eggs that differ from their own. However, a simpler explanation is possible; that is, egg removal by hosts is a response to broken eggs. In at least 7 cases, the missing eggs were known to have been cracked or broken. Other eggs may have been removed immediately after breakage and so would have gone undetected. For example, chicken eggs are more susceptible to breakage than golden-eye eggs (due to their thinner shells), and this could account for the higher disappearance rate of experimental chicken eggs. Furthermore, egg breakage was more common in parasitized nests (6 of 14 nests) than in non-parasitized nests (1 of 6 nests), as has been observed by other authors (Joyner 1976, Talent et al. 1981). This would explain the higher rates of egg tossing in naturally parasitized nests. Removal of broken eggs by hosts would clearly be adaptive. Broken eggs suffer reduced hatchability and the leaking contents could endanger the rest of the clutch by fouling and binding the eggs to each other and to the nest lining (Allen & Parker 1977, Kemal & Rothstein 1988).

The results of the decoy egg experiment suggest further that hosts do not selectively remove parasitic eggs. If parasitism did represent a cost to hosts, then females should avoid nests that already contain eggs or should remove those eggs prior to laying their own (e.g. Brown 1984, Moller 1987). Neither of these responses occurred. Females readily used decoy egg nests even though eggs were present before the host started laying. None of the decoy eggs were removed prior to a female laying her own eggs, and in four cases, females incubated a clutch containing the decoy eggs.

Host Defence in Precocial Birds

Anti-parasite defences are conspicuously absent in most species of precocial birds. Why don't precocial hosts defend against parasitic intrusions? I posed three possibilities in the introduction: (1) genetic or life-history constraints prevent the evolution of host defences, (2) selec-

tion for host defence is weak or sporadic due to infrequent parasitism, and (3) there is little or no cost to being parasitized, negating the utility of host defences.

Rothstein (1975a, 1982) found that several species of altricial birds reject parasitic eggs, while other species accept parasitic eggs at some cost to their own reproductive success. In explaining this pattern, Rothstein (1975a, 1982) argued that the genetic basis for rejection behaviour might simply be lacking in some species. This explanation can not account completely for the absence of host defence behaviours in goldeneyes. Territoriality, nest desertion, breeding dispersal in response to nest failure, and egg removal are all within the behavioural repertoire of goldeneyes. Thus, the fundamental basis for several anti-parasite defences currently exists.

It is possible that hosts cannot determine when they have been parasitized or cannot distinguish parasitic eggs from their own. Unfortunately, this is a difficult hypothesis to test. Defence behaviours may be absent, not because the genetic basis is lacking, but because there simply has not been selection for these abilities. For example, I showed in Chapter 4 that parasitism was detrimental to hosts only when the frequency of parasitism was high. Such levels of parasitism occur infrequently (1 of 3 years) and may affect only a small number of host females. Selection for host defence would therefore be weak. Moreover, even under conditions of intense parasitism, simple host defences might suffice. Nest desertion at extreme levels of parasitism and simple adjustments of clutch size (laying one egg less when parasitized), could minimize the cost of caring for additional young (Andersson & Eriksson 1982). Stealthy behaviour near the nest site might further prevent disclosure of the nest to potential parasites (Sayler 1985, Semel & Sherman 1986). I argue, then, that specialized anti-parasite behaviours would not be expected in goldeneyes, given that parasitism only infrequently affects host fitness (i.e. explanation 2 above).

One other factor could mitigate the costs of parasitism to the precocial host and thereby influence the evolution of host defences. In waterfowl, females are the philopatric sex and Andersson (1984) proposed that parasitism may involve interactions among kin. If so, parasitized females could gain in inclusive fitness, even if direct components of fitness are reduced. Accordingly, there would be little selection for host defences if most parasites are

closely related to hosts. Natal philopatry of females was high on my study area. Of 13 marked ducklings (all females) that have returned to breed on the study area, 10 returned to their natal lake while the remaining 3 bred on the next nearest lake (< 1 km). This sample includes three pairs of sisters. However, the high frequency of parasitism between the two species of goldeneyes (Chapter 4) argues against a kin selection hypothesis, unless hosts discriminate against unrelated parasites. Although I found no evidence of such effects, a more detailed study of individuals of known relatedness is required to test this hypothesis.

CHAPTER 6

THE ADAPTIVE SIGNIFICANCE OF BROOD PARASITISM IN GOLDENEYES

In a variety of species, individuals in the same population adopt strikingly different reproductive tactics (reviews in Rubenstein 1980, Davies 1982, Dunbar 1982, Austad 1984). At one time, such behaviours were viewed as artifacts or aberrations because they contrasted with the view that there should be a single, optimal reproductive strategy. More recently, researchers have considered two other possibilities: (1) individuals pursue alternative tactics when they are unable to breed otherwise, due to inferior competitive ability or to environmental constraints; or (2) alternative tactics yield equal average fitness and are maintained in equilibrium because fitness returns are negatively frequency-dependent (Gadgil 1972, Austad 1984, Parker 1984). To test between these hypotheses, we need to determine whether alternative behaviours represent genetic differences between individuals, whether individuals switch tactics over time, and whether the average fitness returns are equal (Austad 1984). We also need to know how social or environmental factors influence the occurrence of these behaviours. Few studies have successfully addressed all of these questions.

Previous analyses of alternative reproductive behaviours (ARBs) have been limited in two important respects. First, most studies have obtained only very crude estimates of fitness and have rarely determined whether individuals switch behaviours over their lifetimes (Forsyth & Montgomerie 1987). Little attempt has been made to experimentally modify the ecological or demographic factors that might influence the occurrence of ARBs (but see Kodric-Brown 1986). Second, analyses of ARBs have focused on male mating tactics, while female behaviours have largely been neglected (Alcock et al. 1977, Dominey 1980, Gross & Charnov 1980, van den Berghe 1988). It is now evident that females compete vigorously amongst themselves for resources such as nest-sites, brood-rearing sites, high quality foraging areas, and even males (Petrie 1983, Hannon 1984, Davies & Houston 1986, Arcese 1988, and see studies in Wasser 1983). Variation among individuals in the ability to acquire these resources might therefore lead

to the evolution of alternative reproductive tactics in females (Dunbar 1982, Thornhill 1984, van den Berghe & Gross 1988).

In this study, I examine alternative reproductive behaviours in females of two species of cavity-nesting ducks, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). Goldeneye females pursue two nesting tactics: **parental** females lay and incubate eggs in a nest and tend their young for up to two months after hatch; **parasitic** females lay eggs in the nests of other females, and abandon all subsequent care of their young to the host. Facultative brood parasitism has been reported for several species of waterfowl (Weller 1959, Yom-Tov 1980a, Eadie et al. 1988), as well as for some passerine birds (Gowaty & Karlin 1984, Emlen & Wrege 1986, Moller 1987), insects (Wilson 1975, Eberhard 1986, Tallamy 1985, 1986) and fishes (McKaye 1985, Sato 1986). However, there have been few attempts to test explicit hypotheses for this behaviour. Below, I summarize the hypotheses that have been proposed for brood parasitic behaviour, and then describe a 4-year experimental and observational study designed to test these hypotheses.

HYPOTHESES

(1) Reproductive Error

Researchers initially dismissed brood parasitism as a form of reproductive error, resulting from endocrine imbalances (Davis 1940) or "a lack of attunement between environmental cues such as the quality and quantity of available nesting cover, and the female's physiological and behavioural response system" (Siegfried 1976). Such views are no longer tenable. Even if parasitic females differ hormonally or behaviourally from parental females, we also want to know why they differ. The hormonal imbalance and miscue hypotheses do not provide an answer. More importantly, the high frequency of occurrence of brood parasitism among precocial birds argues against reproductive error as a general explanation for the phenomenon (see Davies 1988, Eadie et al. 1988).

(2) Parasitism as an Inadvertent Consequence of Competition for Nest Sites

Brood parasitism could result inadvertently from competition among females for the same nest site (Grenquist 1963, Erskine 1972, Yom-Tov 1980a, Hines & Mitchell 1984). Most ducks do not defend their nests and more than one female might occupy the same site by chance. This hypothesis is most tenable for cavity-nesting ducks in which potential nest sites are discrete and easily located. Goldeneye females lay one egg approximately every other day and egg-laying usually takes only 1-2 hours. Two females could lay several eggs in the same nest without coming into contact. A contest for the nest site might ensue when one female begins to incubate the clutch, resulting in the other female being evicted (Erskine 1972). Thus, joint clutches could arise because a female is forced to abandon the eggs she has already laid in a nest, rather than as a result of any "intentional" attempt to lay the eggs parasitically. If given the opportunity, the putative parasite would readily incubate the clutch. (I hereafter refer to this as the "accident hypothesis").

(3) Brood Parasitism as a Conditional Strategy

Females might parasitize other females when they are unable to, or when it does not pay to, nest on their own. The success of parasitic females might be lower than that of parental females, but at least some reproductive output could be obtained. In such cases, parasitic egg-laying would allow females to make the best of a bad situation (BBS). Four factors have been suggested which might promote parasitic egg-laying as a conditional strategy:

(a) Nest loss - Yom-Tov (1980a) and Haramis et al. (1983) suggested that parasitism is carried out by females that lose their nests to a predator or some other agent before the clutch is complete. If females are unable to renest, or if renesting was not profitable, these birds might lay their remaining eggs in the nest of another female.

(b) Female energetics - Energy or nutrient reserves may limit breeding opportunities of females. Clutch size in waterfowl is thought to be determined by the availability of energy and nutrients for producing eggs (Klomp 1970, Ar & Yom-Tov 1978, Drobney 1980, but see Arnold et al.

1987); females with insufficient resources may be unable to initiate a nest attempt on their own (Ankney & MacInnes 1978, Drent & Daan 1980). These females might, however, lay a few eggs in the nests of other females to salvage some reproductive success (Finney 1975, Pienkowski & Evans 1982).

(c) Age or experience - Age and experience have strong effects on breeding success in waterfowl. Young or inexperienced birds generally produce smaller clutches, suffer higher nest failure, and fledge fewer young than older, more experienced females (Raveling 1981, Rockwell et al. 1983, Afton 1984, and see Chapter 3). Brood parasites may be young females (Grenquist 1963, Grice & Rodgers 1965, Yom-Tov 1980a). Inexperience could reduce a female's ability to secure resources (food or nest sites) necessary for breeding and thereby result in an age-related tendency to lay parasitically. Alternatively, parental investment could vary with residual reproductive value (RRV). Selection should favour behaviours and life histories that minimize reproductive effort during periods of high RRV (Williams 1966, Pianka & Parker 1975). Since RRV is generally higher for young than for old birds, parasitic egg-laying would allow young females to invest in reproduction while avoiding the risks associated with incubation and maternal care.

(d) Nest site limitation - When nest sites are limited, females without their own nests might lay parasitically (Clawson et al. 1979, Heusmann et al. 1980, Andersson 1984). This idea has been favoured especially for cavity-nesting ducks (Jones & Leopold 1967, Clawson et al. 1979, Heusmann et al. 1980, Haramis & Thompson 1985; but see Morse & Wight 1969, Semel & Sherman 1986). There is a critical distinction between this hypothesis and the accident hypothesis described above. Both hypotheses predict an increase in parasitism when population densities are high and nest sites are limited. However, under the limitation hypothesis, parasitism is an adaptive behaviour per se, and parasitic females will not incubate the clutch even if given the opportunity to do so. Under the accident hypothesis, parasitism occurs inadvertently and the "parasitic" hens will readily incubate the clutch if permitted. I used this difference to test between the two hypotheses (see below).

(4) Brood Parasitism as a Mixed Strategy

Andersson (1984) proposed that brood parasitism might evolve to some frequency in a population if parasitic females initially have higher fitness than parental females. Frequency-dependent reproductive success could equalize the success of the two tactics. Accordingly, parasitic females would be more successful when rare and host nests are easily found, and least successful when common and host nests are hard to find (Andersson 1984). Parasites might initially have higher fitness if they were able to channel the time and energy saved by avoiding incubation and brood rearing into increased fecundity or survival.

Parasitic and parental behaviour might be genetically fixed within individuals. In this case, a mixture of the two genotypes could be maintained in an evolutionarily stable state (ESS_t) by either frequency-dependent selection or disruptive selection. Alternatively, parasitic behaviour might be a genetically facultative tactic in a mixed ESS (mESS) with parental nesting. Females would lay parasitic eggs with probability p and frequency-dependent selection would adjust the value of p such that the fitness of the two tactics was equalized (Maynard Smith 1982, Parker 1984).

(5) Brood Parasitism as a Side-Payment Strategy

A final hypothesis is that all females nest parentally, but also lay some eggs parasitically (Brown 1984, Moller 1987, Lank et al. 1988). If some factor constrains the number of eggs that a female can lay in her own nest, it might pay her to lay a few additional eggs parasitically, even if those eggs fare poorly. Alternatively, a female could lay some eggs parasitically at the beginning of the breeding season, replenish her energy/nutrient reserves by feeding intensively for some period of time, and then initiate her own nest.

The placement of this hypothesis in terms of an ESS framework is problematical. The side-payment strategy is a mixed strategy (*sensu* Trivers 1972), in that a female lays some of her eggs parasitically, while tending the remainder on her own. However, unlike the mESS hypothesis above, the fitness of the parasitic tactic need not be equal to that of parental nesting. Parasitic

eggs may do poorly relative to those a female cares for herself, but the strategy will nonetheless be evolutionarily stable if females that do both tactics have greater reproductive success than females that pursue only a single nesting tactic (Brown 1984, Moller 1987).

METHODS

General field methods are described in Chapter 2. As in previous chapters, I combine the results for Barrow's and common goldeneyes. Analyses conducted separately for each species failed to reveal any difference between the species in reproductive performance, parasitic tendencies, or host responses (see Chapters 3 & 4).

Identifying Parasitized Nests and Parasitic Eggs - Methods to identify parasitized nests and parasitic eggs have been described briefly in Chapter 4 and in detail in the Appendix.

Identifying Parasitic Females - Detailed observations were made on a number of parasitized nests to identify females involved in brood parasitism. Several nests were monitored simultaneously using binoculars and 20x spotting scopes. Observations were conducted in the morning (0600-1100) and afternoon (1500-2000) laying periods. I also used Kodak disc cameras rigged with an automatic shutter release to photograph females as they entered and left parasitized nests. Females were identified in the photographs by their nasal saddles. In 1984, I used an automatic neck collaring technique (Heusmann et al. 1980) to mark females as they entered the nest box. Rubber bands with colour-coded streamers were placed on hooks at the nest entrance such that females entering the nest were automatically banded. Finally, females were caught on parasitized nests using a nest trap that closed automatically when a female entered the nest box. Nest traps were set and checked every 2-3 hours; in many cases, traps were used on nests that were under continuous observation. I classified a female as a brood parasite if (1) she was observed to lay eggs in a nest in which at least one other female was laying concurrently, and (2) she did not attempt to incubate the clutch. Females that attempted to incubate a nest were classified as parental for that nest.

Goldeneye females do not breed until 2 or more years of age. Consequently, I had little information on birds of known age since females banded as offspring did not recruit into the population until 1986. I estimated the relative age of parasitic and parental females as the number of years each female had bred (following Dow & Fredga 1984). Unmarked females were assumed to be first time breeders. To test the hypothesis that parasitic females are small or in poor body condition, I compared several measures of size, weight, and body condition for parasitic and parental females. I considered only those females caught and measured during egg-laying, and I analysed Barrow's and common goldeneyes separately since females of the two species differ slightly in size.

Testing for Random Parasitism - I used the binomial distribution to calculate the number of nests that would be parasitized by chance, given only that females are distributed among nest sites at random. This was calculated as:

$$P(X) = \frac{N!}{X! N-X!} \cdot p^X q^{N-X}$$

where

N = the number of breeding females,

X = is the number of females in a given nest box (0, 1, 2, ..., N),

p = the probability that a given nest site is chosen by chance

(= $1/S$ where S = the number of nest sites), and

$q = 1 - p$.

This procedure calculates the expected number of females in each nest, given N trials and a probability p that the nest box is chosen by chance. The expected proportion of "parasitized" nests can be calculated as $P(2+) / \{P(1) + P(2+)\}$ where $P(2+)$ is the proportion of nests with 2 or more females (= $P(2) + P(3) \dots + P(N)$), and $P(1)$ is the proportion of nests with only 1 female.

Nest Predation Experiments - To test the hypothesis that females lay eggs parasitically after their own nests are destroyed, I injected laying females with tetracycline, removed some or all of their clutch and then released the females. Tetracycline chelates calcium ions in the forming eggshell and can be detected by a characteristic fluorescence when exposed to UV light

(Haramis et al. 1983, Eadie et al. 1987). It was therefore possible to trace further egg-laying by the experimental females using a portable UV light. Because of the disruptive nature of this experiment, I repeated the manipulation for only 5 females (each on a different lake). For 3 of the 5 females, I removed the entire clutch of eggs from the nest (range 3-6 eggs). I removed only part of the clutch (1 of 8 eggs and 4 of 9 eggs) from the nests of the other two females. I subsequently checked each nest on the same lake and any other lakes within 1-2 km and used the UV light to detect any eggs labelled with tetracycline.

Nest Manipulation Experiments - I manipulated the availability of nest boxes on several study lakes to determine the influence of nest-site availability on brood parasitism. Two sets of experiments were conducted. In the first, I altered the number of nest boxes on 4 lakes according to the following treatments: (a) control - no change in the number of nest boxes, (b) reduction - a continual reduction in the number of nest boxes each year, (c) a one year pulsed addition - boxes added at the end of year 1 and removed at the end of year 2, and (d) a 2 year pulsed addition - boxes added at the end of year 1 and removed at the end of year 3. All additions or removals of boxes were conducted at the end of the breeding season (August) so that females arriving on the breeding ground in the next year were exposed to the new pattern of nest box availability prior to the initiation of nesting. I followed all nest activities in these boxes over the study period and monitored the frequency of brood parasitism.

In the second set of experiments, I established 2 study plots, each comprising 7-10 small lakes and ponds. There were no nest boxes on these lakes prior to the start of the experiment in 1984. On one plot, I erected a low density of nest boxes (2 per lake = 2.1 boxes/km shoreline) while on the second plot, I added a high density of boxes (5 per lake = 6.5 boxes/km shoreline). I monitored the use and extent of parasitism in these boxes from 1985 to 1987 (none of the boxes were used in 1984).

Female Removal Experiments - I removed host females from parasitized nests to determine whether parasites would incubate a clutch to which they had contributed. I identified hosts by 3 criteria: (i) the female had incubated a nest in the same site in the previous year, (ii) the female

had a developing brood patch, and (iii) the female had been observed or inferred to have laid the majority of eggs in the nest. Most females met at least two of these criteria. As a control, I conducted a reciprocal experiment by removing a small number of parasitic females while leaving the host undisturbed. In all cases, females were trapped on a nest using nest traps and were killed via a lethal overdose of the anesthetic halothane. The females were immediately placed on ice, and the ovaries and reproductive tracts were dissected within 8 h. I estimated clutch size through counts of post-ovulatory follicles and large developing follicles using techniques described in Payne (1966) and Hannon (1981).

Decoy Nest Experiment - To determine whether artificial nests containing eggs would be parasitized, I placed 3 goldeneye eggs or 3 large chicken eggs painted to resemble goldeneye eggs in unused nest boxes. In these cases, I knew that the nest was not attended by a host female, and so I could unambiguously determine whether other females would lay, but not incubate, eggs in a nest that was apparently active. Details of this experiment are provided in Chapter 5.

Measuring Reproductive Success - Reproductive success (RS) of parasitic and parental females was estimated using two approaches. First, I followed the success of individual females over the entire breeding season. It was difficult to follow a large sample of parasitic females, since I needed to identify all the nests used and all the eggs laid by those females. Over 4 years, I followed the entire egg-laying sequence of 12 parasitic females. Several of these females were involved in other experiments, leaving only 6 parasites with complete information on reproductive success. It was easier to monitor the reproductive success of parental females. I present data on 32 females that were followed in detail, and that were not suspected of being involved in parasitic activities.

To obtain a second estimate of reproductive success, I conducted experimental and observational studies to quantify separately each component of reproductive success in a large number of nests. This approach does not provide measures of reproductive success for individual females, but it does provide a more accurate assessment of the success of parasitic and parental eggs. I determined the fate of all eggs in unmanipulated nests (parasitized and non-parasitized)

and in experimental nests, to which I added different numbers of goldeneye eggs. The results presented here are summarized from analyses described in Chapter 4. I estimated the average annual success of parasitic and parental tactics as:

$$RS = (\bar{X} \text{ clutch size}) \cdot (\bar{X} \text{ nest success}) \cdot (\bar{X} \text{ hatch success}) \cdot (\bar{X} \text{ fledge success})$$

where the means for each variable were determined separately for parental and parasitic females. I multiplied this value by the average breeding lifespan of parasitic and parental females, respectively, to estimate average lifetime reproductive success (LRS).

It was not possible to derive error terms for these estimates since they were, in turn, products of other variables. However, I assessed the potential variability in LRS estimates using a simulation approach. I first assumed, for simplicity, that the distribution of each component of RS was normal. For each variable, I then obtained a random normal deviate from a random number generator and scaled this value by the observed mean and standard deviation. Finally, I calculated the product of these pseudo-values for all RS variables to estimate LRS. I repeated this procedure 100 times for parasitic and parental tactics. I calculated annual RS separately for parental females when alone and when parasitized, and obtained an average value of LRS by assuming (i) that 35% of the nests of parental females were parasitized (Table 6.1) and (ii) that survival of females was not affected when they were parasitized (see Chapter 3). This approach is crude, but it provides at least some indication of the range of LRS values that might be expected for each nesting tactic.

RESULTS

Frequency of Brood Parasitism

Brood parasitism occurred frequently in all 4 years of this study (Table 6.1). The proportion of nests that were parasitized ranged from 20% to 46% between years, with an overall mean of 38%. The proportion of parasitic eggs ranged from 8% to 31%, with an overall mean of 17% (I did not estimate the proportion of parasitic eggs in 1987). The two estimates of parasitism

Table 6.1. Annual variation in the frequency of brood parasitism. The mean, SE, and range is calculated for all lakes in each year.

	<u>Proportion of Parasitized Nests</u>		<u>Proportion of Parasitic Eggs</u>		<u>No. Lakes</u>	<u>No. Nests</u>
	<u>$\bar{X} \pm SE$</u>	<u>Range</u>	<u>$\bar{X} \pm SE$</u>	<u>Range</u>		
1984	.45 \pm .09	.17 - .80	.31 \pm .04	.20 - .45	6	71
1985	.20 \pm .05	0 - .60	.08 \pm .03	0 - .35	12	95
1986	.45 \pm .07	0 - .80	.18 \pm .02	0 - .30	13	108
1987 ^a	.46 \pm .07	0 - .75	-	-	12	97
All ^b	.38 \pm .04	0 - .80	-	-	43	371
	.35 \pm .04	0 - .80	.17 \pm .02	0 - .45	31	274

^a The proportion of parasitic eggs was not determined in 1987

^b The first line shows the values for all 4 years; the second line excludes lakes in 1987

(parasitized nests and parasitic eggs) were highly correlated (see Appendix 1). There was considerable variation in the frequency of parasitism among lakes within years (Table 6.1). Parasitism was rare or absent on some lakes, but extremely common on others. Even in years when the overall frequency of parasitism was low (e.g. 1985), up to 60% of all nest attempts on some lakes were parasitized.

The proportion of nests parasitized was identical for Barrow's and common goldeneyes (39% and 36% of all nests, respectively). Moreover, females were as likely to be parasitized by the other species as they were to be parasitized by a conspecific (Barrow's goldeneyes: 48% interspecific parasitism, 52% intraspecific parasitism (N = 48 nests); common goldeneyes: 53% interspecific parasitism, 47% intraspecific parasitism (N = 40 nests)). These frequencies did not differ from those expected by chance (G-test with Williams' correction, $G_w = 0.06$, $df = 2$, $P > .50$).

Brood parasitism involved a large proportion of females in the breeding population. Seventy percent of all marked females (N = 76) were involved in a parasitic interaction at least once in their life, acting either as a parasite or as a host. This estimate is conservative, since I was able to determine the identity of only a small number of parasitic females (see below).

Brood Parasitism Under Natural Conditions

To determine if the observed frequencies of brood parasitism were an artifact of the high density of nest boxes (e.g. Semel & Sherman 1986), I examined data for nests in natural cavities collected by Mary Jackson on the same study area in 1952-1956. Nest boxes were not available during this period. Jackson followed 9 natural cavity nests in detail, making frequent visits to nests during egg laying. Parasitized nests could therefore be identified using the same criteria as in the present study (i.e. clutch sizes greater than 13 eggs, eggs laid after incubation, or 2 eggs laid in a nest on the same day). By these criteria, four of the nine nests (44%) were parasitized and one other case of parasitism was suspected. Less detailed data were available for 35 additional natural cavity nests followed between 1952 and 1962. Eight of these nests were definitely parasitized and two others were suspected (23-29%). Thus, frequencies of brood

parasitism under natural conditions are similar to those that I observed. Moreover, parasitism has occurred at about the same level for over 35 years in the same population.

Do Females Switch Tactics?

Parasitic behaviour was variable within, and among, individual females. I identified 36 females as putative brood parasites. Three of these birds were seen only once and I had little information on their identity or reproductive history. Of the remaining 33 females, 23 acted only as parasites in a given year, while the other 10 laid some eggs parasitically in addition to establishing nests of their own. In all of these last 10 cases, females laid parasitically in a neighbouring nest located within 50 - 500 m. on the same lake or pond. I was able to follow the egg-laying sequence for seven of these females; three laid eggs in their own nests and in a neighbour's nest during the same period, while the other four females parasitized first, and then initiated nests of their own.

Females also switched behaviours between years. I followed 19 marked parasitic females over two or more years (Figure 6.1). In nine cases, females nested on their own in the year prior to being observed as a brood parasite. In three other cases, parasites established their own nests in the following year. There was no evidence that any females were consistently parasitic and only 1 female was observed to act as a brood parasite in two consecutive years. That female also established her own nest in both years. Parasitism clearly is not a fixed behavioural polymorphism, and I therefore reject the hypothesis that parasitic and parental nesting are genetically pure strategies maintained in an evolutionarily stable state (ESSt).

Is Brood Parasitism an Accident of Competition for Nest Sites?

The first prediction of the accident hypothesis is that the proportion of parasitized nests will be correlated with the number of breeding females. Indeed, there was a significant positive correlation between the proportion of parasitized nests and the number of pairs/nest site ($r_s = .49$, $N = 31$ lake-years, $P < .01$; Figure 6.2). Other hypotheses could, however, account for this pattern (see below). I next compared the proportion of nests parasitized on each lake with the

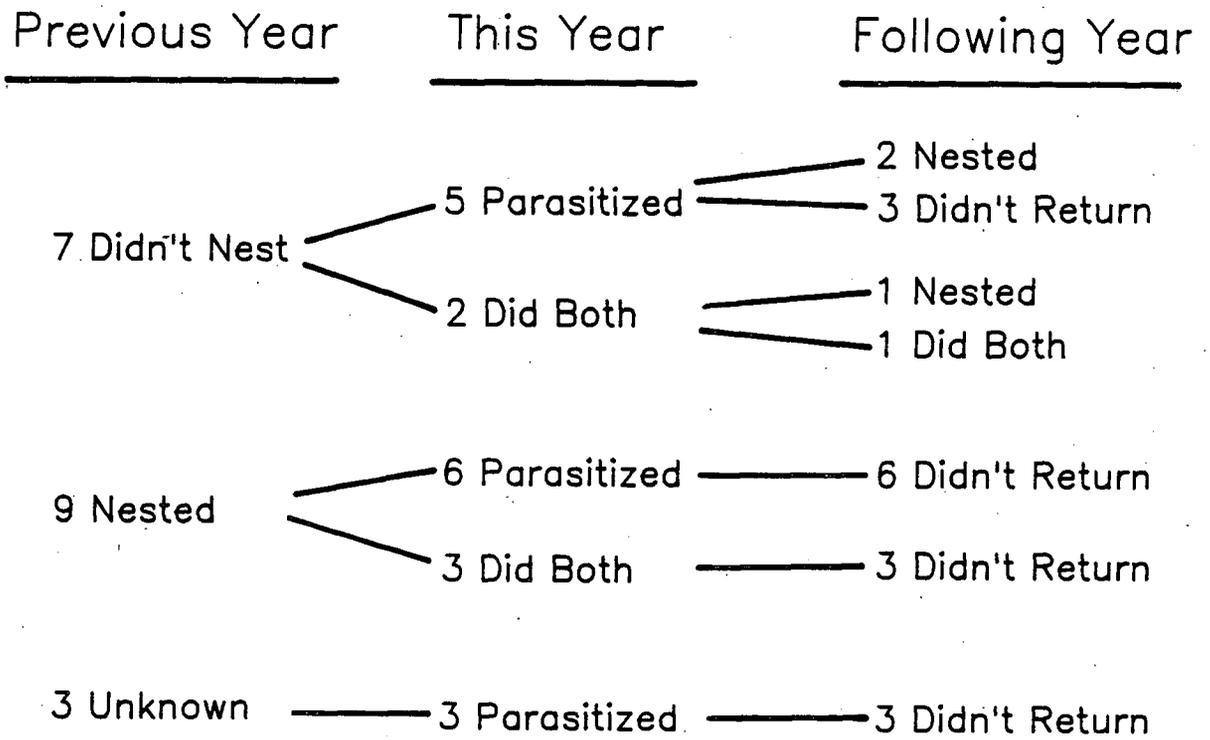


Figure 6.1. Reproductive histories of parasitic goldeneye females.

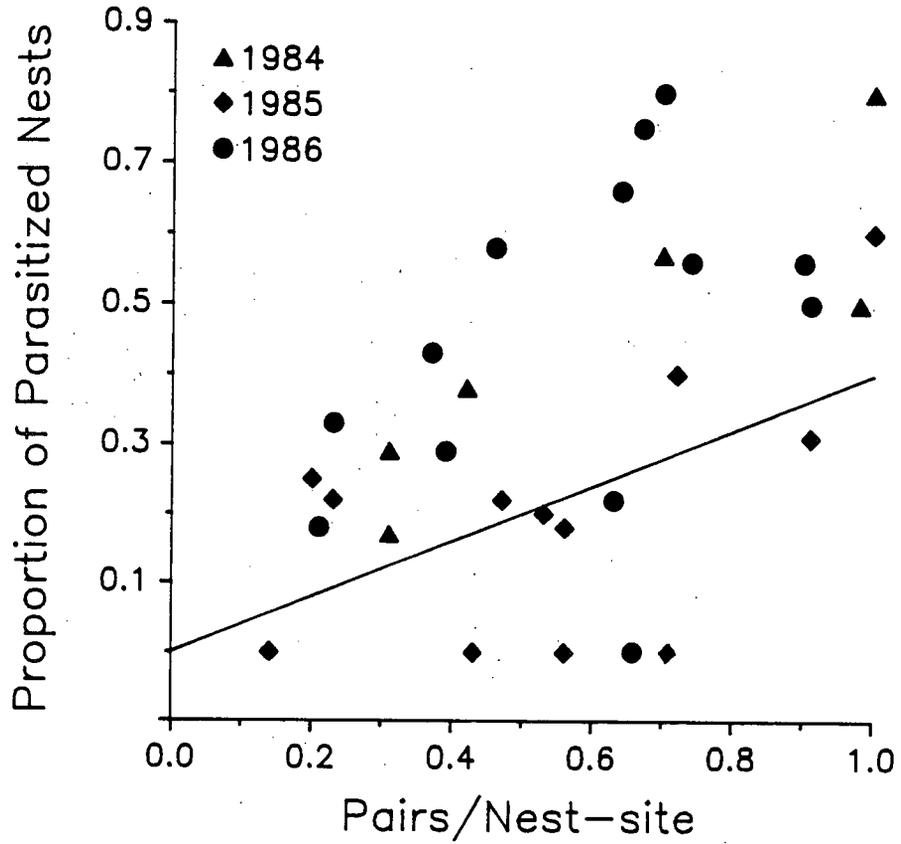


Figure 6.2. The frequency of brood parasitism as a function of pair density. Each point represents one lake in one year. The solid line shows the expected frequency of parasitism under the hypothesis that females are distributed randomly among nest sites.

proportion that would be expected if all of the breeding females on that lake used nest sites at random. Parasitized nests occurred more often than would be expected by chance in 22 of 31 comparisons (binomial test, $P < .02$; Figure 6.2). Analyses for each year separately gave comparable results for 1984 (parasitism greater than expected in all 6 comparisons, $P < .03$) and for 1986 (parasitism greater than expected on 11 of 13 lakes, $P < .02$), but not for 1985 (parasitism greater than expected on only 5 of 12 lakes). In at least 2 years, brood parasitism was not explained by two or more females using the same nest site by chance.

A second prediction of the accident hypothesis is that putative parasites should incubate the clutch if given the opportunity to do so. I tested this prediction by removing the host female from 9 nests before the start of incubation. None of these nests were incubated by the parasite, although egg-laying continued in two nests and parasitic females were observed visiting four nests after the host was removed. In a reciprocal experiment, I removed the parasitic female and left the host undisturbed. Hosts incubated the nest in 4 of 6 cases. The response of parasitic females was significantly different from that of host females (Fisher's Exact test, $P < .02$). Approximately 26% of all nests in my study population were deserted for unknown reasons. I therefore expected 1.6 of 6 nests to be deserted when I removed the putative parasite, i.e. close to the observed value of 2 nests. Similarly, I expected 2.3 of 9 nests to be deserted when I removed the host female. The observation that all 9 nests were deserted is significantly different from expected (binomial test, $P < .001$).

The female removal experiments strongly suggest that parasites are not simply attempting to obtain a nest site for their own use. Two other lines of evidence support this conclusion. First, several of the nests containing decoy eggs were parasitized. Of the 8 decoy nests used by goldeneyes, 4 were never incubated whereas only 1 of 9 control nests was abandoned. Although sample sizes were small, these results suggest that females lay eggs in nests already containing eggs without attempting to incubate the clutch. "Inadvertent competition" cannot explain those occurrences, since there was no host to prevent a female from using the nest.

Second, 30% of parasitic females also established their own nest in the same year. It could be argued that these females initiated a second nest attempt after losing a contest for the first site. However, several females laid eggs in both a neighbour's nest and in their own nest during the same period (see above). Clearly, these females were not simply ousted in a competition for a nest site. Moreover, in most parasitized nests, parasites laid only a few eggs in the nest and often stopped laying several days before the host began incubation. None of the above results are consistent with the accident hypothesis and I therefore reject it as a general explanation for parasitic behaviour in goldeneyes.

Nest Predation

Nest predation occurred infrequently on the study area (8 of 265 nests) and only two of the 33 identified parasites were suspected of having lost an earlier nest to a predator. In both cases, the female was observed laying in a nest, and the nest was later found deserted with eggs missing. None of the 5 females subjected to experimental predation laid parasitic eggs after their clutch was manipulated. I did not find tetracycline-labelled eggs for any of the three females from which I removed the whole clutch. In the 2 cases where I removed only part of the clutch, both females returned to their original nest, laid 1 more egg each, and then incubated the clutch. In both cases, the new egg exhibited the characteristic tetracycline fluorescence, indicating that the marker was effective (see Eadie et al. 1987). I conclude that nest predation cannot account for the high frequency of parasitism observed in goldeneyes. Females appear to be highly faithful to their nests, and will return and incubate their clutch even if several eggs are removed.

Female Condition

I found no statistically significant differences in any measure of size, weight or body condition between parasitic and parental Barrow's goldeneyes, although there was a slight trend for the length of the middle toe and claw to be shorter in parasites (Table 6.2). In common goldeneyes, only culmen length was significantly smaller in parasites. These results do not support the female condition hypothesis.

Table 6.2. Size and body condition of parasitic and parental goldeneye females. Only females caught during egg-laying are included.

	<u>Parasitic</u>	<u>Parental</u>	<u>P^a</u>
a) Barrows			
Culmen L. (mm)	31.8 ± 0.2	31.6 ± 0.2	NS
Tarsus L. (mm)	47.5 ± 0.4	47.4 ± 0.3	NS
MTC (mm) ^b	66.8 ± 0.5	68.0 ± 0.4	< 0.10
Wing L. (mm)	223.6 ± 2.4	224.3 ± 0.8	NS
Weight (g)	794.0 ± 32.1	770.3 ± 19.7	NS
Condition ^c	0.74 ± .03	0.72 ± .02	NS
N	5	12	
b) Common			
Culmen L. (mm)	32.7 ± 0.3	34.0 ± 0.3	< 0.01
Tarsus L. (mm)	45.3 ± 0.2	46.0 ± 0.4	NS
MTC (mm) ^b	67.6 ± 1.1	68.3 ± 0.7	NS
Wing L. (mm)	217.5 ± 1.8	217.1 ± 1.0	NS
Weight (g)	658.7 ± 18.8	693.0 ± 15.6	NS
Condition ^c	0.71 ± .02	0.72 ± .02	NS
N	6	10	

^a Mann-Whitney U-tests; NS, not significant

^b Middle toe and claw length

^c Condition = (Weight / Tarsus³) x 10³

Female Age and Experience

Parasitic females were slightly more likely to be in their first breeding year ($G_w = 3.93$, $P = .076$; ages 2+ and 3+ pooled for analysis; Table 6.3). However, parasitic behaviour was not exclusive to young birds, and two females with at least 3 years of breeding experience laid parasitic eggs (Table 6.3).

Nest Site Limitation

The frequency of brood parasitism was influenced by population density and by the relative availability of nest sites. The proportion of parasitized nests was significantly correlated with relative density of breeding pairs (Figure 6.2 and see above). However, there was a stronger correlation between the frequency of parasitism and the proportion of nest sites used (Figure 6.3). This was true when I used either the proportion of nests parasitized ($r_s = .80$, $N = 31$ lake-years, $P < .001$) or the proportion of parasitic eggs ($r_s = .73$, $N = 31$, $P < .001$) as an index of the frequency of parasitism. Correlations calculated separately for each year were also significant, even though the frequency of parasitism varied considerably among years and between lakes.

Similar results were obtained when I experimentally manipulated the number of nest boxes on four study lakes (Figure 6.4). The frequency of parasitism was strongly influenced by the availability of nest boxes and all changes were in the predicted direction; that is, (1) there was no change in the proportion of parasitized nests on the control lake, (2) the proportion of parasitized nests doubled on the nest reduction lake, and (3) the proportion of parasitized nests decreased sharply and then increased on the two nest addition lakes, with the changes matching closely the duration of the pulsed additions. It was not possible to replicate these treatments, and so I cannot assess the statistical validity of these results.

The second nest addition experiment provided less conclusive results. In all three years, a greater proportion of parasitized nests occurred on the plot with a low density of nest boxes (LD) compared to the plot with a high density of boxes (HD) (Table 6.4). However, the differences were small and not statistically significant (all $G_w < 1.0$, $P > .35$). This experiment was

Table 6.3. The number of parasitic and parental goldeneye females according to breeding age. Values in parentheses are proportions.

<u>Age</u>	<u>Parasitic</u>	<u>Parental</u>
1+	22 (.67)	33 (.46)
2+	9 (.27)	32 (.44)
3+	2 (.06)	7 (.10)

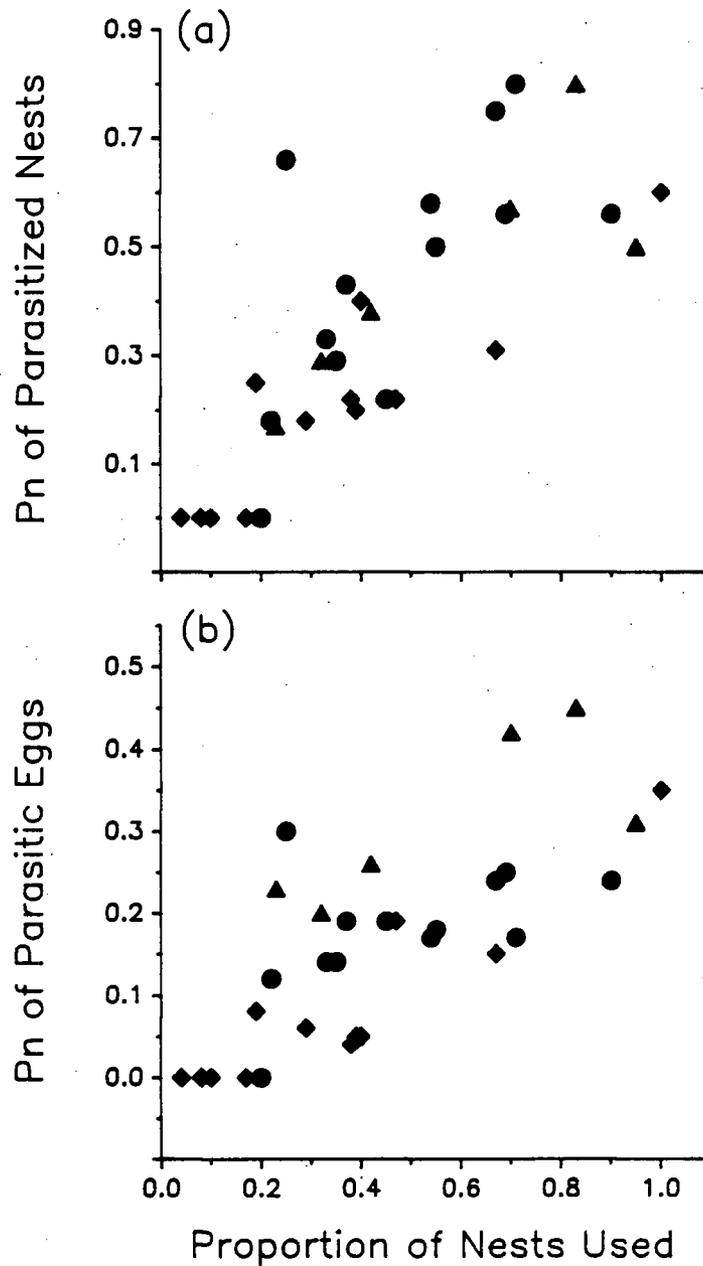


Figure 6.3. The relationship between nest site availability and (a) the proportion of nests parasitized, and (b) the proportion of parasitic eggs. Each point represents one lake in one year. Symbols as in Figure 6.2.

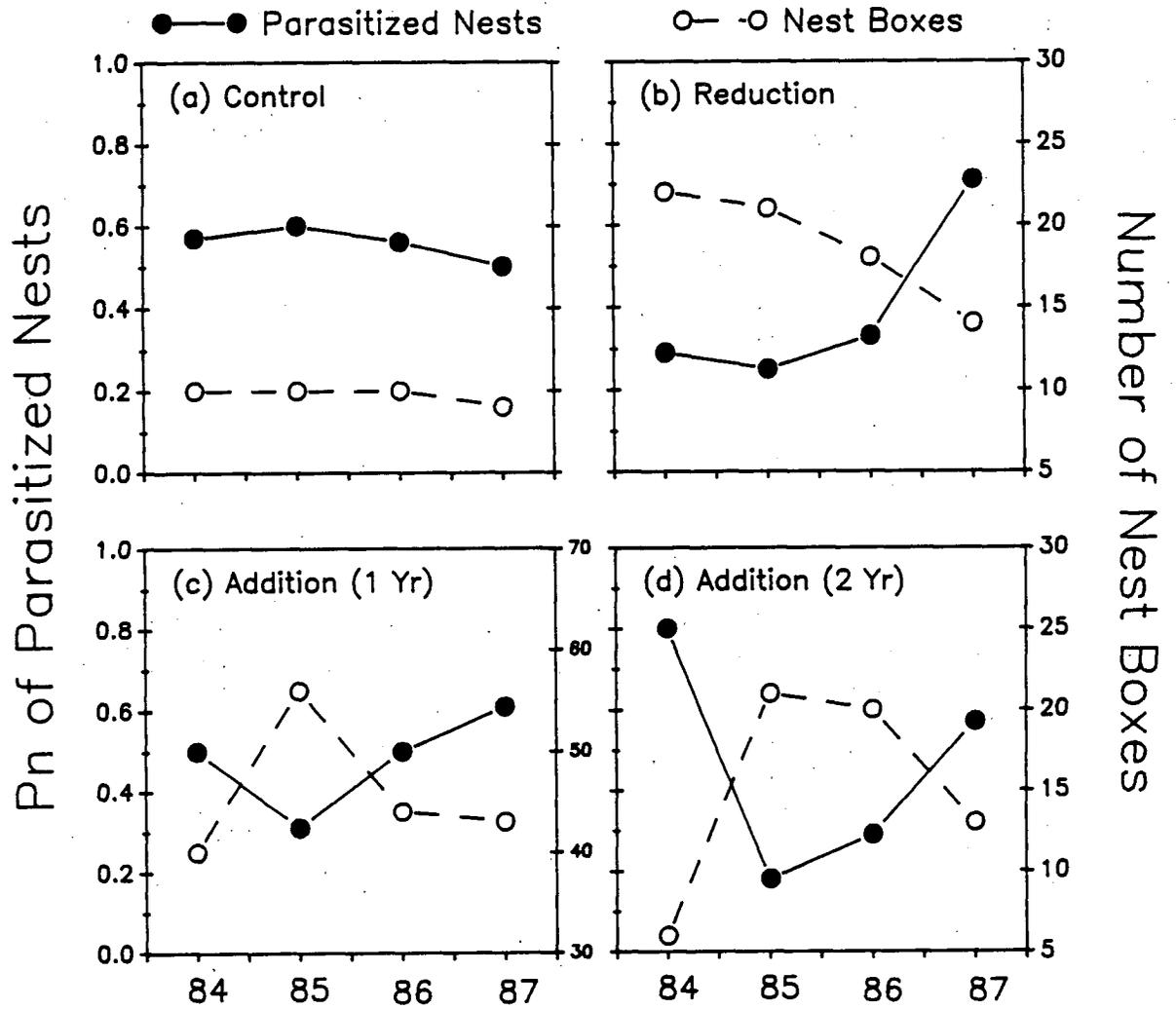


Figure 6.4. The effect of experimental manipulation of nest site availability (open circles) on the proportion of nests parasitized (filled circles). Each treatment represents a separate lake followed from 1985 to 1987.

Table 6.4. The number of nest boxes used and the proportion of nests parasitized on two experimental study plots with a high density (5 boxes / lake) and low density (2 boxes / lake) of nest sites.

	<u>High Density</u>		<u>Low Density</u>	
	<u>No. Used</u>	<u>Parasitized</u>	<u>No. Used</u>	<u>Parasitized</u>
1985	2	0	8	.25
1986	11	.18	9	.22
1987	13	.31	12	.42
All Years	26	.23	29	.31

hindered by the small size of the goldeneye population on the experimental area. Less than half of the available boxes were used (Table 6.4), and the lack of a clear difference between the high density and low density treatments may reflect a surplus of nest sites in both treatments.

Nest Limitation or Host Availability?

An alternative explanation for the relationship between parasitism and nest limitation is that parasitic egg-laying is simply facilitated by the increased availability of potential hosts at high population densities (Rohwer & Freeman 1989). I used partial correlation analysis to separate the effects of host availability and nest limitation. In this analysis, I regarded each lake in each year as an independent sample ($N = 31$ lake-years). The frequency of parasitism was not correlated with the number of host nests when either the number of nest boxes or the proportion of nests used was held constant (Table 6.5). However, when the number of hosts was controlled statistically, the frequency of parasitism remained significantly correlated with both measures of nest availability (Table 6.5). Parasitic behaviour therefore appears to be most strongly influenced by the availability of nest sites.

Reproductive Success of Parasitic and Parental Females

The conditional strategy hypothesis predicts that the reproductive success of parasitic females is less than that of parental females, whereas the mixed ESS hypothesis predicts that reproductive success of the two tactics is equal. Females that laid at least some eggs parasitically produced slightly more eggs in total (Welch's approximate $t = 2.00$, $df = 21.8$, $P < .06$), but hatched and fledged the same number of young as parental females (both $t < 0.6$, $P > .50$; Table 6.6). The power of these comparisons is limited by the small sample of parasitic females.

However, I obtained similar results when I quantified separately each component of reproductive success using a larger number of experimental and naturally parasitized nests (Table 6.7; see methods for details). The data in Table 6.7 are summarized from analyses presented in Chapter 4.

Table 6.5. Partial correlations between the frequency of brood parasitism, nest site availability, and the number of hosts. N = 31 lake-years.

	<u>Pn Nests Parasitized</u>	<u>Pn Parasitic Eggs</u>
a) Controlling No. Boxes Correlation with No. Hosts	.19	.26
b) Controlling No. Hosts Correlation with No. Boxes	-.49 **	-.49 **
a) Controlling Pn Nests Used ^a Correlation with No. Hosts	-.23	-.08
b) Controlling No. Hosts Correlation with Pn Nests Used ^a	.77 ***	.71 ***

^a Proportions were arcsin square-root transformed

*** P < .001, ** P < .01

Table 6.6. Reproductive success of individual parasitic and parental goldeneye females.

	<u>Parasitic</u>	<u>Parental</u>	<u>P^a</u>
Clutch Size	9.0 ± 0.5 ^b (12)	7.8 ± 0.3 (32)	< .06
No. Hatch	5.5 ± 0.3 (6)	5.8 ± 0.6 (32)	> .50
No. Fledge	2.2 ± 0.7 (6)	2.4 ± 0.5 (32)	> .75

^a Welch's approximate t-test

^b Clutch size estimate includes 6 females that were used in other experiments or otherwise disturbed

Table 6.7. Components of reproductive success for parasitic and parental goldeneyes. Results are shown separately for unmanipulated and experimental nests.

	<u>Parasitic</u>	<u>Parental</u>	
		<u>Alone</u>	<u>Parasitized</u>
I. Unmanipulated Nests			
Clutch Size ^{1,2}			
a) Observed	9.0 ± 0.5 a (12)	8.1 ± 0.2 a,b (50)	7.8 ± 0.2 b (66)
b) POF's	10.0 ± 0.3 a (7)	8.0 ± 0.0 b (2)	8.3 ± 0.4 b (7)
Pn Nests Incubated	0.76 ± .04 a (102)	0.72 ± .05 a (71)	0.76 ± .04 a (102)
Pn Eggs Hatch	0.74 ± .04 a (59)	0.92 ± .03 b (40)	0.89 ± .02 b (59)
Pn Young Fledge	0.46 ± .05 a (48)	0.42 ± .06 a (27)	0.46 ± .05 a (48)
Net Egg Success ³	.26	.28	.31
II. Experimental Nests			
Clutch Size	-	7.6 ± 0.3 a (26)	7.1 ± 0.2 a (27)
Pn Nests Incubated	0.69 ± .06 a (39)	0.70 ± .08 a (37)	0.69 ± .06 a (39)
Pn Eggs Hatch	0.69 ± .06 a (19)	0.88 ± .04 b (20)	0.89 ± .03 b (17)
Pn Young Fledge	0.33 ± .10 a (13)	0.33 ± .07 a (18)	0.35 ± .10 a (13)
Net Egg Success ³	.16	.20	.22

¹ Clutch size was estimated by following individual females (Observed) and by counts of post-ovulatory follicles (POFs)

² Values with different letters are significantly different ($P < .05$)

³ Net egg success is the probability that an egg produces a fledgling (pn incubated · pn hatch · pn fledge);

Four main results emerge:

(1) Parasites laid 1-2 eggs more than parental females. There was a significant difference between the observed clutch size of parasitic and host females (Welch's approximate $t = 2.23$, $df = 14.7$, $P < .05$) but not between parasites and non-parasitized parental females ($t = 1.67$, $df = 14.7$, $P < .15$). Counts of post-ovulatory follicles (POFs) showed that parasites laid more eggs than parentals in all cases (Welch's approximate t , parasites versus parasitized parentals: $t = 3.29$, $df = 11.1$, $P < .05$; parasites versus parentals alone: $t = 6.67$, $df = 7$, $P < .05$).

(2) Similar proportions of parasitized nests and non-parasitized nests were incubated. This was true for both unmanipulated nests ($G_w = 0.47$, $P > .50$) and experimental nests ($G_w = 0.01$, $P > .50$).

(3) Hatch success was 20% lower for parasitic eggs in both unmanipulated and experimental nests (Mann-Whitney U tests, both $P < .05$). I discuss reasons for this difference in Chapter 4. The most probable explanation (for nests parasitized naturally) is that some parasitic eggs were laid after the host had started incubation.

(4) There was no significant difference in the post-hatch survival of young from parasitized and non-parasitized nests (Mann-Whitney U tests, $P > .10$). Host and parasite young also survived equally well within parasitized broods ($G_w = 0.05$, $P > .90$).

The probability that a parasitic egg produces a fledged offspring (i.e. net egg success) is therefore similar to that of an egg laid by a parental female (Table 6.7). I estimated annual reproductive success of females as the product of each component of RS (Table 6.8 and see methods). This approach assumes that parasitic females do not establish their own nest. The parasitic tactic resulted in slightly more fledged young than the parental tactic in the observational studies, whereas the reverse applied in the experimental studies (Table 6.8). The differences within each comparison were minimal. These estimates of annual reproductive success were similar to those obtained by following individual females throughout the entire breeding season (Table 6.6).

Table 6.8. Estimated annual and lifetime reproductive success (number of fledglings) of parasitic and parental goldeneye females.

	<u>Unmanipulated Nests</u>		<u>Experimental Nests</u>	
	<u>Parasite</u>	<u>Parental</u>	<u>Parasite</u>	<u>Parental</u>
Annual Reproductive Success^{a,b}				
i) Observed	2.33	2.31	1.45	1.54
ii) POFs	2.59	2.35	1.57	1.68
No. Breeding Years^c	2.11	1.84	2.11	1.84
Lifetime Reproductive Success^{a,b}				
i) Observed	4.92	4.25	3.06	2.83
ii) POFs	5.47	4.32	3.31	3.09

^a Reproductive success was calculated assuming that (i) parasitic females laid all of their eggs parasitically and (ii) 35% of parental female nests were parasitized

^b Estimates were calculated separately using observed clutch sizes (Observed) and clutch sizes estimated from counts of post-ovulatory follicles (POFs)

^c Breeding lifespan was assumed to be the same for females in unmanipulated and experimental nests

Thus, two different methods show that parasitic and parental females produce about the same number of fledged young per year.

Since parasitic females invest less time and energy in rearing offspring, they might live and breed longer than parental females. However, there was no marked difference for goldeneyes. The average breeding lifespan of parasitic females was 2.11 ± 0.19 years ($N = 19$), whereas that for parental females was 1.84 ± 0.11 ($N = 61$; Welch's $t = 1.20$, $P > .10$).

I estimated lifetime reproductive success (LRS) as the product of annual RS and breeding lifespan. Lifetime success of parasitic females was similar to that of parental females (Table 6.8). However, the range of simulated LRS values for parasites was 0-28 young compared to 0-18 young for parental females (Figure 6.5). Both distributions were strongly skewed, but LRS estimates for parasitic females fell more often in the 0-2 class. The median LRS for parasitic females was 2.63 young (interquartile range: 0.51 - 6.85), whereas that for parental females was 3.28 young (1.52 - 6.14). When I repeated the analysis using clutch sizes determined by counts of POFs, the median LRS for parasitic and parental females was 2.94 young (0.56 - 7.61) and 3.32 young (1.68 - 5.87), respectively. These results suggest that brood parasitism is a risky tactic; only a few parasitic females do exceedingly well, while many obtain little or no success.

Negative Frequency-dependent RS?

A final prediction of the mixed ESS hypothesis is that the reproductive success of parasites is negatively frequency-dependent; that is, the success of parasites is high when the parasitic tactic is rare, but declines below that of parental females when parasitism is frequent. This will necessarily be true since the parasitic tactic cannot succeed without at least some parental females in the population. As the proportion of parental females declines, the fitness of parasites also declines, given that potential hosts become increasingly scarce (see Andersson 1984).

Other evidence was consistent with the prediction of negative frequency-dependence. Parasitic goldeneyes laid 1-2 eggs more than parental females (Table 6.7) and the hatch success of eggs in parasitized nests was near 100% when parasitism was rare (Figure 6.6). Thus, brood

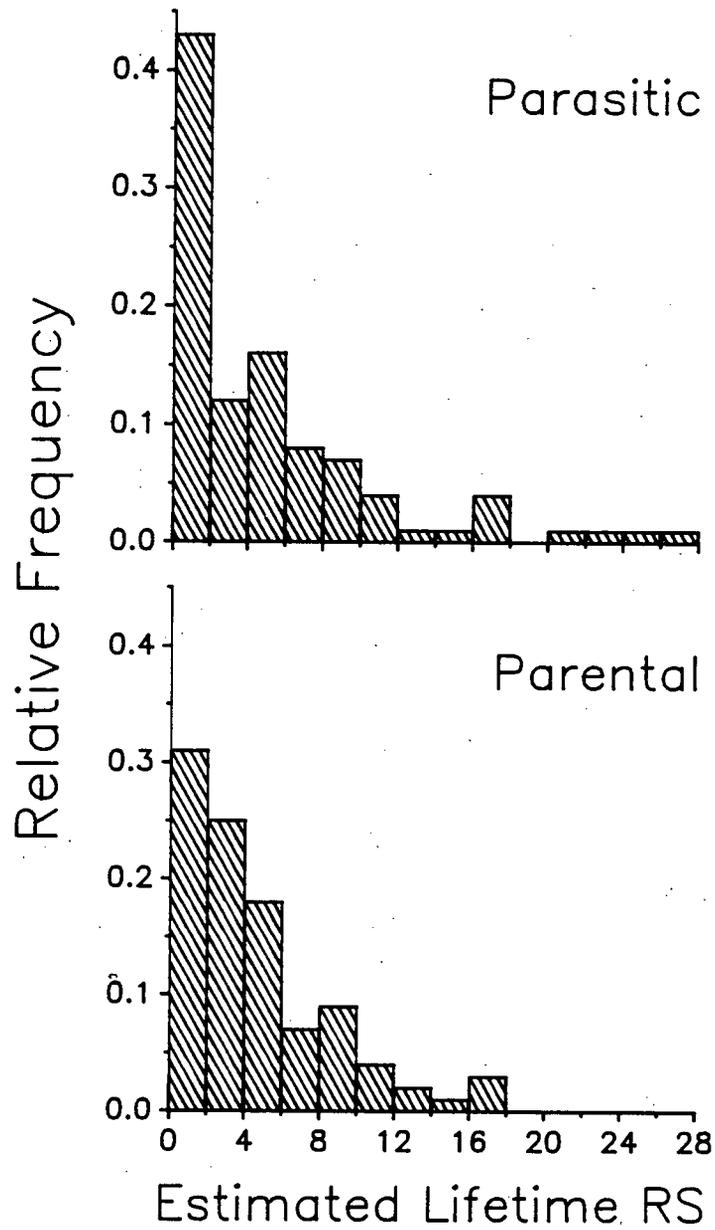


Figure 6.5. The distribution of simulated measures of lifetime reproductive success (number of young fledged) for parasitic and parental goldeneye females. Details of the simulation procedure are given in the text.

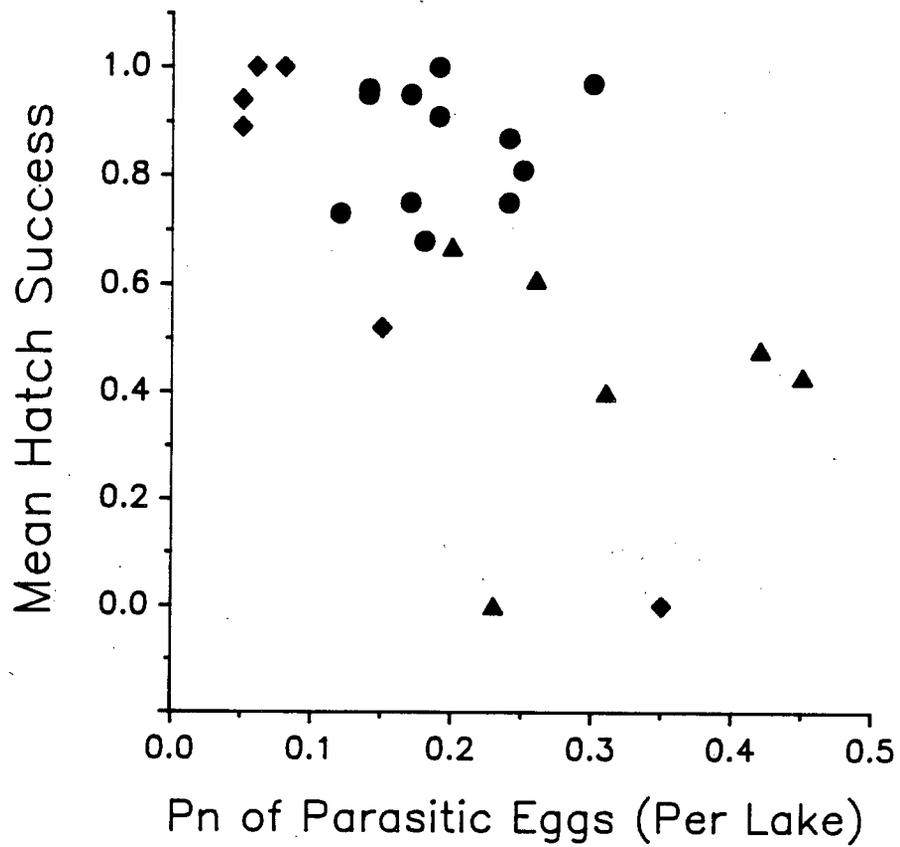


Figure 6.6. Hatch success of eggs in parasitized nests as a function of the frequency of parasitism. Each point represents the average for all parasitized nests on a lake in a single year. Symbols as in Figure 6.2.

parasites had higher fitness than parental females at low frequencies of the parasitic tactic. However, the success of parasitic eggs declined considerably as the frequency of parasitism increased (Figure 6.6). Average hatch success in parasitized nests was negatively correlated with the proportion of parasitic eggs ($r_s = -.59$, $N = 24$, $P < .01$; considering each lake in each year as an independent sample). Since the lower average hatch success in parasitized nests was due primarily to reduced success of parasitic eggs (Table 6.7 and see Chapter 4), the reproductive success of parasitic females falls below that of parental females at increasing frequencies of brood parasitism. Note, however, that the negative relationship between hatch success and the frequency of parasitism is influenced strongly by differences among years (Figure 6.6). When each year was analysed separately, a negative relationship was observed in only one of three years (1985).

DISCUSSION

Accident or Adaptive Behaviour?

Until recently, facultative brood parasitism was considered to be an accidental or aberrant behaviour of little evolutionary significance (Grenquist 1963, Jones & Leopold 1967, Erskine 1972, Siegfried 1976). Few researchers considered that parasitic egg-laying in waterfowl was an adaptive reproductive behaviour in its own right (e.g. see Hines & Mitchell 1984). However, detailed studies have documented facultative parasitism in an increasing number of species and several adaptive hypotheses have now been proposed for this behaviour (Yom-Tov 1980a, Andersson 1984, Eadie et al. 1988). The present study is one of the first to test these hypotheses.

Parasitic behaviour in goldeneyes was not simply an inadvertent consequence of competition among females for nest sites. Putative parasites did not incubate nests into which they had laid eggs, even when I removed the host female. Some females laid eggs in neighbouring nests as well as in their own during the same period, a result that is clearly at odds with the accident hypothesis. In other cases, parasitic laying stopped several days before the host began to incubate

the nest, suggesting that parasitic females were not excluded from nest sites by the presence of an incubating female (*sensu* Grenquist 1963, Erskine 1972).

Some researchers have argued that the high frequencies of brood parasitism observed in studies using nest boxes are an artifact of the unnatural densities of nest sites (Semel & Sherman 1986, Semel et al. 1988). Under such conditions, "pathological" levels of parasitism may develop, rendering futile any attempt to assess the evolutionary significance of the behaviour (Semel & Sherman 1986). I do not believe that such a situation obtained in my study. Research by M. Jackson on this same population over 30 years ago revealed levels of parasitism similar to those found today, yet nest boxes were not available during those earlier studies. Territorial behaviour in goldeneyes might constrain the maximum frequency of brood parasitism by limiting the number of breeding females on a given lake (Chapter 5, Gauthier 1987, Gauthier & Smith 1987). On my study area, goldeneye pairs were well spaced, and nests were parasitized by one or, at most, two females. This contrasts with wood ducks in which breeding pairs are not territorial, population densities increase rapidly in response to the addition of nest boxes, and up to 6 females may lay eggs in the same nest (Semel & Sherman 1986).

Brood Parasitism as a Conditional Strategy

The conditional strategy hypothesis predicts that females become parasitic only when they are unable to breed otherwise. I considered four factors that might promote parasitic egg-laying under such circumstances: (1) nest predation, (2) female size or condition, (3) age or experience, and (4) nest site availability. There was no evidence that females became parasitic in response to natural or experimental nest predation, nor did I find any differences in the size or condition of parasitic and non-parasitic females. In contrast, parasitic females were younger, on average, than parental females, suggesting an influence of age. Moreover, the availability of nest sites had a pronounced effect on the frequency of brood parasitism. There were strong correlations between the frequency of parasitism and nest site availability in all years of the study. A similar pattern was observed when I experimentally manipulated the number of nest boxes on a series of lakes.

These results support the hypothesis that parasitism is a conditional strategy pursued by young females when nest sites are limited.

Although nest limitation is often supposed to influence the frequency of brood parasitism in cavity-nesting birds (McLaughlin & Grice 1952, Grenquist 1963, Grice & Rogers 1965, Clawson et al. 1979, Lank et al. 1988), other studies have failed to find evidence consistent with this hypothesis (Morse & Wight 1969, McCamant & Bolen 1979, Pienkowski & Evans 1982, Semel et al. 1988). A negative correlation between the frequency of parasitism and nest availability could result if parasitism was constrained only by the availability of hosts (Rohwer & Freeman 1989). As the absolute number of hosts increases, the number of unoccupied nest sites necessarily decreases, giving rise to a spurious correlation between parasitism and nest availability. My results do not support this interpretation for goldeneyes. Partial correlation analyses showed that the frequency of parasitism was much more strongly correlated with the availability of nest sites than with the number of hosts. Further, host densities were not altered in the nest manipulation experiments, yet changes in the frequency of brood parasitism closely matched the changes in the number of nest sites. While the abundance of potential hosts undoubtedly affects the costs and benefits of parasitic behaviour (Semel et al. 1988), my evidence for goldeneyes indicates that nest site availability has an over-riding influence.

Three observations, however, challenge the conditional strategy hypothesis as a sufficient explanation for brood parasitism in goldeneyes. First, parasitic egg-laying was not confined to young females. Several females in their second and third breeding year were parasitic (Table 6.3). Second, moderate frequencies of parasitism occurred even when unoccupied nest sites were available (Figure 6.3). Finally, some females laid eggs as brood parasites while also establishing a nest of their own (Figure 6.1). Similar patterns have been reported for other species (Morse & Wight 1969, Clawson et al. 1979, McCamant & Bolen 1979, Pienkowski & Evans 1982, Brown 1984, Gibbons 1986, Semel et al. 1988).

Brood Parasitism as a Mixed Strategy

As alternatives to the conditional strategy hypothesis, I considered three mixed strategy hypotheses. The ESS_t hypothesis proposes that parasitic and parental behaviours are genetically fixed within individuals, and that an equilibrational balance of the two genotypes is maintained by frequency-dependent or disruptive selection. This hypothesis was soundly rejected by the observation that parasitic behaviour was phenotypically flexible. Females switched behaviours within and between years.

The mixed ESS hypothesis instead proposes that parasitic and parental behaviours are alternative tactics at the individual level. Females lay only a proportion of their eggs parasitically, and natural selection adjusts that proportion until the payoffs of parasitic and parental tactics are equilibrated. The mixed ESS hypothesis predicts that the success of the alternative tactics will be equal, and negatively-frequency dependent (Brockmann et al. 1979, Gross & Charnov 1980, reviews in Austad 1984, Dominey 1984). I found evidence consistent with both predictions. First, the probability that a parasitic egg produces a fledged offspring was similar to that of an egg laid by a parental female (Table 6.7), and estimated annual and lifetime success of parasitic and parental females were nearly identical (Table 6.8). Second, the relative success of the parasitic tactic declined significantly as the frequency of parasitism increased (Figure 6.6).

Although these results are consistent with the mixed ESS hypothesis, it is difficult to account for the observed effects of nest site availability if this hypothesis is correct. In a mixed ESS, individuals do not use cues about the environment or about their own phenotype to modify their behaviour. Rather, tactics are played stochastically according to some heritable probability which can be modified only by natural selection over evolutionary time (Maynard Smith 1982, Parker 1984). This expectation conflicts with the observation that the frequency of parasitism varied considerably among years and lakes, and changed rapidly in response to changes in the availability of nest sites. Moreover, the requirement that females lay parasitically with a fixed probability seems unnecessarily restrictive. Females that did so would be at a disadvantage to females that were able to alter their behaviour in response to changes in environmental or

phenotypic conditions (see Austad 1984). In at least some species, parasitic females do use cues about their own reproductive condition or the condition of their mate or nest site to modify their laying tactics (Emlen & Wrege 1986, Gibbons 1986, Evans 1988).

I considered a third mixed strategy hypothesis which proposes that females lay some eggs parasitically on the side (the side-payment hypothesis). I found that goldeneye females produced more eggs in total when they laid at least a few eggs parasitically (Table 6.6). Although this did not translate into more fledged offspring, my sample sizes were small. The side-payment hypothesis could explain why some females laid eggs in neighbour's nests in addition to their own. It cannot, however, account for the effects of nest-site limitation nor for the fact that some females only laid parasitically during a given year (Figure 6.1).

Reconciling the Conflicting Results

I was able to reject several of the hypotheses proposed to explain facultative brood parasitism, but there are clearly some unresolved issues. On the one hand, there is evidence that some females pursue parasitism as a conditional strategy in response to nest limitation. On the other hand, there is evidence that some females pursue parasitism as part of a mixed strategy, possibly obtaining benefits on the side. Conditional and mixed strategy hypotheses are generally viewed as mutually exclusive (e.g. Davies 1982, Parker 1984, Arak 1984). The results of my study are therefore puzzling.

As a resolution, I propose that parasitic behaviour in goldeneyes is an opportunistic tactic that can be pursued by any individual, under a variety of circumstances. Some females act as brood parasites when they are unable to obtain nest sites of their own. For these females, parasitism would be a direct consequence of nest site limitation. Other females lay parasitically as an alternative to, or in addition to, nesting on their own. Parasitic egg-laying by these females would occur even when population densities were low and nest sites abundant. Thus, some background level of parasitism would persist in the population, although parasitism would be more frequent when nest sites were limited.

This argument supposes that a facultative brood parasite might benefit from parasitic egg-laying, even if nest sites were readily available. There are several reasons why this might be so.

(1) Females that lay some eggs parasitically may be able to produce more eggs in total, either by spreading out the demands of egg production, or by reducing the number of eggs/young that they care for themselves. Parasitic goldeneye females laid 1-2 eggs more than non-parasitic females. Heusmann et al. (1980) reported that a parasitic wood duck laid 20 eggs in a single season, nearly double the normal clutch size. Similarly, parasitic swallows of two species laid more eggs and fledged more young than non-parasitic females (Brown 1984, Moller 1987).

(2) Parasitism might be advantageous if some factor other than energy or nutrients limited the number of eggs that a female could lay in her own nest. Arnold et al. (1987) suggested that clutch size in prairie ducks was limited by egg viability. Eggs that were not incubated within 10 days of being laid were less likely to hatch (Arnold et al. 1987). By laying some eggs parasitically prior to establishing their own nests, females could avoid this constraint. In at least three species of birds (wood ducks, Clawson et al. 1979, Heusmann et al. 1980; goldeneyes, this study; moorhens, Gibbons 1986) some females lay parasitically before initiating their own nests.

(3) Parasitism might be advantageous if females were able to secure better care for their offspring than they could provide themselves. This might benefit young females, in particular, if they were able to parasitize older, more experienced hens. I show elsewhere that older females in high quality nests were more likely to be parasitized (Eadie, in prep).

(4) Parasitic behaviour might enhance the survival and therefore, the lifetime fitness of females. Incubation in precocial birds is demanding, and can lead to stress-related mortality or to an increased risk of predation (Ricklefs 1974, Korschgen 1977, Drobney 1980). By avoiding incubation and brood-rearing, parasitic females would not only circumvent these costs, but might also be able to molt and migrate earlier. I did not find any difference in the breeding lifespan of parasitic and parental goldeneye females. Dow & Fredga (1984), however, found that female common goldeneyes in Sweden were less likely to survive if they produced and cared for a large brood in their first year.

(5) By spreading eggs among several nests, a parasite could reduce the risk of total nest failure and thereby increase the probability that at least some young survive (Payne 1977a, Rubenstein 1982). This factor is likely to be of less consequence than the preceding four. Bulmer (1984) demonstrated that the selective advantage of such risk spreading is small. Moreover, simulated estimates of lifetime reproductive success (Figure 6.5) indicate that the success of the parasitic tactic may be more, rather than less, variable than that of parental nesting.

If parasitism provides even some of the above benefits, why doesn't the parasitic tactic sweep through the population? I argue that frequency-dependent reproductive success sets an upper limit to brood-parasitic behaviour. Both logic and evidence suggest that the relative benefit of parasitic behaviour is considerably reduced at high frequencies of parasitism (Andersson 1984, and see above). For example, the hatch success of parasitic goldeneye eggs declined rapidly as the frequency of parasitism increased (Figure 6.6, and see Chapter 4). Similar results have been reported for wood ducks (Haramis & Thompson 1985, Semel et al. 1988). In spite of this element of frequency-dependence, it is unlikely that parasitism will evolve to an evolutionarily stable frequency, because the "payoffs" of alternative nesting tactics are also influenced by factors such as population density and nest site limitation. Thus, the value of parasitic laying differs when population densities are high and nest sites are limited, compared to circumstances in which all females can obtain nest sites of their own. Parasitism as an opportunistic tactic would allow females to adjust their behaviour to changes in social and environmental conditions. As long as these changes occur, there is not necessarily a single equilibrium frequency of parasitism at which the fitness of the two tactics is balanced.

Opportunistic parasitism might also involve frequency-dependent choice (Brockmann & Dawkins 1979), such that the "decision" to lay parasitically depends on the relative abundance of potential hosts (e.g. see Brown 1984, Moller 1987). Frequency-dependent choice on a behavioural time scale could mimic frequency-dependent selection on an evolutionary time scale (Brockmann & Dawkins 1979). However, the advantage of such a mechanism is that it is not probabilistic, and therefore provides flexibility in responding to changing conditions.

Facultative Parasitism in Other Birds

The two patterns observed in my study have also emerged in other recent studies of facultative brood parasitism in birds. For example, females of several species pursue parasitism as a conditional strategy in response to competition for limited nest sites (Clawson et al. 1979, Haramis & Thompson 1985, Evans 1988, Lank et al. 1988), nest disruption (Emlen & Wrege 1986, Evans 1988) or poor breeding condition of the female or her mate (Gibbons 1986, Lank et al. 1988). In a smaller number of species, parasitism is part of a mixed strategy, in which females lay eggs in a neighbouring nest in addition to their own, and thereby increase their own reproductive success (Brown 1984, Moller 1987, Evans 1988).

Most researchers have interpreted their results as supporting one of these two alternatives. However, two recent studies indicate that more than a single factor might be responsible for parasitic behaviour in the same population. Evans (1988) suggested that some starlings became parasitic as a salvage tactic, while other females turned to parasitism as part of a mixed strategy. He argued that both mechanisms acted independently to maintain parasitic behaviour in the population. Similarly, parasitism in wood ducks has been linked to a limited supply of nest sites, yet some females lay parasitically even when nest sites are abundant (Clawson et al. 1979, Haramis & Thompson 1985). Lank et al. (1988) speculated that such contradictory evidence could be resolved if wood duck populations contained both mixed and salvage strategists. Females without a nest site or with insufficient energy reserves might lay parasitically as a salvage strategy, but parasitism would nonetheless persist among females that pursued parasitism as part of a mixed strategy (Lank et al. 1988). These studies closely parallel my own findings.

A potential confounding factor in my study is that I considered intraspecific and interspecific brood parasitism simultaneously. However, I showed earlier that all aspects of reproductive success were identical for Barrow's and common goldeneyes (Chapters 3 and 4). Both species used the same nest sites and breeding areas, reared young in the same way, and effectively functioned as a single "ecological" species. Further, I could not detect any effect on parasitic young of being raised by a female of the other species, although there may be long-term effects,

such as inappropriate species recognition and mate choice behaviours (e.g. Gottlieb 1971, Shapiro 1980). It could be argued that considering both species simultaneously provides an even more powerful test of the adaptive basis of brood parasitic behaviour. Given that the parasitic trait exists in females of both species (as it does), and given that both species are limited by the same resources (as they appear to be), we expect similar frequencies of parasitism to occur in both species. In fact, the frequency of parasitism was identical in both species, and parasitism between the species was as frequent as parasitism within species.

The increasing numbers of reports of facultative brood parasitism indicate not only that parasitism is a widespread reproductive tactic, but also that alternative female reproductive behaviours may be more prevalent than previously thought. I showed previously that there was considerable variation in reproductive success among female goldeneyes, and that some of this variance was the result of exploitative competition for nest sites and brood territories (Chapter 3). Under such conditions, behaviours that allowed females to circumvent these constraints would be adaptive. Parasitic egg-laying is one such option, and it may prove to be a common alternative tactic of females in species that can insert their offspring into another individual's nest or brood. Successful parasitism of conspecifics requires relatively few specializations, and it is probably not coincidental that parasitic behaviour is found frequently in species in which resources required for breeding are limited (e.g. nest cavities, food resources), and in which the opportunity to parasitize conspecifics is high (e.g. colonial nesting species).

CHAPTER 7

DENSITY-DEPENDENCE, FREQUENCY-DEPENDENCE AND ALTERNATIVE
NESTING BEHAVIOURS IN GOLDENEYES

The concept of evolutionarily stable strategies (ESS's) has been a powerful tool in the analysis of animal social behaviour (Dawkins 1980, Arak 1984, Parker 1984, 1985). Unlike optimality theory, ESS theory deals explicitly with frequency-dependent selection and is therefore appropriate whenever the fitness of an individual depends on the actions of other individuals in the population (Maynard Smith 1982, Parker 1984). This is important since many aspects of animal behaviour, and certainly all aspects of social behaviour, meet this condition. However, most ESS models ignore the effects of population density (Brown & Vincent 1987a,b). In fact, ESS models are usually tractable only under the assumption of a stationary, infinitely large population with a stable age distribution (Maynard Smith 1982). Since this assumption is often violated (e.g. Hansell & Brown 1987), there has been increasing interest in determining the effects of population density on the evolutionary stability of behavioural strategies (Sibly 1984, Parker 1985, Brown & Vincent 1987a,b).

In this chapter, I examine the interaction between density-dependent and frequency-dependent selection in maintaining alternative nesting behaviours in two species of cavity-nesting birds, the Barrow's goldeneye (*Bucephala islandica*) and the common goldeneye (*B. clangula*). In Chapter 6, I tested several hypotheses to account for brood parasitic behaviour in goldeneyes, with conflicting results. Some evidence was consistent with the hypothesis that parasitism was a conditional strategy pursued by young females when nest sites were limited. Other evidence suggested that parasitism was a tactic in a mixed strategy, pursued in the absence of other constraints. I proposed that these results could be reconciled if parasitism was an opportunistic tactic, subject to both density and frequency-dependence.

These ideas are formalized in the present chapter. In collaboration with Dr. John Fryxell, University of Guelph, I first construct a simple model which incorporates only the effects of

frequency-dependence and ask whether parasitic behaviour can be maintained under those conditions. I then incorporate the effects of population density and nest-site limitation to determine how density-dependence alters an interpretation based on frequency-dependence alone.

THE MODEL

Alternative strategy games usually involve several players ("n-person" games; Maynard Smith 1982, Parker 1984), and analytical solutions for the ESS are often complex or even impossible (Partridge & Krebs 1978, Poethke & Kaiser 1985). An alternative approach is to use computer simulation models (Partridge & Krebs 1978, Howard 1984, Poethke & Kaiser 1985). Unlike traditional game theory, simulation models allow dynamic games incorporating stochastic variation. Factors that are usually ignored in analytical ESS models, such as population density and nest-site limitation, can be readily included. The simulation models can then be used to predict parameter values or tactic frequencies, and these predictions can be tested with field data (Howard 1984, Poethke & Kaiser 1985). We adopt such an approach here.

The model constructed here calculates the reproductive success of parasitic and parental females for a range of parameter combinations. The reproductive success of a parasitic female is a function of:

- (1) the availability of host females,
- (2) the number of eggs that a parasite lays,
- (3) the probability that a parasitic egg produces a fledged offspring, and
- (4) the probability that other parasites choose the same host.

The reproductive success of a parental nesting female is a function of:

- (1) the probability of getting a nest site,
- (2) the number of eggs that a parental female lays,
- (3) the probability that a parental egg produces a fledged offspring, and
- (4) the probability of being parasitized by one or more parasites.

We made the following simplifying assumptions: (1) females pursue only a single nesting tactic within a breeding season (i.e. parasite or parental), (2) parasites lay all of their eggs in a single host nest, and (3) parasites choose randomly among hosts. I consider the validity of these assumptions in the discussion.

The annual reproductive success of parental and parasitic females was estimated as the number of eggs a female lays, multiplied by the probability that an egg produces a fledgling. This latter probability, in turn, depends on how many (if any) parasitic females also lay eggs in the same nest. We used the binomial distribution to determine the probability that a given parental female is parasitized by 0, 1, ..., N_p parasitic females. Here, the number of trials is simply the number of parasitic females in the population (N_p). The probability that any given parental nest is chosen by a parasite is $1/N_n$, where N_n is the number of parental females in the population. Accordingly, the reproductive success (RS) functions can be written as:

$$RS_n = E_n \cdot \sum_{y=0}^{N_p} \frac{N_p!}{y!(N_p-y)!} \cdot \left(\frac{1}{N_n}\right)^y \cdot \left(\frac{N_n-1}{N_n}\right)^{N_p-y} \cdot S_y, \quad (1a)$$

and

$$RS_p = E_p \cdot \sum_{y=0}^{N_p-1} \frac{N_p-1!}{y!(N_p-y-1)!} \cdot \left(\frac{1}{N_n}\right)^y \cdot \left(\frac{N_n-1}{N_n}\right)^{N_p-y-1} \cdot S_{y+1} \quad (1b)$$

where E_n = the clutch size of a parental female,

E_p = the clutch size of a parasitic female,

N_n = the number of parental females in the population,

N_p = the number of parasitic females in the population,

y = the number of parasites laying eggs in a host nest (0,1,.. N_p), and

S_y = the probability that an egg produces a fledgling in a nest where y parasitic

females also lay eggs (see below).

We assumed that S_y is a function only of the number of eggs in the nest, and we used data from field studies in 1984 and 1985 to determine this relationship. The proportion of young that fledged was a nonlinear function of clutch size (Figure 7.1). This relationship was the result of two factors. First, the proportion of nests that were incubated was a negative function of clutch size ($r = -.60$, $N = 18$, $P < .01$; considering only nest with more than 4 eggs):

$$p(I) = 0.93 - 0.03 \text{ Clutch Size} \quad (2)$$

Second, the probability that an egg produces a fledgling, given that the egg hatched, was a positive function of brood size ($r = .49$, $N = 34$, $P < .01$):

$$p(F) = 0.02 + 0.059 \text{ Brood Size} \quad (3a)$$

The proportion of eggs that hatched (p_H) was negatively related to clutch size but this effect was minimal (see Chapter 4). For the purpose of this analysis, we assumed that hatch success is constant at 0.90 over all clutch sizes. Brood size in equation 3a was converted to clutch size using this constant (i.e. $\text{Brood Size} = 0.90 \text{ Clutch Size}$). Thus,

$$p(F) = 0.02 + 0.053 \text{ Clutch Size} \quad (3b)$$

The total probability that an egg is incubated, hatches, and produces a fledgling is $p(I) \cdot p(F)$. We combined the regression equations algebraically to obtain a general function for the proportion of eggs producing a fledgling:

$$p(F) = (0.93 - .03 \text{ CS}) \cdot (0.02 + .053 \text{ CS}) \quad (4a)$$

$$= 0.02 + 0.05 \text{ CS} - 0.002 \text{ CS}^2 \quad (4b)$$

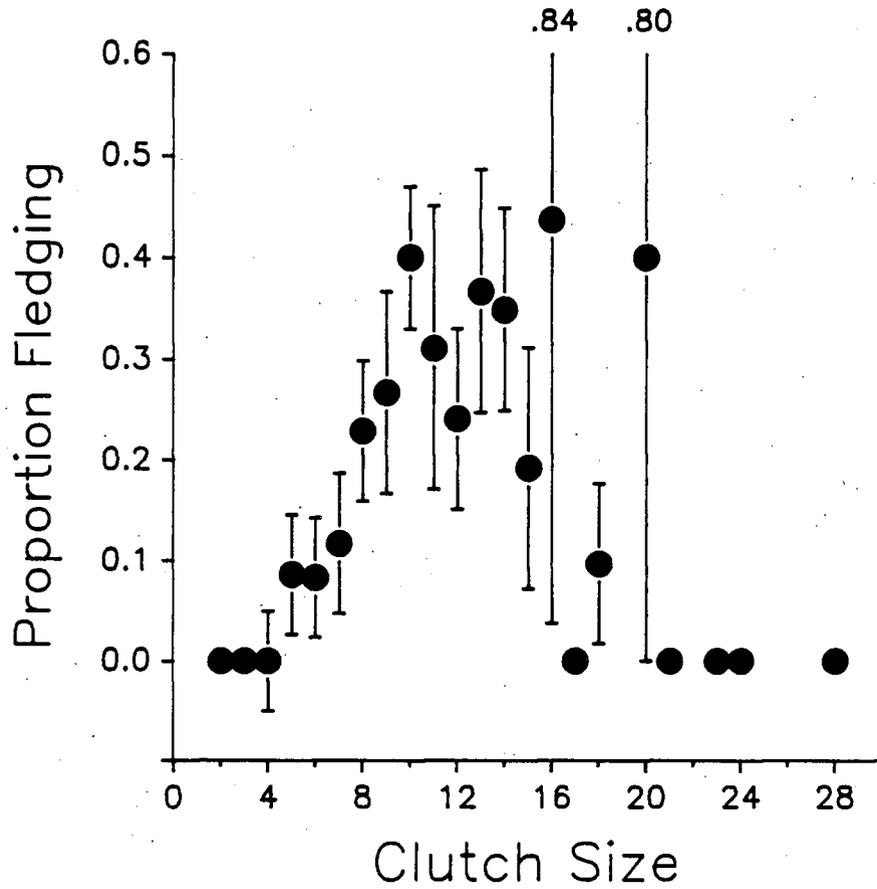


Figure 7.1. The relationship between clutch size and the proportion of eggs resulting in a fledged offspring. Each point is the mean \pm 1 SE for all nests with that clutch size. Points without error bars represent single observations (two nests were observed with 24 eggs).

Since the total clutch size (CS) depends on the number of females that parasitize a particular host nest, the probability that an egg of a parental female produces a fledgling is:

$$S_y = 0.02 + 0.05 [E_n + (y) E_p] - 0.002 [E_n + (y) E_p]^2 \quad (5a)$$

Similarly, the probability that an egg of a parasitic female produces a fledgling is:

$$S_{y+1} = 0.02 + 0.05 [E_n + (y+1) E_p] - 0.002 [E_n + (y+1) E_p]^2 \quad (5b)$$

Equations 5a and 5b were substituted into equations 1a and 1b, respectively, to calculate the reproductive success of parental and parasitic females. We determined the effects of frequency-dependence by systematically varying the number of parasitic females relative to the number of parental females. The reproductive success of each type of female was calculated for a range of frequencies of the parasite tactic and a range of clutch sizes of parental and parasitic females.

In a second set of simulations, we examined the effect of density-dependence by varying the total number of females, while keeping constant the relative proportions of the two types of females. To model the effects of nest site limitation on the reproductive success of parental females, RS_n was devalued by the probability of obtaining a nest site. This probability was set equal to 1.0 if there was a surplus of nest sites, and was otherwise calculated as N_s / N_n where N_s is the number of nest sites available. We assumed that parental females could not breed if they did not obtain nest sites. In cases in which the number of parental females exceeded the number of nest sites, the binomial probabilities in equations 1a and 1b were calculated using the number of females with nest sites ($= N_s$) rather than the total number of parental females (N_n).

Finally, we used a population simulation model to determine whether parasitic behaviour would be maintained in a population when both frequency-dependent and density-dependent selection were operating. We assumed that nesting tactics were perfectly heritable (e.g. parasitic females produced only parasitic daughters) and that all birds returned to their natal area to breed. Annual survival of adults was set to 0.65, the observed value (Savard and Eadie 1989). Recruit-

ment was based on the reproductive success of each tactic, as modelled above. The total number of females of each type in each year was calculated as the number of surviving adults, plus the number of surviving young produced in the preceding year by each female, summed over all females. Starting conditions were varied for different simulations runs, although in all cases E_n and E_p equalled 9 eggs. The time period in each simulation was 100 years (approximately 20-30 generations). Population size was limited only by nest site availability and by the reproductive success of each type of female. As such, the model is deterministic. However, a stochastic component was introduced by assuming that parasitic females were assigned at random to individual parental (host) females. Thus, some hosts were more heavily parasitized than others, and the net effect of parasitism on the success of both parasites and parental females therefore varied.

RESULTS

Is There a Stable Mix of Parasitic and Parental Females?

The model indicates that a stable mix of parental and parasitic strategies can be maintained by frequency-dependence alone. The results are shown in Figure 7.2 for different frequencies of the parasitic tactic (ordinate) and different combinations of clutch size of parasites (E_p ; abscissa) and parentals (E_n ; lines within the figure). Each line represents an isocline for reproductive success. For a given combination of parameters, parental females obtain greater reproductive success above the line, parasites realize greater reproductive success below the line, and the success of the two tactics is equal at the line. Four main results emerge from this analysis:

(1) A range of parameter combinations exist at which the reproductive success of parasitic and parental females is equal. These parameter values are, for the most part, within the range found in natural populations of goldeneyes (clutch sizes ranging from 6 to 14 eggs, and frequencies of parasitism up to 50%).

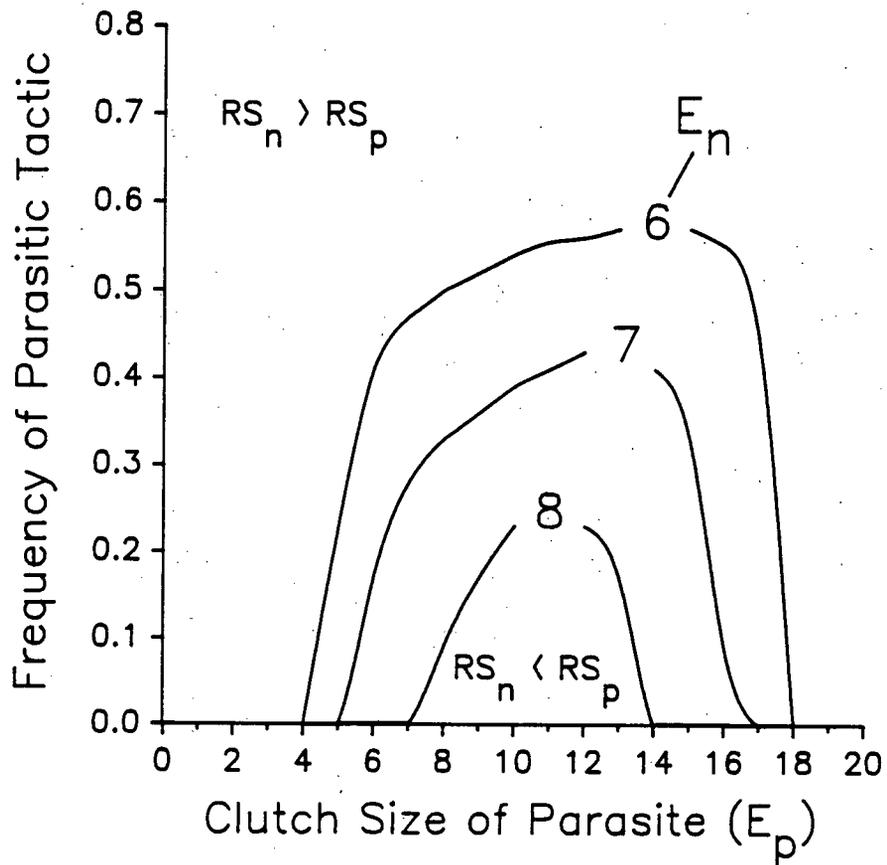


Figure 7.2. Reproductive success isoclines for different frequencies of the parasitic tactic, and different clutch sizes of parasitic (E_p) and parental (E_n) females. The lines show the combinations of parameters at which the success of parasitic (RS_p) and parental (RS_n) tactics is equal.

(2) For a given combination of E_p and E_n , reproductive success is negatively-frequency dependent. The reproductive success of parasites declines relative to that of parental females as the frequency of the parasitic tactic increases above the equilibrium frequency. Conversely, the reproductive success of parasites is superior to that of parentals when the frequency of parasites falls below the equilibrium point (Figure 7.2).

This relationship occurs because of the survivorship function, derived from field data (Figure 7.1 and equation 4b). When the relative abundance of parasites is high, the number of parasitic females that choose the same parental nest by chance is large, resulting in extreme clutch sizes and low reproductive success for all females in those nests (Figure 7.1). Since some parental females are not be parasitized, again by chance, the average reproductive success of parentals under these conditions exceeds that of parasites. Conversely, when the relative abundance of parasites is low, instances of multiple parasitism per host nest are infrequent and total clutch sizes are smaller. Parasites have superior reproductive success if they can lay more eggs than parentals (Figure 7.2). This result mimics the relationship observed between the frequency of parasitism and reproductive success under natural conditions (Chapter 6).

(3) The model indicates that the only stable points on the isoclines shown in Figure 7.2 are those at the apex of the curves. For example, consider the situation in which both parental and parasitic females lay 8 eggs ($E_n = 8$; $E_p = 8$). The reproductive success of the two tactics is equal when the frequency of the parasitic tactic is approximately 0.10 (Figure 7.2). However, a parasite that is able to lay 10 eggs has higher reproductive success than the parasite that lays 8 eggs, and so can become established in the population (Figure 7.2). This parasite also has greater reproductive success than parental females, and the frequency of the parasitic tactic therefore increases (Figure 7.2). The net result is that an evolutionarily stable equilibrium is reached only at the peak of the isocline; i.e. only certain combinations of parameters yield stable equilibria.

(4) The simulations suggest that the evolution of parasitism is closely tied to the factors that limit clutch size. The smaller the clutch size of parental females, the greater the range of conditions over which a parasitic tactic can persist (Figure 7.2). When the clutch size of parental

females exceeds 9 eggs, the parasitic tactic always has lower reproductive success and no frequency of parasitism is evolutionarily stable. Thus, the best response by hosts is simply to lay more eggs, while the best response by parasites is to remove eggs of the host. In either case, the evolutionary viability of parasitic egg-laying clearly depends on factors that limit clutch size in parental and parasitic females.

Testing the Predictions of the Model

Do clutch sizes of females, and frequencies of parasitism match those predicted by the model? I found that parental females lay an average of 8 eggs, while the average clutch size of parasitic females range between 9 and 10 eggs (Chapter 6). These values are in qualitative agreement with the predictions of the model, and indicate that an ESS is possible (Figure 7.2). The predicted frequency of parasitism is 0.17 if parasites lay 9 eggs, and 0.23 if parasites lay 10 eggs (Figure 7.2). The evolutionarily stable frequency of parasitism (i.e. that at the apex of the isocline, given a parental clutch of 8 eggs) is also 0.23. The observed frequency of parasitism (as indicated by the proportion of eggs laid parasitically) is 0.17 ± 0.02 SE ($N = 31$ lake-years, Chapter 6, Table 6.1). This value is close to the frequency predicted by the model.

Density-dependence and Nest Site Limitation

Given the agreement between the predictions of the model and the observed frequency of parasitism, it is tempting to conclude that parasitism and parental nesting are maintained as a mixed ESS. However, that hypothesis fails to account for the observed effects of population density and nest site limitation on the frequency of parasitism (Chapter 6). We therefore conducted a second set of simulations to incorporate both frequency-dependent and density-dependent effects on the reproductive success of goldeneye females. In these simulations, we systematically varied both the total number of females and the relative frequency of the parasitic tactic, while keeping the number of nest sites constant.

The effects of nest site limitation are shown in Figure 7.3. Reproductive success isoclines are plotted for three cases: (i) nest sites are not limited (the number of nest sites (N_s) is equal to

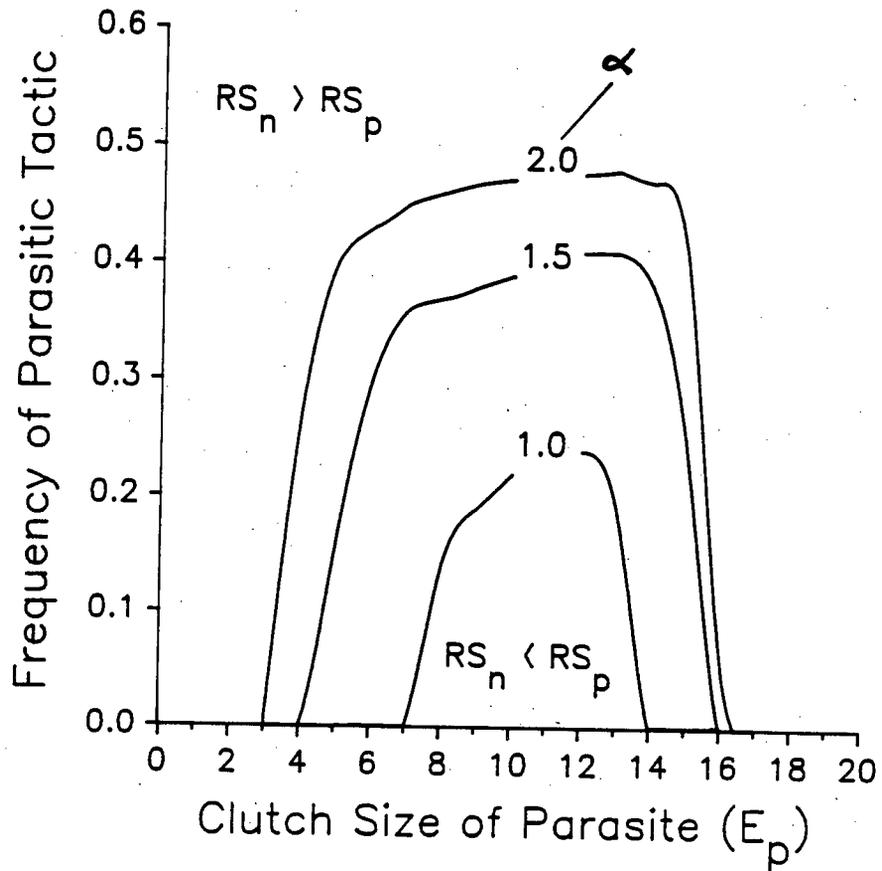


Figure 7.3. The effect of nest site limitation on the relative reproductive success of parasitic and parental females for different clutch sizes and frequencies of parasitic females. Each line represent the combination of parameters at which the success of parasitic (RS_p) and parental (RS_n) tactics is equal. Nest limitation is indexed as $\alpha =$ the number of parental females (N_n) / the number of nest sites (N_s). In all simulations, $N_s = 10$ nests and $E_n = 8$ eggs.

the number of parental females (N_n); $\alpha = N_n / N_s = 1.0$), (ii) nest sites are moderately limited ($N_n / N_s = 1.5$), and (iii) nest sites are severely limited ($N_n / N_s = 2.0$). The equilibrium frequency of parasitism increases with increasing nest site limitation. This result occurs because the expected reproductive success of parental females is reduced when the availability of nest sites is limited. Under such conditions, parasitism becomes a more profitable tactic. Furthermore, as the degree of nest site limitation becomes increasingly severe, the range of conditions over which parasitism can coexist with parental nesting also increases, although the effect decelerates (Figure 7.3).

The interaction between frequency-dependence and population density is shown in Figure 7.4. At a given density of females, the reproductive success of parasites declines relative to that of parentals as the frequency of the parasitic tactic increases (Figure 7.4). Conversely, at a fixed frequency of the parasitic tactic, the relative reproductive success of parasites increases as the total number of females increases. The net result of these two processes is that there is no single ESS. Rather, the equilibrium frequency of parasitism increases in a nonlinear fashion with the total density of females (Figure 7.4).

This interaction has important implications for field studies that attempt to test between conditional strategy and mixed strategy hypotheses. If population density varies, it is possible to obtain results consistent with either hypothesis. I illustrate this in Figure 7.5, where I plot the reproductive success of parasitic and parental females (y-axis) separately as a function of the frequency of the parasitic tactic (x-axis) and the total density of females (z-axis). In this figure, reproductive success is described by tilted 3-dimensional surfaces for each tactic. Because the success of each tactic is influenced differently by density and frequency, the two surfaces are not parallel and therefore intersect (Figure 7.5). The line of intersection gives the combinations of frequency and density at which the success of the two tactics is equal.

Figure 7.5 shows that when population density is low (< 12 females), the reproductive success of parasites falls below that of parentals at all frequencies of parasitism. However, at higher population densities, the reproductive success of parasites and parentals is negatively

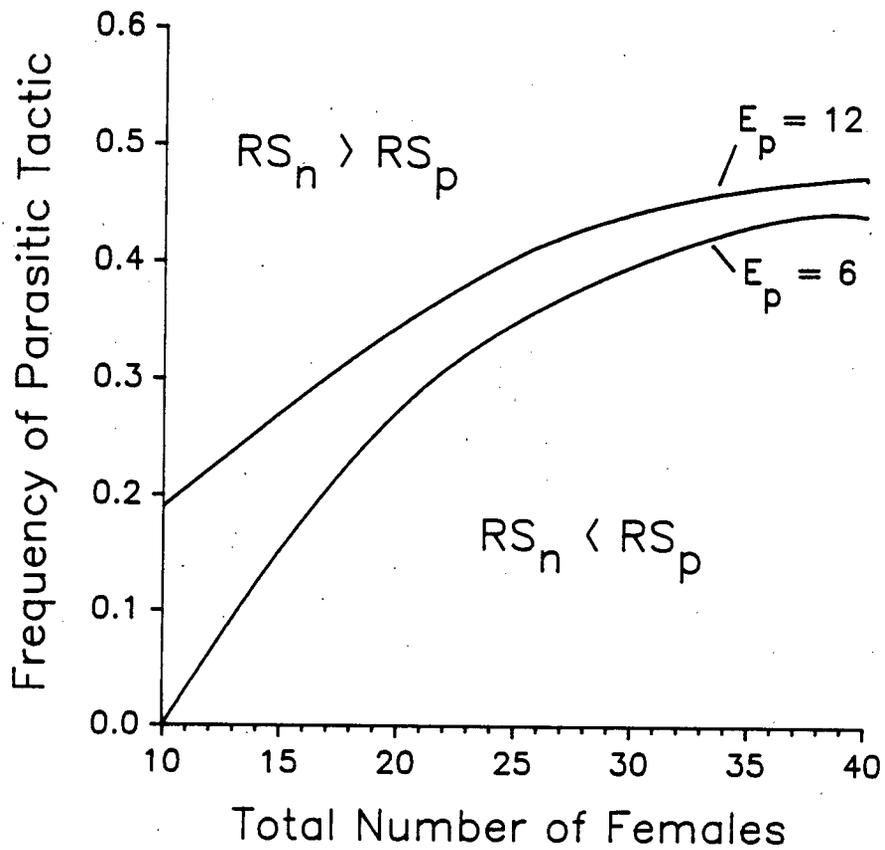


Figure 7.4. The effect of population density on the relative reproductive success of parasitic and parental females for two sizes of parasitic clutches (E_p). Each line represent the combination of parameters at which the success of parasitic (RS_p) and parental (RS_n) tactics is equal. In all simulations, $N_s = 10$ nests and $E_n = 8$ eggs.

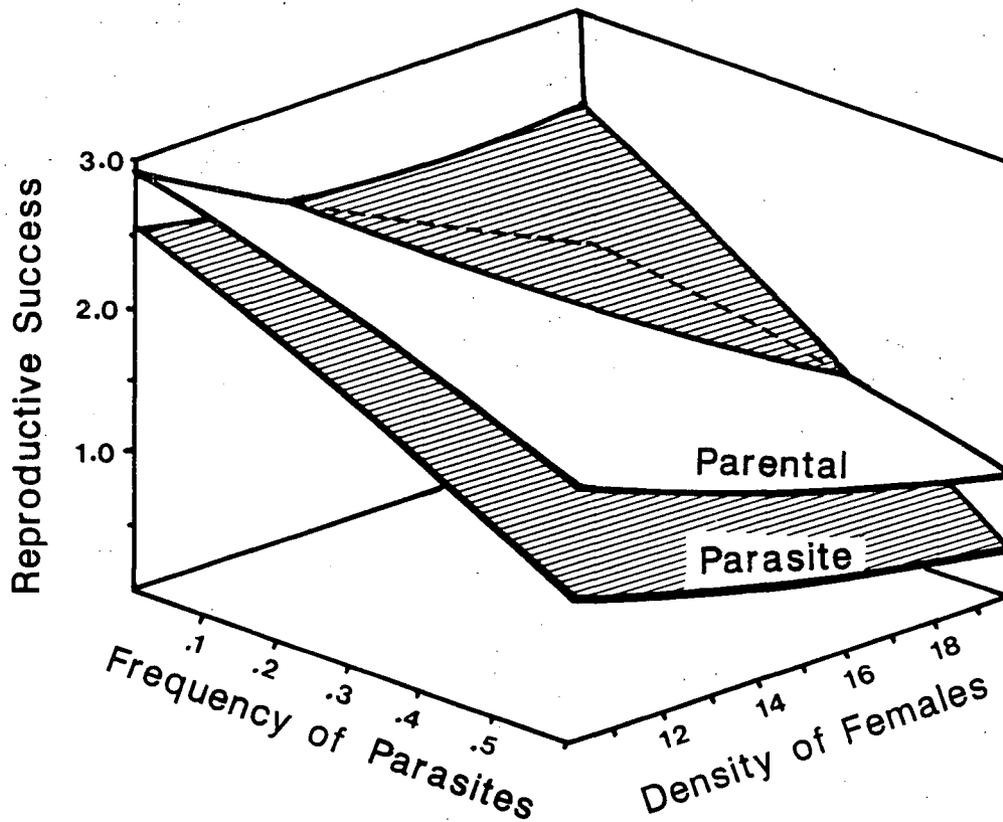


Figure 7.5. The effects of variation in the frequency of the parasitic tactic (x-axis) and the total density of females (z-axis) on the reproductive success of parasitic (shaded) and parental (open) females (y-axis). Reproductive success is plotted as a 3-dimensional surface. The surface for parental females slopes into the back of the figure and cuts through the surface for parasitic females. The line of intersection gives the combinations of density and frequency at which the success of the two tactics is equal. $N_s = 10$ nests and $E_n = E_p = 9$ eggs.

frequency-dependent. Parasites do better when the frequency of parasitism is low, parentals do better when the parasitic tactic is common, and a balance of the two tactics is reached where reproductive success is equal. Moreover, the location of the equilibrium point varies as a function of the absolute population density (Figure 7.5). Thus, if I had studied this population when densities were low, I would have concluded that parasitism was a subordinate tactic, consistent with the conditional strategy hypothesis. Had I studied the same population under high densities, I would have found evidence consistent with the predictions of the mixed ESS hypothesis. Clearly, conclusions about the adaptive basis of alternative nesting behaviours can be influenced strongly by the effects of population density.

Population Simulations

Can parasitic behaviour be maintained in a population by the combined effects of frequency- and density-dependence? To answer this question, we simulated changes in the number of parasitic females over several generations, starting from a variety of different conditions (Table 7.1). In most cases, the parasitic tactic became established (Table 7.1). Of the 90 simulation runs conducted, the parasitic tactic invaded the population in 63 runs (70%). This is an interesting result since all of these simulations were conducted using clutch sizes of 9 eggs for both parental and parasitic females. At these clutch sizes, the reproductive success of parasitic females is always inferior to that of parental females in the absence of density-dependence (see Figures 7.2 and 7.5). By including the effects of density-dependence, parasitic behaviour can be maintained in a population even when it has lower fitness initially.

The effects of population density are evident in those cases in which the parasitic tactic did not become established (Table 7.1). Two conditions, in particular, precluded parasitic behaviour: (1) small population size (runs 1, 6, and 13), and (2) high starting frequencies of parasitic females (i.e. over 80% of all females; runs 12 and 16). In the first condition, the number of hosts was insufficient to maintain a high absolute density of parasites and parasites became extinct through chance fluctuations in density. In the second condition, the extreme frequency of parasitism drove both hosts and parasites to extinction within 10 years.

Table 7.1. Results of a population simulation model showing the number of times that the parasitic trait became established for different starting values for each parameter. In all runs, the clutch size of parental and parasitic females was 9 eggs.

Run No.	No. Nests	No. Parentals	No. Parasites	Pn. Parasites	No. Times ^a Established
1	5	5	2	.28	0/5
2	10	10	2	.17	3/5
3	20	20	2	.09	4/5
4	40	40	2	.05	4/5
5	40	80	2	.04	5/5
6	5	3	3	.50	2/5
7	10	6	6	.50	5/5
8	20	12	12	.50	5/5
9	40	24	24	.50	5/5
10	40	20	20	.50	5/5
11	40	20	40	.67	5/5
12	40	20	80	.80	5/10
13	40	3	3	.50	0/5
14	40	5	5	.50	5/5
15	40	10	2	.17	10/10
16	40	10	40	.80	0/5

^a The parasitic trait was considered to be established if it persisted for the full simulation run (i.e. 100 years).

Under less extreme conditions, the parasitic trait invaded the population when initially rare (runs 2-5 and 15). The parasitic tactic was also maintained in the population when it was initially common (runs 7-11 and 14). Figure 7.6 shows the results for the first 50 years of run #5 (parasites initially rare) and run #10 (parasites common). Note that the frequency of the parasitic trait continued to fluctuate, indicating the absence of a stable equilibrium. However, these fluctuations were dampened after 30-40 years and there was considerable similarity in the final frequency of parasitism. In the 63 simulations in which the parasitic trait became established, the frequency of parasitism at the end of the 100 year runs ranged between 0.20 and 0.40, with most observations between 0.30 and 0.35 (Figure 7.7). This result is impressive given the variety of starting conditions.

DISCUSSION

The Interaction Between Frequency-dependence and Density-dependence

Most ESS models ignore the effects of density-dependence. Our analyses show that incorporating the effects of population density can considerably alter interpretations of behaviours based on frequency-dependent processes alone. In the goldeneye model, there is a density threshold above which a frequency-dependent equilibrium can be obtained, and below which it can not. By simply varying population density, it is possible to obtain results consistent with either the conditional strategy or the mixed strategy hypotheses (Figure 7.5). This result is important for two reasons. First, it provides an explanation for the results of my field study of brood parasitism in goldeneyes, where I found evidence consistent with both hypotheses (Chapter 6). Second, and more generally, it suggests that density- and frequency-dependence can interact in an unanticipated way to maintain alternative reproductive behaviours in a population. ESS analyses usually regard mixed and conditional strategies as mutually exclusive, and researchers have frequently attempted to test these alternatives in field studies (reviews in Maynard Smith 1982, Austad 1984). Our results, however, suggest that it will be difficult to distinguish between these alternatives if population density varies.

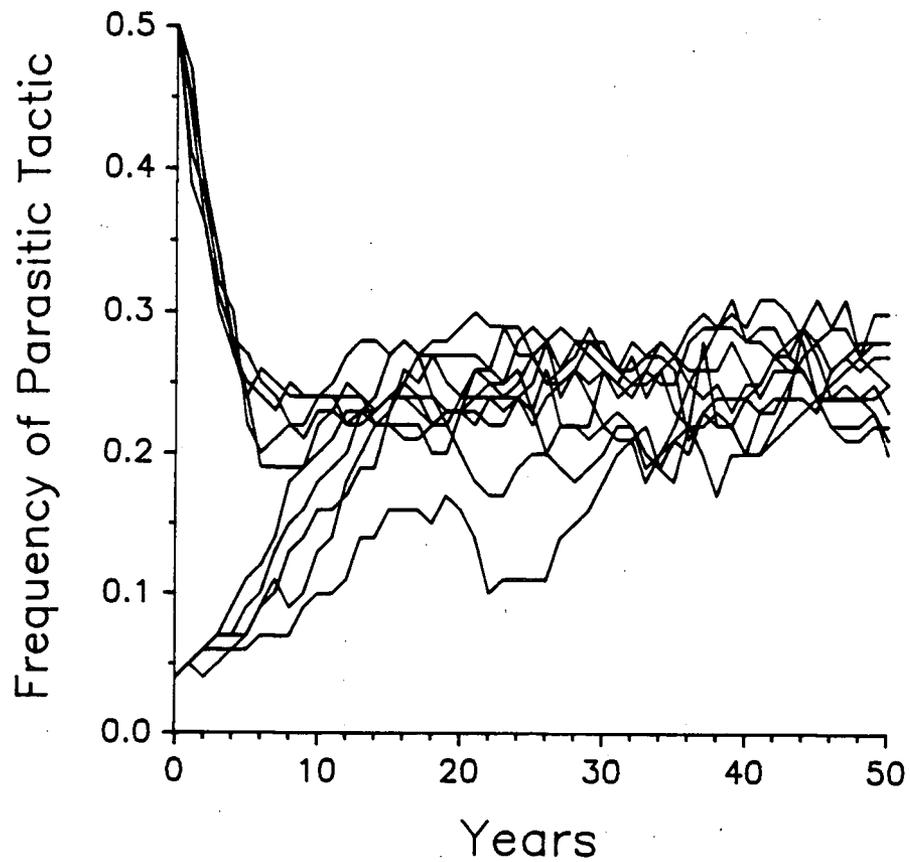


Figure 7.6. Results of a population simulation showing the changes in the frequency of the parasitic tactic over time. The first fifty years of each simulation are shown for two starting conditions: parasites initially rare (Run #5 in Table 7.1), and parasites initially common (Run #10). $E_p = E_n = 9$ eggs for all simulations.

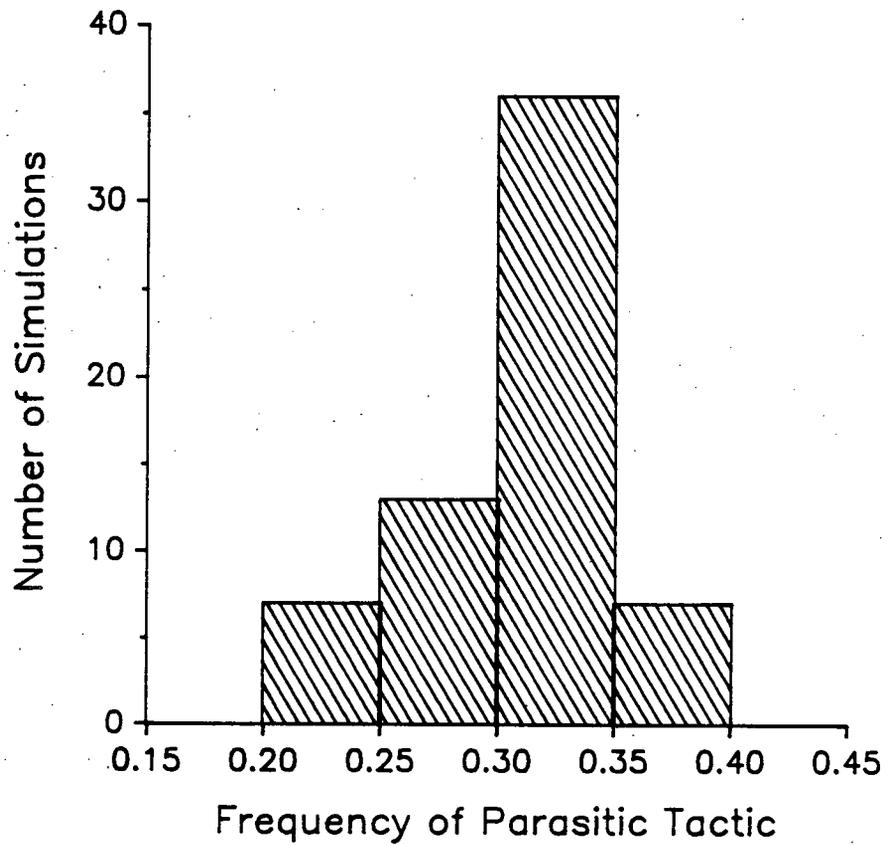


Figure 7.7. Distribution of the final frequency of the parasitic tactic (after 100 years) in the 63 simulation runs in which the parasitic tactic became established (see Table 7.1).

These findings are probably not unique to our study system. For example, similar results may obtain whenever: (1) the success of one tactic (e.g. parasite) depends on the proportion of individuals playing the second tactic (e.g. parental); and (2) resources required by individuals playing the second tactic are limited (e.g. nest sites). Under these conditions, reproductive success is affected both by tactic frequencies, and by the total number of individuals competing for the limited resource. Species in which some individuals scrounge resources from other individuals meet these conditions, and are particularly good candidates for further study (e.g. Barnard & Sibly 1981, Sibly 1984).

The idea that frequency-dependence and density-dependence can operate simultaneously is not new. Population geneticists have previously considered the combined effects of density-dependent and frequency-dependent selection (review in Slatkin 1979), and at least a few ecologists have recognized the potential interaction between these processes (Dunbar 1982, Sibly 1984, Parker 1985, Brown & Vincent 1987a,b). Dunbar (1982), for example, explicitly stated that there may be a density-threshold below which frequency-dependent effects on behaviour are unlikely to occur. Sibly (1984) incorporated the effects of frequency-dependence and population density in a general model of producer-scrounger relationships. He showed that a balance of the two tactics depends on both the relative and absolute number of individuals playing each tactic. Finally, some empirical evidence is consistent with the notion that alternative tactics are maintained by both frequency- and density-dependent processes (Cade 1979, Gerhardt et al. 1987, and see discussion in Greenfield & Shelley 1985 and Gardner et al. 1987).

Incorporating the effects of density-dependence may resolve ambiguous results reported in other studies of alternative reproductive behaviours. Brockmann et al. (1979) found that digging and entering tactics of female digger wasps (*Sphex ichneumoneus*) conformed to the predictions of a mixed ESS hypothesis for a population in New Hampshire, but not for a population in Michigan. They speculated that gene flow or recent environmental change may have displaced the Michigan population from its equilibrium frequency (Brockmann et al. 1979). An alternative explanation is that density-dependent factors played a role similar to that observed in our system. If population density differed between the two locations, it would be possible to obtain results

consistent with a mixed ESS in one population yet not in another, without having to invoke gene flow or environmental instability (Figure 7.5). The Michigan population has apparently since gone extinct, an observation that supports the claim that demographic factors differed between the two populations.

Brood Parasitism and Population Dynamics

Will parasitic behaviour be maintained in a population if both density-dependent and frequency-dependent processes are operating? This ultimately depends on the factors that limit population size. If variation in density is largely stochastic, there will never be a single frequency of parasitism that is evolutionarily stable (Figures 7.5 and 7.6). However, since parasitism can influence the reproductive success of all females, there can be feedback between the behaviour and population dynamics. High frequencies of parasitism reduce the success of all females, leading to reduced recruitment and lower densities in the next generation. In these smaller populations, there is less competition for nest sites, the frequency of parasitism is reduced, and, consequently, the reproductive success of all females is improved. This feedback could lead to a balanced, or bounded, frequency of the parasitic tactic. Our population simulations provide support for this notion (Figures 7.6 and 7.7).

One interesting result of such a feedback loop is that selection acting on parasitic behaviour could not only balance the parasite/parental frequency, but also lead to an equilibrium population density. Parker (1985) and Brown & Vincent (1987a,b) showed that an ESS results in stable equilibria for both the strategy frequencies and the population size, when the effects of density-dependence are included. Even when population size and strategy frequencies are subject to large fluctuations, coalitions of strategies may still emerge as an ESS (Brown & Vincent 1987a,b).

Evaluation of the Assumptions of the Model

Our model is based on several simplifying assumptions. The most critical component of the model is the survival function. The relative payoffs to parasitic and parental females were deter-

mined largely by the relationship between the clutch size in the nest and the probability that an egg produces a fledged offspring (S_y). The survival function used in the model was derived from field data (Figure 7.1). However, other studies on the same or similar species have reported different survival functions (Andersson & Eriksson 1982, Dow & Fredga 1984). How might this affect our conclusions?

Dow & Fredga (1984) found no relationship between clutch size and fledging success in common goldeneyes. Accordingly, there is no constraint on number of young that can be reared in a single brood. A parasitic female that lays a single egg more than a parental female has higher fitness and so can become established in the population. If nest sites are limited, the parasitic tactic is viable even if parasites lay fewer eggs, since the success of the parental tactic is devalued by the probability of obtaining a nest site. Thus, under a constant survival function, the conditions for the establishment of the parasitic tactic are less restrictive than those given by our model.

Andersson & Eriksson (1982) reported a negative relationship between brood size and duckling survival for goldeneyes in Sweden. We repeated our simulations using their survival function ($p(F) = 1.038 - 0.066$ Brood Size, and $\text{Brood Size} = -0.076 + 0.963$ Clutch Size). When population densities were low, parasitic females always had lower reproductive success than parental females. This remained true until there were four times more females than nest sites. At that point, parasites had higher success and could become established (for $E_p = 6-10$ eggs and $E_n = 8$ eggs). We tried a less negative relationship between brood size and duckling survival ($1.0 - 0.033$ Brood Size). Again, parasites could invade when relatively rare, but some degree of nest limitation was required. Thus, the results of simulations using a negative survival function were similar to ours, except that nest limitation had to be more severe before parasitic egg-laying became the more profitable tactic.

A second assumption of our model is that there is a causal basis for the relationship between clutch size and the probability that an egg produces a fledgling. This may not be true. For example, the positive relationship between brood size and survival (Eqn. 4.0) could stem from

brood sizes being larger early in the breeding season and duckling survival being higher from early nests (Chapter 3). However, by using the observed relationship between brood size and survival, we have captured these patterns, even if we are uncertain of their mechanistic basis.

Two additional assumptions of our model are that females use only a single tactic in a given breeding season and that parasitic females lay all their eggs in a single nest. Neither of these assumptions is valid. Females switch nesting tactics within years, and some parasitic females lay eggs in two or more nests (Chapter 6). The flexibility of the parasitic tactic should not unduly influence our model provided that the same proportion of parasitic eggs is laid. This is analogous to comparing genetically fixed tactics maintained in an evolutionarily stable state, with genetically flexible tactics maintained as a mixed evolutionarily stable strategy (see Maynard Smith 1982). In most cases, the calculated ESS is the same (but see Brown & Vincent 1987a,b).

Violation of the second assumption is more serious. If parasites spread their eggs among several nests, and/or if parasites avoid heavily parasitized host nests, then the total clutch sizes in host nests will remain small until the frequency of the parasitic tactic is high. Consequently, reproductive success of both hosts and parasites will be higher than estimated by our model, and greater frequencies of parasitic behaviour can be maintained in the population. Our assumption is therefore conservative with respect to the conditions under which parasitic behaviour can become established.

We do not claim that our model accurately depicts the evolutionary basis of brood parasitic behaviour in goldeneyes. Moreover, because many of our assumptions are simplistic, we do not attach any great significance to the close fit between the predicted frequency of parasitism and that observed in the study population. Rather, we view the real value of the model as heuristic, particularly in showing how density-dependence and frequency-dependence can interact to maintain parasitic behaviour in a population. Our results indicate that studies of alternative reproductive behaviours need to consider not only tactic frequencies, but also demographic factors such as population density. Although ESS theory continues to provide the main framework for studies of alternative reproductive behaviours, there has been increasing concern over

the difficulty in testing ESS theory in the field (Davies 1982, Austad 1984, Dominey 1984). Our study suggests that the effects of density-dependence further complicate such attempts. However, unlike Dominey (1984) and Caro and Bateson (1986), we do not advocate abandoning the ESS approach. Rather, we suggest that more progress will be made by incorporating both density-dependent and frequency-dependent processes in ESS models. Recent attempts to do so have revealed unanticipated links between population dynamics and the behaviour of individuals (Sibly 1984, Parker 1985, Brown & Vincent 1987a,b). These insights would not likely have resulted from descriptive studies of proximate or ontogenetic factors alone.

CHAPTER 8

GENERAL DISCUSSION

This thesis makes contributions in three areas: (1) I demonstrate that alternative reproductive behaviours are not the exclusive domain of males; females can and do pursue alternative tactics; (2) I present new insights into the interaction between density-dependent and frequency-dependent selection in maintaining alternative reproductive behaviours in a population; and (3) I provide one of the most detailed studies of facultative brood parasitism in a precocial bird.

Alternative Reproductive Behaviours in Females

Until recently, analyses of alternative reproductive behaviours have focused almost exclusively on mating tactics of males. That focus reflects the prevailing notion that reproductive competition among females is rare, that variance in female reproductive success is low relative to males, and that alternative tactics are therefore unlikely to evolve in females (e.g. see Payne 1979, Hafernik & Garrison 1986). In contrast, I found that variance in reproductive success among goldeneye females was substantial. Some females were consistently more successful than others, indicating considerable variation in individual breeding ability. Reproductive success was also closely tied to the quality of resources such as nest sites and possibly brood territories, and there was evidence that females compete exploitatively or aggressively for these resources. My results therefore join other studies in suggesting that females compete for resources essential for reproduction (Wasser & Waterhouse 1983, Hannon 1984, Davies & Houston 1986, Arcese 1988). Under such circumstances, some females might opt out of this competition and pursue less costly routes to reproduction. Parasitic egg-laying is one such alternative.

Because of the current interest in sexual selection theory, researchers have emphasized the contribution of mating success and mate choice to fitness. As studies begin to examine intrasexual competition for resources other than mates, I predict that alternative tactics of females will become more evident. Specifically, we might expect to find female alternative

reproductive behaviours in species where females compete exploitatively or aggressively for resources that are essential to reproduction, such as nest sites or breeding territories. This prediction has already been confirmed for some insects (Brockmann et al. 1979), birds (Stutchbury & Robertson 1987), and fishes (van den Berghe & Gross 1989). Brockmann et al.'s (1979) study on joint-nesting in digger wasps provides a particularly striking parallel to my study.

ESS Theory and The Interaction Between Density- and Frequency-dependence

The application of game theory to the study of animal behaviour has been heralded as one of the most important recent developments in evolutionary and behavioural ecology (Parker 1984). In particular, the concept of evolutionarily stable strategies (ESSs) has provided the central theoretical framework for most research on alternative reproductive behaviours (Rubenstein 1980, Davies 1982, Austad 1984, Dominey 1984). Nonetheless, there is growing discontent with this approach, in part because of the difficulty in testing ESS theory in the field (Austad 1984, Dominey 1984, Caro & Bateson 1986). For example, a formidable effort is required to obtain more than a crude measure of the success of alternative tactics. Moreover, tactics may appear to have equal fitness (as predicted by a mixed ESS hypothesis) simply because the sample size is too small or the variance is too high to detect any differences in fitness that do exist (Davies 1982, Austad 1984). Field studies are further complicated by the need to follow marked individuals over long periods of time, in order to determine the flexibility or ontogenetic development of alternative behaviours (Caro & Bateson 1986). Such long-term studies are only now becoming popular.

My study represents one of the most thorough attempts to test ESS theory for a natural population. I quantified in detail the costs and benefits of alternative nesting tactics using both observational and experimental studies. These analyses allowed me to estimate the lifetime reproductive success of parental and parasitic females. I also followed the behavioural tactics of individuals over several years and so could assess the flexibility in nesting behaviours. Finally, I determined the effects of several social and ecological factors on the frequency of alternative

tactics, again using both an observational and experimental approach. In spite of these efforts, I was unable to resolve clearly between the hypotheses posed by ESS theory.

That failure, however, led to the most novel result of this study; that is, that the effects of density-dependence can considerably alter interpretations of behaviour based on frequency-dependent selection alone. Using a simple simulation model, I showed that there is a density threshold below which frequency-dependent effects are minimal, but above which frequency-dependence becomes a prominent force. That result provides an explanation for the contradictory results observed in my field study (see below). However, the implications are more far-reaching; specifically, my research indicates that it will be difficult or impossible to distinguish between conditional and mixed ESSs in field studies where population density varies. Incorporating both density-dependent and frequency-dependent processes in ESS models may yield new insights into the interactions between social behaviour and population dynamics (Parker 1985, Brown & Vincent 1987a,b).

Facultative Brood Parasitism in Goldeneyes

Thirty years after Weller's (1959) inaugural study, we still have little understanding of the factors that promote and maintain the high frequencies of parasitism observed in the Anatidae. One very simple contribution of my study was to examine the phylogenetic distribution of brood parasitism in North American waterfowl (Fig. 1.1). That analysis indicates that parasitism is a primitive trait in the Anseriformes, such that all species have, or at least had, the ability to lay eggs parasitically. This does not, however, explain the wide variation among species in the frequency of brood parasitism. To address the source of that variation, we need to know (1) how parasites benefit from parasitic egg-laying, and (2) how various ecological, social, and phenotypic factors influence the frequency of facultative parasitism. Because the success of a brood parasite ultimately depends on the response of the host, we also need to determine the effects of parasitism on host females. A major goal of this study was to address these objectives.

My efforts led to three major findings. First, I found that parasitism had few deleterious effects on the reproductive success of hosts. On average, parasitized females reared as many of

their own young as non-parasitized females, and there was no effect on the growth of host young or on the survival of the host female. These results contrast with earlier studies on precocial birds. However, except for Andersson & Eriksson's (1982) study, virtually all previous analyses have relied on observational methods. I argue in Chapter 4 that such an approach does not readily permit an unbiased assessment of the effects of parasitism on the host, particularly in cases where one cannot distinguish easily between host and parasite eggs or offspring. Further, the effects on the host will undoubtedly be influenced by spatial and temporal variation in the frequency of parasitism. My results suggest that some hosts may suffer reduced success when parasitism is extremely frequent, but that there is little effect on host success under low to moderate rates of parasitism. It is not surprising, then, that studies of the same species under different conditions yield opposite conclusions.

Second, I found that goldeneyes exhibit few defences against parasites. This was not surprising, given that parasitism has little negative effect on host fitness. However, my results contrast with those of Andersson & Eriksson (1982) in that goldeneyes in my study did not adjust their own clutch size when parasitized. My findings also refute Gauthier's (1987) predictions; there was no evidence that goldeneyes defend territories near their nest site as a defence against parasitism. The only host response that might be considered an anti-parasite defence was that of nest desertion when clutch sizes were extreme. Such a response would be adaptive since hatch success of host eggs declines considerably when more than 16-20 eggs are present in the nest. Similar patterns have been reported for other species, and I argue that simple but robust responses to parasitic intrusions may be sufficient for many precocial hosts.

Finally, I used observational and experimental studies to examine the adaptive significance of brood parasitism in goldeneyes. This led to the rejection of several hypotheses that have been proposed to explain parasitic behaviour in waterfowl. Specifically, brood parasitism in goldeneyes was not: (1) an inadvertent consequence of competition for nest sites; (2) an artifact of high densities of artificial nest sites (boxes); or (3) a function of nest predation or female body size/condition. Parasitic behaviour was, however, (1) more frequent in young females and (2) strongly related to the availability of unoccupied nest sites. Further, egg success, annual

reproductive success, and lifetime reproductive success were nearly identical for parasitic and non-parasitic females, and the relative success of a nest parasite declined as the frequency of parasitism increased in the population.

These results were initially puzzling, since they are consistent with two different hypotheses (the conditional strategy and the mixed strategy hypotheses). The dilemma was resolved through the simulation model described above; results consistent with both hypotheses are possible when the effects of both density-dependence and frequency-dependence are incorporated. I argued further that parasitic egg-laying is a flexible behaviour that can be pursued by any individual under a variety of circumstances. Some females become parasitic when they can't breed otherwise, while other females lay parasitically to obtain additional benefits on the side. Density-dependence will operate primarily through nest site limitation, thereby promoting parasitism as a salvage tactic. Parasitism as a side-payment tactic, on the other hand, will be limited by frequency-dependent factors such as reduced success of parasitic eggs at high frequencies of parasitism. Both factors, operating simultaneously, could maintain parasitic behaviour in the population (Chapter 7). Flexibility in parasitic behaviour would allow females to adjust their behaviour to these changing ecological and social conditions.

Similar themes have emerged from other recent studies of brood parasitism (Emlen & Wrege 1986, Moller 1987, Evans 1988, Lank et al. 1988) and it is possible to identify three general conditions that promote facultative brood parasitism in birds. These are:

(1) Constraints on parental nesting. Facultative parasitism is more common in species for which (i) resources necessary for breeding (e.g. nest sites, food resources, or brood rearing sites) are limited, or in which (ii) age, inexperience, or frequent nest failure limit the nest success of parental females (reviews in Yom-Tov 1980a, Andersson 1984, Eadie et al. 1988).

(2) The potential to benefit on the side. In a few species, parasitic females lay more eggs and fledge more young than non-parasitic females (Brown 1984, Moller 1987). However, these females also rear broods of their own, indicating that parasitism is an additional rather than alternative tactic to parental nesting. Such side-payment tactics are profitable only if some factor

constrains the number of eggs a female can lay in her own nest. This appears to be the case for many altricial birds (see Appendix 2). Parasitic females might also benefit through reduced variance in reproductive success (bet-hedging; Payne 1977a, Rubenstein 1980) or improved care of offspring if host females are more experienced or better parents, but such effects have yet to be demonstrated.

(3) The opportunity to parasitize other individuals. The success of the parasitic tactic ultimately depends on the availability of suitable hosts. It is not surprising, then, that facultative parasitism occurs more frequently in species that (i) nest in dense aggregations such as colonies or on islands, (ii) have long laying seasons, (iii) produce large clutches, (iv) use easily located nest sites, and (v) do not defend their nest sites (Andersson 1984, Haland 1986). All of these factors relate to the availability of hosts, or to the ease in finding and parasitizing host nests.

One question remains - why is the frequency of facultative parasitism higher in precocial birds than in altricial birds? Andersson (1984) suggested that facultative parasitism is not over-represented in precocial birds other than the Anatidae, although Rohwer & Freeman's (1989) analyses suggest otherwise. For example, intraspecific brood parasitism has been reported for several species of Galliformes and Charadriiformes. Moreover, there are at least four other reasons to expect higher frequencies of parasitism in precocial birds. First, precocial birds share many of the traits described above, such as large clutch sizes, long laying seasons, and easily located nests. Therefore, the conditions favouring parasitism are more prevalent in precocial birds. Second, precocial hosts generally lack defences against parasites, possibly because of the reduced cost of parasitism (Chapters 4 and 5). Accordingly, parasites have an easier task laying in a host nest, and Rohwer & Freeman (1989) argued that barriers to the evolution of brood parasitism are thereby reduced for precocial birds.

Third, precocial brood parasites are less constrained by the need to find a host that provides suitable care, given that precocial young are relatively independent of parental care (Andersson 1984). The availability of potential hosts is therefore considerably enhanced. For example, many precocial birds are able to successfully parasitize other species as well as conspecifics. Of

the 28 species of North American anatids that are intraspecific brood parasites, 21 also parasitize other species of waterfowl (Eadie et al. 1988). Finally, the high frequency of intraspecific parasitism in waterfowl may reflect the influence of kin selection (Andersson 1984). In most ducks and geese, females are the philopatric sex. Andersson (1984) proposed that hosts and parasites might be closely related, such that both gain in inclusive fitness through brood parasitism.

It is apparent that brood parasitism is a more common reproductive tactic in birds than previously thought. The application of molecular genetic techniques to field studies will undoubtedly add to the growing list of species that are known to lay eggs in the nests of other individuals. However, parasitic behaviour need not be confined to birds, and it will be interesting to determine the extent to which these behaviours occur in other taxa such as insects (e.g. Tallamy 1985, 1986) or fishes (Sato 1986). These groups will be especially important in providing alternative study systems to test hypotheses that have, so far, been generated primarily for birds.

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APPENDIX 1

METHODS TO ESTIMATE THE FREQUENCY OF FACULTATIVE BROOD PARASITISM

Intraspecific brood parasitism in many species of birds is more common than once suspected (Brown 1984, Emlen & Wrege 1986, Gowaty & Karlin 1986, Moller 1987, Evans 1988). Analysis of this behaviour has been hindered by the inability to identify eggs laid by different females in the same nest (Yom-Tov 1980a). New developments in molecular genetic techniques hold promise (e.g. Burke & Bruford 1987, Wetton et al. 1987, Quinn et al. 1987), but such applications are in their infancy. Researchers have therefore had to rely on indirect and circumstantial evidence to infer the occurrence of egg-dumping and to determine maternity of the eggs and offspring. With the exception of Yom-Tov (1980a), there have been few attempts to assess the reliability of these methods.

This appendix evaluates 6 criteria that have been used frequently to infer brood parasitism. My primary aim is to validate these criteria for use in this thesis, but the results may prove useful to studies of other species. A second objective is to analyze the degree of association between the 6 criteria in order to identify a smaller subset that would be of greater utility in field studies. Finally, I compare two different estimates of the frequency of brood parasitism: (i) the proportion of nests parasitized, and (ii) the proportion of parasitic eggs laid. Most studies report only the former (Brown 1984, Moller 1987, Evans 1988), whereas I show that the latter may be more appropriate in analyses of the evolutionary basis of brood parasitic behaviour.

Criteria for Detecting Brood Parasitism

I considered six criteria that have been used extensively to detect facultative brood parasitism (see Morse & Wight 1969, Yom-Tov et al. 1974, Clawson et al. 1979, McCamant & Bolen 1979, Yom-Tov 1980b, Eriksson & Andersson 1982, Pienkowski & Evans 1982, Brown 1984, Hines & Mitchell 1984, Giroux 1985, Emlen & Wrege 1986, Gibbons 1986, Moller 1987, Evans 1988).

(1) More than one egg laid per day:

No species of bird is known to lay more than one egg in a period of less than 24 hours (Welty 1982, Brown 1984). For example, goldeneyes lay one egg approximately every other day (mean: 0.64 ± 0.03 , $N = 112$ nests). Thus, two or more eggs appearing in a nest within a 24 hour period will not belong to the same female.

(2) Eggs laid after the host has started incubation:

In goldeneyes, hatching is synchronous and incubation does not start until the clutch is complete. Eggs that appear in a nest after the start of incubation are likely to belong to another female. The use of this criterion in the present study was partly undermined because it was often difficult to determine the exact day when a female started incubation. As a conservative measure, I considered eggs as being parasitic only if they were laid 2 or more days after I thought incubation had started.

(3) Abnormally large clutch size:

Extreme clutch sizes are often interpreted as evidence of brood parasitism, although this criterion is almost always subjective. Yom-Tov (1980a) proposed that clutches greater than twice the size of the average clutch could be considered as parasitized. For goldeneyes, this equals 21 or more eggs (mean clutch size for all nests was 10.4 eggs). This is a highly conservative criterion.

To assess the maximum clutch size of a single female, I collected 16 females at or near the end of egg-laying (see Chapter 6 for details). These females included birds that were preparing to incubate clutches (with developing brood patches) and parasitic females. I dissected the ovaries and reproductive tract of each bird, and counted all post-ovulatory follicles and large developing follicles, following Payne (1966) and Hannon (1981). Based on these counts, the average clutch size of an individual female was 9 eggs with a maximum of 11 eggs (Figure A.1). Similar estimates were obtained for clutches in nests that were apparently unparasitized (based on criteria independent of clutch size - # 1, 2 and 4 above). The average clutch size in those nests was 8.2 eggs, with a maximum of 12 eggs (Figure A.1). Clutches of 13 or more eggs are

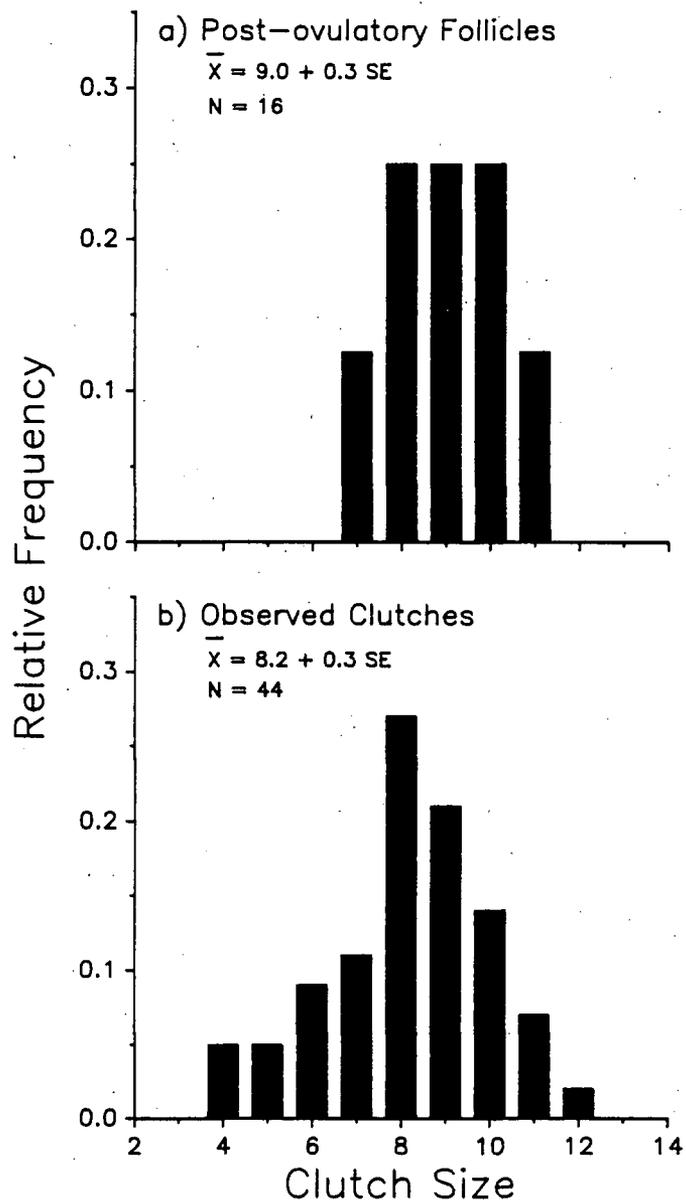


Figure A.1. Clutch sizes of individual goldeneye females determined by (a) counts of post-ovulatory follicles and (b) observations of natural nests.

therefore the product of more than one female. I used this value as a criterion to classify parasitized nests.

(4) Direct observation of 2 or more females laying eggs in the same nest:

This criterion is straightforward. I obtained direct evidence for two or more females laying in the same nest using a variety of monitoring procedures, including nest observations, nest trapping, automatic cameras, and collar markers (see Chapter 6).

(5) Differences in the morphology or appearance of eggs:

Some authors have distinguished eggs of different females in the same nest on the basis of egg size, shape, or pigmentation (Yom-Tov 1980a,b, Gibbons 1986, Moller 1987). I analysed the size and shape of goldeneye eggs to determine whether variation in egg morphology could be used to identify parasitized nests. In the field, I measured the length, width, and weight of eggs in all nests. I then performed cluster analyses on these measures for all eggs in each nest, using complete linkage clustering with Euclidean distance as the distance metric. Each egg size variable was first standardized by its mean and standard deviation to ensure that all variables contributed equally to the cluster analysis.

A sample of these analyses is shown in Figure A.2 for parasitized and non-parasitized nests (nests were classified as being parasitized using criteria 1, 2, 3, and 4; i.e. those independent of egg morphology). In several parasitized nests, we knew the identity of some or all of the host eggs (via nest trapping, nest cameras, etc.). Two points emerge from this analysis. First, eggs that belonged to different females did cluster into separate groups, as would be expected if egg shapes and sizes are characteristic of individual females. Second, differences in egg morphology were greater in parasitized nests. The distance between the two most dissimilar eggs in each nest (i.e. the maximum Euclidean distance (MED) increased with clutch size in both parasitized nests ($r = 0.32$, $N = 57$, $P < .02$) and non-parasitized nests ($r = .54$, $N = 32$, $P < .001$; Figure A.3). While there was no difference in the slopes of regressions calculated for each group of nests ($F = 0.38$, $df = 1,85$, $P > .50$), the intercept of the parasitized nests was significantly larger ($F = 35.91$, $P < .001$).

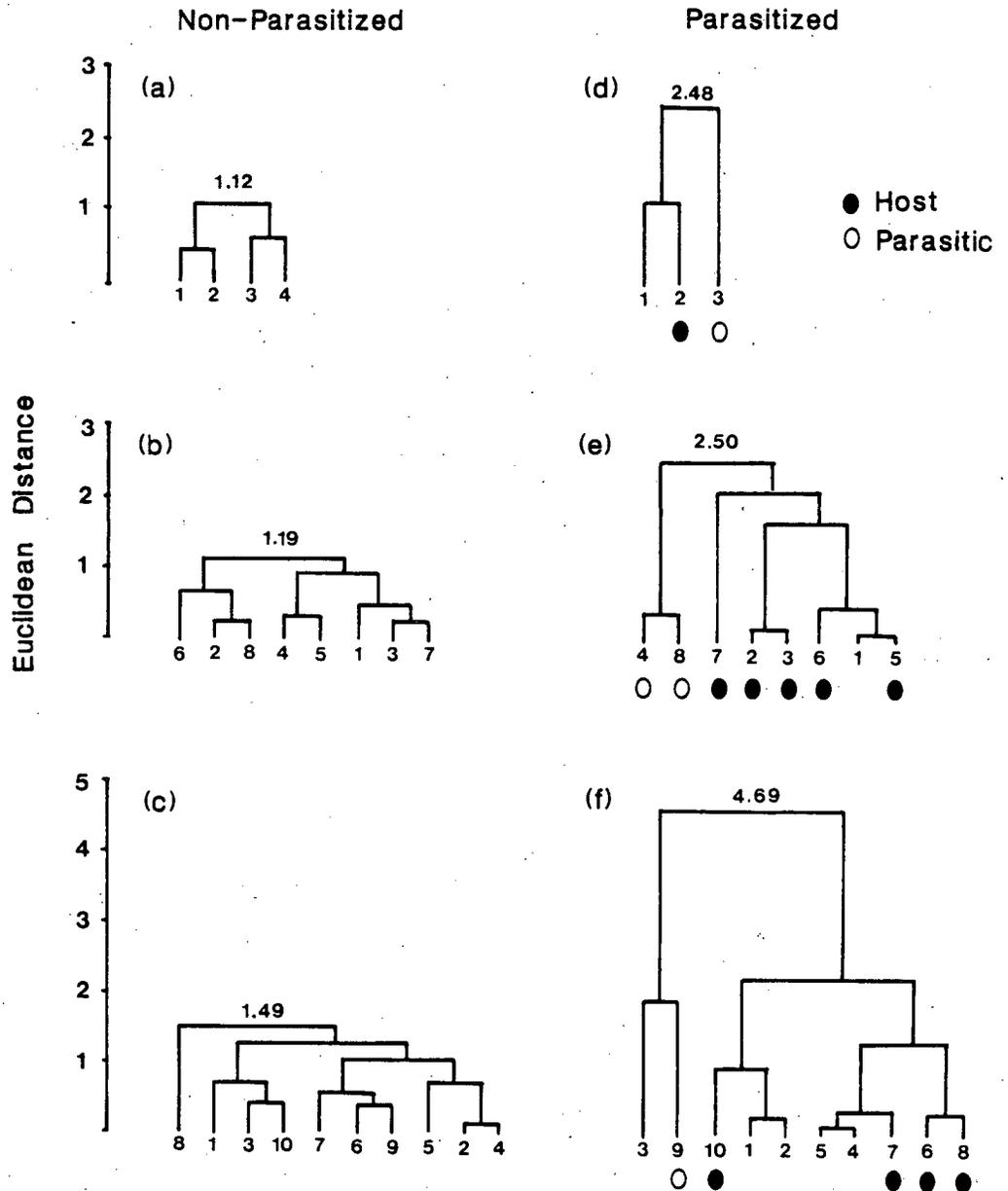


Figure A.2. Cluster analyses on egg size variables for non-parasitized and parasitized clutches. Examples are shown for small (a,d), medium (b,e) and large (c,f) clutches. The value above each dendrogram is the maximum Euclidean Distances among eggs in that clutch. Eggs that were known to belong to either the host or the parasite are shown for parasitized nests.

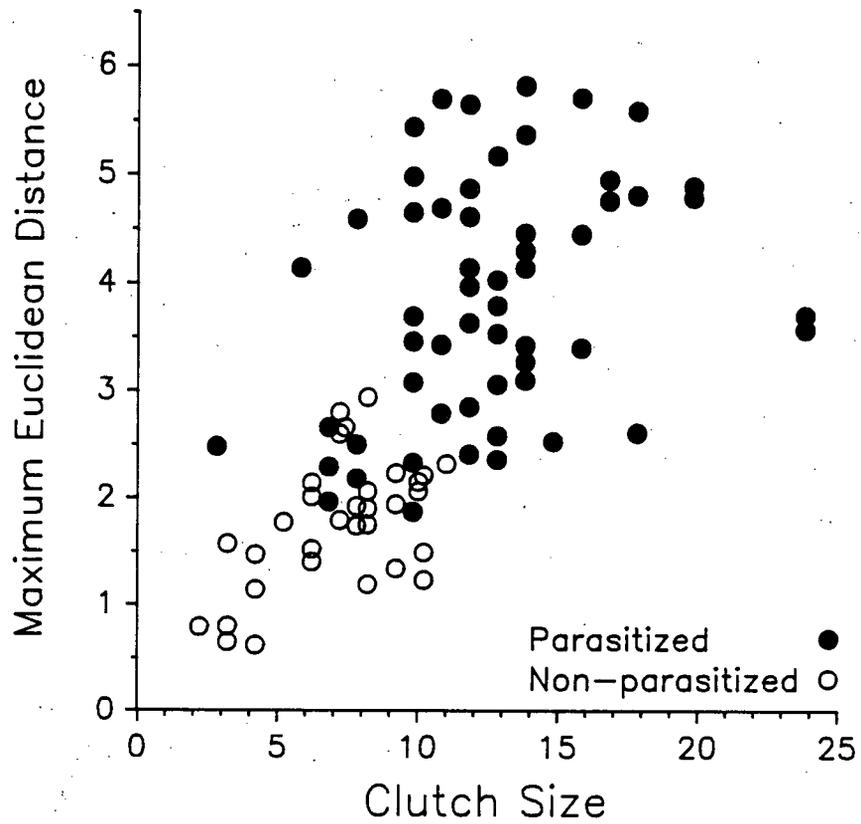


Figure A.3. Maximum Euclidean Distance for each clutch as a function of clutch size. Parasitized and non-parasitized clutches are shown separately.

This analysis confirms that differences in size are greater among eggs in parasitized nests, and suggests that it is possible to use egg morphology to identify parasitized nests and parasitic eggs. Comparisons of Euclidean distances for non-parasitized and parasitized nests shows that MED's in non-parasitized nests rarely exceed 2.5, and are never greater than 3.0 (mean = 1.74 ± 0.11 SE, N = 29). In contrast, MED's in parasitized nests are almost always greater than 2.5 (mean = 3.85 ± 0.15 , N = 57). Considering only those parasitized nests with clutch sizes in the range found in non-parasitized nests (i.e. < 12 eggs) yields similar results, with most MED's being greater than 2.0 - 2.5 (mean = 3.46 ± 0.27 , N = 20; Figure A.3). I therefore used a Euclidean distance of 2.5 as an objective criterion to identify parasitized nests on the basis egg morphology. Any nest for which the maximum Euclidean distance (MED) between eggs was greater than 2.5 was considered to be parasitized, while nests with MED's less than 2.5 were considered to be non-parasitized. Note that some nests will be misclassified by this criterion (4 of 29 non-parasitized nests and 8 of 57 parasitized nests; Figure A.3).

I also used this procedure to separate eggs of different females within parasitized nests. Eggs that were known to be laid by the same female rarely differed by a Euclidean Distance greater than 2.0, and in most cases, this value was substantially less (see Figure A.3). Accordingly, I considered eggs that differed by a Euclidean distance of greater than 2.5 to have been laid by different females. Undoubtedly, this measure is conservative, and parasitic eggs may be misclassified as non-parasitic. However, it was often possible to further discriminate among eggs of different females using other lines of information (e.g. laying patterns, colour, direct observations of females laying).

(6) Skips in egg-laying:

Some authors have used evidence of long skips in the appearance of eggs in a nest as an indication of nest parasitism (Eriksson & Andersson 1982). Long breaks in egg-laying would not be expected if the nest represented the efforts of a single female. However, I observed skips of up to 4 days in cases in which I was certain that only a single female was using the nest. Accordingly, I considered skips in egg-laying as evidence for brood parasitism only if the breaks were greater than 6 days, or if 2 or more skips of 4+ days duration were observed.

Association Between Criteria:

Fifty-four (54) parasitized nests were followed in sufficient detail that I could assess all 6 criteria. Three criteria were most often met: variance in egg morphology (98% of nests), 2 eggs/d (63% of nests), and clutch sizes exceeding 13 eggs (43% of nests; Table A.1). Observations of 2+ females laying in a nest, and skips in egg-laying were observed in only 20% of the nests (Table A.1).

Two or more criteria were met in over 94% of nests, with an average of 2.7 criteria per nest. Only three nests met just a single criterion. Thus, these criteria appear to be reliable indicators of parasitism, given that most are corroborated by at least one other line of evidence. I did not find any nest which passed all 6 criteria, although there were several cases in which 4 or 5 lines of evidence were documented. Jaccard's dichotomy coefficients (Wilkinson 1988; shown below the diagonal in Table A.1) ranged from 0.08 to 0.65. The average for all 15 possible pairs of criteria was $0.24 \pm .04$, indicating that any given pair of criteria would occur together in approximately 1 of 4 nests.

A principal components analysis identified three groups of criteria: (1) a group loading on clutch size > 13 eggs, eggs laid after incubation, variance in egg morphology, and 2 eggs/day, (2) a group loading on 2+ females, with moderate loadings on egg morphology and 2 eggs/d, and (3) a group loading only on skips in egg-laying (Table A.2). Five of the six criteria therefore have some degree of redundancy. The other criterion, skips in laying, occurred infrequently and was not strongly associated with any of the other criteria. It may therefore be an unreliable indication of brood parasitism.

Previous studies of brood parasitism in birds have relied extensively on three criteria: 2 eggs laid per day, eggs laid after incubation, and clutch sizes beyond some upper limit (Clawson et al. 1979, Heusmann et al. 1980, Eriksson & Andersson 1982, Moller 1987, Evans 1988). I examined the effectiveness of various combinations of these 3 criteria for goldeneyes. The

Table A.1. Association matrix among criteria used to infer brood parasitism. Values above the diagonal are the number of nests in which both criteria occurred (N = 54 nests). Values below the diagonal are Jaccard's dichotomy coefficients. Values in the diagonal are the number of nests in which only that criteria was met.

Criteria	(1)	(2)	(3)	(4)	(5)	(6)	(N)
(1) 2+ eggs /Day	[0]	7	14	8	34	4	34
(2) Eggs after incubation	.16	[1]	10	3	15	2	17
(3) Clutch size > 13 eggs	.36	.33	[0]	3	22	5	23
(4) 2+ females on nest	.27	.11	.09	[0]	13	2	13
(5) Variance in egg morphology	.65	.28	.42	.25	[2]	9	53
(6) Skips in laying	.10	.08	.18	.10	.17	[0]	10

Table A.2. Principal components analysis on criteria used to infer brood parasitism. Loadings are based on a Varimax rotation (N = 54 nests).

Criterion	PC1	PC2	PC3
Clutch size > 13 eggs	.69	.07	.13
Eggs after incubation	.69	-.14	-.13
Variance in egg morphology	.68	.53	.18
2+ eggs/day	.53	.58	.08
2+ females on nests	-.12	.85	.04
Skips in laying	.04	.01	.98
Eigenvalue	1.70	1.36	1.03
% Variance	28.4	22.6	17.2
Cumulative % Variance	28.4	51.0	68.2

proportion of nests that were correctly identified as parasitized were:

Clutch size > 13 eggs and Eggs after incubation:	30/54 nests (56%)
Clutch size > 13 eggs and 2 eggs/d:	43/54 nests (80%)
2 eggs/d and Eggs after incubation:	44/54 nests (82%)
All three:	48/54 nests (89%)

Some combinations of criteria were only marginally successful in identifying parasitized nests (e.g. clutch size exceeding 13 eggs and eggs after incubation). Researchers using only those criteria risk misclassifying a large number of nests. On the other hand, it was possible to correctly identify 89% of parasitized nests using all 3 criteria. These criteria loaded highly on the first principal component (Table A.2), indicating that association analyses provide a means to identify subsets of criteria that accurately detect brood parasitism while being relatively easy to measure in the field.

One additional indication of parasitism was discovered after the above analyses were complete. There was a marked difference in the number of consecutive days on which an egg was laid in parasitized and non-parasitized nests (Figure A.4). It was unusual to find an egg laid on more than 2 or 3 consecutive days in a non-parasitized nest (mean: 1.7 days \pm 0.1 SE; Figure A.4a). In contrast, it was not unusual to find a new egg on up to 9 or 10 consecutive days in a parasitized nest (mean: 5.9 \pm 0.5 SE; Figure A.4b). Thus, nests with a new egg on each of 4 or more consecutive days are probably parasitized.

Estimating the Frequency of the Parasitic Tactic

The frequency of brood parasitism has traditionally been measured as the proportion of nests parasitized (e.g. Clawson et al. 1979, Heusmann et al. 1980, Hines & Mitchell 1984, Evans 1988). However, analysis of the evolutionary basis for brood parasitism requires an estimate of the frequency of the parasitic tactic in the population. The proportion of nests parasitized will provide only an approximation since (i) more than one parasitic female might lay in the same host nest, and (ii) the same female might parasitize several different nests. Two alternative measures of parasitism are the proportion of parasitic females, and the proportion of parasitic

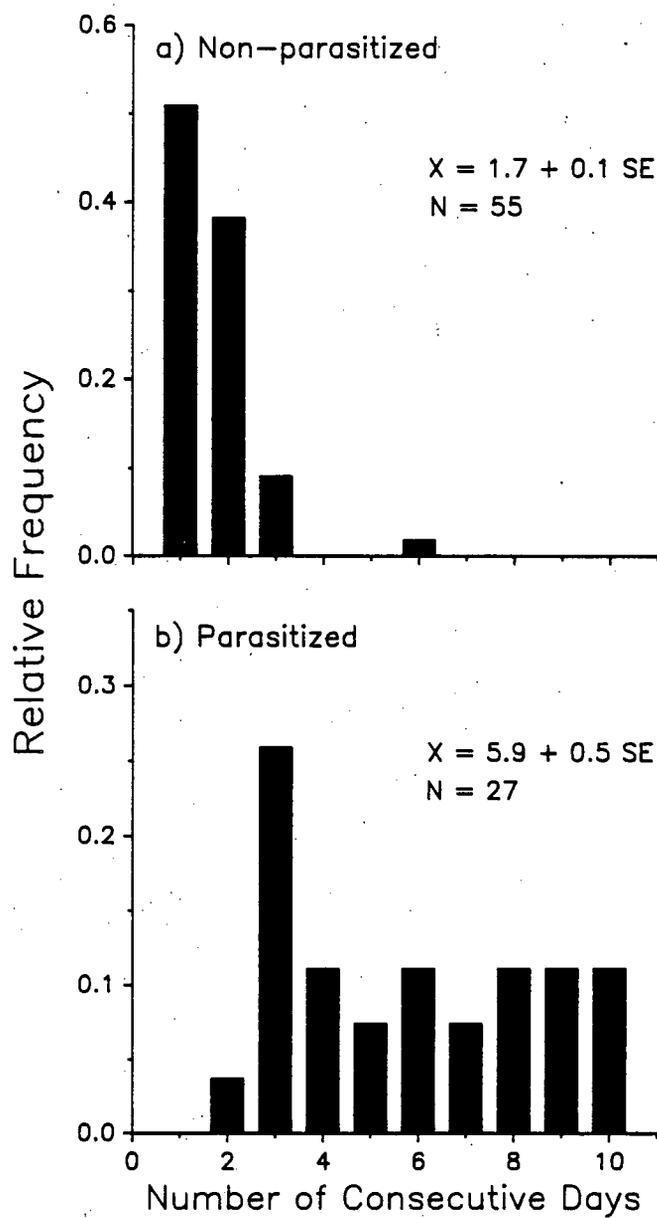


Figure A.4. The number of consecutive days on which an egg was laid in (a) non-parasitized nests and (b) parasitized nests.

eggs. If parasitic females lay approximately the same number of eggs as non-parasitic females, then these two measures should be similar.

It is often difficult to distinguish between host and parasite eggs and, hence, direct counts of parasitic eggs are not feasible. I estimated the number of parasitic goldeneye eggs in each nest using two methods:

Method A - The number of parasitic eggs in each parasitized nest was calculated as

$$\text{Total clutch size} - \text{Average clutch size in a non-parasitized nest}$$

This assumes that hosts lay a full clutch when parasitized, and that all eggs beyond this clutch size are parasitic.

Method B - I obtained a direct count of the number of parasitic eggs laid in each parasitized nest using comparisons of egg morphology (see below), and using information on egg-laying patterns (i.e. eggs laid on the same day as a host egg, or eggs laid after the host initiated incubation). I assumed the host laid the majority of eggs in the nest.

I compared the two estimates using data from 14 lakes over 3 years (each datum is the number of parasitic eggs laid on a single lake in a single year). The two estimates were highly correlated ($r_s = .986$, $N = 14$, $P < .001$). The number of parasitic eggs ranged from 1 to 120 among lakes but the net difference between the two methods was less than 1 egg (mean: 0.34 eggs ± 1.26 SE). Although Method B represents a more direct count of parasitic eggs, Method A gave a reasonable and comparable estimate. This is encouraging since Method A can be used in studies in which it is not possible to distinguish eggs of different females. An investigator need only be able to identify parasitized nests and to estimate the average clutch size in non-parasitized nests.

The proportion of parasitic eggs (Method A) was also correlated among lakes with the proportion of parasitized nests, both within years (1984: $r_s = .94$, $N = 6$, $P < .01$; 1985: $r_s = .83$, $N = 12$, $P < .001$; 1986: $r_s = .62$, $N = 13$, $P < .05$), and for all years combined ($r_s = .76$, $N = 31$, $P < .001$; Figure A.5). However, the two values were not equal. On average, the proportion of

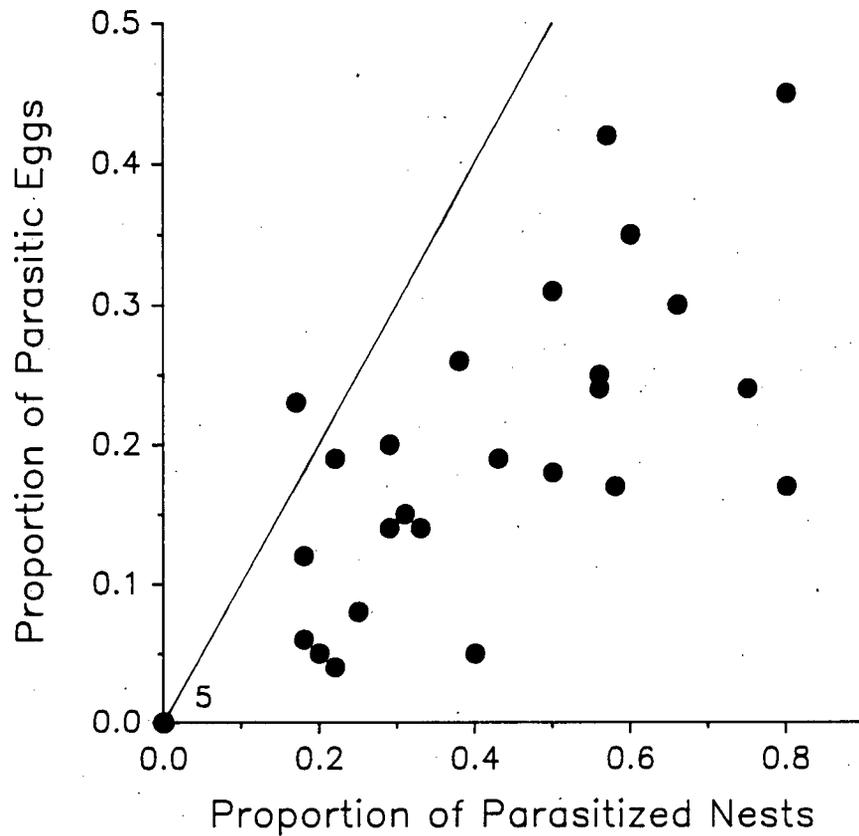


Figure A.5. The relationship between the proportion of nests that were parasitized and the proportion of eggs that were parasitic. The line shows the expected relationship if the two measures of parasitism are identical.

parasitized nests ($0.35 \pm .04$ SE, $N = 31$) was twice the proportion of parasitic eggs ($0.17 \pm .02$ SE). Even at relatively low frequencies of brood parasitism (e.g. 20% of eggs laid parasitically), a high proportion of nests may be parasitized (e.g. up to 80% on some lakes; Figure A.5). One explanation for such variation is that some females lay parasitic eggs in more than one nest.

CONCLUSIONS

Facultative parasitism represents a challenge in terms of understanding the evolution of such parasitic reproductive behaviours, and in evaluating the effects of such behaviour on the structure of mating and social systems (Harvey 1986, Davies 1988). As more researchers study this phenomenon, facultative parasitism will likely be recorded for an increasing number of species. Much of this research will rely on the kinds of evidence examined here and current methods must therefore be evaluated early in this pursuit, if we are to use these comparative data efficiently.

Although my study focused on brood parasitism in goldeneyes, the findings should prove useful to studies of facultative brood parasitism in other species. In particular, I emphasize four results. First, there is considerable redundancy among the 6 criteria used to infer brood parasitism - more than one criterion was met in all but 3 of the parasitized goldeneye nests. This is encouraging and, indeed, expected if these criteria do accurately detect brood parasitism. Nonetheless, no single criterion was met in all nests and investigators should be cautious when inferring rates of parasitism from only one or two lines of evidence.

Second, some criteria were more reliable indicators of parasitism than others. In particular, evidence of 2 eggs laid per day, eggs appearing after incubation, and extreme clutch sizes were found in a majority of parasitized nests. I was also able to use egg morphology to identify parasitized nests. These criteria will likely be the most useful in future field studies. On the other hand, skips in egg-laying appear to be poor indicators of parasitism and researchers should be wary of using this criterion.

Third, principal components analysis identified subsets of criteria that could be used effectively to identify parasitized nests with reduced effort. The three criteria that loaded highly on the first principal component (2 eggs/day, clutch size greater than 13 eggs, and eggs laid after incubation) correctly identified 89% of the parasitized nests. Robust subsets of criteria that are easy to measure may greatly facilitate field studies of brood parasitism.

Finally, I have argued that the proportion of parasitized nests can provide an inaccurate measure of the frequency of the parasitic tactic in the population. I suggest that the proportion of parasitic eggs will be a more useful measure for analyses of the evolutionary basis of facultative brood parasitism. I used a simple method to estimate this frequency and showed that it provided estimates that were comparable to those based on direct counts of parasitic eggs in each nest.

APPENDIX 2

THE DISTRIBUTION OF OBLIGATE BROOD PARASITISM IN BIRDS

I opened this thesis by noting that the distribution of obligate versus facultative brood parasites differs considerably according to developmental mode in birds (Chapter 1). In this appendix, I return to this pattern and offer some speculation on its origin. I do not attempt to explain the origin of the parasitic trait itself; Hamilton & Orians (1965) and Payne (1977a) provide lucid reviews of the factors that have favoured the evolution of parasitic behaviour. Here, I deal only with the question of whether parasitism will become obligate, once the ability to parasitize another species arises.

Of the 87 species of obligate brood parasites, only one is a precocial bird. In contrast, of 29 species that have been recorded as facultative interspecific parasites, 27 are precocial. I suggested in Chapter 1 that this discrepancy is related to the different costs and benefits of parasitism to altricial and precocial birds. Bruce Lyon, of Princeton University, and I have formalized this idea in a simple model. The following is an abstract of these ideas (Lyon & Eadie, MS). We envision the evolution of obligate brood parasitism as a tradeoff between fecundity (F) and the survivorship of the eggs and offspring (S). The product of these two components ($F \cdot S$ = the number of young fledged) yields an estimate of fitness. Obligate parasitism will evolve when the fitness of a brood parasite (bp) is greater than that of a parental bird (pt); that is, when

$$F_{bp} \cdot S_{bp} > F_{pt} \cdot S_{pt}, \text{ or}$$

$$F_{bp} / F_{pt} > S_{pt} / S_{bp}.$$

In other words, parasitism will evolve when the relative increase in fecundity of a brood parasite is greater than the relative reduction in the survival of eggs or chicks laid in a host nest. This equation represents a benefit / cost threshold for the evolution of obligate parasitism (Figure A.6 and Lyon & Eadie, MS).

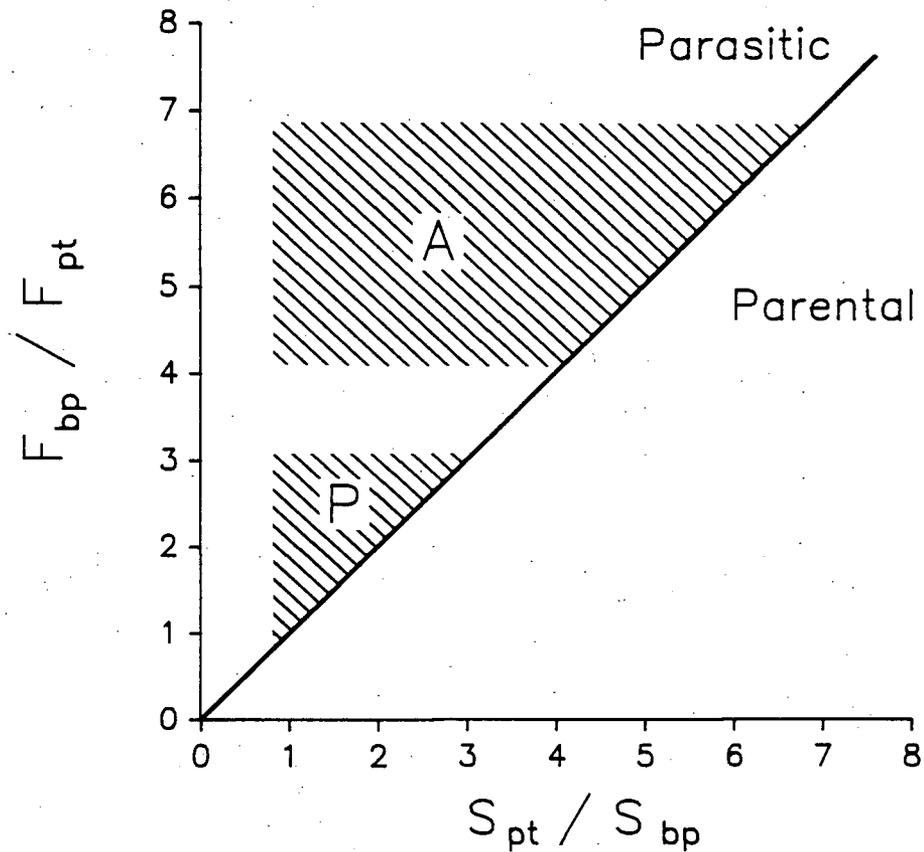


Figure A.6. A benefit/cost threshold for the evolution of obligate brood parasitism. Obligate parasitism is favoured when the relative increase in realized fecundity of a brood parasite (F_{bp} / F_{pt}) exceeds any reduction in egg success (S_{pt} / S_{bp}). The hypothetical increase in fecundity for an altricial brood parasite (A) and a precocial brood parasite (P) is shown by the shaded regions.

The crux of our argument is that the benefit / cost ratio differs considerably for altricial and precocial birds. Specifically, the relative gain in increased fecundity via emancipation from parental care will be substantial for an altricial bird, but will be minimal for a precocial bird. Clutch size in altricial birds is thought to be limited by the demands of post-hatch parental care (Lack 1968, Klomp 1970). Emancipation from parental duties via parasitism would thereby allow an altricial parasite to channel the energy saved into egg production. Parasitic cowbirds, cuckoos, and finches all lay than more 5-8 times the number of eggs laid by non-parasitic relatives. Egg removal experiments show that altricial birds, such as flickers (*Colaptes auratus*) or wrynecks (*Jynx torquilla*), can lay up to 60-70 eggs in a single breeding season; i.e., 8-10 times the number of eggs laid in a normal clutch (references in Welty 1982). The relative fecundity gain for an altricial parasite (F_{bp}/F_{pt}) will therefore be 4-8 times that of a non-parasitic bird. An altricial parasite could sustain considerable egg losses before parasitism becomes unproductive (Figure A.6). Consequently, we argue that parasitism in altricial species should rapidly proceed to the obligate state, once the ability to parasitize another species arises (see also Hamilton & Orians 1969).

In contrast, the young of precocial species require little post-hatch care and clutch sizes may be closer to their potential limit (Ankney & MacInnes 1978, Ar & Yom-Tov 1978, Drobney 1980; but see Winkler & Walters 1983, Arnold et al. 1987). There is little evidence that a precocial parasite would gain substantially through emancipation from post-hatch parental care. Parasitic redheads lay about the same number of eggs as non-parasitic females (Weller 1959). Parasitic wood ducks (Clawson et al. 1979) and goldeneyes (this study) lay a few eggs more than non-parasitic females, but the increase is small. Egg removal experiments with willow ptarmigan (*Lagopus lagopus*) resulted in a doubling of the normal clutch size (17 eggs compared to an average clutch of 8-9 eggs), while there was only a slight increase in clutch size when eggs were removed from the nests of captive mallards (Rohwer 1984). These results suggest that precocial birds gain a slight increase in fecundity by laying parasitically, but the advantage is considerably less than that for altricial birds (i.e. $F_{bp} / F_{pt} = 2$). Any reduction in the success of parasitic eggs

could reduce the net benefit of parasitism for a precocial parasite below the threshold in Figure A.6. We therefore expect obligate parasitism to be uncommon in precocial birds.

Our model provides one explanation for the greater frequency of obligate brood parasitism in altricial birds. It does not account for the frequent occurrence of facultative parasitism. There are two possible explanations for facultative parasitism. First, periodic reductions in either the fecundity (F_{pt}) or egg survival (S_{pt}) of the parental tactic may favour occasional parasitism. In other words, the threshold for parasitism may be crossed periodically, thereby promoting parasitism as a facultative tactic. Second, parasitism in combination with parental nesting may be more profitable than parental nesting alone. In terms of our model, this would require:

$$(F_{bp} \cdot S_{bp}) + (F_{pt}' \cdot S_{pt}) > F_{pt} \cdot S_{pt}$$

where F_{pt}' = the fecundity of a female when she lays F_{bp} eggs as a parasite, and then lays and cares for F_{pt}' eggs on her own. Rearranging gives the benefit / cost threshold for the mixed tactic:

$$F_{bp} / (F_{pt} - F_{pt}') > S_{pt} / S_{bp}$$

Thus, facultative parasitism as a side-payment tactic (i.e. in addition to parental nesting) will pay when the additional fecundity realized through parasitism exceeds (i) any loss in parental fecundity (F_{pt}') that occurs as a result of acting as a parasite, and (ii) any reduction in the success of eggs laid parasitically. Note that if females can lay as many eggs in their own nest when they act as a parasite as when they do not (i.e. $F_{pt} = F_{pt}'$), then it will always pay to lay some eggs parasitically, provided that at least some of those eggs hatch ($S_{bp} > 0$).

These ideas are developed in more detail by Lyon & Eadie (MS). We do not pretend that the simple models above represent an accurate depiction of the evolution of either obligate or facultative brood parasitism. However, we do suggest that consolidation of the many diffuse ideas scattered throughout the literature into a more formal theoretical framework will facilitate future research into the ecology and evolution of brood parasitism.

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