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**THE BREEDING ECOLOGY OF THE MOORHEN, *GALLINULA*
CHLOROPUS, IN AN ARTIFICIALLY CREATED WETLAND
ENVIRONMENT AT WWT LLANELLI, SOUTH WALES**

A Thesis Presented by Daniel William Forman

for the degree of

Doctor of Philosophy

of the

University of Wales

School of Biological Sciences

University of Wales Swansea

June 2001

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Abstract

An intensive three year study on a wild population of moorhens (*Gallinula chloropus*) at the Wildfowl and Wetlands Trust Centre Llanelli, South Wales revealed that monogamy was the dominant breeding system. Significant numbers of individuals, however, bred annually in polyandrous, polygynous and polygynandrous groups. In contrast to communal groups formed by unrelated individuals and siblings, breeding groups formed by parents and offspring rarely persisted longer than one breeding season. Successful laying in multi-female groups only occurred when both females laid synchronously in the communal nest. The reproductive success of individuals in all communal groups over the duration of the study was generally lower than in monogamous pairings. Some females laid parasitically in the nests of neighbouring conspecifics in all years of the study. This intra-specific brood parasitism (IBP) appeared primarily restricted by host availability. Non-territory holding “floater” females laid a significant proportion of the annual number of IBP eggs. Territory holding IPB’s laid parasitically before and after they had laid in their own nests with equal frequency. Host responses to IBP were limited by their ability to discriminate between their own eggs and those laid parasitically. As the success of IBP was generally poor, most hosts appeared in to incur little cost by being parasitised.

Moorhen broods hatched over several days, creating distinctive size hierarchies based on chick age. To combat parental care monopolization, parents fed small chicks at greater rates per minute than large chicks. Large chicks were also tousled more frequently than smaller counterparts. Parents used tousling to enforced foraging independence on the entire brood. An investigation of parental behaviour using chick sex data derived from a genetic sexing technique revealed that female parental care was sex biased in several ways. In contrast, male parental care was uninfluenced by the chick’s sex.

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List of Animals Mentioned in the Text

Acorn woodpecker (*Melanerps formicivorus*)
Alpine accentor (*Prunella collaris*)
American coot (*Fulica americana*)
American kestrel (*Falco sparverius*)
Bar-headed goose (*Anser indicus*)
Barn swallow (*Hirundo rustica*)
Bewick swan (*Cygnus columbianus*)
Blackbird (*Turdus merula*)
Black kite (*Milvus migrans*)
Bronze-winged jacana (*Metopidius indicus*)
Brown-headed cowbird (*Molothrus ater*)
Brown rat (*Rattus norvegicus*)
Budgerigar (*Melopsittacus undulatus*)
Buzzard (*Buteo buteo*),
Carolina wood duck (*Aix sponsa*)
Canvasback duck (*Aythya valisineria*)
Carrion crow (*Corvus corone*)
Collared flycatcher (*Ficedula alleicollis*)
Common goldeneye *Bucephala clangula*
Common grackle (*Quiscalus quiscula*)
Common gull (*Larus canus*)
Common pochard (*Aythya ferina*),
Common moorhen (*Gallinula chloropus*)
Common shelduck (*Tadorna tadorna*).
Common tern (*Sterna hirundo*)
Cliff swallow (*Hirundo pyrrhonota*)
Crested coot (*Fulica cristata*)
Crimson rosella (*Platycercus elegans*)
Domestic cat (*Felis domesticus*)
Dunnock (*Prunella modularis*)

Dusky moorhen (*Gallinula tenebrosa*)
Eastern bluebird (*Sialis sialis*)
Eastern kingbird (*Tyrannus tyrannus*)
Eurasian kestrel (*Falco tinnunculus*)
European coot (*Fulica atra*)
European fox (*Vulpes vulpes*)
European starling (*Sturnus vulgaris*)
Golden lion tamarin (*Leontopithecus rosalia*)
Great reed warbler (*Acrocephalus arundinaceus*)
Great tit (*Parus major*)
Grey heron (*Ardea cinera*)
Grey starling (*Sturnus cineraceus*)
Guira cuckoo (*Guira guira*)
Herring gull (*Larus argentatus*)
House wren (*Troglodytes aedon*)
Hottentot teal (*Anas punctata*)
Jackdaw (*Corvus monedula*)
Lesser black-backed gull (*Larus fuscus*)
Lesser snow goose (*Chencaerulescens caerulescens*)
Magpies (*Pica pica*)
Mallard (*Anas platyrhynchos*)
Mink (*Mustela vison*)
Mexican jay (*Aphelocoma ultramarina*)
Peregrine falcon (*Falco peregrinus*)
Pied avocet (*Recurvirostra avocetta*)
Pukeko (*Porphyrio porphyrio*)
Purple gallinule (*Porphyryula martinca*)
Raven (*Corvus corax*)
Red-billed whistling duck (*Dendrocygna autumnalis*)
Redhead duck (*Anas americana*)
Red-winged blackbird (*Agelius phoeniceus*)
Ringed dove (*Streptopelia risoria*)

Ring-necked pheasant (*Phasianus colchicus*)
Ringed teal (*Callonetta leucophrys*)
Ross's goose (*Anser rosii*)
Shiny cowbird (*Molothrus bonariensis*)
Sparrowhawk (*Accipter nisus*)
Song Sparrow (*Melospiza melodia*)
Tasmanian native hen (*Gallinula mortierii*)
Tree swallow (*Tachycineta bicolor*)
Tufted duck (*Aythya fuligula*)
Weasel (*Mustela nivalis*)
White-fronted bee-eater (*Merops bullockides*)
White-headed duck (*Oxyura leucocephala*)
Yellow hammer (*Emberiza citrinella*)
Yellow-winged blackbird (*Agelius thilius*)
Zebra finch (*Taeniopyga guttata*)

ABBREVIATIONS

BBS	Breeding Bird Survey
BL	Bill Length
BST	British Summer Time
BTO	British Trust for Ornithology
CBC	Common Bird Survey
CL	Culmen Length
DNA	Deoxyribonucleic Acid
ESS	Evolutionary Stable Strategy
HA	Hatching Asynchrony
HP	Hatch Period
IP	Incubation Period
IBP	Intra-specific Brood Parasitism
MC	Maximum Chord
OSM	Optimal Skew Model
PCR	Polymerase Chain Reaction
RHP	Resource Holding Potential
S.E.	Standard Error
SRS	Seasonal Reproductive Success
SW	Shield Width
T+t	Tarsus and toe
U.K.	United Kingdom
WeBS	Wetland Bird Survey
WWT	Wildfowl and Wetlands Trust

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Finally, I would like to thank the moorhen, one of the most intriguing species one could ever hope to study and a joy to behold.

CHAPTER 1

INTRODUCTION

“And near unpeopled stream-sides, on the ground,

by her spring-cry the moorhens nest is found”

D.G. Rossetti (Spring, 2000, New Amsterdam Books, Amsterdam)

1.1 General Introduction

The Moorhen *Gallinula chloropus* is an adaptable species that is able to spread relatively rapidly and colonise a wide range of habitats (Cramp & Simmons, 1986; Ritter & Sweet, 1993). This ability is partly due to its behavioural flexibility and its remarkably diverse breeding biology (see section 2.2). The breeding biology and ecology of Moorhens has been extensively studied over the last 30 years. Initially, British researchers described and examined the fundamentals of Moorhen breeding biology, such as courtship and hatching success (see Relton, 1972; Wood, 1974; Huxley & Wood, 1976). Since the early 1980s, several research projects in the UK have begun to reveal the fascinating and complex diversity of Moorhen social and reproductive behaviour (see Petrie, 1982; Gibbons, 1985; Eden, 1987; Eden *et al.*, 1988; Leonard *et al.*, 1988; 1989; McRae, 1994). These studies focused on two Moorhen populations, both located in East Anglia (UK). In particular, the vast majority of published research has been undertaken at the former WWT site at Cambridge Botanical Gardens, some 250 miles from the current study location (e.g. Gibbons, 1985; Leonard *et al.*, 1988; 1989; McRae, 1994).

1.2 Ongoing Population Surveys and Monitoring

The British Trust for Ornithology (BTO) undertakes annual reviews of the breeding success of many avian species through amateur-led nest record surveys and censuses. In particular, this is done on all wildfowl and rail species via the Wetland Bird Survey (WeBS) in conjunction with the WWT, the Joint National Conservation Council (JNCC) and the Royal Society for the Protection of Birds (RSPB). Features such as clutch size, egg predation, national population fluctuations and fledging success are assessed annually. Trends and data revealed in WeBS and these other monitoring programmes allows one to make comparative and temporal analyses of the Moorhen's UK distribution and basic breeding success.

In 1995, the BTO Nest Record Scheme issued a "Low Alert" for the Moorhen following alarming increases in daily nest failure rate (nest failure rates have doubled in the last 30 years) and a decrease equivalent to circa half an egg in mean clutch sizes (Crick *et al.*, 1996). The Common Bird Census (CBC) also revealed that the UK's Moorhen population declined by 15-20% over this period. According to "The New Breeding Atlas" (Gibbons *et al.*, 1993), this decline was approximately 9%. The WeBS survey is, however, more sensitive to waterfowl and rail species than the CBC or Breeding Bird Surveys (BBS). It found a progressive increase in the UK Moorhen population since the Breeding Atlas's first publication in 1974. The exact status of this widely distributed species is, consequently, unclear. It is, however, likely that in certain key areas Moorhen populations are increasing (e.g. WWT properties, the Severn and Thames estuaries). Elsewhere, the Moorhen may be experiencing the effects of climate alterations of the UK, with drier springs and summers which would modify seasonal reproductive performance and even cause a population decline in some areas (Crick *et al.*, 1996).

1.3 Avian Reproduction

1.3.1 The Importance of Egg Size in Avian Reproduction

Larger avian eggs contain greater absolute amounts of nutrients than smaller eggs (Carey 1996). Egg size varies more than egg composition (the total amount of energy per egg). For example, American coot *Fulica americana* egg size accounts for 70% of the variation in total energy per egg, whereas only 30% of this variation is explained by egg density (Arnold *et al.*, 1991). Larger eggs generally produce larger chicks (Birkhead & Nettleship 1984; Rhymer, 1988; Magrath, 1992; Erikstad *et al.*, 1998). Eggs have greater yolk and energy contents in precocial and semi-precocial species than in species that produce less advanced young at hatching (Sotherland & Rahn, 1987). The increased egg size in precocial and semi-precocial species provides the raw materials and supports the metabolic costs of synthesizing feather, muscle and other tissues of non-dependent chicks (Rahn & Ar, 1974).

1.3.2 Costs of Egg Production

Egg production is assumed to be relatively inexpensive in terms of total parental investment in altricial species (Monaghan & Nager, 1997). Egg production can, however, only be inexpensive in situations where the resources required for egg synthesis (energy, protein and calcium) are not limiting (Nager *et al.*, 1997). The costs of egg production vary greatly between species, being 13-41% of Basal Metabolic Rate for passerines, 82-128% for shorebirds to over 200% in waterfowl (Carey, 1996). This variation in egg production cost appears related to the life history strategies of individual species. The higher cost of large eggs in precocial species is likely to be offset by reduced parental care costs after hatching. It is worth pointing

out that, although precocial species do not provide much food to chicks, they have other costs associated with raising young (see Lepage *et al.*, 1998).

Intraspecifically, hatchlings from larger eggs are more likely to survive than those from smaller eggs (Carey, 1996). For example, American coot chicks hatched from larger eggs have more mature tissue, insulation and better heat retaining properties which could improve their survivability compared to smaller chicks (Alisauskas, 1986).

1.3.3 Constraint of Clutch Size on Egg Size

There is a trade off between the advantage of laying larger eggs and selection pressure for larger clutches (Rohwer, 1988). Large eggs may produce bigger, fitter chicks but there may be, in turn, an increased adult investment to these more “costly” chicks. This may have consequences for the total number of chicks that can be successfully raised from a clutch (Ojanen, 1983; Pettifor *et al.*, 1988; Rhymer, 1988; Monaghan *et al.*, 1995). If egg size cannot be modified, females of some species could physiologically vary egg composition instead. Partitioning egg constituents in similar sized eggs, means that females could produce different sized chicks under particular environmental conditions. This inter- and intra-clutch control on variations in egg size then promotes the female’s fitness (Alisauskas, 1986; Erikstad *et al.*, 1998).

Optimality theory predicts an inverse relationship between egg and clutch size (Brockelman, 1975). This would theoretically arise because larger chicks have an advantage over smaller chicks and the additional energy used to synthesise larger eggs would ultimately reduce overall clutch size. Lack (1947; 1968) suggested that the evolution of clutch size is a function of both proximate (nutritional and hormonal) and

ultimate (life history strategy) controls. He postulated that avian clutch size was shaped by natural selection and corresponded directly to the number of young for which the parents of altricial young could successfully provision. Lack's theories on optimal clutch size have proved hard to verify but they have stimulated a wide-ranging debate.

Clutch manipulation experiments on a wide range of avian species suggest that clutch sizes are usually lower than the number that would give rise to the most fledglings (Pettifor *et al.*, 1988; Krebs & Davies, 1993; Monaghan *et al.*, 1995; Carey, 1996; Monaghan & Nager, 1997; Lepage *et al.*, 1998). Various adaptations of Lack's hypothesis have been suggested to deal with this discrepancy (Linen & Møller, 1989; Monaghan & Nager, 1997). Many of these have 'trade-offs' reflecting the conflict over maximal reproductive success and parental fitness (they incorporate parental survival and future reproductive attempts). Parents essentially have three choices in the reproductive decision, all of which affect individual fitness and determine parental investment allocated to chicks (Bell, 1980). Firstly, parents can allocate only part of their resources to breeding and the rest to their own survival (iteroparity). Secondly, parents can allocate all of their resources to reproduction, even at the expense of their own survival (semelparity). Thirdly, they could entirely forgo breeding for that season.

1.3.4 Seasonality and Clutch Size

Total seasonal reproductive success (SRS) is determined by the number of young produced. This depends on the number of broods produced and their size. A comparative study of British birds (Crick *et al.*, 1993), found that multi-brooded birds tend to lay earlier with respect to the date of the modal population clutch size than did

single brooded species. Multi-brooded species, therefore, do not 'wait' for optimal conditions before breeding (see section 1.3.6).

1.3.5 Mating Systems, Communal Breeding and Reproductive Success

Great diversity of reproductive strategies and mating systems may be evident within species (Krebs & Davies, 1991; Davies, 1992). It is thought that diverse mating systems arise through the behaviours of individuals attempting to maximise their reproductive success (Emlen & Oring, 1977). Furthermore, evolution of different mating systems appears related to varying intensities of environmental and social selective pressure (Gowaty, 1981; Davies, 1992). Lack (1968) postulated that monogamy is the dominant mating system in birds as males and females can leave more descendants if they share the costs of raising a brood. According to the theory of sexual selection, however, males should mate with as many females as possible and females should mate or pair with those males providing the best care/resources for offspring in order for individuals to maximise their fitness (Trivers, 1972; Parish & Coulson, 1998).

Monogamy may arise as the best available option in the face of limited opportunity for polygyny (Davies, 1992). In territorial species, males generally control the resources necessary for female reproduction (e.g. nesting sites). They are thus able to monopolise females perhaps leading to polygyny (Davies, 1989). The relative costs and benefits of polygyny to each sex have been assessed in several studies (e.g. Davies & Houston, 1989; Kormpimäki, 1991; Veiga, 1992; Johnson *et al.*, 1993). In Dunnocks *Prunella modularis*, males appear to breed best in polygamous groups and do worse in monogamous and polyandrous groups (Burke *et al.*, 1989). The situation is reversed in females who breed in polyandrous groups (Davies & Houston, 1986,

Burke *et al.*, 1989). Reproductive sharing and the degree of relatedness between co-breeding individuals are possible mechanisms mediating the stability and cohesion of polygamous groups (see sections 3.4.5 & 4.4.9; Jamieson *et al.*, 1994; Keller & Reeve, 1994; Jamieson, 1997). Male co-operation may be more frequent in harsh environments (Gowaty, 1981).

1.3.6 Factors Affecting Reproductive Success in Birds

It is apodictic that reproductive success declines seasonally in most temperate breeding avian species (Gibbons, 1989; Hochachka, 1990; Tinbergen & Daan, 1990; Perdeck & Cavé, 1992; Brinkhof *et al.*, 1993; Brinkhof & Cavé, 1997). There can be, however, considerable variability in reproductive effort and success between breeding individuals and groups within a population (Drent & Daan, 1980). Individual reproductive success can be influenced by many environmental and physiological factors. For example, experimentally manipulating hatching times and clutch size (Wiggins *et al.*, 1994) revealed that environmental changes and differences in parental and territory quality affected the seasonal decline in reproductive success in the Collared flycatcher *Ficedula albicollis*.

Multi-brooded species (e.g. Moorhens), unlike single brooded species, often breed in sub-optimal conditions (Davies, 1992). Such individuals should adapt their reproductive strategy (e.g. by either laying larger eggs or producing smaller clutches) in relation to their nutrient reserves and territory quality if they are to maximise their fitness at a particular moment (Arnold, 1994). These adaptations could be crucial during poor breeding seasons and at times of the year when adverse weather and limitations in the availability of food supply can significantly reduce reproductive success (Wiggins *et al.*, 1994).

The time of year when Temperate Zone species commence breeding can restrict individual annual reproductive success (Price *et al.*, 1988; Tinbergen & Daan, 1990; Norris, 1993). Seasonal fluctuations in the abundance and availability of food (Hagen, 1969; Perrins, 1970; Martin, 1987; Vehulst & Tinbergen, 1991; Brinkhof & Cavé, 1997), parental and territory quality (Petrie, 1982; Gibbons, 1989; Brinkhof *et al.*, 1993), local predator numbers (Swennen, 1989), nest parasites (Møller, 1994) and weather conditions (Bengston, 1972; Wiggins *et al.*, 1994) have also been found to affect reproductive success in some birds. Mallard *Anas platyrhynchos* brood survival, for example, was highest for ducklings hatched early in the breeding season when food was plentiful and predator numbers low (Dzus & Clark, 1998).

1.3.7 Age and Reproductive success

Age-related differences in reproduction occur in many avian species (Wooller *et al.*, 1990; Hamer & Furness, 1991; Perdeck & Cavé, 1992). It is apodictic that young birds lay fewer and smaller eggs than older birds (e.g. Crawford, 1980; Curio, 1983; Soether, 1990). First time breeding may impair the ability of females to breed the following year, as recorded in Lesser snow geese *Chencaerulescens caerulescens* (Viallefont *et al.*, 1995). Furthermore, younger birds may have lower reproductive success than that of older birds with more breeding experience (Wooller *et al.*, 1990).

In the 'state-based' approach to life history, age may not, however, necessarily determine reproductive success (McNamara & Houston, 1996). This approach suggests that individual quality (e.g. the ability of individuals to lay large clutches or to maintain a good condition) is more important than simply age (McNamara & Houston, 1996). Indeed, the breeding success of Common terns *Sterna hirundo* is

associated with the body condition of the parents rather than their age (Wendelin & Becker, 1999).

1.3.8 Avian Incubation

Incubation in birds occurs when physiological zero (the threshold at which embryonic development begins, i.e. 20-27°C, see Meijerhof, 1992 for a review) is exceeded within an egg. Incubation behaviour appears to be stimulated by reproductive hormones e.g. prolactin and progesterone (Wiebe *et al.*, 1998). Recent evidence on the flexibility and variability of different incubation behaviours within species suggests, however, that incubation behaviour is not as rigidly controlled by hormones as had been previously thought (Wiebe *et al.*, 1998; Grenier & Beissinger, 1999).

1.3.9 Incubation and Hatching Asynchrony

Incubation in many bird species commences before clutch completion despite the theoretical advantages of initiating incubation when laying has ceased (Caldwell & Cornwell, 1975; Afton, 1979; Nilsson, 1995; Wilson & Verbeek, 1995). Commencing incubation during laying results in eggs initially receiving different periods and amounts of heat. This results in differential chick embryo development within the clutch (Caldwell & Cornwell, 1975). Ring-necked pheasants *Phasianus colchicus* often lay eggs after clutch incubation has begun causing an asynchronous development of embryos of between 1-3 days (Persson & Göransson, 1999). Despite this, clutches can still hatch synchronously, possibly as a result of auditory cues from neighbouring eggs at the time of hatching (Vince, 1968). The disparity in the development of individual chicks may, however, also produce a staggered hatching

pattern whereby eggs within the clutch hatch over a period of days (Hahn, 1981; Stenning, 1996; Persson & Göransson, 1999).

Parents of synchronously hatched clutches tend to have greater fledging success than asynchronous counterparts (Nilsson, 1995). Despite this apparent benefit to parents of ensuring hatching synchronicity, hatching asynchrony (HA) is regularly observed (Magrath, 1990). HA is a much-debated topic in ornithology because of its implications in brood reduction (see Stenning, 1996 for a recent review). As chicks are fed and grow from the time they hatch, HA results in the creation of a size hierarchy between siblings. In these hierarchies, the smaller last hatched chicks often have a higher pre-fledge mortality or are in poorer condition than first hatched chicks (Horsfall, 1984; Bryant & Tatner, 1990; Magrath, 1990; Hörak, 1995).

Many hypotheses have been advanced to explain the adaptive significance of HA. These range from brood reduction (Ricklefs, 1965), sibling rivalry (Mock & Plover, 1987) and nest failure (Hussell, 1982). It is entirely possible, however, that HA is simply an example of convergent evolution (Stenning, 1996). Those who consider HA adaptive, believe that females can manipulate hatching patterns by adjusting their incubation behaviour but this has rarely been tested experimentally (Wiebe *et al.*, 1998). Incubating females could vary the degree of HA by altering the commencement of incubation or altering the rate at which incubation increases during laying (Wiebe & Bortolotti, 1994; Wiebe *et al.*, 1998; Grenier & Beissinger, 1999).

1.4 Intra-specific Brood Parasitism

1.4.1 A Comparison of Inter- and Intra-specific Brood Parasitism

The reproductive strategy of brood parasitism, where a bird lays an egg in the nest of another female who then provides parental care, is common in several bird taxa

(Payne, 1977). This reproductive strategy also occurs in insects (e.g. Eickworth, 1975; Tallamy, 1985; Zink, 2000) and fish (e.g. Tetsu, 1986). Avian obligate interspecific brood parasitism, where the parasitic species is totally dependent on the host species for parental care, has been extensively studied and is generally considered to be well understood (Hamilton & Orians, 1965; Payne, 1977; Rothstein, 1990a). By contrast, the strategy of IBP is less well documented. IBP is a complex reproductive strategy where a female ‘steals’ the parental care of a conspecific (Petrie & Møller, 1991; Lyon, 1993a; McRae, 1994; Eadie & Lyon, 1998). This strategy has recently been described in a wide range of avian species with differing social systems and life histories (Yom-Tov, 1980; Møller, 1987; Emlen & Wrege, 1986; Brown & Brown, 1988; Lank *et al.*, 1989a; Lyon, 1993a; Sandell & Diemer, 1999; Zink, 2000).

The benefits of IBP are balanced by the costs to the host. This leads to a consequent evolutionary “arms race” between parasite and host, similar in nature to that observed between predators and prey (Rothstein, 1975; Petrie & Møller, 1991). Inter-specific brood parasites may select potential hosts by many means over evolutionary history. Species laying eggs of a similar size (Payne, 1967; 1974; 1977), feeding chicks with a similar diet and at a rate that parasite chick requires (Jenson & Jenson, 1969; Payne, 1977), live in similar habitat and are sympatric to the brood parasite are deemed suitable hosts. These complex selection factors are obviously unnecessary in IBP. This phenomenon is likely to be primarily limited by conspecific host nest availability and the ability of hosts to counteract parasitism.

1.4.2 The Strategy of IBP

IBP has often been considered as a “making the best of a bad job” strategy with the female laying parasitically because of reproductive failure or her inability to secure a

nesting site (Petrie & Møller, 1991). This “best of a bad job” aspect of IBP is supported by the fact that it may be utilised by young females or females in poor condition (Lyon, 1993a, McRae, 1994). IBP may also be a prudent and effective fitness gaining-strategy for females under certain circumstances (Lank *et al.*, 1989a). For example, female European starlings *Sturnus vulgaris* are more likely to utilise IBP after clutch loss (Feare, 1991). In addition, female Lesser snow geese utilised IBP when the resources required to rear their own offspring were inadequate (Lank *et al.*, 1989a). IBP can therefore be viewed as a conditional strategy whose frequency within the population is altered by specific factors (Lank *et al.*, 1989a; Lyon, 1993a; McRae, 1994). It is also likely that IBP is only a secondary reproductive strategy to parental care (Lyon, 1993a; McRae, 1994).

1.4.3 Selection of IBP

Several mechanisms may facilitate IBP within a population. Firstly, parasitism can be viewed as a risk-spreading strategy. Complete losses of reproductive investment are avoided as eggs are laid in several nests. The theoretical fitness benefits of such a strategy are, however, only evident in extremely risky environments (Bulmer, 1984; Lyon, 1993a). Secondly, parasitism may reduce sibling competition as parasite siblings compete with non-kin for a share of parental care. If a parasite chick received a disproportionate share of these resources, it would be more likely to survive, favouring IBP as a reproductive strategy (Petrie & Møller, 1991). The majority of species in which IBP has been described are, however, precocial (Yom-Tov, 1980; Andersson, 1984) meaning that parental resources (e.g. food provision) are not shared between the relatively independent young (but see also Lank *et al.*, 1989b). Finally,

the most convincing suggestion for the continuation and selection of IBP is that of exploiting the energetically expensive task of parental care (Petrie & Møller, 1991).

It would pay to use IBP in two situations. Firstly, where the fitness of an individual is limited by the number of offspring it can successfully rear to independence. Secondly, in species whose eggs are relatively cheap to produce (i.e. the resources used to produce eggs do not markedly diminish resources available for parental care). This “side-payment” strategy is likely to be conditional. IBP will be selected for as long as the cost of opportunistic parasitism is less than its benefit, (Petrie & Møller, 1991).

When individuals can act as both host and parasite, a evolutionary conflict of interests arises. Pursuing parasitism opportunities may increase the chance of the bird becoming parasitised herself as a consequence of decreased nest attendance. If this is so, selection should favour a female laying parasitic eggs before she lays in her own nest (Brown & Brown, 1989). The majority of studies thus far have confirmed that parasitic eggs are usually laid immediately before a parasite’s own clutch is initiated (Gibbons, 1985; Davies, 1988; Petrie & Møller, 1991; Sorenson, 1991; Lyon, 1993b; McRae, 1994; Robertson, 1998).

1.4.4 Host Egg Recognition and Discrimination

The host’s skills and abilities to recognise their own eggs is likely to be of evolutionary importance in determining a response to IBP. Species or individuals with locatable nests but with good powers of egg discrimination appear poor prospective hosts (Monadjem, 1996). A female may increase her chance of detecting a parasite’s egg by producing consistent but distinctively patterned and coloured eggs (Møller & Petrie, 1990). Evidence for intra-specific egg discrimination and ejection

is, however, weak (e.g. McRae, 1995) compared with that for inter-specific egg ejection (e.g. Rothstein, 1990a). The high frequency of acceptance of IBP eggs suggests there is little discrimination within individual species. IBP may, therefore, be a relatively new reproductive strategy (McRae, 1994).

The risk of ejecting the wrong egg (particularly in those species where eggs are expensive to produce) is a factor mediating against intra-specific egg discrimination. Furthermore, the majority of studies on this subject have found that egg ejection (when it occurs) takes place before the host has laid (Brown, 1984; Møller, 1987; Stouffer *et al.*, 1987) or early in the host's laying period (McRae, 1995). This conditional behaviour minimises the risk of egg misidentification.

Lack of discrimination between host and parasite the eggs may be subject to other constraints. Acceptance by the host of the parasite's eggs could be mandatory as parasite females could destroy the host's clutch if their eggs were not accepted (Petrie & Møller, 1991). Moreover, destruction of host eggs by the parasite could also synchronise laying between the parasite and host, thereby increasing the benefits of a successful parasitic attempt (Petrie & Møller, 1991). If a nest contains disproportionately more eggs of parasites, it would pay the host to desert the nest rather than accept the enhanced parental care costs of rearing that particular brood (Andersson & Eriksson, 1982; Fenske & Burley, 1995).

1.4.5 The Implications of Cuckoldry on Parental Care

If parasitism is a possibility, it would pay for the host parents to reduce their input to the suspect brood. Such reduced parental input could occur if there is an ongoing risk of parasitism (a non-faculative response) or non-kin are identified within the brood by parents (a faculative response) (Owens, 1993). There may be a trade-off between the

host group's current and future reproductive effort. If so, parasitised parents should decrease their care if the mean relatedness of their clutch is less than that of future attempts (Westneat & Sherman, 1993). Furthermore, if a facultative response to parasitism is possible (parents can identify clutches likely to contain non-kin), parental care should be reduced in those clutches containing a lower proportion of kin (Owens, 1993; Westneat & Sherman, 1993).

With only a finite amount of resources available to individuals for reproduction, a strategy of reducing investment in suspect broods would maintain sufficient resources for future reproductive success of a more kin-biased brood. There is, however, a need for rigorously controlled long term studies of the reproductive success of individuals in order to test this hypothesis (Owens, 1993).

1.4.6 The Tactics of Brood Parasites: Host Nest Monitoring

The success of many parasitic events depends on the stage in the host's laying period when the egg of the parasite is laid (Gibbons, 1986; Lyon, 1993a; b; McRae, 1994; 1995). It would pay a parasite to carefully monitor a host's nest. This could explain the tendency of eggs of parasites to be "dumped" in the nests of close neighbours (Gibbons, 1986; Davies, 1988; McRae, 1995). As the eggs of parasites are not distributed evenly throughout the host's laying sequence there appears to be some level of nest monitoring by the parasite (Møller, 1987). Indeed, female White-fronted bee-eaters *Merops bullockides* and Barn swallows *Hirundo rustica* are reported to visit the territories of potential hosts (Emlen & Wrege, 1986; Møller, 1987).

1.4.7 The Relationship Between Communal Breeding and IBP

Communal breeders may be more prone to parasitism as individuals are concentrated within an area and dramatic changes in behaviour occur during the laying period. Both may increase the ability of parasitic females to locate host nests (Monadjem, 1996). In addition, communal laying may depress parasite egg discrimination by the presence of many eggs in multi-female nests (McRae, 1996a). If communal breeders attract higher rates of parasitism, this potential cost must be viewed against the benefits of breeding communally. Recent reviews of Australian and South African passerine avifauna suggest, however, that the frequency of cuckoo (inter-specific) parasitism is similar in communal and non-communal species. This suggests that communal breeders do not suffer from increased parasitic loads (Poiani & Elgar, 1994; Monadjem, 1996). A similar result was also found in a previous study on IBP in Moorhens where communal groups were as likely to be parasitised as monogamous pairs (McRae, 1994). Extra adults at the nest can facilitate nest detection but this may be countered by increased vigilance against brood parasitism (Poiani & Elgar, 1994).

1.4.8 IBP and Reproductive Success

The adaptive role of IBP has been subject to considerable debate (see section 5.1). In particular, much attention has been directed to the identification of IBPs and their associated reproductive success (Lyon, 1991a; Petrie & Møller, 1991; McRae, 1994). It was suggested formerly that IBPs were reproductively or competitively inferior birds attempting to capitalise on the parental care of others to increase their own fitness (Petrie & Møller, 1991). An increasing number of studies have revealed, however, that females that lay parasitically are as reproductively successful in their

own nests as non-parasitic females (e.g. Møller, 1987; Lyon, 1991a; McRae, 1994; Brown & Brown, 1998; Hotker, 2000).

1.4.9 IBP and Host Reproductive Success

The laying of parasitic eggs in conspecific's nests, shunts the high costs of parental care onto other breeding groups (Brown, 1984). Ultimately, this behaviour could impair the annual and lifetime reproductive success and fitness of host groups through increasing the host's energy expenditure in the incubation and chick rearing phases of parental care. Recently, Brown & Brown (1998) found that the annual survival probability of female Cliff swallows *Hirundo pyrrhonota* was greatest for IBPs and least for hosts. Furthermore, hosts were found to have lower individual lifetime and annual reproductive success than IBPs (op. cit.).

IBP may impose direct cost to the host group in many ways. For example, the laying of parasitic egg(s) may prolong incubation (e.g. Gibbons, 1985); affect hatching patterns/brood hierarchies and increase competition between chicks for parental care. Few studies have found any effect on the survival of host adults and chicks. The survival of parasite and host chicks are likely to be consequences of the expression of different phenotypes (McRae, 1994; Brown & Brown, 1998).

1.5 Parent-offspring Interactions

1.5.1 Parental Investment and Care

There are a wide range of differing parental investment strategies within avian breeding systems (Trivers, 1974; Linden & Møller, 1989; Clutton-Brock 1991; Clutton-Brock & Godfray, 1991; Lessells, 1991). Parental expenditure (e.g. in terms of time and energy) peaks during the nestling period (Drent & Daan, 1980). This is

particularly apparent in altricial species, where offspring are entirely dependent on parental care for survival. In his seminal work, Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving at the cost of the parent’s ability to invest in other offspring”. Natural selection should, therefore, favour parental ability to allocate their resources to maximise their own reproductive success (Dijkstra *et al.*, 1990; Albrecht, 2000). Parents must seek to maximise their lifetime reproductive success by balancing the investment demands of current and future reproductive efforts (Trivers, 1974; Stearns, 1976). This can be achieved by ensuring a high fledgling mass of as many young as possible whilst individually maintaining a healthy physical condition.

The costs of parental investment can have a serious detrimental affect on the survival of adults (e.g. Nur, 1984a; Houston & Davies, 1985) and the success of future reproductive efforts (e.g. Roskaft, 1985; Dijkstra *et al.*, 1990; Godfray, 1991; Lessells, 1991). Brood size manipulation studies have found that parents can often provision at greater rates (e.g. Mock & Ploger, 1987) and care for more young (e.g. Nur, 1984b; Finke *et al.*, 1987; Dijkstra *et al.*, 1990 but see Högstead, 1980) than they actually do. Such increased feeding rates can increase the growth, survival and eventual adult size of offspring (Ricklefs, 1984; Stamp *et al.*, 1985; Skagen, 1988). The benefit to parents of producing high quality offspring is crucial, since the relative survivorship of offspring and their associated reproductive success can account for fitness differences between parents (Skagen, 1988; Daan *et al.*, 1990; Tinbergen & Daan, 1990; Amat, 1995). Parents will reach, however, an intrinsic or extrinsic parental energy expenditure ceiling or “Optimal Working Capacity” (Royama, 1966; Drent & Daan, 1980). Survival and future reproduction is negatively affected beyond this capacity (Houston & Davies, 1985; Tinbergen & Verhulst, 2000).

Age, experience and condition of parents (as well as territory quality and food availability) influence levels of parental care and reproductive success in birds (Gibbons, 1985; Desrochers & Ankney, 1986; Skagen, 1988; Verhulst & Tinbergen, 1991; Norris, 1993; Brinkhof *et al.*, 1993; Amat, 1995; Wright *et al.*, 1998). Parents are thus limited by many factors in the amount of care or effort they can allocate to a brood. To maximise lifetime reproductive success, parental provisioning effort per brood should be optimised with respect to the current condition of each parent, (Trivers, 1972; 1974).

1.5.2 Parent-Offspring Conflict and Brood Reduction

Trivers (1974), based on Hamilton's (1964) inclusive fitness theory, was first to introduce the concept of conflict between parents and offspring. He suggested that they are in conflict over the exact amount of investment parents are willing or able to provide and the offspring is willing to receive. Empirical evidence confirms the predictions of parent-offspring conflict theory but research discerning the connection between this evidence and the divergence of fitness benefits suggested by the theory are, as yet, not forthcoming (Mock & Forbes, 1992).

One potential outcome of parent-offspring conflict is brood reduction through infanticide or siblicide (e.g. O'Connor, 1978; Horsfall, 1984; Mock, 1984b). Under certain circumstances (e.g. adverse conditions, decreased food availability) parents may be unwilling or unable to provide sufficient care to successfully rear all members of a brood (Horsfall, 1984; Mock, 1987 but see Nilsson, 1995). It would, therefore, be prudent for parents to optimise brood size to maximise their fitness at that given time rather than attempt to rear a larger number of poorer quality chicks.

This intriguing and complex behaviour may be facilitated through HA creating a size hierarchy based on age (Bryant & Tatner, 1990; Amundsen & Slagsvold, 1991). Brood reduction may be active, with individual chicks attacked by parents (e.g. Horsfall, 1984), or passive, leaving the larger siblings to exclude smaller, later hatched chicks from receiving parental provisioning (e.g. O'Connor, 1978). Both will result in selective mortality of specific siblings or offspring (Mock, 1984a; 1987; Forbes, 1993; Slagsvold, 1997).

Despite the number of studies on this subject, empirical support for parent-offspring conflict over brood size is not evident (see Drummond *et al.*, 1986). The parents of siblicidal species do not interfere in siblicide. This indicates that offspring “co-operate” with parents over brood reduction (Drummond *et al.*, 1986; Mock, 1987; Forbes, 1993). O'Connor (1978) modelled the inclusive fitness threshold over which it pays a sibling to eliminate a nest-mate rather than a parent committing infanticide finding that such a situation could arise in certain circumstances. Siblings could “co-operate” with their parents by decreasing brood size (through siblicide) in anticipation of future food shortages. This would maximise not only their own survival but also the fitness of their parents at that particular time (Forbes, 1993; Nilsson, 1995).

1.5.3 Parental Effort and Food Provisioning

Feeding behaviour is energetically expensive to parents (Drent & Daan, 1980; Reyer & Westerterp, 1985). Parental effort increases with brood size (e.g. Nur, 1984b; Wright & Cuthill, 1990; Wright *et al.*, 1998). Such increases are not, however, proportional to the number of chicks in the brood (Wright *et al.*, 1998). Parents of some species may be able to “absorb” the extra effort required in rearing additional chicks in large broods at the expense of non-parental activities (e.g. European

starlings *op. cit.*). This flexibility of parents in their ability to adjust their energy expenditure is further supported by a failure to find long-term survival or fecundity costs following brood size manipulations in some species (see Linden & Møller, 1989; Dijkstra *et al.*, 1990; Lessells, 1991). In contrast, parental effort invested per offspring decreases with increasing brood size in some studies. This may be due to foraging and energy restrictions or food limitation. This is seen in American coots (Desrochers & Ankney, 1986) and Great tits *Parus major* (Tinbergen & Verhulst, 2000). In addition, human influence (e.g. disturbance) can result in parents expending more energy in non-reproductive activities. This may reduce nestling condition by decreasing parental care, particularly food provisioning (Ferdandez & Azkona, 1993).

As expected, decreases in food availability and provisioning can influence chick growth and survival rates (Houston & Davies, 1985; Skagen, 1988; Fernandez & Azkona, 1993) as well as altering offspring recruitment to the breeding population (Tinbergen & Daan, 1990; Amat, 1995). Parents can choose to increase the level of parental care provided under adverse conditions (Wright *et al.*, 1998). By doing so, they may be able to increase the prospect of the survival and subsequent recruitment of offspring (McGinley *et al.*, 1987; Lessells, 1991; Amat, 1995).

1.5.4 Brood Size, Hatching Asynchrony and Sibling Competition

HA has many implications for parental care and offspring survival and there is considerable debate on its adaptiveness (see Magrath, 1990; Stenning 1996 for reviews). For example, HA can reduce the energetic load of sibling rivalry as demonstrated in the American kestrel *Falco sparverius* (Weibe & Bortolotti, 1994). HA creates a feeding rank hierarchy based on age and not sex, increasing the

probability of producing some high quality offspring of both sexes (Mock, 1987; Simmons, 1988 but see Albrecht, 2000).

Both nestling survival and variability in chick size are related to brood size and HA (Horsfall, 1984; Skagen, 1988; Smith *et al.*, 1989; Bryant & Tatner, 1990; Slagsvold, 1990). Older chicks from HA broods are more competitively able to position themselves either at the front of the nest or closer to parents to monopolize parental care (Horsfall, 1984; Mock, 1984b; Skagen, 1988; McRae *et al.*, 1993; Cotton *et al.*, 1999; Albrecht, 2000).

Offspring of altricial (and, to a lesser extent, semi-precocial species) are dependent upon parental food provision. Such offspring solicit food from parents by begging (Godfray, 1991; Redondo & Castro, 1992). Begging is an energetically expensive activity for offspring (Leech & Leonard, 1996) and is adjusted by its relative cost (energy) and risks (predation) but less by its effectiveness (Mock & Forbes, 1992). Chicks also vary their intensity of begging depending on their level of satiation (Redondo & Castro, 1992; Whittingham & Robertson, 1994). Intra-brood sibling competition may also change begging levels. Signal models suggest chicks should beg more as the level of competition posed by other siblings increases (Cotton *et al.*, 1999). For example, smaller Tree swallow *Tachycineta bicolor* nestlings beg more frequently and for longer than their larger, older siblings (Leech & Leonard, 1996). Presumably, increasing begging levels in smaller chicks incur a greater energetic cost than in their larger siblings. If that cost is not compensated by parents in terms of provisioning, the survival of smaller chicks is impaired.

Parents may adopt strategies to reduce potential offspring age/size-related conflict during the period of parental care (see also section 1.5.2). For example, “tousling” (Horsfall, 1984) larger, more competitive chicks more frequently than younger

smaller chicks, reduces the monopolization of food by larger chicks in Moorhens (Gibbons, 1985; Leonard *et al.*, 1988). Parents could also preferentially feed smaller, less competitive chicks (Stamps *et al.*, 1985; Boland *et al.*, 1997). Crimson rosellas *Platyercus elegans* often show HA, creating a distinct size hierarchy although no difference in the survivorship or growth of last hatched chicks has been recorded (Krebs, 1999; Krebs *et al.*, 1999). To mitigate potential sibling competition, adult Crimson rosellas selectively feed smaller, last hatched chicks. The act of compensating for such competition may, however, incur an energetic/survival cost to parents (Stamps *et al.*, 1985; Krebs, 1999; Krebs & Magrath, 2000). Food size and availability may have important indirect influences on sibling competition caused by HA (Mock, 1984b; 1987; Mock *et al.*, 1986). The shares of parental investment available become more equal and competition within the size hierarchy decreases when food is abundant (Mock *et al.*, 1986; Parker *et al.*, 1989).

1.5.5 The Implications of Sex Ratios, Sexual Conflict and Size Dimorphism on Parental Care

Parental investment in offspring may be sex-biased (see Stamps, 1990; Gowaty & Droge, 1991; Westneat & Sargent, 1996). Modelling allows revealing insights into selection pressures involved in the sex biasing of parental care (Lessells, 1998). Population sex ratios may be distorted (from a primary sex ratio of 1:1) by inequalities in parental care allocation to different sexes (Halliday, 1994). Local resource competition (the difference between male and female offspring in their use of local high productivity areas) may also produce sex ratio variation in the progeny of avian species (Clark, 1978; Gowaty, 1993).

Selection should act against departures from a 1:1 sex ratio (Fisher, 1930; Halliday, 1994). It has been maintained that parents should expend equal amounts of effort in producing sons and daughters (Fisher, 1930; Clutton-Brock, 1991; Halliday, 1994). In agreement, the sex ratio at hatching is indeed, unity for most avian species (Breitwisch, 1989; Clutton-Brock, 1986; 1989; Slagsvold *et al.*, 1989). Equal parental investment can only occur if the relative costs of rearing sons and daughters are equivalent. This is not always the case in sexually dimorphic species (Howe, 1977; Fiala & Congdon, 1983; Slagsvold *et al.*, 1986; Breitwisch, 1989; Torres & Drummond, 1999).

If parents invest equally in sons and daughters in dimorphic species, differential mortality of the sexes may occur during the period of parental care (Howe, 1977; Clutton-Brock *et al.*, 1985; Slagsvold *et al.*, 1986; Slagsvold, 1990). Equal investment by the Common grackle *Quiscalus quiscula* parents to male and female offspring results in a greater mortality of male chicks which are, on average, 20% heavier than females at fledging (Howe, 1977). Since, however, dominant young receive the most food, size hierarchies created by HA and not sex may be more important reflecting observed mortality patterns (e.g. Horsfall, 1984; Mock, 1984; Drummond *et al.*, 1986; Skagen, 1988; Albecht, 2000). Differential mortalities recorded may be confounded by the larger sex requiring more food and being more prone to starvation (Slagsvold, 1990).

Parents of dimorphic species must compromise between producing high quality large chicks of the more costly sex, whilst not investing too heavily in that sex (Slagsvold, 1990; Krebs, 1999; Albrecht, 2000). Gowaty & Droge (1991) suggested the proportion of care received from each parent depends on the sex of the offspring. Partition of parental care would occur if the fitness value of a given sex differs for the

two parents. Such value differences might arise through alloparental or competitive behaviour by one offspring sex with one sex of parent (Gowaty & Droge, 1991).

Parents may skew the offspring sex ratio by changing the quality of the parental care, producing more of the higher quality chick sex when conditions are good (Trivers & Willard, 1973). Parents might also modify their parental investment by varying the amount of care to specific sexes or by adapting the sex ratio of the brood (Lessells *et al.*, 1998; Albrecht, 2000). Parents of some avian species can recognise offspring sex (e.g. Zebra finches *Taeniopyga guttata*) and differentially allocate parental care to them (Burley, 1986) but this is hardly the general rule (Slagsvold *et al.*, 1986).

1.6. Study Aims and Objectives

This study attempted to:

1. Examine aspects of clutch and egg dynamics in Moorhens.
2. Investigate (and contrast) aspects of reproduction and social formation within different Moorhen breeding social systems.
3. Evaluate and discuss the relative frequency IBP within the population and investigate the success of this strategy using an individual approach.
4. Examine the response of host groups to IBP and attempt to confirm that the host's reproductive success was impaired.
5. Investigate and evaluate aspects of parental-offspring relationships within Moorhen family groups, with the emphasis on food provision and aggression.

CHAPTER 2

MATERIALS AND METHODS

2.1 The Study Site

An intensive study was undertaken on a resident breeding population of *circa* 200 wild Moorhens at the Wildfowl and Wetlands Trust (WWT) Centre at Llanelli, South Wales (grid reference SS 532 984). This is an artificially-created wetland environment, which is home to captive collection of 1200 wildfowl of some 90 species. These are supported by twice-daily additions of wheat grain and specialist wildfowl food at regular sites around the grounds. The design of the grounds incorporates an intricate system of ponds fed by an Artesian well. It also includes patches of scrub, ditches and ancient hedgerows and extends over some 45 acres. The Centre is surrounded by a 2.5m high-electrified fence (10,000 volts) to repel large terrestrial predators (e.g. foxes *Vulpes vulpes* and domestic cats *Felis domesticus*) although several avian and mammalian predators were active in the grounds. Potential predators recorded within the enclosure included Grey herons *Ardea cinera*, Sparrowhawks *Accipiter nisus*, Buzzards *Buteo buteo*, Peregrine falcons *Falco peregrinus*, Lesser blackbacked gulls *Larus fuscus*, Herring gulls *Larus argentatus*, Common gull *Larus canus*, Magpies *Pica pica*, Carrion crows *Corvus corone*, Ravens *Corvus corax*, Jackdaws *Corvus monedula*, Mink *Mustela vison*, Weasels *Mustela nivalis* and Brown rats *Rattus norvegicus*.

The presence of the above-mentioned regular supplement of food and the availability of potentially viable habitat resulted in a wild population of Moorhens becoming established since the creation of the Centre in 1989 (N.Williams, pers.

comm.). The above features conspired to facilitate the study of a large number of Moorhens within the confines of a relatively small area.

2.2 The Study Organism

The Common Moorhen (Family *Rallidae*: Order *Gruiformes*) is a territorial and adaptable member of the rail family that usually inhabits slow moving or still waterbodies (Wood, 1974; Cramp & Simmons, 1980). Moorhens are distributed in suitable habitats throughout the world. The exception is Australia where the congeneric Dusky moorhen *Gallinula tenebrosa*, is found. The current British breeding population is estimated to be in the region of 2-3 million pairs (see Gibbons *et al.*, 1993). This figure usually increases in the winter months due to an influx of over-wintering birds from the continent (Lack, 1986).

Moorhens in Britain flock in relatively large numbers during the winter months, often on agricultural land (Anderson, 1965; Howes, 1976; Petrie, 1982; Pollack & O'Halloran, 1995). They feed on open grassland, whilst swimming and on the water's edge (Cramp & Simmons, 1980). Their diet is generally omnivorous, although vegetation takes up the bulk of food ingested (Witherby *et al.*, 1945; Wood, 1974; Petrie, 1982). Pair formation occurs towards the end of winter (around January and February in the UK). Moorhens are unusual in that females are the more active sex in mate choice (Petrie, 1983). Territories are established through aggressive displays and fights (Wood, 1974). These areas are maintained and defended from conspecifics by both sexes during a breeding season that in Britain generally lasts between March and September (Petrie, 1982; Gibbons, 1985). Although the vast majority of Moorhens breed monogamously, they may also breed communally in

polyandrous (Petrie, 1982; McRae, 1996a), polygynous (Wood, 1974; Gibbons, 1985) and polygynandrous (McRae, 1994) groups.

A number of platforms and nests are usually constructed prior to laying. These are generally located in cover close to water or emergent vegetation (Wood, 1974; Huxley and Wood, 1976). Eggs are laid from around mid-March to late August (Huxley & Wood, 1976). In Britain, eggs are produced at a rate of one per night until a clutch is complete (McRae, 1994). Clutch sizes can range between 1 and 13 eggs; although 5-7 eggs is typical (Relton, 1972; Wood, 1974; Huxley & Wood, 1976). Moorhens may also lay additional eggs in the nests of conspecifics (Gibbons, 1985; McRae, 1994). Incubation takes approximately 21 days (Wood, 1974) with both sexes sharing this task (Siegfried & Frost, 1976). The ptilopaedic, semi-precocial young hatch asynchronously and are dependent for 21 days upon their parents for food provision (Gibbons, 1985). They may be fed for up to 60 days (pers. obs.) and at approximately 70 days of age, juveniles become fully independent (Wood, 1974). The length of the Moorhen breeding season means that it is not unusual for this bird to be multi-brooded (up to four broods have been recorded in a year). Juveniles from previous clutches often remain on the natal territory and may assist with the raising of siblings from later clutches in that same year (Eden, 1987; Gibbons, 1987; Leonard *et al.*, 1989).

2.3 Fieldwork

The study was conducted between 1997 and 1999 from February to October between the hours of 08:00 and 16:00 hours British Summer Time (BST). During the research period, the entire breeding and non-breeding populations were initially subjected to a census during early February each year. Twice weekly censuses of the

grounds were subsequently undertaken throughout the breeding season to accurately determine recruitment and mortality (where possible) within the resident population. The number and type of breeding groups were also assessed annually during the breeding season throughout the study period. The numbers of mature (sexually active) and immature (juvenile and sub-adult) males and females in all breeding groups were recorded by direct observation. In addition, the number of adults participating in the reproductive effort (i.e. those individuals that mated) was recorded in each breeding group. Individuals deemed to be helpers (not observed to breed but involved in the care process) were also identified in each group. An attempt was made to genealogically determine (by direct observation of known individuals) the nature of relationships between members and helpers of breeding groups. This could only be ascertained, however, in two of the three years of research (1998 and 1999).

2.4 Nest searches

During early spring, daily focal observations were made of behaviour and any territorial disputes recorded. Territories were then mapped and their area measured using 30m tapes. Nest searches were conducted every morning between 08:20 and 11:00 hours BST by observing nesting behaviour (adults carrying nesting material) and by looking in likely locations around the grounds. When a nest was located, the vegetation type in which it was found and its height of growth above the structure was recorded. This height measurement followed a procedure similar to that utilised by Petrie (1982).

2.5 Nest and Clutch Data

Nests were revisited each day to determine the exact dates on which each egg within a clutch was laid. When an egg was found, it was individually labelled with a nest code and egg number using an indelible black pen. Measurements of egg weight were made using a 50g Pesola spring balance (obtained from the BTO, The Nunnery, Nunnery Place, Thetford, Norfolk, IP24 2PU) with 2g divisions and an accuracy of 0.2g. The maximum egg length and width were also determined at this time using Vernier callipers (obtained from the BTO, The Nunnery, Nunnery Place, Thetford, Norfolk, IP24 2PU) with 1mm divisions, and an accuracy of 0.1mm. Eggs laid by Moorhens in nest-boxes were collected regularly (under license) by avicultural staff at the centre and were similarly measured. Care was taken to attempt to weigh eggs within 24 hours of being laid in order to assess the fresh weight. Weights taken after this time are inaccurate due to continuous losses of water vapour (Rahn & Ar, 1974). Egg volume was calculated using an equation described by Hoyt (1979) for individual eggs, namely:-

$$V = 0.51 \cdot LB^2$$

where V = egg volume (cm³), L = egg length (cm) and B = maximum egg diameter (cm). Clutch volume was calculated by summing the volumes of all eggs within the clutch.

Total clutch size (the total number of eggs present in a nest when laying was complete) was recorded for each nest noting what breeding group types they belonged to. In the case of parasitised nests (see section 2.7), this included eggs laid by IBPs. The dates when individual eggs were laid and the individual laying it (in the case of

multi-female groups) were recorded. On completion, clutches were assigned to an arbitrary week number (e.g. week 1=9th – 15th February, week 2=16th –22nd February etc) to facilitate seasonal analysis (see also Gibbons, 1985). The numbers of eggs laid by each breeding group and their respective fates in located nests were recorded daily. Only complete clutches were used in the analysis of clutch size. In addition, only the host's clutch size was used in nests identified as being parasitised (see section 2.7).

2.6 Multi-female groups

The analysis of multi-female communal groups involved assigning females to a category based on age, total number of eggs laid and their genealogical relationships to other females in the group. In the case of mother-daughter relationships, senior and junior females were respectively the eldest and youngest hens in the group. In sister-sister and unrelated multi-female group analysis, senior females were those that laid the most eggs. This classification system is somewhat arbitrary and may not reflect dominance hierarchy within the social group.

2.7 IBP Data

The occurrence of parasitically laid eggs within a nest was determined using a protocol similar to Gibbons (1985) and McRae (1994; 1997b). Nests were regarded as parasitised if more than one egg appeared in it within the same 24 period and if the egg size, pattern and colouration also supported this (female Moorhens lay distinctly coloured and sized eggs (see Gibbons, 1986; McRae 1994 but see also McRae, 1997b). In addition, eggs laid more than three days after the host stopped laying were also assumed to be from parasites. The laying of parasite eggs was recorded in

relation to the IBPs own laying sequence and was rated as being in one of three categories (before, during and after IBP's had laid their own clutch).

Parasite hens were identified (where possible) by examining detailed records of the laying behaviour of known individual females in neighbouring territories. Comparing specific egg sizes (to see if they fell within the ranges of non-parasitic eggs), patterns and colourations of individual females were also used as a general guide to facilitate the identification of parasitic hens (see McRae, 1997b). The location of each parasitised nest with respect to that of the female identified as laying parasitically was noted. The breeding type of each parasite hen was also recorded.

The host's breeder type was recorded when a parasitised nest was identified. The number of host eggs already present in the host nest when a parasite's egg was deemed to have been laid and eventual complete clutch size were recorded for each parasitised nest. It was noted whether the host nest was being incubated at the time of parasitism. The fates of the eggs of parasites on their first day in the host nest were recorded. The laying of a parasite's egg(s) were noted in relation to the stage in the host's laying sequence (rated as before, during and after the host had laid). On subsequent nest visits, the fates of both parasite egg(s) and host eggs were monitored carefully. Chick mortality was recorded when the clutch hatched and 45 days after hatching.

2.8 Incubation Data

A record of the onset of incubation for each clutch was made by regular monitoring of egg heat throughout the laying sequence. All eggs within a nest were carefully felt and the incubation stages of each clutch rated as belonging to one of three categories (cold, partially incubated and fully incubated). This was done during each nest visit

until the onset of full incubation. Full incubation was defined as all eggs within a clutch being fully warmed. When a clutch was complete, a photograph was taken of the eggs using a Sigma SA-300 camera with a long distance Sigma Zoom 28-200mm and a close up Tokina SAF 35-80mm lens as to provide a permanent record of each hen's eggs over the three years. Nests were checked daily throughout the incubation period to monitor the fate of eggs and to discover whether IBP had taken place.

2.9 Hatching Data

Hatching period (HP) was the number of days over which all eggs in a clutch hatched whereas the incubation period (IP) was the total number of days between the onset of full incubation and clutch hatching. These were determined for each clutch. Only complete clutches for which the dates that individual eggs were laid, incubation undertaken and corresponding hatch dates were known were used in the IP, HP and chick survivorship analyses for the groups. In addition, groups known to have been parasitised, with inaccurately documented breeding attempts or who had laid in nest boxes were excluded from the analysis of overall group reproductive success.

When eggs hatched, each chick was caught and weighed with the 50g Pesola spring balance. Maximum chord (MC) and tarsus and toe (T+t) were measured using a 150mm wing rule (obtained from the BTO, The Nunnery, Nunnery Place, Thetford, Norfolk, IP24 2PU) with 1mm divisions and an accuracy of 1mm. In addition culmen length (CL), bill length (BL) and maximum shield width (SW) were measured using the Vernier callipers. Each chick caught was ringed with an individual combination of colour rings, cut to size and adjusted with adhesive foam (Gibbons, 1985). A sample of down was also taken at this time by quickly pulling out a pinch of feathers from each chick's flank. This down was sealed in polythene bags (3x4 cm),

individually labelled and stored in a freezer at -18°C until PCR analysis was undertaken (see sections 2.11-2.13 for specific details).

Chicks caught throughout the breeding season were re-ringed with full sized colour rings and their biometrics re-recorded. Chick survivorship was noted for each brood 5 days after the last egg(s) in the clutch had hatched, had been abandoned or predated and also at 45 days of age. The population was monitored by carrying out a twice-weekly census over the entire breeding season in each year of research. Adults were caught at night using a million-candle power “Clulite” lamp (obtained from Killgerm Chemicals Ltd, Denholme Drive, Ossett, West Yorkshire, WF5 9NB) and hand nets (supplied by WWT). Catches took place at night between 20:00 and 23:30 hours BST throughout the breeding season. The lamp was shone directly at individual Moorhens and a net used to catch them whilst they were temporally stunned. These birds were ringed with a unique colour ring combination and a BTO metal ring. Weight, T+t, BL, CL, SW and MC were recorded. Each adult was sexed in the hand via a discrimination technique involving weight and T+t measurements (Anderson, 1975) and was later confirmed by behavioural observations. Not all breeding adults were caught and ringed as the WWT restricted the use of ‘walk-in’ cage traps within the grounds. Distinguishing physical features (principally details of the white stripe pattern on the flanks of birds see plate 1.1 page 35) were in some cases, used to identify individuals on specific territories.

2.10 Behavioural Observations

Behavioural observations usually took place between 09:00 and 16:00 hours BST using a pair of Boots 10 x 50mm wide-angle binoculars, Pentax 10 x 24mm UCF V binoculars and an Opticron Classic IF scope. Moorhen broods predominately show



Plate 2.1 Male moorhen showing the stripe pattern used in the identification of specific individuals.

HA, leading to the chicks having a distinct size hierarchy (Gibbons, 1985). This results in considerable age differences between large and small chicks (*circa* 2-3 days, with larger chicks generally being older than their smaller siblings). The relative sizes of chicks within individual broods at hatching involved measuring chick weight, T+t, SW, CL and MC (section 2.9). In each session, the relative sizes of each individual chick (rated as large, intermediate or small) within each study brood was recorded by direct observation (see below). Individual monogamous broods with no adult helpers were randomly selected for behavioural observation throughout the study period. Clutches in which eggs had been laid parasitically were excluded from the experimental broods. A total of 23 of such broods were observed with 9, 6 and 8 broods being studied in 1997, 1998 and 1999, respectively. The largest and the smallest chick from each brood were subsequently used in the analysis. In total, data from 16 male (8 large and 8 small) and 12 female (6 large and 6 small) chicks were used in the sex-based analysis. Care was taken not to observe the same parental groups each year to avoid pseudo-replication. Chicks from each brood were individually observed at 4-day increments of age from hatching up to 60 days (producing a total of 15 observation sessions per chick per brood).

At least 20 minutes lapsed before the recording of any information, allowing broods to adjust to the observer's presence. Behavioural observations were recorded for individual broods at different times (morning, middle of the day and afternoon) on a rotational basis to negate possible temporal influences on feeding and parent-offspring tousing behaviour. Individual chicks were observed continuously for a minimum of 20 minutes per session. Although the research was orientated towards the largest and smallest individuals, efforts were made to view all the chicks in study broods.

Feeding was observed for identified chicks at 4-day increments of age, by continuously recording the number of times that the chicks fed themselves per minute over a set time period. The provisioning behaviour of both parents was similarly observed individually on these days after the brood had hatched until the chicks reached 60 days of age. The number of times individual parents fed chicks and which chick they fed was recorded continuously every minute for a minimum of 20 minutes. If a chick or parent disappeared from view during data collection, recording of behavioural data was suspended until the individual(s) could be seen again.

Parent-offspring “tousling” (Horsfall, 1984) behaviour observed between identified parents and siblings was recorded during each parental observational period. Tousles were defined as being either pecks (parent striking a chick with its beak), chases (parent aggressively pursuing a chick), peck/chases (a combination of pecks and a chase) or shakes (parent enclosing the head/neck of a chick with its beak and shaking bodily). The estimated approximate distance between individual chicks and parents was recorded before and after tousle events. The duration of each tousle, the behaviour of the chick before the event (categorised as begging, resting or feeding) and the type of tousle were recorded at this time. Care was taken to observe all possible feeding and tousling interactions between each parent and chick respectively within each study brood. Data was collected on the behaviour of chicks prior to a tousle event, type of parental attack, as well as duration and the position of chicks before and after this response in 895/977 of cases.

2.11 Sexing Technique and DNA Extraction Protocols

The sexing technique for Moorhens was optimised by using brain tissue from four adults (removed under Trust licence). These birds had been sexed on the basis of

dissection. DNA was extracted from brain tissue using the following standard phenol-chloroform protocol (see Milligan, 1998). First, 300 μ l of SET (100 mM NaCl, 1 mM ethylene diamine tetra acetic acid [EDTA] and 100 mM Tris-borate [2-amino-2-(hydroxymethyl) propane-1,3-diol]), 30 μ l of 10% sodium dodecyl sulphate and 6 μ l of proteinase K (10 mg/ml Gibco BRL) were added to the brain tissue. The mixture was agitated and then incubated over night in a heat block at 55°C. Next, 300 μ l of phenol was added and the solution briefly vortexed. It was then centrifuged for 15 minutes at 8000 rpm. The aqueous layer was removed and 300 μ l of 1:1 phenol:chloroform was added to the aqueous layer. This solution was mixed for 10 minutes on a rotary mixer and then centrifuged for 10 minutes before removing the aqueous layer. This last step was repeated once more with 300 μ l of 1:1 phenol:chloroform added to the aqueous layer and then finally with 300 μ l chloroform. Following this, 40 μ l of 3 M NaAc (pH 5.2) and 800 μ l of 100% ethanol were added to the recovered aqueous layer and the mixture centrifuged for 10 minutes. The aqueous layer was removed after this time and discarded. The remaining solids were washed thoroughly with 80% ethanol, dried in a heat block for 30 minutes at 55°C and resuspended overnight in 300 μ l of Millipore-filtered water overnight in a rotary mixer.

Down feathers had been collected from 28 chicks (12 from 1998 and 16 from 1999). As only small quantities of material were involved, DNA from these downy feathers were extracted with DNeasy Tissue Kit (Qiagen) using the manufacturer's protocol. Two feathers were added into a 1.5 ml Eppendorf tube to which 180 μ l of ATL Buffer (supplied by Qiagen) and 20 μ l of proteinase K (supplied by Qiagen) was added. The solution was thoroughly mixed by vortexing briefly. The solution was then incubated at 55°C for three hours in a heat block in order to lyse the tissue. The feathers were

then removed from the solution. 200 μ l of AL Buffer (supplied by Qiagen) was added and the solution was vortexed and then incubated at 70°C for 10 minutes. After this incubation period, 200 μ l of 100% ethanol was added and mixed by vortexing. The mixture was then pipetted into a 1000 μ l DNeasy mini column. The column was centrifuged at 8000 rpm at room temperature for 1 minute and the flow-through discarded. Subsequently, 500 μ l of AW1 Buffer (supplied by Qiagen) was added and the column was centrifuged as before with all flow-through being discarded. 500 μ l AW2 Buffer (supplied by Qiagen) was then added and the column centrifuged for 3 minutes at full speed (>8000 rpm) at room temperature to completely dry the membrane, with the flow-through discarded. The column was then put into a 1.5 ml micro-centrifuge tube and 50 μ l of Buffer AE (supplied by Qiagen) was added. This tube was incubated at room temperature for 1 minute and then centrifuged for a further minute at 8000 rpm. This last elution step was repeated to provide a backup extract (Qiagen DNeasy Handbook, 1999).

2.12 The Polymerase Chain Reaction (PCR) Protocol

The extracted DNA were used in PCR with the avian sexing primers P2 and P8 (P2- 5'-TCTGCATCGCTAAATCCTTT-3'; P8- 5'-CTCCCAAGGATGAG(A/G)AA(C/T)TG -3') (Griffiths *et al.*, 1998). A Yellow hammer *Emberiza citrinella* female served as a positive control in the initial PCRs with DNA from tissue samples. The DNA from the Moorhen tissue samples provided positive controls for subsequent analyses of down feathers. A blank (negative) control was included in every set of reactions. Up to 2 μ l of the extracted DNA from feathers was used in 10 μ l PCR reaction mixes. These also contained 50 ng of each primer, 0.2 mM of each nucleotides (Promega), 0.4 units of 'Red Hot' *Taq* DNA polymerase (ABGene), 1 μ l of 10x PCR reaction

buffer (ABGene) and 2 mM of MgCl₂ (ABGene). The reaction began with an initial denaturation step of 94°C (1.5 min). This was followed by thirty cycles of annealing at 48°C (30 sec), extension at 72°C (30 sec) and denaturation at 94°C (1 min). This reaction was completed by two minutes at 48°C followed by another two minutes at 72°C.

2.13 DNA Separation and Identification

Polyacrylamide gel electrophoresis and silver staining were carried out according to standard laboratory protocol (Sambrook *et al.*, 1989). Two glass plates (Hoefer) were sprayed with ethanol and wiped clean. Using clean spacers, the plates were held in place by clamps and then locked into a rack using screws to make a seal at the bottom. 3.75 ml of 0.09 M Tris-borate (Sigma Ltd), 6.25 ml of 29:1 acrylamide and 27 ml of de-ionised water were added to a glass flask and de-gassed for five minutes at room temperature. Subsequently, 250 µl of 10% ammonium persulfate, (Gibco BRL), and 33 µl tetra ethylene diamine (TEMED) (Gibco BRL) were added to set the gel. The solution was mixed and then poured into the glass frame. A comb of the required size was inserted between the two glass sheets and the gel allowed to set. Subsequently, the comb was removed and sample wells were irrigated 3 times with Tris-borate buffer.

Five µl of sucrose loading buffer (40% Fisons sucrose, and 0.25% Sigma Ltd Bromophenol blue) were added to the samples. Ten µl of each sample were pipetted into a comb space using long pipette tips to avoid the mineral oil layer. A molecular ladder (4 µl of H₂O, 4 µl of loading buffer and 1 µl of Boehringer Mannheim Marker VI) was also added to one well. A glass blank was constructed and added to the rack

and both plates were put into an electrophoresis tank (Hoefer) filled with Tris-borate buffer. The gel was run for 2-2.5 hours at 30 volts.

After removing the gel from the glass frame, it was washed twice in solution A (360 ml H₂O, 40 ml 100% ethanol and 2 ml acetic acid) for 3 minutes on a shaker. The gel was then soaked in solution B (200 ml H₂O and 0.2 g silver nitrate) for 10 minutes and put on a shaker. The gel was then washed twice in distilled water before finally being placed in solution C (300 ml H₂O, 4.5 g sodium hydroxide, 0.03 g sodium borohydride, and 1.2 ml formaldehyde) for ten minutes, on a shaker. The stained gels were photographed with a Bio-print digital system (Vilber Lourmat). Males were identified by the presence of only one PCR product, and females by two PCR products (Griffiths *et al.*, 1998).

2.14. Statistical Analysis

The analysis of data was conducted using “Microsoft Excel Office 97” spreadsheet and “Analyse-It” General Module v1.5 statistical package. Data was assessed for normality and distribution prior to analysis and appropriate tests undertaken. Statistical tests were conducted with a significance level of $p=0.05$, with all tests being two tailed unless stated to the contrary in tests. Means are stated with Standard Errors (S.E.) and medians with ranges.

CHAPTER 3

THE BREEDING ECOLOGY OF MOORHENS AT WWT LLANELLI

“Some folks rail against other folks, because other folks have what some would be glad of”

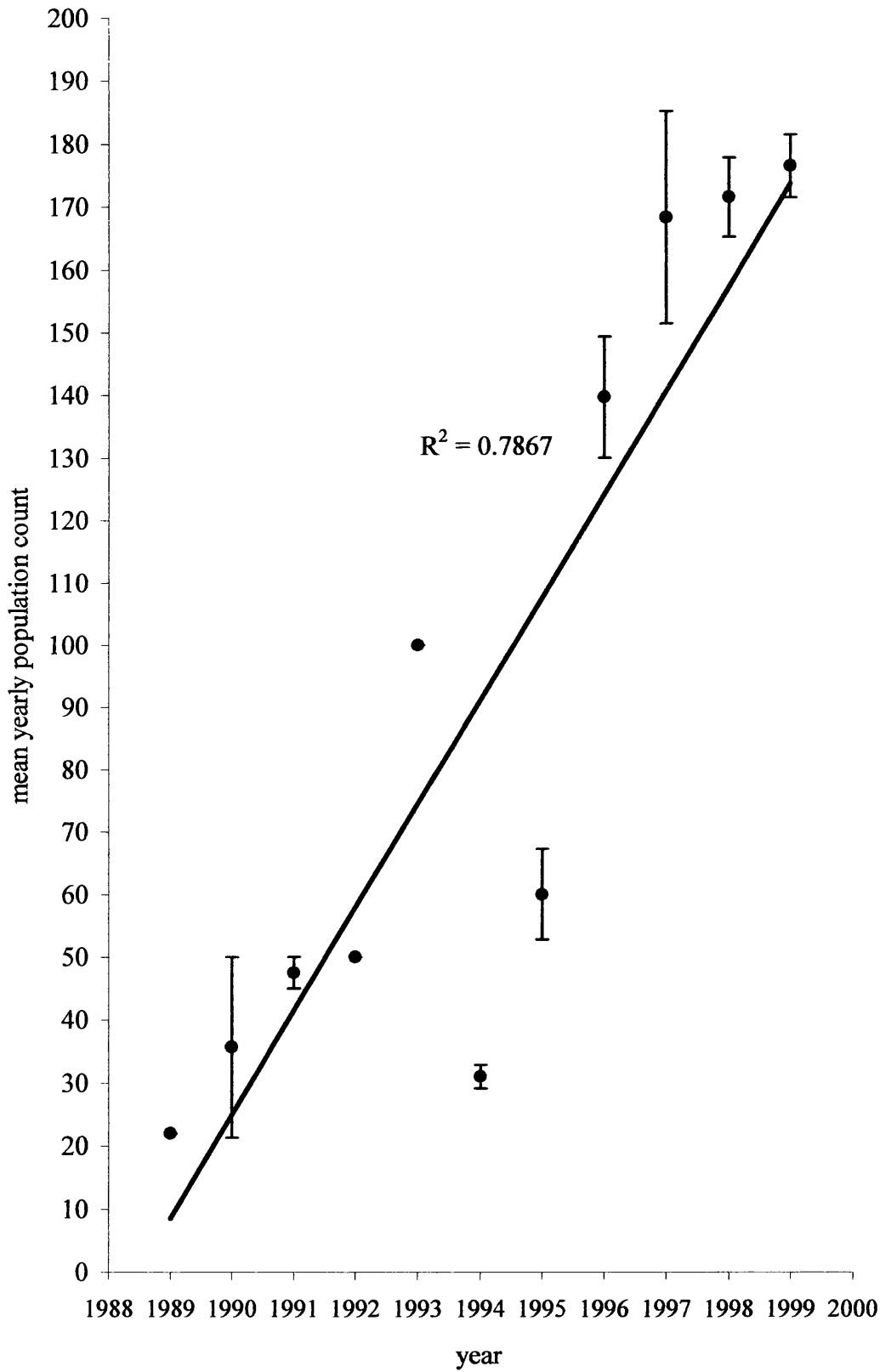
Henry Fielding (Joseph Andrews, 1999, Penguin Books, London)

3.1 Introduction

There are substantial numbers of Moorhens in Carmarthenshire and Glamorgan, the Severn estuary and the WWT centre at Llanelli. Indeed, WWT Llanelli and the Burry Inlet have the greatest density of such birds in the area (Carmarthenshire Birds, 1996; 1997; 1998; Waters *et al.*, 1996; 1998; Cranswick *et al.*, 1997; 1999). The population growth of the resident population at WWT Llanelli and the yearly influx of non-territory holders from outside the grounds had been assessed using mean monthly counts undertaken since the Centre's creation in 1989 (N.Williams, pers.comm.). The Moorhen population has increased steadily (Pearson's Product moment: $r = 0.887$, $p < 0.001$, $df = 10$; see figure 3.1 page 43). This population growth rate has, however, begun to plateau in recent years.

A wide diversity of breeding strategies are evident within Moorhen populations (see section 2.2). The relative frequency and occurrence of these intra-population strategies is likely to be influenced temporally by localised social and environmental pressures (McRae, 1994). Detailed information on the behaviour and reproductive performance of populations will undoubtedly reveal fascinating insights into the developmental processes and patterns of Moorhen social group formation and the temporal expression of differing reproductive strategies.

Figure 3.1 The growth of the Moorhen population at WWT Llanelli since the Centre's creation



3.2 Aims

This chapter aimed to:

1. Describe and assess the establishment of the Moorhen population at WWT Llanelli
2. Determine, quantify and discuss the relative numbers of breeding adults and groups over the three years of study.
3. Describe the different types of breeding groups located at the study site
4. Determine the numbers of eggs laid in each breeding season and their fates

3.3 Results

3.3.1 Breeding Group Numbers

The number of breeding groups recorded within the grounds of WWT Llanelli increased progressively in each year of research. There were respectively 58, 79 and 84 breeding groups in 1997, 1998 and 1999.

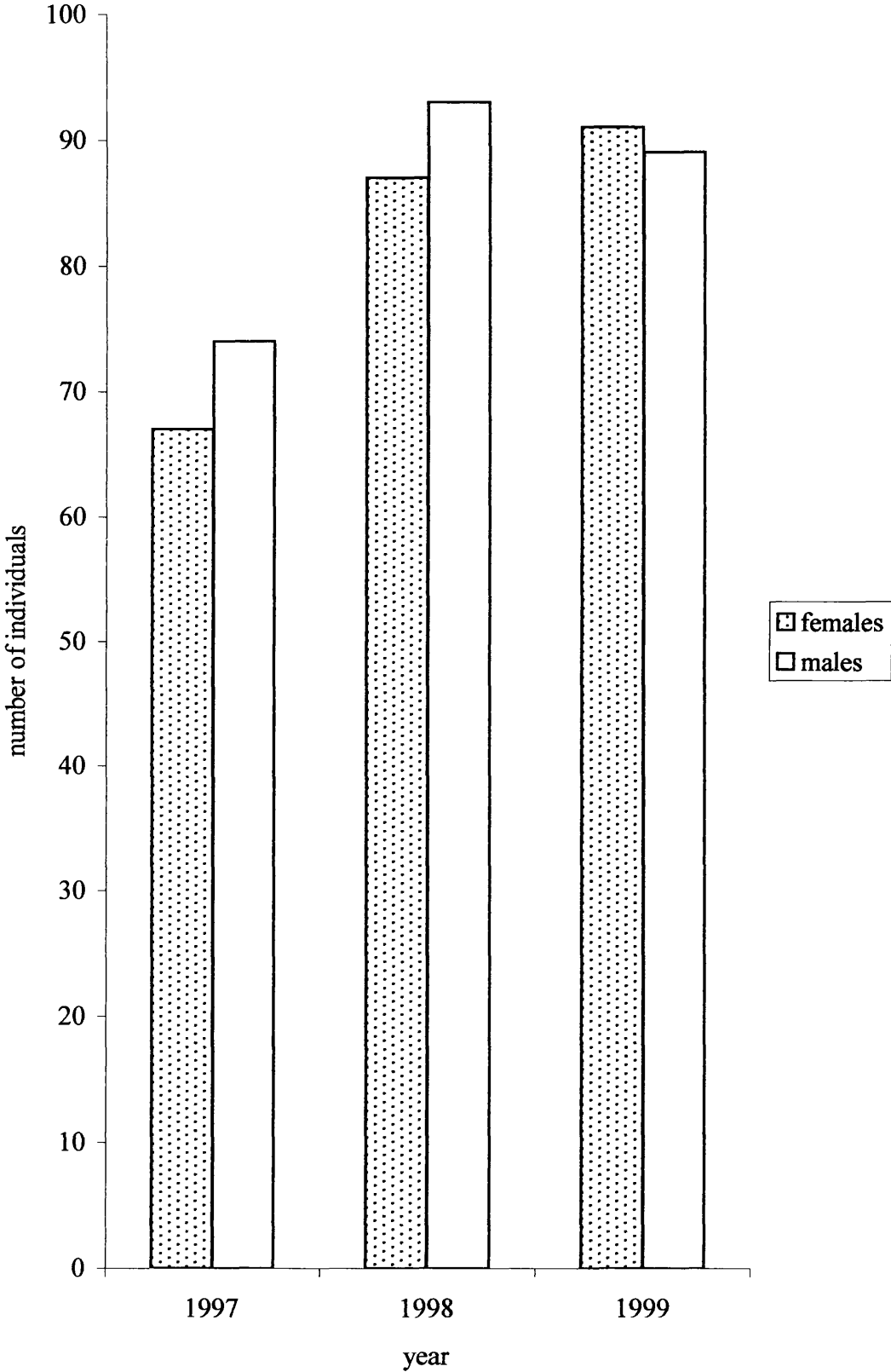
3.3.2 The Number and Sex Ratio of Breeding Adults

The total numbers of adults breeding in each year of research is shown in figure 3.2 (page 45). More adults bred in 1998 and 1999 than in 1997. The sex ratio of the breeding population over the duration of the study was slightly biased towards males (female:male=0.94). This sex ratio did not, however, differ significantly from unity over the duration of the study ($X^2=0.33$, $p=0.84$).

3.3.3 Types of Moorhen Breeding Group

Four main types of Moorhen breeding group were identified over the 3 years of study. These were monogamous, polyandrous, polygynous and polygynandrous groups (see table 3.1 page 46). The vast majority of Moorhen breeding groups

Figure 3.2 The number of males and females in the breeding groups over the duration of the study



recorded in each year were monogamous. Approximately 12-30% (n=10-19) of the breeding groups each year were, however, communal. The most frequently occurring communal group types over the three years were polyandrous and polygynous, there being respectively n= 20 and n=16 such groups. Only a few polygynandrous groups (n=7) were recorded over the three years of research. Overall, the percentage of communal groups progressively decreased over successive years of research. Most (75%) members within polyandrous and polygynous groups in 1998 and 1999 were first order relatives (brothers, sisters or offspring). The exact relationship between members of one polygynous group found in 1998 was unknown. Members of the polygynandrous group recorded in 1999 were a core parental group (mother and father) and three mature offspring (two females and one male).

Breeder type	1997	1998	1999
Monogamous	37	61	68
Monogamous + 1 helper	1	2	3
Monogamous + 2 helpers	1	2	2
Monogamous + 3 helpers	-	-	1
Polyandrous (2 males and 1 female)	10	5	3
Polyandrous + 1 helper	-	1	-
Polyandrous + 3 helpers	-	-	1
Polygynous (1 male and 2 females)	3	7	5
Polygynous + 1 helper	-	1	-
Polygynandrous (2 males and 2 females)	6	-	1

Table 3.1. The frequency and composition of different breeding group types in the 3 years of study

The number of groups having one or more non-breeding adult helper at the nest varied greatly from year to year (see table 3.1 page 46). The number of groups with helpers were similar in 1998 and 1999. In 1997, however, only 2 groups with a total of 3 helpers were recorded. The sexes of these helpers was determined for all breeding groups in 1998 and 1999 (see table 3.2 below).

Sex of helper	1998	1999
male	3	4
female	5	9
Total	8	13

Table 3.2 The number of male and female adult helpers recorded in 1998 and 1999

The majority of helpers over these two years of research were female (66.7% of the total). The overall proportion of adult helpers that were female was not, however, significant (G test: $G_{adj}=0.051$, N.S.). These birds were offspring from the previous breeding season in all groups (n=21) in which they were recorded in 1998 and 1999.

3.3.4 The “Floater” Population

Several individuals (between 4 and 12 members located in various pens) within the population did not appear to defend territories or form observable breeding bonds with other birds. “Floating” individuals were recorded in each of the study years.

3.3.5 The Total Number of Eggs Laid

Table 3.3 (page 48) illustrates the numbers of eggs laid each year of the study. In the last two years, similar numbers of eggs were recorded and both were greater than

that found in the first year of research. A total of 2565 eggs were found in nests during the three years of study. In addition to these eggs, a further 264 eggs were laid in wildfowl nest boxes (used for captive bird breeding programmes) and 324 chicks were recorded as having hatched from unlocated nests.

Year	Number of eggs recorded
1997	873
1998	1138
1999	1142

Table 3.3. The number of eggs recorded annually during the period of study

Interestingly, the number of eggs laid annually in nest boxes varied dramatically between 1997 and the 1998/1999 breeding seasons. In 1997 24% (n=203) of all Moorhen eggs were laid in nest boxes. In 1998 and 1999, however, the proportion of eggs laid in nest boxes ranged from 1.9% (n=18) to 1.1% (n=43) respectively.

3.3.6 Overall Fates of Eggs Laid

The relative fates of the 2565 eggs recorded over the three years of research within the Centre's grounds is shown in figure 3.3 (page 49). The vast majority (84.8%) of eggs either hatched (*circa* 45%) or were predated (40%). The remaining 15.2 % (n=388) were abandoned, ejected, died whilst hatching, killed by flooding, destroyed in the nest or were addled.

The percentages of eggs predated and hatched in the different years is shown by figure 3.4 (page 50). The percentage of eggs predated was highly variable from year to year. The highest and lowest predation rates occurred in 1997 and 1998,

Figure 3.3 The overall fates of eggs laid during the three year study period

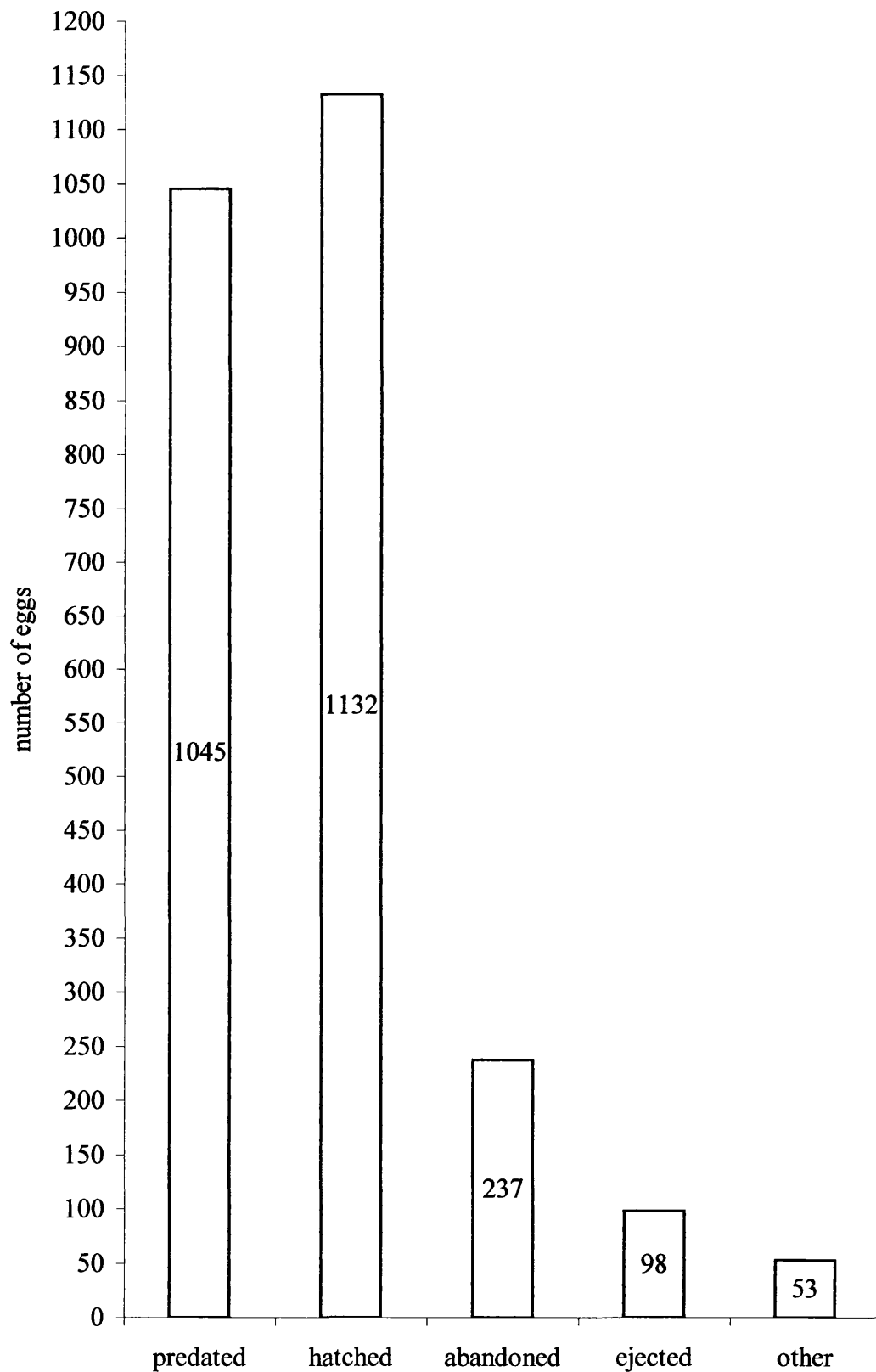
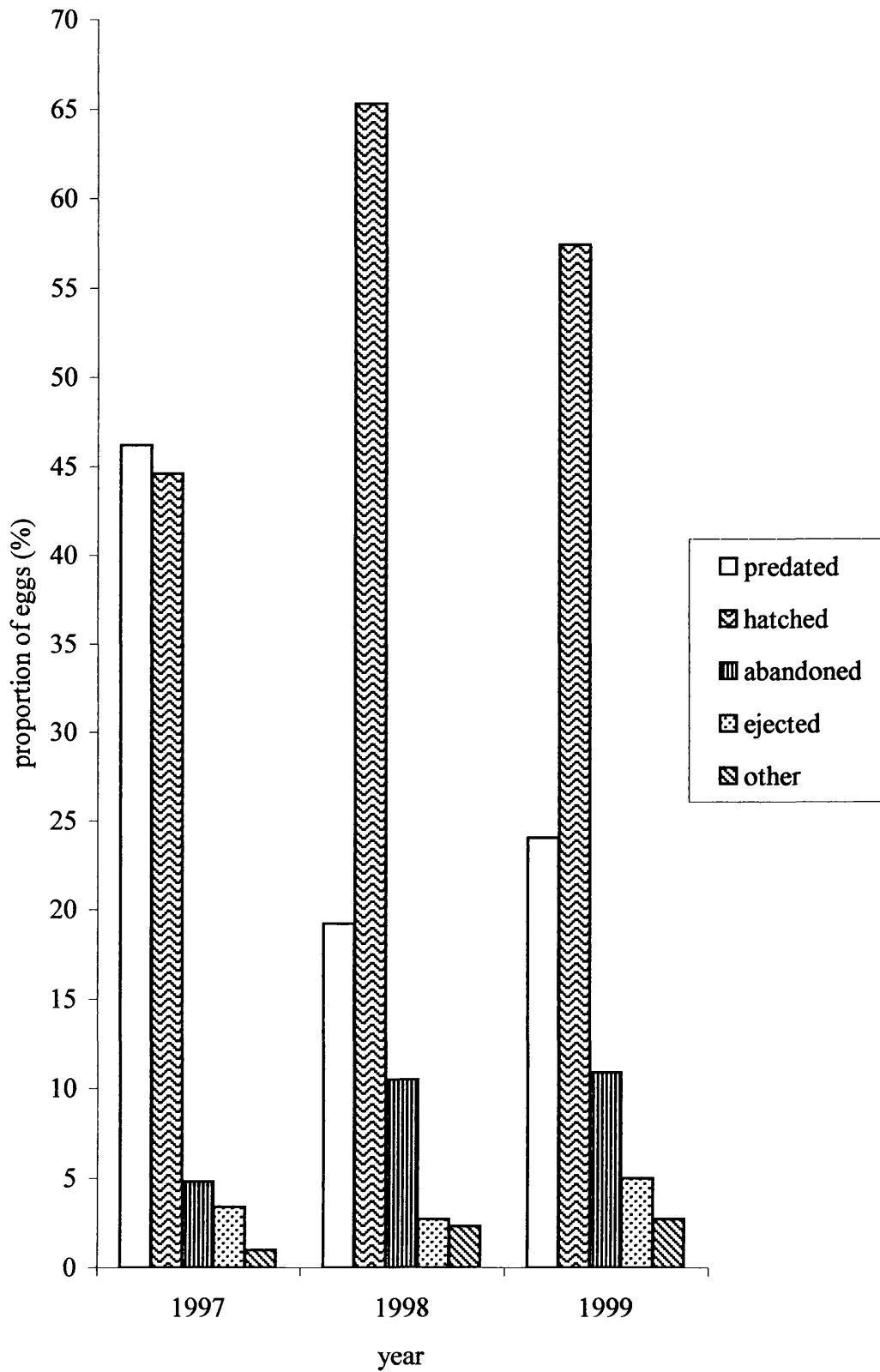


Figure 3.4 Proportional fates of eggs laid each year during the study period



respectively. In addition, the percentage of eggs hatching was also very variable from year to year (highest and lowest hatch success in 1998 and 1999, respectively).

3.4 Discussion

3.4.1 Population Growth

It is likely that Moorhens from the surrounding habitat (in the rough pasture, ditch and pond systems outside the Centre's perimeter fence) initially migrated into the grounds. These migrants rapidly assumed permanent resident status supplementing the existing small number of Moorhens already found within the site (N.Williams, pers. comm.). This movement seems partly due to the creation of suitable habitat for both breeding and over-wintering and partly to the readily available supply of food provided daily to the captive wildfowl collection. The population has expanded rapidly in recent years and Moorhens are now found on all ditch, pond and lake systems within the grounds (pers.obs). In addition, the Moorhen population of WWT Llanelli was noted to increase in the winter months due to the immigration of birds from the surrounding area. Evidence from other WWT properties that provide regular food to captive wildfowl collections suggest that, although breeding sites may be saturated, Moorhens remain on site in "floater" groups (N.Williams, pers.comm.). They may do so simply because of the presence of food and absence of large terrestrial predators.

The Moorhen population growth at WWT Llanelli is not dissimilar to that observed in the other WWT Centres and bird reserves which provide daily food. In particular, the WWT centres at Arundel, Martin Mere and Slimbridge have large populations of Moorhens well above the natural carrying-capacity of the habitat. It is frequently

maintained that these high-density concentrations of Moorhens are important breeding sites for this species (Waters *et al.*, 1996; 1998; Cranswick *et al.*, 1997; 1999).

3.4.2 The Problems of Artificially Supported Populations of Moorhens

The colonisation of WWT sites with captive collections of wildfowl by Moorhens has led to many problems for the Trust. Moorhens defend territories and nests from conspecifics (Wood, 1974; Gibbons, 1985; McRae, 1994) and from other wild and collection species (pers.obs). Moorhens also frequently lay clutches in nest boxes designated for the Trust's captive-breeding programme (see section 3.4.11). As a consequence of this vigorous defence of breeding and nesting areas, they may reduce the potential breeding success of collection species who are unable to lay their eggs in safe nest boxes (R.Edwards, pers.comm.). More seriously, Moorhens may be a permanent locus and vector for infections and parasites that can then enter the collection population. The captive populations of wildfowl in Trust properties are known to be affected by a wide range of bacterial, viral and fungal diseases including Duck viral enteritis, Candidiasis and several strains of Avian tuberculosis (Brown, 1995). Evidence from veterinary staff at WWT Slimbridge further suggests that various avian diseases could enter the captive population via seasonal immigration and resident populations of passerine and non-passerine species (M. Brown, pers.comm.). Brown (1995) suggested that an increase in the number of parasitic infections (e.g. from the nematode *Acuaria unicinta*) recorded in collection birds at Slimbridge was directly related to the increasing numbers of visiting waterfowl to the site.

The Moorhens also have an economic cost by consuming foods provided for captive birds. The Trust consequently annually culls and removes (under license) a specified

number of Moorhen adults and eggs as well as other “pest” (e.g. Mallard and corvid) species. The precise influence of such removals on levels of disease in Trust properties is, as yet, unquantified and clearly needs further research. It seems probable that the removal of up to 80 eggs per year (the present licence quota) is insignificant compared to overall numbers of egg laid each year at WWT Llanelli (see section 3.3.5). Moorhens are annually able to lay several replacement clutches relatively quickly after clutch loss (Wood, 1974; Huxley & Wood, 1976). The removal of a small number of clutches is, therefore, unlikely to affect the population as a whole. Removal of specific group’s eggs may, however, ultimately affect the current reproductive performance of those particular groups.

Supplemental food provided to wild Moorhens at Peakirk Botanical gardens in Cambridge (UK) decreased inter-clutch intervals in experimental broods although it did not increase the number of broods raised (Eden *et al.*, 1988). A regular artificial supply of food may therefore, allow Moorhens to compensate for clutch losses by providing sufficient resources to produce replacement eggs (see section 4.4.3).

One may even suggest that the presence of Moorhens could also be beneficial to the Trust. As stated earlier, many other avian species are attracted in large numbers to WWT Llanelli. Some of these (e.g. corvid species) are, at certain times of the year, the principal predators of eggs. The large numbers of Moorhen eggs available to these predators may reduce the predation pressure on the captive breeding species’ eggs.

3.4.3 Population Increases and the Number of Breeding Groups per Year

Observation and yearly mapping of territory locations in the study site indicated that a degree of territory fragmentation occurred. This was particularly evident in areas of

high Moorhen density possibly as result of kin selection (parents may allow offspring to share existing territories under certain circumstances) or high recruitment rates (section 3.1). Competition for resources (i.e. territories) within the population appeared to progressively increase over the three years of study.

3.4.4 The Sex Ratio of Breeding Adults and Breeding Group Types

McRae (1994) recorded a sex ratio in a Moorhen breeding population that slightly favoured females. This is somewhat different to the present study (see section 3.3.2). The different sex ratios seen in these two isolated populations separated in space and time may be consequences of different environmental and population pressures acting on each population. Mating systems generally seem to be determined by both the ecological features of the environment (Oring, 1969; Emlen & Oring, 1977) and conflicts of interest arising between individuals (Trivers, 1972; Davies, 1992). The vast majority of Moorhen breeding groups over the three years of research were monogamous. A variable number of groups were, however, identified each year in which more than two individuals bred communally (see plate 3.1 page 55). Communal breeding has been recorded in a number of closely related species to the Moorhen, namely the Australian Dusky moorhen (Garnett, 1980), the Tasmanian native hen *Gallinula mortierii* (Gibbs *et al.*, 1994; Goldizen *et al.*, 1998) and the Pukeko *Porphyrio porphyrio* (Craig, 1980; Jamieson & Craig, 1987).

Evidence from a number of UK locations suggest that communal breeding by Moorhens is not atypical. Such breeding systems have been recorded in areas of relatively low population density in the Avon valley (Wood, 1974) and on the river Orwell in Bury St Edmunds (pers. obs). McRae (1994) and Gibbons (1985) both recorded communal breeding in a high-density Moorhen population at Peakirk



Plate 3.1. Moorhen polygynous nest.

Botanical Gardens. McRae (1996a) recorded a higher overall percentage of communal breeders than that found by Gibbons (1985). McRae (1994) suggested that these differences at the same location were due to the influence of population recruitment between the two study periods. In the later period, population pressure, coupled with an ever-increasing limitation on available territory, was thought to have forced individuals to form communal groups to breed successfully. This suggests that availability of territories suitable for breeding is an influential factor in the decision on whether to breed communally in the Moorhen (see also sections 4.4.5, 7.4.3. & 7.4.4). In contrast, some birds e.g. Guira cuckoos *Guira guira* breed communally despite a lack of territory saturation (Macedo & Bianchi, 1997a).

3.4.5 Relationships Between Individuals in Communal and Cooperative Groups

The majority of communal groups observed in the present study were relatively stable from year to year (although their number decreased over the study period). Genealogical information from 1998 and 1999 revealed that these groups typically consisted of parents (the core pair, defined as being the eldest male and female in the group) and between one to three male and female offspring from the previous breeding season (12 out of 24 cases) and between brothers or sisters (6 out of 24 cases). Both Gibbons (1985) and McRae (1994; 1996a) found that the majority of polygynous and polyandrous communal groups consisted of parents and daughters or sons breeding together. In polygynous situations, mothers allowed daughters to lay in the nest although father-daughter incest generally resulted in a low survival rate of offspring (McRae & Burke, 1996). Similarly, in polyandrous trios, males tended to be father and son (Petrie, 1982).

In the current study, equal numbers of communal groups were comprised of either sister-sister (n=3) or brother-brother (n=3) partnerships. A similar number of communal groups (n=6) consisted of unrelated individuals. McRae (1995) determined (through genealogical and DNA “fingerprinting”) that only one communal group consisted of unrelated birds in her three years of research. It is highly likely that this difference between these two geographically isolated populations could have arisen due to the aforementioned differences in population density at the two study sites. In addition, the significantly older Moorhen population at Peakirk (established in 1958) is located on a much smaller, namely 7ha (McRae, 1994) than the current study site (see section 2.1).

The availability of breeding territories may also influence the nature of relationships between communal breeders. In situations where territory is a limiting resource and the chance of successful dispersal is low, more communal groups would be expected to be comprised of relatives (Emlen, 1982; Jamieson *et al.*, 1994). In the current study, the population is still expanding (albeit at a reducing rate) within the Centre’s confines. Consequently, territories may not have been limiting by the end of the study. Moorhens, under these circumstances, would be able to disperse from natal areas, form partnerships (communal or monogamous) and obtain new territories in which to breed. The fact that the number of breeding groups increased in each year of the study supports this suggestion. Communal groups formed by partnerships between unrelated individuals might be more frequent in this situation as there is less pressure from increasing population density and territory saturation to remain in natal areas and breed in kin groups. If this is the case, it would be expected that, as the Moorhen population at WWT Llanelli increases and the availability of territories decreases, more communal groups should be formed and be more frequently

comprised of related individuals (as is the case at Peakirk Botanical Gardens). The decision to breed communally may well, however, be influenced by a variety of other behavioural and ecological factors.

3.4.6 Helpers at the Nest

Parental investment by non-breeding helpers has received considerable attention since its relevance to kin selection was postulated (Hatchwell, 1999). Many hypotheses have been advanced to explain this complex behaviour (see Emlen, 1991). In the last 20 years, heated debate has centred around whether so-called “helpers-at-the-nest” (Skutch, 1935) are a functional (kin-related) response by non-breeding individuals or reflect an unselected instinctive response by non-breeders to the presence of chicks (in particular see Jamieson, 1986; 1989; Jamieson & Craig, 1987; Koenig & Mumme, 1987; Ligon & Stacy, 1989; Mumme & Koenig, 1991).

In a majority of cooperatively breeding species, non-breeding helpers are assumed to gain inclusive fitness benefits by assisting with the rearing of kin (Brown, 1978; 1987; Emlen, 1991; 1997). The non-breeder’s care should decrease with declining relatedness to the recipient (Hamilton, 1964; Houston, 1995). A benefit of helper on the survival of breeders and the number of young reared to maturity has been reported in a variety of different species, including Moorhens (Brown and Brown, 1981; Reyer, 1983; Gibbons, 1985; Hunter, 1985; Eden, 1987; Mumme *et al.*, 1989; Emlen, 1997; Hatchwell, 1999). Such alloparental behaviour is strongly mediated by physiological factors, namely hormones such as prolactin and progesterone (Mays *et al.*, 1991; Schoech *et al.*, 1991; Vleck *et al.*, 1991; Schoech *et al.*, 1996).

Unpaired Moorhen individuals essentially face four possible fitness choices at the start of the breeding season. Should they leave the natal territory and secure a

territory and partner(s) of their own? It is generally considered that this is the best fitness option open to non-breeding adults (Koenig, 1981). Should they could remain and breed within the kin group or remain as a non-breeding helper within the kin group (Hunter, 1987)? Finally, should they could become a population “floater” (section 3.4.7)? All such choices are limited by a variety of ecological factors including the degree of territory saturation (Emlen, 1982) and population pressure (Rowley, 1981).

Support for the view that kin selection facilitates cooperative breeding in birds has come from many sources (e.g. Craig, 1980; Emlen, 1981; Reyer, 1983; Woolfenden & Fitzpatrick, 1984; Jamieson *et al.*, 1994; but see Reyer, 1980). In the present study, adult Moorhen non-breeding helpers were all surviving offspring from that particular group’s previous breeding season (see also McRae, 1996a). Both the numbers of Moorhen groups with non-breeding helpers and the number of non-breeding helpers per group increased successively over the study. The increase in the study population and its effect on territory saturation may restrain the dispersal of juvenile and sub-adult birds, encouraging the formation of stable social groups with non-breeding helpers.

The ratio of offspring should be biased towards the more helpful sex (Emlen *et al.*, 1986). This model incorporates the established concept that helpers repay part of the cost of their parent's investment and thus reduce the net cost of their production (Emlen, 1991). The sex ratio of Moorhen adult helpers was close to unity. This indicates that, at least in Moorhen social groups, the sexes are equally helpful (see also section 8.5.10). Koenig & Walters (1999) concluded, however, that a sex ratio bias in helpers-at-the-nest is unlikely to occur in natural circumstances. Indeed, they claimed any sex ratio biases recorded are likely to reflect local population sex ratio

variations. The unity of the sex ratio in Moorhen helpers may also not be related to any sex facilitated repayment behaviour.

3.4.7 “Sneaky Breeders” and the Significance of the “Floating” Population

A number of IBP events were recorded over the three years of research where the responsible hen could not be identified (see also sections 5.4.2 & 5.4.3). These females could have been sexually mature “floaters” within the population (Brown, 1969). There were several such adult and sub-adult individuals in small groups in each year of the study. The majority of these non-territory holding individuals were identified as surviving offspring of birds within the Centre from the previous breeding season. These individuals may have elected not to migrate out of the Centre’s grounds due to risks of dispersal (Emlen, 1982), or have been unable to secure a breeding territory (Watson & Moss, 1970) or mate for that season (Ridpath, 1978; Smith, 1978). In this situation it might be prudent for individuals to remain as non-breeding helpers, thereby increasing their inclusive fitness (section 3.4.6), or stay near to their natal territory (Brown, 1978). Population “floaters” also lived in small groups at Peakirk Botanical Gardens (Gibbons, 1986; McRae, 1994). At WWT Llanelli, the non-breeders typically inhabited similar habitats to those utilised by over-wintering Moorhens. These areas consisted of open grassed areas with trees and hedgerows in close proximity to water. These core areas for population “floaters” were similar in location in each of the three years of study and were directly adjacent to areas of high-density Moorhen breeding activity.

The non-breeder’s strategy of occupying areas close to Moorhen breeding territories could be advantageous in many ways (Emlen, 1982). “Floaters” are freed from the responsibility and costs of territory defence and parental investment (Koenig &

Pitelka, 1981). They can spend considerably more time searching for breeding opportunities than non-breeding helpers in cooperative groups (Atwood, 1980). A breeding adult on a territory may die or be weakened by disease allowing a challenge for the territory (Koenig, 1981) or the surviving member of the pair may mate with the “floater” (Smith, 1978). Indeed, known “floater” individuals were observed to acquire a mate or territory on a few occasions in the present population. This opportunistic strategy typically succeeded in cases where breeding adults succumbed to disease (such as avian TB) in the early or mid-stages of the breeding season. A large number of “floaters” were recorded in a South American population of cooperatively-breeding Purple gallinule *Porphyryula martinca* (Hunter, 1987). As in the case of Moorhens, these individuals were surviving offspring from previous breeding seasons and their presence seemed a consequence of limited habitat availability.

3.4.8 The Number and Success of Eggs Laid During the Study

The marked increase in the number of eggs laid at WWT between the 1997 and 1998 breeding seasons may be due to observer inefficiency in the first year or (more likely) an increase in the population density and the number of breeding groups in 1998. The numbers of adults and breeding groups in 1998 and 1999 were similar, perhaps accounting for the similar number of eggs laid in both years.

Nest predation is a major source of egg loss in most avian species (Nice, 1957; Huxley & Wood, 1974; Martin, 1988). A review of 36 studies on Neotropical migrant species concluded that predation was the primary cause of nest failure and resulted in a loss of approximately 44% of eggs laid (Martin, 1991). Wood (1974) found that, of 267 Moorhen eggs laid over two years, only 47 (17.6%) hatched. In contrast, Huxley

& Wood (1976) reviewing 18 years of nest record data on Moorhens from the BTO, found that 65.3% of clutches hatched. The authors considered that hatching success was over-estimated as many nests were predated before a complete clutch was laid. Such nests are unlikely to be recorded in nest searches.

Unsurprisingly, there was a strong relationship in the present study between the percentage of eggs predated and those hatching in each of the three years of research. The highest percentage of eggs predated occurred in 1997. The number of eggs hatching that year was correspondingly low. There was less egg predation in 1998 and 1999. The lowest value for predation occurred in 1998, which corresponded to the greatest percentage of eggs hatching.

3.4.9 Causes of Nest Failure and the Impact of Predation

The principal egg predators within the grounds of WWT Llanelli were Magpies, Carrion crows, Jackdaws, weasels and rats. Much effort is expended annually by staff in attempts to control rats and corvids. These control measures have, however, varying degrees of success (R.Edwards, pers.comm.). The control of corvid species (particularly Jackdaws) seems largely ineffective due to difficulties in trapping significant numbers of these animals during the breeding season.

The population of rats in the Centre's grounds in 1997 was thought to be greatly expanded on the previous year. Consequently, the ground staff targeted this species at the start of 1998 in an intensive control programme. This appeared very successful and the rat population that year was very low (based on regular rat distribution surveys). Egg predation decreased substantially as the rat population declined. Rat numbers began, however, to increase throughout 1999 and egg predation levels began to rise. It is, therefore, likely that rats are a principal egg predator of Moorhens and

other bird species within the grounds. Moreover, the number of egg predators within the Centre had a direct impact on the number of eggs successfully hatching and consequently the annual recruitment into the Moorhen population. Rats were also important predators of Moorhen eggs in Peakirk Botanical Gardens (McRae, 1994).

Other studies (notably Wood, 1974; Huxley & Wood, 1976) maintain that foxes (excluded at WWT Llanelli), mustelids and corvids are important predators of Moorhen eggs. Moreover, flooding can also be an important cause of nest failure. BTO data suggests that Moorhen nest failure in the UK has doubled over the last 30 years (Crick *et al.*, 1996). This alarming increase may be linked to increased frequency of flooding events in the UK throughout the year as well as localised increases in fox and corvid populations.

3.4.10 Effects of Human Disturbance on Moorhen Nesting Success and Behaviour

The present study involved visiting nests frequently throughout the laying, incubation and hatching stages. It was hoped to equalise the potential confounding effects of the accompanying disturbance on nest success by visiting all nests with equal frequency. On some occasions, Petrie (1982) was unable to standardise the frequency of visits to all Moorhen nests, as she found them at different stages of incubation. Successful nests were, however, on average visited more often than unsuccessful nests. Successful nests are viable for longer and hence will be visited more frequently.

Götmark (1992) produced a comprehensive review of the effects of human investigators on several orders of nesting birds. He found that disturbance was reported in over half the studies reviewed and was particularly pronounced for Charadriiformes. Furthermore, nesting success in some species was decreased by up

to 40% in disturbed pairs. Disturbance of breeding birds can have many effects on their behaviour and reproduction. In the present study on Moorhens, the number of nests adversely affected by disturbance was difficult to evaluate. Several nests appeared, however, to have been abandoned or predated during the laying and incubation stage perhaps as a consequence of the regular disturbance by the researcher producing nest desertion by adults. Desertion rates can, however, be quite high during the laying stage even in the absence of human disturbance (Knopf, 1979). A few breeding groups over the three years of research, with some hatched chicks abandoned unhatched or piping eggs in response to investigator disturbance. An attempt was made to mitigate these potential risks to Moorhen broods by reducing time spent at the nest site and by being sensitive to parental behaviour. Exposed nests were not visited in adverse weather conditions because of the potential effects on chick development of high egg cooling rates during the temporary periods when incubation was halted.

Neither parents nor chicks appeared to become habituated to the researcher's presence as reported by others (e.g. Parsons & Burger, 1982; McNicholl, 1983). Interestingly, the behaviour of the study population appeared to alter over the three years. This seemed related to the level of disturbance to particular nests and areas. The majority of Moorhen adults and chicks responded immediately to the observer's presence in the territory. They reacted as to a predator producing an alarm call followed by rapid movement to cover. This behaviour was still evident in frequent visits to the study site throughout 2000 and 2001, despite the fact that no field research was then being carried out on this species. Moorhen responses were very different to "unknown" humans passing through their territories where they appeared largely impartial and showed little significant avoidance.

Care was taken to avoid flattening vegetation around the nest site. This was not always possible due to the wide range of vegetation in the locality where Moorhens nested and their differing resilience to trampling disturbance. Consequently, some nests appeared to become more exposed to predators but it is uncertain whether this influenced the overall fates of eggs and clutches. Towards the end of each breeding season, Jackdaws were observed to follow or watch the observer during nest searches and researchers should be aware of their potential role in exposing nest sites to nearby predators. There is a need to assess the true effects of this “uncertainty principle” (Lenington, 1979) on the study of reproduction and (in particular) nesting success in wild species.

3.4.11 Nest Box Eggs and Vegetation Management

The number of Moorhen eggs laid in the nest boxes located in all areas of the Centre’s grounds in each of the three breeding seasons varied dramatically. These wooden constructions (see plates 3.2a & b page 66) were designed to provide collection species refuge from both the elements and potential predators. They were often positioned standing in water for use by the various waterfowl species and to reduce rates of rat predation on bird eggs. Moorhens utilised these convenient and relatively safe nesting sites throughout the three breeding seasons. Indeed, Moorhens often-laid replacement clutches in them after staff had removed their previous nests.

Vegetation management may adversely affect Moorhen reproductive success through removal of potential nesting sites or reducing cover around the nest (Taylor, 1984; Ritter & Sweet, 1993). Nest boxes located in areas with an abundance of vegetative cover in which to nest were rarely used by Moorhens (pers.obs).



Plate 3.2a Typical nest box set-up at WWT Llanelli (with moorhen construction visible)



Plate 3.2b Moorhen nest constructed in a nest box

Moorhens are subject to considerable predation (Wood, 1974; Huxley & Wood, 1976; Hornbuckle, 1981) particularly in nests which are most exposed and accessible to predators (Relton, 1972). The intensity of egg predation and degree of vegetation management in the Centre may therefore, influence the number of nest boxes utilised annually by Moorhens. Interestingly there was a direct negative relationship between the level of egg predation (section 3.4.2) and the number of eggs laid in nest boxes (section 3.4.1). Moorhens are more likely to lay in nest boxes when egg predation levels are high. It is uncertain, however, whether the level of egg predation is the proximate factor stimulating this behaviour.

3.5. Conclusions

1. The relatively young Moorhen population at WWT Llanelli is currently steadily expanding. The number of eggs laid, breeding groups recorded and recruitment at the site increased successively over the duration of the study.
2. The fate of Moorhen eggs varied annually throughout the study. Predation accounted for significant egg and clutch losses. Annual changes in the populations of key egg predators (e.g. Brown rats) affected the relative success of Moorhen clutches in each year of research.
3. Moorhens at the study site form a variety of different social and breeding groups. In particular, four distinct breeding systems were identified. Variation in the occurrence and frequency of these different systems appeared to be due to ecological and environmental constraints.
4. The presence of large numbers of this territorial rail may have important effects on the health and captive breeding success of certain wildfowl at WWT Llanelli.

Predation and disease trends in the Moorhen population may also reveal issues pertinent to the management of collection birds at this site.

CHAPTER 4

EGG PRODUCTION, CLUTCH SIZE AND REPRODUCTIVE SKEW

“Society is indeed a contract....it becomes a partnership”

Edmund Burke (Reflections on the Revolution in France, 1982, Viking Press, London)

4.1 Introduction

Factors such as egg quality (Monaghan *et al.*, 1995), food availability (Nager *et al.*, 1997), territory quality (Högsteadt, 1980), female condition (Dent & Daan, 1980), incubation (Williams, 1996), population density (Both, 1998) and predation (Martin, 1992) influence clutch size in a variety of bird species. Few studies have examined, however, intra-specific clutch variation between different breeding group types (with some notable exceptions e.g. Craig, 1980; McRae, 1994; 1996a; Goldizen *et al.*, 1998). This type of analysis would enable one to determine the proximate constraints on clutch size in a variety of breeding situations where more than two breeding individuals are present.

Optimal skew models (OSMs) have been created to assess the degree of cooperation in communal breeding systems (Vehrencamp, 1983a; b; Reeves & Nanacs, 1992; Reeves & Ratnieks, 1993; Emlen, 1995; Keller & Reeves, 1994; Reeves & Keller, 1995; Cant, 1998). These reproductive skew models provide a general framework, examining the partitioning of reproduction between individuals in social groups and investigate factors shaping the evolution of social groups (Keller & Reeves, 1994; McRae, 1994). The suitability of these models has been debated (see Cant, 1998; Clutton-Brock, 1998) as all are based on the simplifying assumption that reproductive

conflict is resolved by a dominant individual (Vehrencamp, 1983a; b). It is likely, however, that the existing models will be adapted to include incomplete or absent dominance situations, increasing their utility for investigating social evolution.

4.2 Aims

This chapter aimed to:

1. Examine egg size variation between Moorhen females.
2. Assess and contrast clutch sizes of different Moorhen breeding systems.
3. Investigate and discuss aspects of reproductive skew and conflict within multi-female social groups.

4.3 Results

4.3.1 Egg Biometrics

The mean (\pm S.E.) egg weight, length and width over the duration of study were 22.52 ± 0.05 g, 44.97 ± 0.04 mm and 32.05 ± 0.02 mm respectively. There were no significant differences (one-way ANOVA) in egg weight or width between years. There was, however, a significant difference in egg length between years (one-way ANOVA: $F_{2,2329}=15.61$, $p<0.01$). The mean volume of eggs laid were significantly different between individual females within each year of research (see table 4.1 page 71).

Year	Number of females	Number of eggs	Mean yearly egg volume (cm ³)	One-Way ANOVA output	
				F-statistic	<i>p</i>
1997	34	344	51.10±0.51	8.20	<0.01
1998	42	664	51.62±0.64	11.03	<0.01
1999	51	636	51.60±0.43	8.62	<0.01

Table 4.1. The mean (\pm S.E.) egg volume of eggs laid annually and one-way ANOVA F-statistic of the significant differences within each breeding season of the mean volumes of eggs produced by individual females

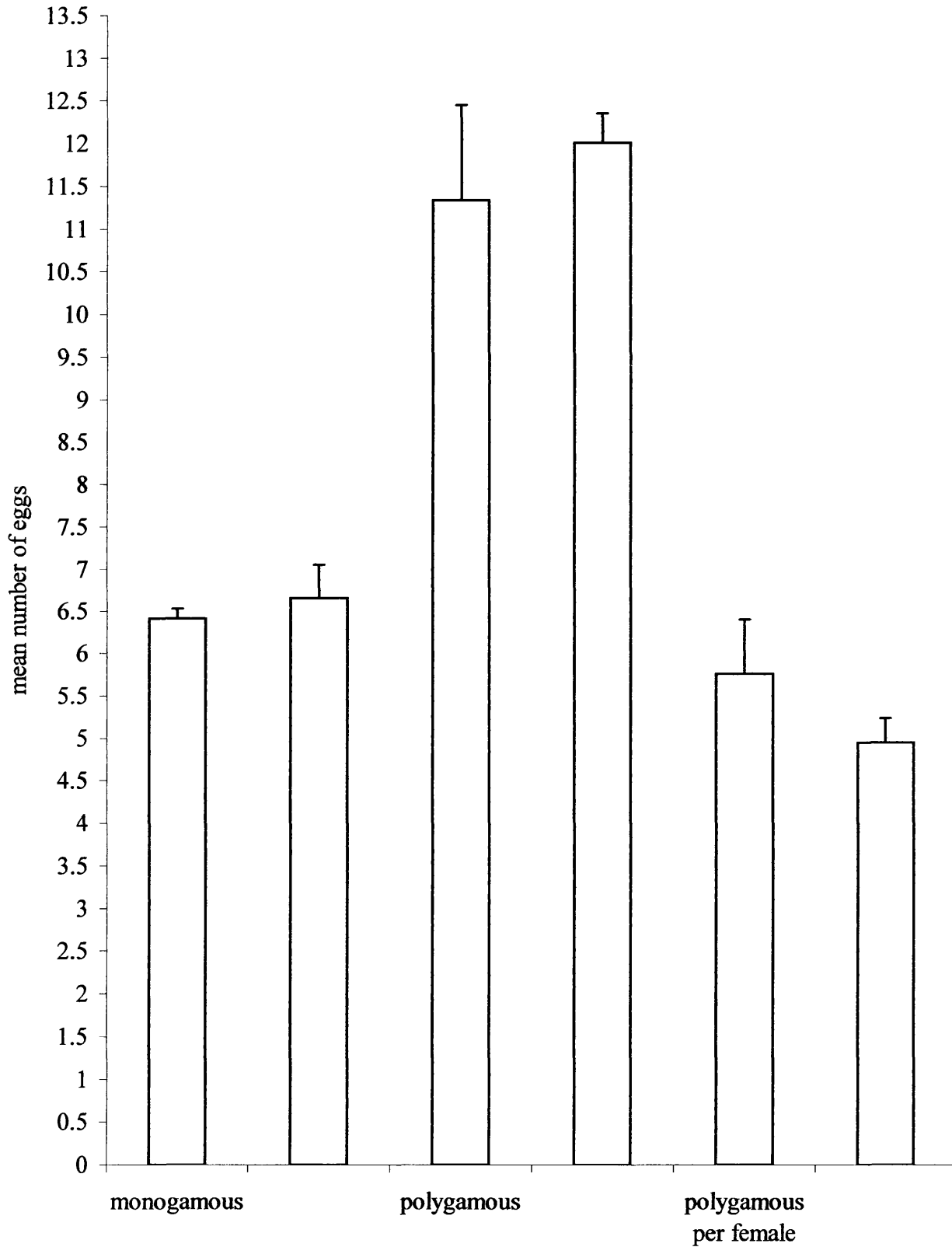
4.3.2 Seasonal Egg Weight Variation

Pearson's correlation coefficients were calculated using egg weights and the corresponding date of lay for each of the three years independently to determine whether seasonal variation was evident. Egg weight did not significantly differ with time of year in any of the years tested.

4.3.3 The Clutch Sizes of Monogamous Groups

A total of 230 complete monogamous clutches were recorded during the study. The mean clutch sizes of monogamous groups varied from year to year (table 4.2 page 73) but one-way ANOVA showed that this variation was not significant. The data was pooled and the mean clutch size for monogamous clutches over the three years calculated (see figure 4.1 page 72).

Figure 4.1 Mean clutch sizes per breeder types and per female in multi-female groups



Year	Number of clutches	Mean clutch size
1997	33	6.42±0.26
1998	98	6.24±0.15
1999	99	6.58±0.21

Table 4.2. The mean (\pm S.E.) clutch sizes of monogamous groups in the different years of the study.

4.3.4 The Clutch Sizes of Polyandrous Groups

The mean sizes for the 23 complete polyandrous clutches recorded over the three years are shown in table 4.3 (below). There was no significant difference between the mean polyandrous clutch sizes over the three years on one-way ANOVA, although there was a progressive increase in mean clutch size over the 3 years of study. The data from each year was pooled and the mean polyandrous clutch size calculated (see figure 4.1 page 72).

year	Number of clutches	Mean clutch size
1997	8	6.13±0.30
1998	10	6.70±0.58
1999	5	7.40±0.44

Table 4.3. The mean (\pm S.E.) clutch sizes of polyandrous groups over the three years of the study

4.3.5 The Clutch Sizes of Polygynous Groups

A total of 18 complete polygynous clutches were recorded in the three years of study. The mean polygynous clutch sizes are shown and progressively decreased over the 3 years of the research (see table 4.4 below). This decrease was not, however, significant using a one-way ANOVA. The data was pooled and the mean polygynous clutch size over the 3 years of study calculated (see figure 4.1 page 72).

Year	Number of clutches	Mean clutch size
1997	2	12.00±1.00
1998	10	11.40±1.12
1999	6	11.00±0.37

Table 4.4. The mean (\pm S.E.) clutch sizes of polygynous groups over the three years of the study

4.3.6 The Clutch Size of Polygynandrous Groups

Only 7 complete polygynandrous clutches were recorded during the duration of the study. The mean clutch sizes for these groups in 1997 and 1999 are shown in table 4.5 (page 75). The mean polygynandrous clutch size in 1999 was found to be highly significantly greater than that laid in 1997 (Student's two-tailed t-test: $t = 4.65$, $p < 0.01$) but this may simply reflect the extra female in 1999.

Year	Number of clutches	Number of males	Number of females	Mean clutch size
1997	5	2	2	10.00±0.93
1999	2	2	3	15.50±0.50

Table 4.5. The mean (\pm S.E.) clutch sizes of polygynandrous groups and their composition over the 3 years of the study

4.3.7. Multi-Female Groups: Clutch Sizes Per Hen

In communal groups with more than one breeding female, a mean clutch size per female was calculated. These are shown for polygamous and polygynandrous groups in table 4.6 (below). Clearly, the number of eggs produced by polygynous females was greater than for polygynandrous hens in all comparable years. There were no significant differences in clutch sizes per female on one-way ANOVA between years for either polygynous or polygynandrous individuals.

Year	Number of females	Mean clutch size for polygynous hens	Number of females	Mean clutch size for polygynandrous hens
1997	4	6.00±1.50	10	4.82±0.44
1998	20	5.70±0.41	none recorded	none recorded
1999	12	5.75±0.25	6	5.17±0.60

Table 4.6. The mean (\pm S.E.) clutch size per female in polygynous and polygynandrous groups over the 3 years of study

The mean numbers of eggs per hen for polygynous and polygynandrous females over the duration of the study are shown in figure 4.1 (page 72).

4.3.8 Reproductive Skew in Multi-female Groups

Table 4.7 (below) shows the relative level of reproductive skew between related and unrelated females in communal groups. In the case of the analysis between mother and daughter, skew was calculated based on the ratio of the senior (mother) and junior (daughter) females. Conversely, in the analysis between sister-sister and unrelated female groups, skew was calculated based on the female laying the most eggs.

Female Relationship	Year	Group number	Number of eggs laid in total	Skew	Mean (\pm S.E.) skew
Sister-sister	1998	7	15	0.53	0.51 \pm 0.01
	1998	33	22	0.50	
	1998	51	37	0.51	
Mother-daughter	1998	10	13	0.62	0.57 \pm 0.02
	1998	55	11	0.55	
	1998	46	13	0.62	
	1998	34	15	0.53	
	1999	20	11	0.54	
	1999	30	12	0.50	
	1999	40	20	0.65	
unrelated	1998	40	24	0.54	0.52 \pm 0.01
	1999	63	12	0.50	
	1999	74	13	0.53	

Table 4.7. Reproductive skew in different categories of multi-female groups

The level of reproductive skew varied, depending on the nature of the relationship between breeding females within each group. When two sisters laid together, reproductive skew was relatively slight with females laying similar numbers of eggs in each laying attempt. Reproductive skew was similarly unpronounced when two unrelated females laid together. In contrast, generally when mother and daughter (first order relatives) laid together, reproductive skew generally favoured the mother and was indicative of a despotic social system. The pooled mean of both semi-social group types (0.52 ± 0.01 , $n=6$) was significantly less than that of Mother-daughter groups (T-test: $t = -2.26$, $p=0.04$, $df=11$).

4.3.9 Multi-female Groups – Which Female Initiated Laying Attempts?

Table 4.8 (below) illustrates the degree of laying synchronicity in multi-female groups. Females were rated as laying synchronously, or whether one female laid first.

Female breeding relationship	Laying attempt		
	Senior	Junior	Synchronously
	Female	Female	
Sister-sister	4*	2**	5
Mother-daughter	5†	1††	3
Un-related females	1°	1∞	3

*in 3 of these attempts the junior female destroyed the eggs laid by the senior hen, only one attempt to initiate laying was successful

**both of these attempts by the junior hen were successful but in one case the senior did not attempt to lay communally

†in 3 of these cases the mother laid one day and in two cases laid 2 days before the daughter

††in this instance the egg laid by the daughter was destroyed by the mother

°the initiation of a clutch attempt by the senior hen was successful

∞the senior hen destroyed the egg

Table 4.8. The degree of female synchronicity in all multi-female laying attempts

It appeared that successful egg laying by unrelated multi-female and sister-sister breeding groups is generally synchronous. When one female laid before the other, eggs were usually destroyed by the second female. In comparison, the majority of clutch attempts in mother-daughter communal groups were initiated by the mother (the senior female) and only rarely did both the females lay synchronously. In the only recorded case where a daughter attempted to lay before her mother, the latter destroyed the egg.

4.3.10 Clutch Sizes per Female (see also section 3.4.8)

The pooled mean of the complete clutch size and the mean number of eggs laid per hen for each of the four breeding group types found at WWT Llanelli over the 3 years of study are shown in figure 4.1 (page 72). Individual females in the breeder groups laid significantly different numbers of eggs per clutch attempt (one-way ANOVA: $F_{3,302}=5.096$, $p<0.05$). Females in monogamous and polyandrous groups had similar clutch sizes. Females laying in multi-female groups (polygynous and polygynandrous) had smaller clutches than single female breeding groups.

4.3.11 Seasonal Clutch Analysis

Spearman's correlation coefficients between complete clutch size and the week each was laid were calculated for each breeder type. Clutch size decreased over the breeding season in all breeder types, although the association was only significant for monogamous clutches ($r_s=-0.328$, $p<0.01$).

4.4 Discussion

4.4.1 Egg Size

Significant variations in egg size can be evident in different populations of the same species (Carey & Morton, 1976; Manning, 1978). Lack (1968) suggested this variation was adaptive but it has yet to be demonstrated whether this variation alters reproductive success in most avian species (Carey, 1996). The mean (\pm S.E.) weight of Moorhen eggs in the present study (25.22 ± 0.05 g) was only slightly greater than that found in England by Wood (1974), (24.88g). It is possible that greater differences in egg size and mass may be evident in more geographically isolated populations of Moorhens. A study on Crested coots *Fulica cristata* in Spain and Morocco found that egg size was significantly different in the two geographically isolated populations (Makow, 2000). Such population differences in egg size are likely to reflect the effects of differing environmental pressures.

It may be prudent for females to limit the sizes of eggs laid under certain situations to maximise clutch size. For example, females might produce larger eggs in years when food is limited (Carey, 1996). Analysis in the differences in egg volume in female Moorhens in this present study confirm that individual females produce eggs of different size. In addition, egg weight also varied significantly from female to female each year. Unfortunately, it was impossible to discern whether these differences resulted from environmental, physiological or genetic variables, (or a combination of these factors).

4.4.2 Environmental and Physiological Constraints on Egg Size

Egg composition and mass may be considerably influenced by environmental factors at the time of laying. Two independent studies on American coots at the same

geographical location found different relationships between egg mass and their composition (Alisauskas, 1986; Arnold *et al.*, 1991). In the case of Moorhens in this present study, egg weight and width did not significantly vary over the three years of research. Egg length, however, showed significant differences between years. It is likely that these differences in egg length had little effect on overall egg size within the Moorhen population.

Female body mass and condition (Ricklefs, 1984), age (Newton, 1989; Viñuela, 1997), laying date and order (Clark & Johnson, 1992; Viñuela, 1997; Erikstad *et al.*, 1998) all influence egg size. Combinations of these influences might explain the observed significant differences in egg volume between females in each year of the study. In most avian species, egg composition and size varies more between females than within the same female (Hepp *et al.*, 1987). Observations on a wide range of avian species suggest that egg size is also likely to be genetically controlled (Carey, 1996). For example, several studies on Mallards have indicated that egg mass variation has a strong genetic component (Prince *et al.*, 1970; Rhymer, 1988). There is, however, a lack of empirical evidence across a wide spectrum of avian orders (Carey, 1996) and scope clearly exists for research into the genetic control of egg size. Casual observations of the similarity in egg sizes (weight, length and width) between Moorhen sisters in this present study suggests that egg size could be a heritable trait in this species. It must be noted, however, that the confounding effects of female condition and territory quality on egg size were not controlled in this present study.

4.4.3 The Effect of Supplemental Food on Moorhen Reproduction

Lack (1968) suggested that food exerts ultimate control on reproduction in most bird species. Food abundance may be a proximate control on the initiation of breeding and

egg synthesis (Carey, 1996). The twice-daily addition of food supplied to the captive collection at the Centre may have provided sufficient resources to breeding females for the synthesis of eggs of relatively consistent size, within and between each breeding season. Food supplementation may have also affected the number of clutches produced, the inter-clutch interval and even the number of eggs laid over each breeding season (see Eden *et al.*, 1988; Arnold, 1994).

A study on the effects of supplemental food on egg production in American coots found, however, that it did not affect egg size (Arnold, 1994). It is, therefore, likely that egg size is only weakly influenced by supplemental food availability in Moorhens. Only a few studies have found species where egg size is significantly altered by artificially augmented food e.g. Black Kites *Milvus migrans* (Viñuela, 1997), Lesser Black-backed gulls (Hiom *et al.*, 1991) and Song Sparrows *Melospiza melodia* (Smith, 1988). Supplemental food did, however, effect first laying dates and clutch size in American coots (Arnold, 1994).

It is likely that egg size plays an important (but small) part in overall chick fitness (Carey, 1996). Qualities of parents and territories both had a greater influence on nestling mass than egg and chick size at hatching size in the altricial Blackbird *Turdus merula* (Magrath, 1992b). Moorhen parents provision their semi-precocial chicks for an extended period (see section 8.5.1). Although egg size is an important factor in determining initial chick size, parental and territory quality are likely to be pivotal for the successful rearing of chicks.

4.4.4 Clutch Size and Mating Systems

The mean clutch size per female did not differ significantly between years for all breeding group types. This is unsurprising in an environment in which artificial

augmented food resources were readily available to breeding females all year round (see sections 2.1 & 4.4.3). Arnold (1994) found that supplemental feeding induced female American coots to lay circa one additional egg compared to female controls. These larger clutch sizes of experimental females represented, however, only 3% of the observed total variation in American coot clutch sizes suggesting that the female's ability to lay larger than average clutches is only weakly influenced by supplemental food.

All multi-female communal groups had lower clutch sizes per female than single female breeding groups. Younger, inexperienced females tend to lay smaller and fewer eggs per attempt (Crawford, 1980; Curio, 1983; Soether, 1990; McRae, 1994). Most females laying in communal nests were first time breeders (i.e. daughters of the breeding group; see also McRae, 1996a). These females tended to lay fewer eggs than older females (e.g. their mothers) within the group (section 4.4.5). These age-related trends in egg production capacity are likely to explain the overall lower average clutch sizes per female recorded in multi-female groups.

4.4.5 Reproductive Skew in Multi-female Groups

The decision to breed communally can be affected by many ecological and behavioural factors (see also sections 1.3.5 & 7.4.4). As ecological conditions become challenging, the expected profitability of an individual's solitary reproduction (limited by population density, territory quality and vacancies) decreases (Emlen, 1991; Reeves & Ratnieks, 1993). Individual Moorhens may then maximise their fitness by forming a communal partnership. The formation of communal partnerships does not, however, imply that such 'arrangements' are equally beneficial to group members (Davies, 1992). Communally breeding females may gain from mutual

cooperation but probably do better by exploiting the cooperative behaviour of a conspecific (Axelrod & Hamilton, 1981; Krebs & Davies, 1993). As individuals strive to maximise their fitness (Trivers, 1972), conflict may occur over the exact share of reproduction obtained by each group member (see also section 7.4.2).

OSM's predict that ecological constraints on solitary reproduction and an individual's relative fighting ability influence the level of reproductive skew in social groups (Vehrencamp, 1983a; b; Emlen, 1991; Reeves & Ratnieks, 1993; Keller & Reeve, 1994). When relatedness between group members increases and the profitability of solitary success decreases, reproductive skew is expected to increase (Reeve & Keller, 1995). Skew may also increase as the fighting ability of subordinate decreases (Reeve & Keller, 1995). It appeared possible to evaluate the social partitioning of reproduction in a variety of differing breeding situations by assessing the relative reproductive skew of Moorhen communal groups. It also seemed possible to use this information to test the underlying theories of OSMs.

Pukekos (Craig & Jamieson, 1990; Jamieson *et al.*, 1994), Tasmanian native hens (Gibbs *et al.*, 1994; Goldizen *et al.*, 1998) and Acorn woodpeckers, *Melanerpes formicivorus* (Koenig & Stacy, 1990) all have a range of diverse social and breeding systems. They also have reproductive skews that are similar to Moorhens. Reproductive skew is predicted (and found) to be higher in matrilineal (partnerships between mother and daughter) than in semi-social (partnerships forged between individuals of the same generation e.g. sisters) associations (Keller & Reeve, 1994; Reeve & Keller, 1995). Variability in reproductive sharing may also represent different stages in the social evolution of communal species such as the above (Sherman *et al.*, 1995).

4.4.6 Semi-social Female Partnerships

OSMs predict that reduced relatedness would lower reproductive skew and consequently minimize dominance behaviour between individuals of the same sex (Reeve & Ratnieks, 1993). In unrelated multi-female groups, successful clutch attempts generally only occurred when both female Moorhens laid synchronously (see table 4.8 section 4.3.9). If one female began to lay before its partner, that egg was generally destroyed. This suggests some conflict over the proportion of reproduction each female was allowing the other to receive. Similarly, in sister:sister partnerships successful laying was initiated only when both laid together. In both of these semi-social groups, skew levels indicated an equal sharing of reproduction.

4.4.7 Matrifilial Groups

In contrast to the above, the majority of successful clutch attempts in matrifilial (mother:daughter) groups occurred when the senior (mother) female laid first (section 4.3.9). Daughters often laid their first egg some one to two days after their mothers laid. In the only recorded instance when a daughter laid an egg first, it was immediately destroyed by the mother. Furthermore, mothers and daughters laid synchronously in only a small number of instances. This suggests a dominance conflict between mother and daughter over the timing of breeding. This is a further indication of a despotic social system, in which the balance of power and reproduction are unequally shared between the mother and daughter. Matrifilial groups had the highest level of reproductive skew in this study. Caution should be exercised however, in interpretation of this result. The high skew value recorded in matrifilial groups may be an artefact of the age-related differences in Moorhen egg production, with daughters laying fewer eggs per clutch attempt than mothers (section 4.4.4). As

daughters are less experienced breeders, they may have been unable to synchronise egg production with their mothers. This may also account for the asynchronous laying pattern observed between mothers and daughters. Interestingly, there was no recorded instance of daughters destroying their mother's eggs. Mothers may have exerted a reproductive dominance over their daughters, perhaps by deterring them from the nest. Such behaviour could initially prevent daughters from accessing the nest in the early stages of laying. This is further suggested by the observation that mothers occasionally chased daughters away from the nest when they were laying.

The discussion presented so far has dealt with the conflict and cooperation between females. Little mention has been made of the influence of the male in polygamous reproduction decisions. No study has yet ascertained what influences and control males (fathers) have on their daughter's reproductive input in Moorhen kin-related groups. This information would clearly be extremely useful in determining the relative balance of kin-related and sex dominance between individuals in Moorhen social groups.

4.4.8 Reproductive Sharing and the Importance of Female Quality

Offspring with a low competitive ability are less able to disperse and secure the resources necessary for breeding (Emlen, 1997). In addition, dispersal rates are also likely to be lower in those offspring produced at the end of the breeding season (see Gibbons, 1985). These factors are likely to force some offspring to remain with their parents for a second year (see sections 3.4.5 & 3.4.6). The majority of these individuals originated from clutches hatched towards the end of each breeding season. Their age, experience and body size puts these offspring at a competitive disadvantage to their parents.

Female quality may be an integral part in the formation and stability of communal groups (Cant, 1998). In the specific case of matrifilial groups, female quality and competitiveness may determine whether a daughter breeds communally with her mother. Since daughters are likely to have a lower competitive ability than their mothers, they will be socially suppressed. Mothers may, therefore, be able to control their daughters potential share of reproduction. If the competitive ability of daughters remains lower than their mothers, they may be unable to compete for a direct share of reproduction. This conflict may lead to the formation of a cooperative partnership, in which offspring gain fitness (indirectly) by assisting parents in breeding (section 3.4.6).

In contrast, those daughters equally matched with their mothers are likely to be capable of competing for a share of reproduction. They would then contribute directly to the group's reproductive effort by mating with their father or group male. Despite obtaining a share of the group's reproduction, daughters may still be suppressed by the mother (i.e. the control of clutch initiation by the mother; section 4.4.7).

4.4.9 Group Stability, Communal and Cooperative Breeding

Skew theory predicts that groups of competitively matched females will persist longer than counterparts comprised of unequally matched counterparts (Keller & Reeve, 1994). If one female is dominant, she should attempt to monopolise reproduction to maximise her own fitness (Davies, 1992; Cant, 1998). "Peace incentives" (*sensu* Keller & Reeve, 1994), such as synchronous laying and equally sharing group reproductive output may promote group stability and cooperation over several breeding seasons. When one breeder yields to another as an inducement to

stay and help, it might be said that a “social contract” is established over reproductive sharing (Reeve & Keller, 1995). This “social contract” in Moorhen social groups, is likely to be based on the competitive ability and reciprocity of the partners.

Both matrilineal (and patrilineal) cooperative and communal groups in this study were unstable from year to year. With a few notable exceptions these groups disbanded at the end of each breeding season. By comparison, all semi-social partnerships were more stable and persisted for more than one breeding season. It is plausible that the difference between the stabilities of matrilineal and semi-social communal groups is related to the degree to which reproductive sharing occurs. Aspects of social dominance and competitiveness may also influence group stability, particularly in matrilineal groups (section 4.4.8).

For reproductive sharing to occur, each individual must benefit by its continued association with the other (Emlen, 1995). Unrelated females breeding together do not obtain kin-related fitness gains from helping rear each other’s offspring. These females may, however, have several benefits from communal living (e.g. increased survival and lifetime reproductive success; Koenig & Stacey, 1990). It may be in each female’s interest, therefore, to cooperate in creating a stable, egalitarian social system in which to breed. This would potentially maximise each individual’s direct fitness. Social systems sharing reproduction equally may, therefore, be a pre-requisite for the formation of stable Moorhen communal groups comprised of unrelated individuals. Such egalitarian systems have been similarly observed in breeding groups of other communal avian species, such as the Pukeko (Jamieson *et al.*, 1994) and Acorn woodpeckers (Koenig & Stacy, 1990).

4.4.10 Female Conflict at the Nest: A Test of Optimal Skew Models

OSMs predict that intense dominance related aggression should occur between related members of a partnership. This prediction appears to hold true for Moorhen multi-female groups in this study. There were many recorded instances of each female attempting to lay before the other in matrilineal and sister-sister groups. In these cases, the second female at the nest destroyed her conspecific's eggs (table 4.9 section 4.3.9). This behaviour may restrict the ability of one female to monopolise breeding at that particular time. In comparison, unrelated female partnerships had the lowest frequency of females attempting to lay first. Clutch initiation was, therefore, more synchronous in unrelated groups than partnerships comprised of related females.

A number of sources suggest that control of breeding is incomplete and or absent in most social species (in particular see Cant, 1998; Clutton-Brock, 1998). Females can monopolise reproduction if they eliminated their female partner's young. This could be achieved in birds at the egg or chick stage. In order for this strategy to be successful, however, each individual would have to be able to distinguish their own offspring from those of other conspecifics. Moorhens are known to destroy the eggs of conspecifics when laid parasitically and within communal groups (sections 4.4.6, 4.4.7 & 6.4.5). This behaviour, however, only occurs early in the laying sequence when few egg are present in the nest (McRae, 1994). This suggests that Moorhens are unable to distinguish their own eggs from those of conspecifics. McRae (1996a) considered that the inability to recognize individual eggs facilitated communal breeding in the Moorhen. If offspring are costly to produce, the risk of destroying one's own progeny restricts infanticide in species in which discrimination is weak (Johnstone & Cant, 1999).

Females of other communal avian species e.g. Acorn woodpeckers (Mumme *et al.*, 1983; Koenig *et al.*, 1995) and Mexican jays *Aphelocoma ultramarina* (Trail *et al.*, 1981), also destroy eggs of other communally nesting females. This behaviour in Acorn woodpeckers (similar to that in Moorhens) ceases when females lay synchronously, also suggesting poor individual egg discrimination within this species (Mumme *et al.*, 1983). An indirect fitness cost incurs when related individuals (e.g. mothers and daughters) destroy each other's eggs (Reeve & Ratnieks, 1993), and this may counter a tendency to develop mechanisms for egg (and chick) discrimination in many communal avian species.

4.5 Conclusions

1. The eggs produced by individual females differed in size over the duration of the study.
2. Total clutch size and clutch size per hen were influenced by each breeder type. In particular, multi-female groups had the greater total clutch sizes than the other groups. Daughters from multi-female groups, however, had the lowest average clutch size per female.
3. Reproductive skew and the frequency of egg destruction within multi-female groups varied with respect to the competitive ability and relatedness of each female within the group. Matrilineal groups were despotic in character, reflected by a bias in reproductive skew and asynchronous laying in favour of senior females (mothers). Semi-social groups persisted longer than matrilineal groups and were characterised by a low reproductive skew. Such groups were indicative of an egalitarian breeding system.

CHAPTER 5

MOORHEN INTRA-SPECIFIC BROOD PARASITISM:

AN INDIVIDUAL APPROACH

“Do not put all your eggs in one basket”

18th Century Proverb

5.1 Introduction

It is increasingly apparent that females of many avian species (particularly colonial and precocial species) regularly utilise IBP as an additional reproductive strategy (see section 1.4.3). Examining the use of IBP using an individual approach may facilitate a greater understanding of this intriguing and complex strategy (Soether, 1991; Lyon, 1993a; McRae, 1994). Such an approach may also enable the recognition and classification of intra-population IBP strategy variations whilst giving insight into the fitness benefits of adopting this behaviour.

5.2 Aims

This chapter aimed to:

1. Determine the annual frequency of IBP within the study population.
2. Identify those females utilising IBP and to describe the different types of IBP within the population.
3. Evaluate and discuss the possible reasons for the occurrence of IBP within the population using an individual approach.
4. Assess the relative success of parasitically laid eggs.

5. Determine the clutch size and fecundity of parasitic females and contrast this information with that from non-parasitic females.

5.3 Results

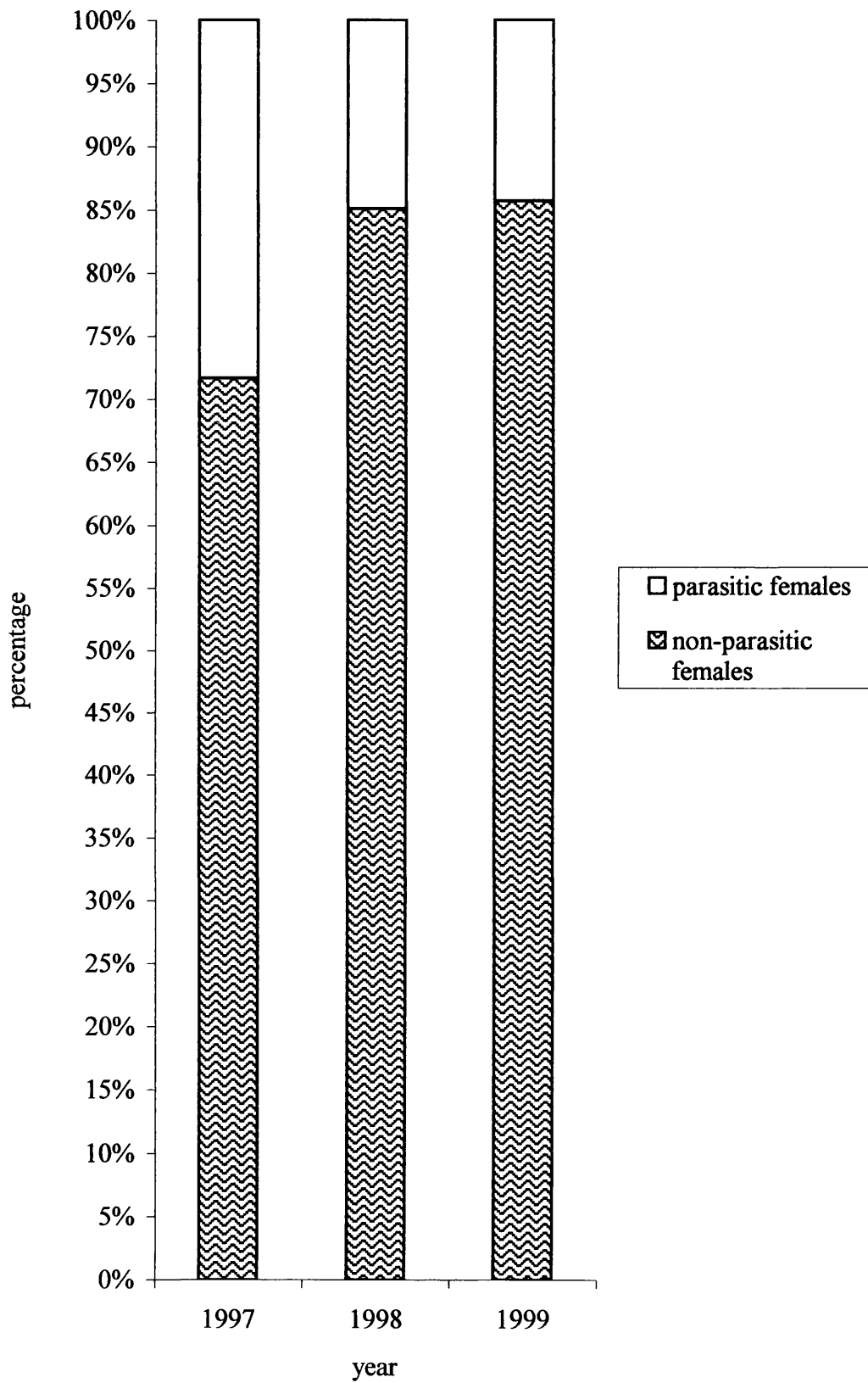
5.3.1 The Number of Females Using IBP

The numbers of breeding females in 1997, 1998 and 1999 were 67, 87 and 91, respectively. Of these females, a variable percentage were identified as parasitising a conspecific's nest in each year (see figure 5.1 page 92). The numbers of females identified as parasitic were similar in the 1998 and 1999 breeding seasons but the number of parasite females was greatest in the first year of research (1997). A number of parasitic events occurred over the three years where the hen responsible could not be identified (n= 25). These eggs were considered to have been laid by females from the "floater" population (see sections 5.4.2 & 5.4.11). The number of parasitic eggs laid by these females varied considerably from year to year, being 7 (17.01%), 18 (28.13%) and 13 (38.23%) of the total number of parasite eggs laid in 1997, 1998 and 1999, respectively. It was impossible, however, to determine the number of "floater" females laying parasitically in each year due to difficulties with their individual identification.

5.3.2 The Number of Eggs Laid Parasitically Per Female

The median number of parasitic eggs laid per host nest and the total number of eggs laid per identified parasitic female are summarised in table 5.1 (page 93). On average, parasite females laid one egg per parasitic attempt, but generally laid at least 2 eggs parasitically over each breeding season.

Figure 5.1 The annual percentage of females that laid parasitically



Year	Eggs laid per host nest	Eggs laid per IBP female
1997	1 (1-5)	2 (1-7)
1998	1 (1-6)	2 (1-8)
1999	1 (1-7)	2 (1-7)

Table 5.1. The median numbers (with ranges) of parasitic eggs laid per host nest per IBP female

5.3.3 A Comparison of the Fates of IBP and Non-IBP Laid Eggs

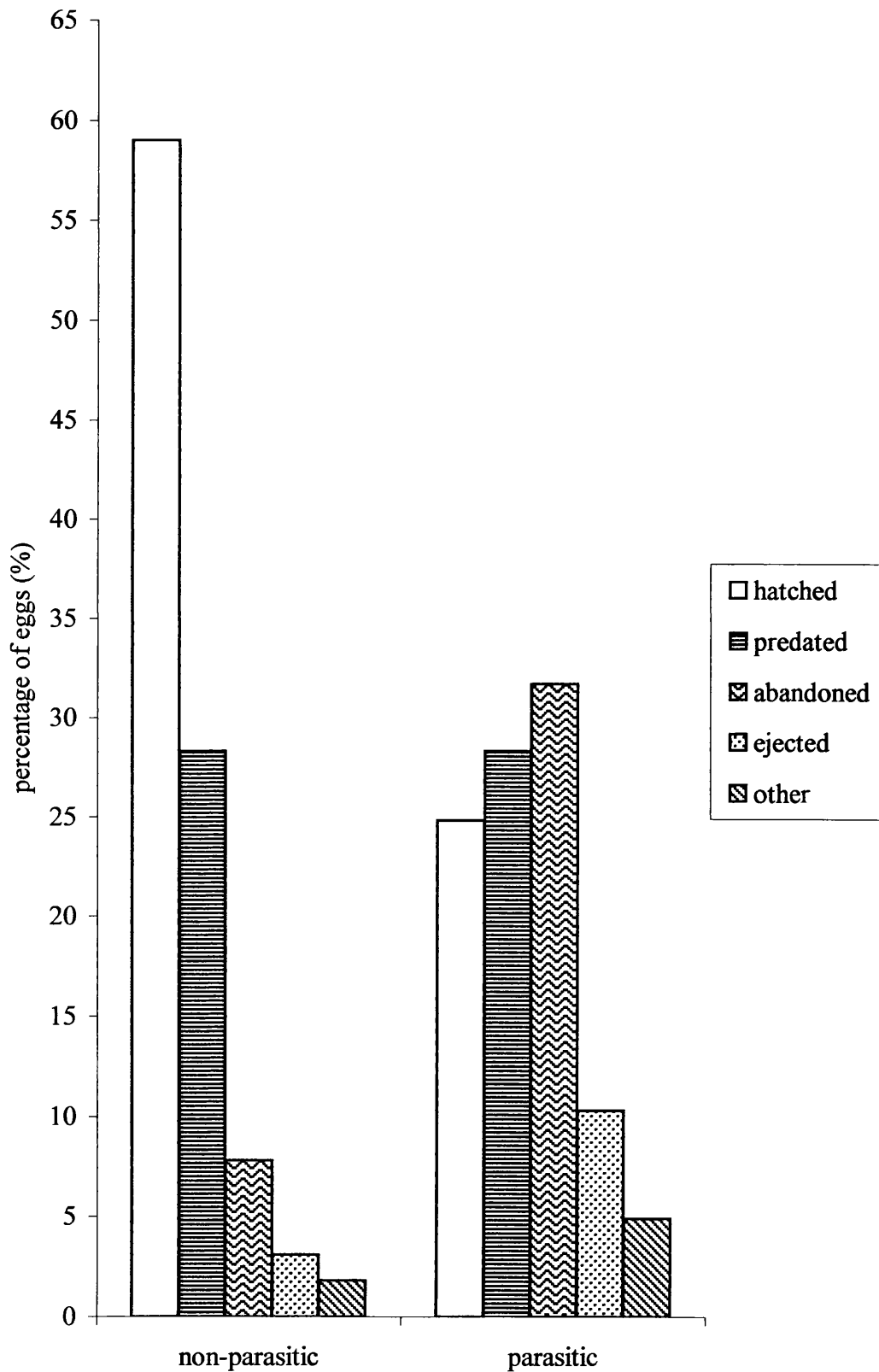
The total number of eggs laid parasitically as a proportion of the total in each year, was initially high and decreased progressively over the entire study. There was no obvious relationships between the numbers of parasite eggs laid, the number of nests parasitised and the number of eggs and nests that were predated each year (table 5.2 below).

Year	Number of nests parasitised	Number of parasitic eggs laid	Number of nests predated	Number of eggs predated
1997	36 (21.3%)	48 (7.4%)	100 (59.17%)	282 (47.56%)
1998	35 (17.95%)	64 (6.89%)	34 (17.44%)	167 (19.31%)
1999	22 (11.64%)	34 (3.42%)	81 (42.86%)	235 (24.45%)

Table 5.2. The numbers of parasitised nests and eggs laid parasitically as well as the levels of egg and nest predation in each year of research.

A comparison of the fates of the total number of parasitic and non-parasitic eggs over the three years of research is illustrated in figure 5.2 (page 94). Non-parasitic and parasitically laid eggs clearly suffered similar levels of predation over the three years.

Figure 5.2 A comparison of the fates of parasitically and non-parasitically laid eggs over the duration of the study



A greater proportion of parasitically laid eggs were ejected, abandoned and or destroyed than those laid non-parasitically. In particular, the percentage of parasitic and non-parasitic eggs abandoned varied dramatically. A similar pattern was evident for both ejection and egg destruction frequencies. Accordingly, the hatching success of eggs laid parasitically was considerably lower compared to that of non-parasitic eggs. Overall, approximately 25% (n=36) of all eggs laid parasitically hatched, compared to 60% (n=1427) of non-parasitic eggs.

5.3.4 The Breeding Status of IBPs

It was possible to identify the parasite female responsible in 66 (71%) of the separate parasitic events recorded during this study. The vast majority of these parasitic events were clearly undertaken by females from monogamous breeding groups (see table 5.3 below).

Parasitic female's breeder type	Number	Percentage
Monogamous	53	80.3
Polyandrous	6	9.09
Polygynous	1	1.52
Polygynandrous	6	9.09

Table 5.3. The number and percentage of events for IBP females from different breeder types identified over the course of the study

Monogamous females appeared significantly more likely to lay parasitically than any of the other three breeder types recorded during the study (G Test: $G_{adj}= 46.35$, $p<0.01$).

5.3.5 Clutch Sizes of IBP and Non-IBP Females

The mean (\pm S.E.) clutch sizes are shown for parasitic and non-parasitic females in table 5.4 (below). Since non-parasitic females laid significantly different clutch sizes between years (one-way ANOVA: $F_{2,218}=4.61$, $p<0.01$) and females laying parasitically did not (one-way ANOVA: $F_{2,60}=1.29$, N.S.) clutch size analysis was undertaken within each year of the study. Females that laid parasitically produced similar clutch sizes as counterparts restricted to laying in their own nests (see table 5.4 below). Two-tailed independent t-tests revealed no significant differences between the 2 types of female in any of the years.

Year	Clutch size of non-IBP females	Clutch size of IBP females
1997	6.21 \pm 1.73	5.74 \pm 1.57
1998	6.07 \pm 1.58	6.44 \pm 1.78
1999	6.97 \pm 2.55	6.62 \pm 2.33

Table 5.4. Mean (\pm S.E.) clutch sizes of IBP and non-IBP females for the three years of study

5.3.6 Egg Production of IBP and Non-IBP Females

The mean numbers of eggs laid by IBP and non-IBP females are shown in table 5.5 (page 97). IBP females produced significantly variable totals of eggs in the different

years of study (one-way ANOVA: $F_{2,30}=4.38$, $p=0.021$). In contrast, non-parasitic females laid similar numbers of eggs in each year (one-way ANOVA: $F_{2,148}=3.26$, N.S.). Independent t-tests were subsequently conducted between each year and revealed no significant differences in the numbers of eggs laid by the 2 types of female in any of the 3 years of study.

Year	Non-IBPs	IBPs
1997	11.82±7.55	11.86±5.16
1998	15.46±7.84	21.10±9.28
1999	15.05±8.46	18.33±9.62

Table 5.5. The mean (\pm S.E.) total number of eggs laid by IBP and non-IBP females in the three years of study

5.3.7 When Did Females Lay Parasitically in Their Own Laying Sequence?

Over the three years, 104 (71.2%) parasite eggs were identified as being laid by specific hens. For these individual females, it was possible to relate the laying of the parasite egg to the parasite's own nearest clutch attempt. Eggs laid parasitically were rated to one of the following categories in relation to the parasite's own laying behaviour: (1) before, (2) during and (3) after laying her own clutch (see section 2.7).

Over the three years, 55 (52.88%) parasite eggs were laid before a parasite's own clutch attempt, 3 (2.89%) were laid whilst a parasite was laying her own clutch and 46 (44.23%) were laid after a parasite had laid/completed her own clutch. A highly significant difference was found between when females laid parasite eggs in relation to their own laying sequence (G Test: $G_{adj}=31.40$, $p<0.001$). Females tended not to

lay eggs parasitically during their own laying sequence. They were equally likely to lay before or after they had laid their own clutches (G Test: $G_{adj}=0.40$, N.S.).

5.3.8 The Use of IBP by Females Before They Laid Their Own Clutches

Over the three years of research, 55 parasite eggs were laid by females before they had laid their own clutch. The majority of these parasite eggs were generally laid within a week of the female attempting her own clutch. The frequency of parasite eggs laid decreased significantly with days before a parasite's own clutch was attempted (Spearman's Rank Correlation coefficient: $r_s=-0.70$, $p=0.0001$).

5.3.9 The Use of IBP by Females During the Laying of Their Own Clutch

Only two instances were recorded of females laying parasitically whilst they were in the process of laying their own clutch ($n=3$ eggs laid). These events occurred at variable times (2, 4 and 6 days) during the hen's own laying sequence.

5.3.10 The Use of IBP by Females After They Have Laid Their Own Clutches

A total of 46 parasitically laid eggs were laid by females after they had completed laying their own clutch. The number of eggs laid parasitically decreased with the number of days after clutch completion (Spearman's Rank Correlation coefficient $r_s=-0.80$, $p<0.0001$).

5.3.11 The Fates of IBP Female's Clutches at the Time of Parasitism

For those females laying parasitically after laying their own clutches, the fate of their clutch attempts were recorded to assess whether loss was a significant factor in the decision to parasitise (see table 5.6 page 99). In the analysis, "nest loss" was

defined as nests where all eggs failed to hatch as a result of nest predated or abandonment. No single clutch status category was significantly related to the occurrence of parasitism (G Test: $G_{adj}= 1.53$, N.S.).

Status of the IBP's clutch at the time of parasitism	Number
Nest lost	18
Own clutch laid and currently incubated	18
Own clutch hatched	10

Table 5.6. The number of IBP eggs produced in relation to the status of IBP's clutches at the time

5.3.12 Proximate Factors Influencing the Frequency of IBP

To determine the possible proximate influence of a parasite's own previous clutch loss on the decision to parasitise, four stages of each parasite female's breeding in relation to laying were collated (see table 5.7 page 100). Failed clutches were defined as those that had been predated or abandoned. Only data from the parasite's last attempt prior to laying individual parasite eggs were used in this analysis. Only a few eggs were laid parasitically after clutch completion. The majority of parasite eggs were laid after a clutch failure or when the IBP females had not laid their own clutch. Similar proportions of eggs were laid parasitically after these events in both 1997 and 1998. The data from 1998 indicated, however, that although clutch failure commonly occurred before a parasitic attempt, many parasitic events took place after the parasite's own clutch had hatched.

IBP hen's prior clutch status	Number of IBP eggs			
	1997	1998	1999	Total
Not laid	16	9	6	31
Clutch attempt failed	14	13	9	36
Clutch completed	4	7	1	12
Own clutch hatched	5	18	2	25

Table 5.7. The number of individual IBP eggs laid in relation to the IBPs clutch status recorded prior to the event in each of the years of study.

The proportion of eggs laid parasitically at different stages in the parasites own breeding history varied between years (G-Test R x C: $G=-89.26$, $p<0.001$; see table 5.8 below).

Overall fates of eggs laid parasitically	Number and % of IBP eggs per year		
	1997	1998	1999
Hatched	10 (20.83%)	19 (29.69%)	7 (20.59%)
Predated	25 (52.08%)	11 (17.18%)	4 (11.76%)
Abandoned	8 (16.67%)	25 (39.06%)	15 (44.11%)
Ejected	4 (8.33%)	7 (10.94%)	4 (11.77%)
Destroyed in nest	1 (2.09%)	2 (3.13%)	4 (11.77%)

Table 5.8. The fates of all IBP eggs laid in each year (the percentages shown are calculated from yearly totals)

The success of parasitic eggs also varied between years. The greatest proportion of parasitically laid eggs to hatch occurred in 1998, the year of the lowest predation risk (see table 5.8 above).

5.3.13 The Regularity of Use of IBP by Specific Females

Over the duration of the study, 34 females were positively identified as brood parasites (excluding “floater” females). Whilst it was impossible to establish whether any of these females had parasitised in years subsequent to the study, approximately 20% (n=7) of these females laid parasitically over at least two breeding seasons. The proportion of females laying parasitically over just one breeding season varied, being greatest in 1997 (n=13 females) and least in 1998 (n=6 females). Only one female was recorded as laying parasitically over the three years of research.

5.4 Discussion

5.4.1 IBP: An Individual Approach

A significant but variable proportion (14–30%) of the female breeding population were identified as laying parasitically in each of the years. Female age and breeding experience may be important factors influencing the frequency and use of IBP. Female Moorhens exhibiting IBP tended to have had some breeding experience (Gibbons 1985; McRae & Burke, 1996; McRae, 1998).) In contrast to Moorhens, Lesser snow geese IBPs are predominately younger females (Lank *et al.*, 1989a). Furthermore, low-ranking older females laid parasitically in nests of high-ranking female Bar-headed geese *Anser indicus* (Weigman & Lamprecht, 1991). It was generally impossible to accurately age individuals within the population in the current study, except for individuals hatched and ringed during the period of study (see also section 5.4.2). Most females laying parasitically appeared, however, to be least 2-3 years old (on the basis of plumage and moult).

The clutch size and total number of eggs produced by females that laid parasitically were similar to those laid by non-parasitic females (see also McRae, 1998). This



suggests that IBP and non-IBP females in this population have similar fecundities. In contrast, American coot IBPs, although producing similar clutch sizes to non-parasitic females, produced significantly more eggs (Lyon, 1993a). They may, therefore, have had greater fecundities than non-parasitic females. Detailed information of the ability of IBPs to produce similar numbers of eggs as non-IBP females goes some way to refute the suggestion that IBPs have low fecundities (Yom-Tov, 1980). The low success rate of parasitically laid eggs compared with the success of IBPs own clutches in this and other studies implies that risk-spreading is not necessarily the primary reason for IBP (Lyon, 1993a; McRae, 1998).

The majority of IBPs in this study were monogamous. This is unsurprising, however, as the relative proportions of breeder type recorded at the study site was heavily biased towards monogamy over the three years of research (section 3.3.3). In contrast, the relatively low number of communally breeding females that were IBP suggests that such individuals do not have a predisposition for IBP. Current theory suggests that subordinate females (i.e. daughters) can increase their fitness by adopting IBP (Zink, 2000). There was no evidence, however, that subordinate Moorhen females from communal groups laid parasitically. Since daughters appear to have lower fecundities than mothers (section 4.4.4), they do not have the necessary resources and reproductive experience to allow them to utilise the complementary strategy of IBP in conjunction with laying in the communal nest.

4.5.2 “Floater” Females and IBP

In many avian species, varying proportions of sexually active females do not breed but are present on breeding grounds (Stutchbury & Robertson, 1988). If these individuals are unable to secure breeding territories, these “floater” birds (Brown,

1969) may increase their fitness by adopting a ‘best of bad job’ IBP strategy (section 1.4.2). “Floater” females in European starlings (Sandell & Diemer, 1999) and Bar-headed geese (Weigman & Lamprecht, 1991) have been similarly reported to use IBP. In the study on European starlings, 47% of “floating” females engaged in IBP whilst awaiting breeding opportunities (Sandell & Diemer, 1999). Furthermore, over a quarter of American coot eggs in one study were laid by non-territory holding “floater” females (Lyon, 1993a). Variable proportions (between 17-38%) of eggs per year were laid parasitically by Moorhen “floater” females within the population. It was impossible to ascertain the exact identity and number of those females responsible. In similar studies, however, McRae (1994; 1998) identified five Moorhen “floater” females as being responsible for the laying of 25% of parasitic eggs.

“Floater” females generally have a low reproductive success when using IBP (Sorenson, 1991;1993; Lyon, 1993a; Sandell & Diemer, 1999). They are generally younger, smaller or in poorer condition than territory holders (Lyon, 1993a; Sandell & Diemer, 1999). As a consequence, “floaters” may lay fewer, smaller eggs (Crawford, 1980; Curio, 1983; Soether, 1990; Lyon, 1993a). Eggs laid parasitically by “floater” females were generally viable, although a few were infertile. These eggs were as likely to hatch and were similar in size to those eggs laid parasitically by resident IBPs.

Most “floater” IBP occurred in territories nearby to large “floater” social groups (section 3.4.7). Importantly, “floater” females laid a greater proportion of their eggs parasitically during the host’s laying period than did territory-holding females. As they are free from the time constraints of territory defence and parental investment, “floater” females may be able to spend more time than territory holding counterparts

in locating suitable host nests. By laying parasitically, “floater” females are able to increase their direct fitness in a situation where breeding territories are a limiting factor. IBP in “floater” females is, therefore, confirmed as a ‘making the best of a bad situation’ strategy (Yom-Tov, 1980; Petrie & Møller, 1991; McRae, 1998). The overall reproductive success of Moorhen “floaters” using IBP is likely, however, to be considerably lower than that of territory holding parasites (Lyon, 1993a; Sandell & Diemer, 1999). Lyon (1993a) calculated that American coot “floaters” would have to lay on average, 78 eggs to equal the reproductive success of territory holding females! Clearly, Moorhen “floaters” similarly failed to lay sufficient numbers of eggs parasitically to equal the reproductive success of territory holding females.

5.4.3 “Floater” Breeding Strategies

Without the aid of genetic analysis and detailed observation it was impossible to determine the paternity of “floater” eggs. Quasi-parasitism where parasitic females mate with the host male (Emlen & Wrege, 1986; Wrege & Emlen, 1987; Birkhead *et al.*, 1990; Alves & Bryant, 1998), has not been recorded in Moorhens (McRae & Burke, 1996). This suggests that “floaters” secure mates during the winter (see Petrie, 1982). Indeed, copulations between “floater” males and females have been observed in Moorhens by Gibbons (1985) and in the present study. Young Bar-headed geese females have also been reported to form pairs but not to lay in their own nests (Weigman & Lamprecht, 1991).

Female European starling “floaters” laid parasitically at the start of breeding seasons but often joined communal groups as either breeders or helpers later in the year (Sandell & Diemer, 1999). There was no evidence that Moorhen “floaters” in this population joined existing breeding groups as secondary breeders or helpers at any

stage in the breeding season. Some “floater” females in the Moorhen populations may have formed pairs but were unable to secure territories (see section 3.4.7). In subsequent years, “floaters” were observed to establish breeding territories. Future studies could examine the breeding behaviour of moorhen “floater” individuals in high-density populations to determine what breeding strategies and systems occur. As non-breeding American coots (Lyon, 1993a) and Moorhens have been observed to rapidly fill vacant territories during the breeding season, it is clear that these individuals would benefit most by breeding as territory holders rather than remaining as specialist IBP “floaters” (Yom-Tov, 1980; Andersson, 1984).

5.4.4 The Estimation of IBP

Not all eggs laid parasitically may have been correctly identified due to difficulties in discriminating between eggs destroyed by hosts and those predated by avian predators. The actual numbers of eggs laid parasitically and number of parasitic females per year may, therefore, be an underestimate (Gibbons, 1986; Lank *et al.*, 1989a). It was thought, however, that the rigorous examination and identification of suspect parasite eggs and their origin would lead to a very low bias in the present study (see also McRae 1997b).

A number of parasitic attempts may have been unsuccessful. For example, females attempting to lay parasitically could be deterred from the nest by the host or be restricted by a lack of available and suitable host nests. Failed parasitic attempts have been documented in some studies (e.g. Semel & Sherman, 1986; Møller & Petrie, 1990; McRae, 1994; 1995). Since hosts may be constrained in their ability to defend their nest by the risk of damaging their own clutch, the laying of eggs parasitically is more likely be successful (Sorenson, 1991, 1993; McRae, 1995).

Detailed video analysis has revealed the behavioural patterns of Moorhen hosts and IBPs during the critical times of the parasitic event (McRae, 1994; 1996b). During the evening, IBPs approached and forcefully occupied the host's nest. This pattern occurred even when the host confronted the intruder or remained sitting on the nest. During laying, the parasitic female was repeatedly and forcibly harassed by the host adults at the nest (usually the male, Siegfried & Frost, 1975; McRae, 1994; pers.obs). To minimise the exposure to this physical attack, IBP eggs are laid significantly faster than those of the normal clutch (McRae, 1996a). Although this may minimise time spent at the host nest (see Sealy *et al.*, 1995), females of a low competitive ability could be deterred from the nest by host aggression before they have laid parasitically. The female may then be forced to "dump" eggs parasitically in another host's nest (see sections 6.3.6 & 6.4.8) or lay in her own nest or deposit eggs nearby. This is supported by the observation that single eggs considered to have been laid by parasitic females were found close to nests by McRae (1995) and in the present study. All these uncertainties will have to be resolved if a realistic and accurate assessment of the population level of IBP is to be achieved.

5.4.5 The Frequency of IBP

Studies on a variety of species revealed a considerable range of population frequencies of IBP (see Pienkowski & Evans, 1982; Møller, 1987; Romagnano *et al.*, 1990; Young & Titman, 1988; Feare, 1991; Weigman & Lamprechi, 1991; McRae, 1994; Lyon & Everding, 1996; Alves & Bryant, 1998; Post & Seals, 2000). The frequency of IBP at WWT Llanelli was not the same as that recorded in the older, denser Moorhen population at Peakirk Botanical Gardens (Gibbons, 1985; McRae, 1994). The proportion of eggs laid parasitically (as a percentage of all eggs laid per

year) at Peakirk was less than that found at WWT Llanelli. Differing rates of temporal evolution of anti-IBP tactics, such as nest guarding (Møller, 1987; Burgham & Picman, 1989) and secretive behaviour around nests (Uyehara & Narins, 1995) in geographically isolated populations may account for the observed variances in IBP frequency (see also Jamieson *et al.*, 2000).

5.4.6 The Regulation and Occurrence of IBP

Moorhen parents are restricted by the number of young they can individually successfully rear (Gibbons, 1985; McRae, 1998). IBP allows direct fitness gains through the laying of additional eggs in a conspecific's nest, thereby shunting the costs of incubation and chick rearing onto the host group (Møller, 1987). Since Moorhen eggs are small in relation to the size of females, it is assumed that the cost of egg production is quite low in this species (McRae, 1997a). If eggs are cheap to produce, (as has also been suggested for Cliff swallows by Brown & Brown, 1989 but see also Carey, 1996) and the condition of the female permits the formation of eggs, why are not more eggs laid parasitically?

IBP may be restricted by several factors. Firstly, success of IBP is enhanced when females lay parasitically in synchrony with the host group. Eggs laid parasitically too early or late in the host's laying sequence have a low probability of hatching (see sections 6.4.3 & 6.4.8). Secondly, injury or predation risks during inter-territory movements might restrict the opportunities available to females for laying parasitically. Finally, host nests are available for successful parasitism for only a short period throughout a breeding season. For example, American coot nests are available to IBPs for a maximum of 9 days per year (Lyon, 1993a) and this is likely to

be also a feature of the Moorhen population studied here. All restrict the use and frequency of IBP as a viable reproductive strategy.

5.4.7 Proximate Influences on IBP

A number of collection and wildfowl species were observed to parasitise conspecifics on a regular basis (e.g. Ross's goose *Anser rossii*, Mallard, White-headed duck *Oxyura leucocephala*, Bewick Swan *Cygnus columbianus*, Red-billed whistling duck *Dendrocygna autumnalis*, Carolina wood duck *Aix sponsa* and Common shelduck *Tadorna tadorna*). Nest site limitation probably facilitated parasitism in the majority of these cases (pers.obs and see also Evans, 1988; Gowaty & Bridges, 1991 but see Poysa, 1999). Age (and hence experience) may contribute to the occurrence of IBP. For example, a 1 year-old White-headed duck laid four fertile eggs in an older female's nest despite suitable alternative nesting sites being available. Although territory size is unlikely to influence whether a female Moorhen lays parasitically, aspects of territory quality (e.g. the amount of vegetative cover available in which to nest) may facilitate the use of IBP (Gibbons, 1985).

5.4.8 The Influence of Nest Predation on IBP

Evidence favouring the hypothesis that predation pressure is an important factor regulating the frequency of parasitism within a population has been obtained (Yom-Tov, 1980; Sorenson 1991, 1993; McRae, 1994; 1997a; Poysa, 1999; Jamieson *et al.*, 2000). This is unsurprising given that nest predation is considered a principal driving force in the evolution of breeding strategies (Martin, 1992). The present study provided support for this hypothesis finding that most of the IBP eggs laid occurred when clutch loss was highest (section 5.3.3). The numbers of IBP females were

similar, however, in 1998 and 1999 despite a 2.5 fold increase in nest predation in the latter. Furthermore, the number of eggs laid parasitically and number of nests parasitised in 1999 was approximately half that recorded in 1998 (see also Robertson, 1998). Levels of nest predation therefore, had little effect on the actual number of eggs laid parasitically and nest parasitised. Both of these variables progressively decreased throughout the study (but see McRae, 1994).

The status of individual female's clutch attempts prior to laying parasitically was not linked to the annual use of IBP. Clutch loss in this study was clearly not the only cue stimulating this complex behaviour (but see McRae, 1997a; Poysa, 1999). Similarly, despite clutch loss being frequent in American coots, only 14% of IBP events occurred after nest predation (Lyon, 1993a). Other studies examining possible proximate cues of IBP have also concluded that nest predation is a negligible factor (e.g. Brown 1984; Gibbons, 1986; Stouffer & Power, 1991; Sorenson, 1991).

Despite the lack of a discernible effect of predation on the number of Moorhen nests parasitised annually, nest loss may have influenced the occurrence of IBP in other ways (McRae, 1994; 1997a). The greatest number of females only laying parasitically in one year of the study occurred in 1997 (the year of highest nest predation). This suggests that nest predation influences the number of females that are opportunistic IBPs within the population. These females may attempt to negate fitness losses incurred by clutch predation, using IBP as a conditional one-off strategy. In contrast, several females were identified as regularly laying parasitically over 2 (and in one case, 3 breeding seasons, see section 5.3.13). It is unlikely that these individuals are responding to the proximate and conditional influence of clutch loss. IBP in these females is more likely, therefore, to be part of a mixed reproductive

strategy employed by certain individuals attempting to maximise their current and lifetime fitness (Lyon, 1993a).

5.4.9 Nest Predation and Local Breeding Synchrony

Local nesting synchronicity between separate breeding groups may reduce the risks of nest predation and parasitism, particularly in colonial species (Brown & Brown, 1989; McRae, 1994). Nesting synchronicity may, however, also facilitate successful parasitism. Localised predation events may reset the reproduction timing of neighbouring breeding groups so that laying is more or less synchronous within certain areas (McRae, 1994; 1997a). Nest predation at the current study site was often localised in time due to the foraging behaviour of egg predators e.g. Jackdaws and rats. As a consequence, localised breeding synchrony often occurred. Breeding synchronicity can facilitate successful IBP by promoting host availability at a time when the parasite is in the process of producing eggs (McRae, 1997a; 1998).

In the present study, peak numbers of eggs laid parasitically corresponded to similar peaks in the number of non-parasitic eggs laid. This does not mean, however, that egg production by non-IBP females *per se* promotes the production of eggs by IBPs. These eggs are merely produced in synchrony with other breeding female's egg production within the population. This is likely to arise through visual cues associated with breeding (see section 5.4.13).

The occurrence and timing of IBP may be influenced if localised nest predation synchronises laying between different breeding groups. Under these conditions, IBPs should theoretically lay more eggs during the host's laying period. Furthermore, such IBP-host laying synchronicity should be particularly pronounced in years of heavy and widespread nest predation. These predictions remain, however, unsubstantiated

in the current study (but see McRae, 1997a). No clear trend was observed between nest predation levels and the number of eggs laid parasitically during the hosts laying period. IBP-host synchronicity appears, therefore, to act independently from the influence of localised nest predation.

5.4.10 Host Group Size

Approximately one quarter of all IBP events occurred in the nests of communal groups. The presence of several adults does not appear to deter an opportunistic female from laying parasitically. The nesting behaviour of several individuals, such as nest construction and shift changing during incubation, might attract the attention of IBPs. Group size is unlikely to prevent IBP in Moorhens as all eggs are laid at night (Wood, 1974; McRae, 1994; 1996b). Only one adult (usually a male, Siegfried & Frost, 1975) incubates and attends the nest during this period. Their mate(s) were occasionally observed, however, to roost in close proximity to the egg nests. Individuals on the target nest becoming aware of the presence of an intruding female, do not vocalise to attract other group members to repel the intruder (McRae, 1996b). Such alarm vocalisations could presumably attract opportunistic nocturnal predators e.g. rats (McRae, 1997a) and weasels (pers.obs). The need to minimise this risk may prevent the development of an effective group defence against IBP.

5.4.11 The Impact of “Floaters” on the Frequency of IBP

Costs of communal breeding and nest failure amongst early breeders may account for variation in the rate of observed IBP between years (Sandell & Diemer, 1999). The presence of “floater” females may be another factor responsible for yearly differences in the occurrence of IBP. The population and number of breeding groups

increased successively throughout the duration of the study (see section 3.4.3). Under conditions of increasing population density and habitat saturation, individuals of lower competitive ability may be forced into communal, helper or “floater” roles (Brown, 1969; Sandell & Diemer, 1999). This could encourage “floater” groups within the population (section 3.4.7). These population increases might encourage IBP by augmenting host nest site availability (Evans, 1988; Gowaty & Bridges, 1991; Robertson, 1998 but see also Poysa, 1999). Notably, in the final year of the study, “floaters” laid *circa* 40% of IBP eggs. A substantial increase in “floater” density was also recorded in this year. Further research is needed to determine whether the actual number of “floaters” laying parasitically increased progressively.

5.4.12 IBP and the Temporal Plasticity of Laying

In contrast to the majority of studies on IBP (see section 1.4.3), female Moorhens in this study laid parasitically before, during and after laying in their own nests (see also Møller, 1987). Those eggs laid parasitically after the IBP’s own laying period may have been assigned to the wrong female. The criteria for parasite egg and female identification was, however, rigorous and robust and well used in this species (see section 2.7). This study is the first to document temporal plasticity in the ability of female Moorhens to lay parasitically at all stages of their laying periods.

Females laid parasitically before and after laying in their own nests with equal frequency suggesting that the risks of both strategies are less than the benefits of opportunistic IBP. Selection should favour females able to produce and lay parasite eggs when suitable host nests become available. There may be different costs and benefits associated with females laying parasitically before and after producing their own clutches. For example, females laying parasitically before they attempt their own

clutches incur no increased risk of predation or parasitism to their own clutch (Brown & Brown, 1989). Personal risks (e.g. by predation or conspecific aggression) may, however, be associated with locating host nests and laying parasitically. Although female behaviour whilst laying parasitically may limit the period of time exposed to host attack (see McRae 1996b), physical injuries may occur during this time. If these injuries affect the physical condition of females, they may impart a short-term fitness cost to IBPs reducing the resources available for the subsequent production and rearing of their own clutches. The social organisation used in Moorhen incubation allows females, that have already begun laying, to leave their territory at night to lay parasitically, as male partners “guard” the clutch (section 5.4.10). On one notable occasion, females in neighbouring territories parasitised each other over two nights (pers.obs). This indicates a decline in nest vigilance at this time and, more importantly, that IBPs are not excluded from becoming hosts themselves.

5.4.13 Laying Synchronicity and the Production of IBP Eggs

Many colonially nesting bird species achieve reproductive synchrony through socially-mediated stimuli and environmental cues. This “Fraser Darling Effect” (Daly & Wilson, 1978), is thought to dilute the risk of individual predation within the breeding population. Female Moorhens (and their mates) maybe similarly be stimulated into reproductive behaviour via visual and auditory cues from neighbouring breeding groups. For example, Ringed doves *Streptopelia risoria* commence reproduction when stimulated by courtship and mating behaviour of neighbouring pairs (Lott *et al.*, 1967).

The spatial distribution and density of the breeding population (as well as predation) at WWT Llanelli may facilitate this local synchronisation of reproduction (section

5.4.9). As each territory was usually closely surrounded by several other breeding groups, individuals have direct access to potential reproductive cues (e.g. mating signals) that may stimulate reproduction. Certainly, many of the Moorhen groups laid synchronously. This socially-mediated reproduction might also stimulate the production of eggs by IBPs that would benefit from the availability of host nests.

Moorhen eggs take approximately 24 hours to form (McRae, 1994). The ability of females to lay replacement clutches without a significant decline in clutch size shortly after nest predation (Wood, 1974; McRae, 1998) suggests that they are able to produce eggs in addition to those laid earlier with relative ease. In support of this argument, IBPs occasionally produced eggs that were laid parasitically an extended period from their last laying attempt. Many of these events were characterised by females laying several parasitic eggs in succession. Furthermore, most of these eggs were laid within 7 days of the female completing her clutch. Eggs laid parasitically after this time were laid by females whose clutches were currently being incubated or by those whose clutches had already successfully hatched.

If IBP egg production is influenced by neighbours, laying should be synchronized such that the majority of eggs were laid parasitically during the host's laying period. The overall timing of IBP in relation to the host's laying period was, however, generally poor (see section 6.4.3). Only 45% of eggs laid parasitically were laid during the host's laying period. Nevertheless, it is possible that hormonal and physiological influences on egg production causes a time delay between the onset of the cue and egg production, fertilisation and laying. This might, in many cases, reduce synchronicity between IBPs and hosts. Further research is clearly required to investigate this point.

5.4.14 IBP During the Laying Period

Very few eggs were laid parasitically during the IBP's own laying sequence (section 4.4.9). Incubation may be a factor potentially restricting such laying (see sections 7.3.4 & 7.4.8). Laying parasitically during the normal sequence of one egg per day, produces a staggered laying pattern. If incubation commenced prior to laying parasitically, a time-delay proportional to the number of eggs laid parasitically would occur when the IBP next laid in her own nest. As different eggs would receive differing amounts of heat in relation to when they were laid, this could result in an exaggerated HA pattern which may not be advantageous (see section 7.3.6). Females could avoid this if they commenced incubation after they have laid parasitically. In agreement with this, at the time when the two females laid parasitically during their own laying period, their clutches were not currently incubated.

5.4.15 The Benefits of IBP to Male Partners

IBP in Moorhens is exclusively a female strategy (McRae, 1994; 1996b and see also Cunningham & Birkhead, 1997; Petrie, 1983; 1986). Male Moorhens play no discernible part in its accomplishment except for providing sperm. By contrast, male Lesser-snow geese aid their partner by distracting hosts, allowing their female to lay parasitically in or near the host nest (Lank *et al.*, 1989b). Despite the general lack of assistance by male Moorhens in their partner's IBP attempts, it is clear that they do derive a fitness gain from those parasitically laid eggs that hatch successfully. Male Moorhens would consequently benefit from pairing with a female capable of IBP. Such additional fitness gains to males may possibly be a factor in mate choice in this species but this remains untested at present.

5.5 Conclusions

1. The number of females adopting IBP varied between years. The number of eggs and nests parasitised by IBPs similarly differed between years. Altering levels of nest predation, “floater” density, host availability and local laying synchronicity may all influence the relative number of nests parasitised by IBPs.
2. Three separate categories of females using IBP were identified. “Floater” females laid parasitically as a “Making the Best of a Bad Job” strategy. Some females laid parasitically as a conditional response to nest loss thereby reducing fitness losses incurred by egg predation. Other females appeared to use IBP regularly as a complimentary fitness gaining strategy to that of parental care.
3. Territory-holding IBPs had similar fecundities to females not using this strategy
4. Few females laid parasitically when they were laying in their own nests. In contrast, IBPs predominately laid parasitically either before or after they laid their own clutch.
5. The overall success of eggs laid parasitically was poor in relation to non-IBP eggs.

CHAPTER 6

HOST-PARASITE INTERACTION

“Its them that take advantage that get advantage in this world”

George Elliot (Adam Bede, 1980, Penguin Books, London)

6.1 Introduction

Because of the theoretical costs of successful IBP, selection should favour development of host anti-parasite behaviour to minimise its potential risk (Rothstein, 1990a). Similarly, selection should also favour the establishment of IBP behaviours that facilitate the success of each parasitic attempt (Yamaguchi, 2000). In order for IBP to be successful, IBPs must be able to locate and gain access to the nests of suitable host groups. Hosts can, however, effectively counter the threat of IBP by nest guarding during the critical period of egg laying and incubation (Møller, 1987; 1989; Burgham & Picman, 1989; Poiani & Elgar, 1994) and by discriminatory behaviour to suspect eggs within their clutches (Petrie & Møller, 1991).

6.2 Aims

It was attempted in this chapter to:

1. Describe spatial and temporal variations in the occurrence of IBP in relation to the host's laying period, territory location and breeder type.
2. Discuss the relative success of IBP in relation to parasite-host synchronicity.
3. Discuss and evaluate host responses to IBP

6.3 Results

6.3.1 Host Breeder Type

Ninety-three parasitic events were recorded, including those eggs laid parasitically by “floater” or unidentified females. The breeder type of each host group can be seen in table 6.1 below). Monogamous groups were significantly more likely to be the hosts of IBP than communal breeding groups (G-Test: $G_{adj}= 54.55$, $p<0.01$).

Breeding system of host group	Number and percentage of IBP events	Absolute incidence (and percentage) of each breeding group type during the study
Monogamous	71 (76.3%)	178 (80.9%)
Polyandrous	8 (8.6%)	19 (8.6%)
Polygynous	6 (6.5%)	16 (7.3%)
Polygynandrous	8 (8.6%)	7 (3.2%)

Table 6.1. The number and percentage of IBP events recorded throughout the study in relation to the breeding system of host groups and the absolute incidence of each breeding group type over the duration of the study

6.3.2 The Location of Host Territories

The location of host territories in relation to that of the parasite territory is summarised in table 6.2 (page 119). Eggs were predominately laid parasitically in the nests of groups adjacent to that of parasites (G-Test: $G_{adj}= 56.13$, $p<0.001$). Interestingly, there was a general decrease in the frequency of parasitic events with increasing distance from the parasite’s own territory.

Location of host's territory	Number and percentage of IBP events
Adjacent to IBPs territory	56 (84.85%)
2 territories away	7 (10.60%)
3 territories away	2 (3.03%)
4 territories away	1 (1.52%)

Table 6.2. The location of host territories in relation to the IBPs own territory

6.3.3 The Timing of IBP: The Importance of Host-parasite Laying Synchronicity

Individual eggs laid parasitically in host nests were assigned to one of three stages in terms of the host's laying sequence. These were being laid (1) before (in an empty nest), (2) during (whilst the host group was still laying) and (3) after (when the host group had completed their clutch) (see table 6.3 below). The total proportions of eggs laid parasitically in each of these three host laying stages differed significantly (G-Test: $G_{adj}= 21.39, p<0.01$).

Year	Hosts laying sequence at the time of IBP		
	Before	During	After
1997	-	17	32
1998	6	31	26
1999	9	16	9
Total	15	64	67

Table 6.3. The number of eggs laid parasitically with respect to the host's laying period

Females, however, were as likely to lay parasitically during the host's laying period as they were after the host had ceased laying (G-Test: $G_{adj}= 0.03$, N.S.). Interestingly, the total proportion of eggs laid in each host laying category differed significantly between years (G-Test RxC: $G=24.78$, $p<0.01$).

Differences were observed between the proportion of parasite eggs laid at each of the three stages in the host's laying period for "floater" and resident groups (see table 6.4 below). Specifically, the percentage of eggs laid parasitically by "floater" females during the hosts laying period was greater than that recorded for resident females.

Host's stage when IBP occurred	Percentage of eggs laid parasitically by resident females	Percentage of eggs laid parasitically by "floater" females
Before	10.19	10.53
During	42.59	55.26
After	47.22	34.21

Table 6.4. The percentages of eggs laid parasitically by "floater" and resident IBP females at different stages of the hosts laying period.

6.3.4. The Fate of Eggs Laid Parasitically on Their First Day in Host Nests

Table 6.5 (page 121) illustrates the number of eggs laid parasitically that were accepted or rejected (defined as those eggs that were abandoned, destroyed or ejected) on their first day in the host's nest (see also sections 6.3.6-6.3.8). This analysis excluded eggs that were predated on their first day in the host nest. Eggs laid parasitically before the host had laid were always rejected (G-Test: $G_{adj}=10.73$, $p=<0.05$). In contrast, eggs laid parasitically during and after the host had laid were significantly likely to be accepted (G-Tests: $G_{adj}=13.57$ and 20.40 respectively, both

$p < 0.001$). The relative proportion of eggs that were accepted on their first day in the host nest was similar for those eggs that were laid during and after the host had laid (Fisher's Exact Test: =0.049, N.S.).

Host's stage when IBP occurred	Number of eggs	
	accepted	rejected
Before	0	15
During	54	13
After	56	8

Table 6.5. The fate of parasitically laid eggs on their first day in host nests in relation to when they were laid in the host's own laying sequence

6.3.5 The Eventual Fate of Eggs Laid Parasitically

The numbers of eggs laid parasitically that hatched or failed (defined as those eggs abandoned, ejected or destroyed in the nest) can be seen in table 6.6 (below).

Host stage when IBP occurred	Number of eggs laid parasitically	
	hatched	Failed to hatch
Before	0	15
During	16	15
After	16	33

Table 6.6. The hatching success of eggs laid parasitically at different stages of the host's laying sequence

Eggs predated were excluded from this analysis. The hatching success of eggs laid parasitically depended on when in the hosts laying period they were laid, (G-Test RxC: $G=1121.98$, $p<0.001$). Eggs laid parasitically before hosts had laid their clutch failed to hatch (G-Test: $G=10.73$, $p<0.05$). By contrast, equal numbers of eggs laid parasitically during and after the hosts laying period hatched and failed. Within these two categories, the proportion of parasitically laid eggs that hatched were similar (Fisher's Exact Test: $=0.059$, N.S.).

6.3.6 IBP Before the Hosts Have Laid

Less than 11% ($n=15$) of eggs laid parasitically were in an empty host nest (6 in 1998 and 9 in 1999, see table 6.3 page 119). In all cases, parasitised nests were abandoned by the host prior to the initiation of a clutch attempt (see section 6.3.5).

6.3.7 IBP During the Host's Laying Period

In total, 67 eggs were laid parasitically during the host's laying sequence over the 3 years. The majority of these eggs (65.15%, $n=43$) were laid during the first 4 days of the host's laying sequence. The range of days over which these eggs were laid was, however, quite large varying from 1 – 12 days into the sequence. The number of eggs laid parasitically decreased significantly with duration into the host's laying period (Spearman's Rank Correlation Coefficient: $r_s=-0.85$, $p=0.0009$).

The number of IBP eggs laid parasitically accepted and rejected on their first day in the host nest with respect to the number of host eggs already present can be seen in table 6.7 (page 123). Eggs laid parasitically during the host's laying period were as likely to be accepted as rejected on their first day in the host nest when only one or two host eggs present. After host females had laid at least 3 eggs, parasitic eggs were

uniformly accepted. The analysis could not be continued past four host eggs but the observed trend in table 6.7 continued, with the relative survivorship of parasitically laid eggs on their first day in the host's nest increasing with the number of host eggs already present.

Number of host eggs resent	Number of eggs laid parasitically		G-Test Output	
	accepted	rejected	G_{adj} value	significance
1	5	6	0.04	NS
2	5	5	0	NS
3	9	1	3.87	<0.05
4	12	0	8.66	<0.01

Table 6.7. Host responses to eggs laid parasitically in relation to the number of host eggs present when IBP occurred

Of the 55 parasitically laid eggs that were accepted during the host's laying period, less than 24% (n=16) hatched. Interestingly, these accepted eggs were as likely to hatch as they were to be abandoned (G-Test: $G_{adj}=0.064$, N.S.). IBP eggs hatched if they were laid early in the host's laying period (Spearman's Rank Correlation coefficient: $r_s=-0.75$, $p=0.033$, n=8). Host clutch size had no apparent effect on whether eggs laid parasitically during the host's laying sequence hatched (Spearman's Rank Correlation coefficient: $r_s=-0.10$, N.S.). Only two parasitically laid eggs were ejected from host's nests during the hosts laying period, both occurring in 1999 when 2 host eggs were present. The ejected eggs were found some 50cm from the host nest and appeared to have no discernible damage (e.g. puncture marks). Host eggs were undamaged and still within the confines of the nest. In both cases, the host female

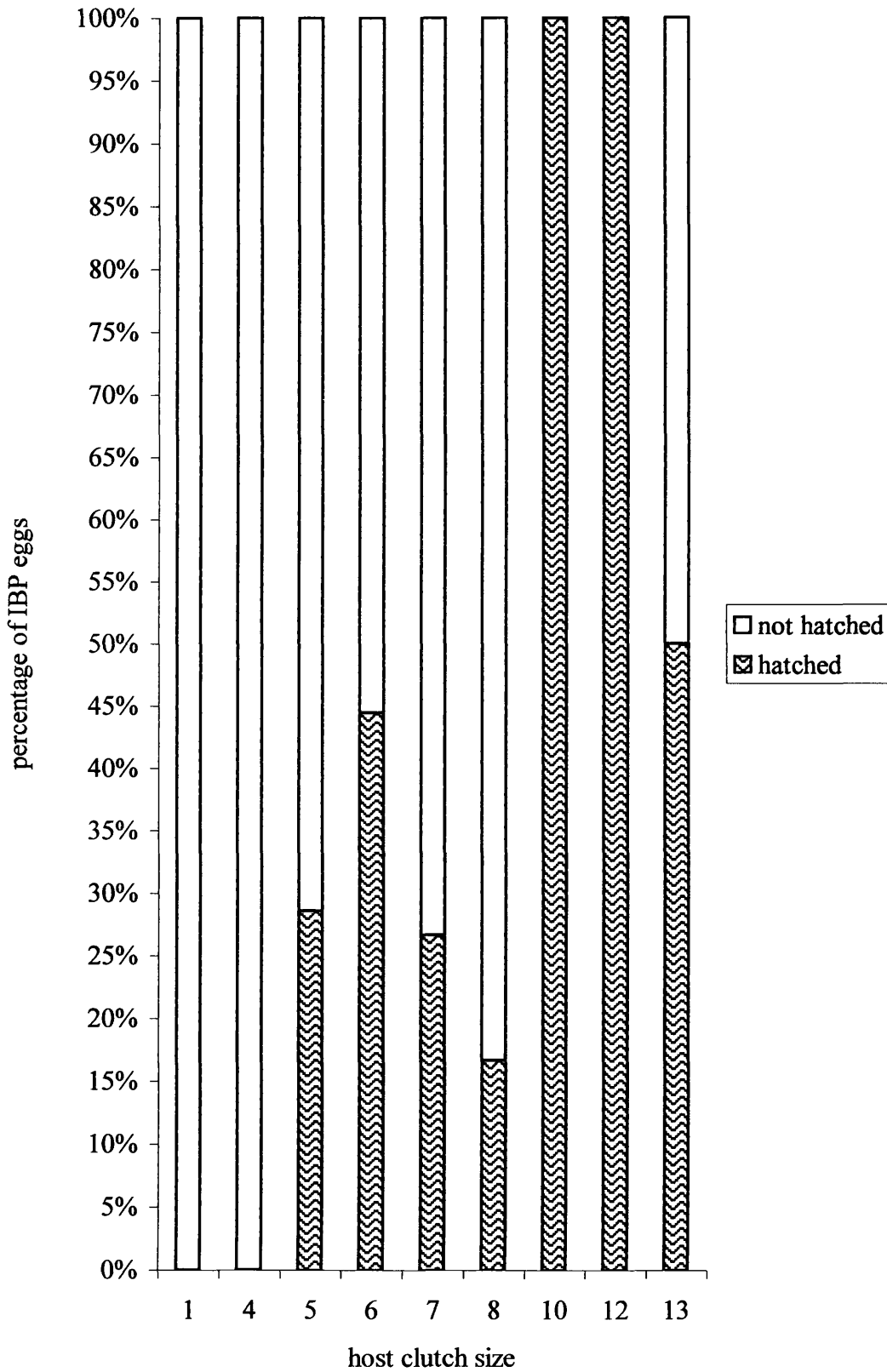
continued to lay. Two nests were abandoned by the host group after a parasitic female had laid a single egg at day 2 and 3 respectively of the hosts laying sequence. A further seven nests were judged destroyed by hosts in response to IBP. The majority (n=6) of these occurred when the host had laid only one egg.

6.3.8 IBP After the Host had Ceased Laying

Over the duration of the study, 64 IBP eggs were laid parasitically after the host had completed her clutch. The number of IBP eggs declined with the number of days after the host had stopped laying that IBP occurred (Spearman's Rank Correlation coefficient: $r_s = -0.78$, $p < 0.0001$). Only 16 (i.e. 25%) of these successfully hatched. Figure 6.1 (page 125) illustrates the increasing probability of IBP eggs hatching with increasing host clutch size. The number of IBP eggs hatching progressively decreased with increasing time between the host initiating incubation and IBP occurring (Spearman's Rank Correlation coefficient: $r_s = -0.51$, $p = 0.017$, $n = 21$).

Six (9.34%) eggs laid parasitically after hosts had ceased laying, were ejected from the host nest during incubation. These ejection events occurred 1 - 20 days after the host female had stopped laying. The median (with range) incubation time lag for IBP eggs after hosts had stopped laying was 7 (2-29) days. Interestingly, five IBP eggs that were laid with a host incubation time lag of 11 - 29 days hatched successfully. Over the same period, however, 10 IBP eggs were either abandoned or ejected from other host nests. Eggs laid parasitically by "floater" females after the host had stopped laying were as likely to hatch as those IBP eggs laid by territory holding females (1 tailed Fisher's Exact test: $= 0.073$, N.S.).

Figure 6.1 The influence of host clutch size on the probability that IBP eggs laid after the host has laid will hatch



6.4 Discussion

6.4.1 Host Breeder Type and the Significance of Host Group Location

Although the majority of host groups in this study were monogamous, over a quarter were communal breeders. The apparent significance of this IBP selection towards one specific breeder type is skewed by monogamy being, by far, the dominant breeding system in the population. One might well expect such breeders to receive greater numbers of parasitic eggs (see also sections 3.3.3 & 5.4.1). Multi-female breeding groups may be attractive potential hosts from the perspective of IBPs. The increased number and diversity of eggs present in communal group nests (sections 4.3.6 & 4.3.7) may dilute the host's potential to discriminate between eggs (McRae, 1995). In addition, the larger group size in communal breeding could improve vigilance against predators and parental care thus benefiting IBP chicks (Poiani & Elgar, 1994; Monadjem, 1996 and see also section 5.4.9). On reflection, however, the group-breeding system of the host appeared to be an insignificant factor influencing IBP.

In contrast, the proximity of host group's territory (and nests) to that of IBPs had a profound effect on the latter. Approximately 85% of IBP eggs were laid in their nearest neighbour's nests. Previous studies on Moorhens and other IBP species have found similar trends (e.g. Brown, 1984; Gibbons, 1986; Davies, 1988; Brown & Brown, 1989; Møller, 1989; Lokemon, 1991; Lyon, 1993b; McRae, 1994). There may be risks (e.g. predation and conspecific aggression) associated with movement into neighbouring territories and this could limit the distance that IBPs are willing to travel in search of host nests.

One of the affects of the increasing population size at the study site (section 3.1) was that breeding territories became more densely packed. This progressive process may have facilitated observation by IBP females and their direct access to many

neighbouring territories. On average, each breeding group was closely surrounded by between two to three neighbouring territories. Since success is often dependent on the detection of viable host nests (Petrie & Møller, 1991; Brittingham & Temple, 1996; McRae, 1994), the ability of females to closely observe the nesting behaviour of neighbouring groups is likely to be beneficial (see also section 6.4.9). Brown-headed cowbirds *Molothrus ater* locate host nests by direct observation of the latter's nest building (Norman & Robinson, 1975). This could be one mechanism by which neighbouring Moorhen females identify viable host nests. By monitoring the nests of their neighbours, IBPs may be able to respond quickly to potentially favourable situations by laying parasitically (Emlen & Wage, 1986; Møller 1987; Massoni & Reboreda, 1999).

6.4.2 Host Selection

Moorhen host groups are as likely to be experienced as inexperienced breeders (Gibbons, 1985). It is highly unlikely, therefore, that Moorhen IBPs select hosts based on their ability to provide parental care (McRae, 1998). Similarly, Grey starlings *Sturnus cineraceus* IBPs failed to use host characteristics to direct them to high quality hosts (Yamaguchi, 2000). In contrast, high-ranking Bar-headed geese are more likely to be hosts than lower ranking counterparts (Weigmann & Lamprecht, 1991). In this last species, hosts may be selected based on their social ranking and associated parental ability.

In dense Moorhen populations, ecological constraints by offspring dispersal increase the likelihood that close neighbours are related (McRae, 1994). Consequently, there is a high probability that IBPs will lay parasitically in the nests of first or second order relative [i.e. parents, offspring or siblings] (McRae & Burke, 1996). This will reduce

the fitness costs to hosts providing care to parasitically laid eggs (*sensu* Hamilton, 1964). This indirect benefit may, therefore, ameliorate the negative effect of IBP on host fitness. It is presently unknown, however, whether Moorhen IBPs preferentially select hosts on a kin-basis. Further research is clearly required on this intriguing point.

6.4.3 The Success of IBP: The Importance of Host-IBP Laying Synchronicity

Although host acceptance of IBP eggs appeared generally high (see also section 6.4.5), the number that actually hatched was very low. Only 25% of all IBP eggs hatched compared with over 60% of non-IBP eggs hatching. A further 32% of IBP eggs were abandoned prior to hatching. The relatively low success of IBP within this population, contrasts with that previously recorded in Moorhens at Peakirk (Gibbons, 1985; McRae 1994) and may be due to the poor laying synchronicity between IBPs and host groups (see also section 6.4.9). Over half of IBP eggs were laid after the hosts had ceased laying and had commenced incubation. Despite the majority of these eggs being laid within four days of hosts completing their own clutches, this usually resulted in a considerable time-lag between host incubation and the timing of IBP. Consequently, IBP eggs laid after hosts had laid were incubated for shorter times than that required for hatching. These eggs were then usually abandoned by hosts (section 6.3.8; see Gibbons, 1985; McRae, 1995 but see also section 6.4.4).

Since Moorhens rarely commence incubation when their clutches are complete (section 7.3.3), a similar abandonment trend was seen in IBP eggs laid towards the end of the host's laying period (section 6.3.7). Female Redhead ducks *Anas americana* also usually lay eggs parasitically within the host's laying period. Less than 46% of these eggs, however, eventually hatched (Sorenson, 1991). The poor

success of IBP eggs laid during the host's laying period may be related to the ability of host groups to recognise cues early in their laying sequence indicating the occurrence of IBP (section 6.4.5).

IBPs could enhance the survival of any parasitic eggs by removing host eggs prior to laying (Evans, 1988; Feare, 1991) but Moorhen IBPs never, however, removed host eggs before they laid parasitically (see also McRae, 1995; Yamaguchi, 2000). Interestingly, host clutch size increased the probability that IBP eggs laid after hosts have laid will hatch. Since incubation duration is strongly associated with clutch size (section 7.3.3), IBPs benefited from laying in nests containing many host eggs.

The overall poor success of eggs laid parasitically and general lack of IBP-host laying synchronicity suggests, however, that Moorhen IBPs are unable to recognise the stage in the hosts laying period giving the greatest success (see also Yamaguchi, 2000). IBP is, therefore, unlikely to be costly to the majority of hosts as most eggs are laid parasitically at inappropriate times and consequently, fail to hatch (McRae & Burke, 1996 and see section 7.4.11). Furthermore, the ability of Moorhen hosts to detect eggs laid parasitically both early in their own laying sequence and in empty nests also reduces the success of IBP (see also sections 6.4.5 & 6.4.8).

6.4.4 The Effect of Host Brood Mortality on the Success of IBP

Despite most IBP events being unsuccessful, under certain conditions, IBP eggs laid well after the hosts ceased laying, occasionally hatched successfully. In several notable cases, when a host's chicks had hatched but had subsequently perished (by predation, disease or exposure), IBP eggs continued to be incubated. These IBP chicks subsequently hatched and may then have benefited from reduced intra-brood competition for parental care. Interestingly, after the loss of their own chicks, host

groups incubated IBP eggs for a considerable periods- up to 32 days was observed (see also sections 7.3.3 & 7.3.5). This behaviour was particularly evident in years of high chick mortality (e.g. 1997 and 1999) suggesting that IBP can be an effective “risk-spreading” strategy under some ecological conditions (Bulmer, 1984).

6.4.5 Host Responses to IBP: Egg Discrimination and Critical Timing

The earlier in the host’s laying period that IBP eggs were laid by Moorhens, the greater the probability those eggs will eventually hatch. Females should, therefore, direct their efforts into laying parasitically in synchrony with hosts if they are to facilitate the success of IBP (Yamaguchi, 2000). The vast majority of IBP eggs are laid early in the host’s laying period in a number of species (Lyon & Everding, 1996; Roberston, 1998 but see also section 6.4.3). For example, approximately 83% of IBP eggs in Cliff swallows are laid within the first two days of a host laying (Brown & Brown, 1989). The success of IBP may be constrained, however, by host tactics including ejection of suspect eggs (McRae, 1995).

The evolution of distinctively coloured and patterned eggs within host species might be a response to the threat of inter-specific brood parasitism (Møller & Petrie, 1990). Many host species, e.g. Eastern kingbirds *Tyrannus tyrannus* can discriminate between their eggs and those laid by other species (Bischoff & Murphy, 1993). Moorhens appear to be unable to make such discriminations between the eggs of different species and their own. For example, Moorhen clutches laid in nest boxes (section 3.4.10) were occasionally parasitised by several collection bird species, e.g. Ringed teal *Callonetta leucophrys* and Carolina wood duck. Despite considerable differences in shape, colour and size, these eggs were accepted and duly incubated by the Moorhen host prior to their removal by Trust staff (pers.obs). Colour-dyed

Hottentot teal *Anas punctata* eggs added experimentally to Moorhen clutches were similarly accepted (McRae, 1994; 1995). As the frequency of inter-specific brood parasitism of Moorhen nests by native wildfowl and rail species is practically zero (pers.obs; see section 9.3), there is likely to be no selection pressure for the evolution of egg discrimination in this species.

Moorhens also appear generally unable to distinguish their eggs from those laid by a conspecific (McRae, 1995; 1996a). The acceptance of IBP eggs by hosts is, however, conditional to the number of eggs (hence the investment) already present within the nest when IBP occurs. In the current study, there was an equal chance that eggs laid parasitically would be accepted or rejected when laid concurrently with the host's first or second egg (see section 6.3.7). After hosts laid their third egg, however, there was strong tendency for the IBP eggs to be accepted. In a similar study on Moorhens, hosts rarely accepted a conspecific's egg unless three eggs had been laid previously by the host (McRae, 1995 and see also Jamieson *et al.*, 2000). In other species, hosts do not abandon or eject eggs once they have begun to lay e.g. Common goldeneyes *Bucephala clangula* (Andersson & Erikson, 1982) and European starlings (Stouffer *et al.*, 1987). Under these circumstances, the host's decision to accept or abandon nests in which IBP eggs have been laid is constrained by the level of prior investment. This decision may be influenced by the host's previous reproductive success as well as their ability to lay a replacement clutch (Lyon, 1993a).

The ability of hosts to discriminate between their own eggs and those of IBPs may be constrained by the dangers of ejecting the wrong eggs (Petrie & Møller, 1991; Hosoi & Rothstein, 2000). As egg number in the host's nest increases, the probability (and associated cost) of mis-identifying eggs also rises. This may restrict the

probability of hosts discriminating against IBP eggs at a time when the laying of such eggs is costly (Møller & Petrie, 1990; Petrie & Møller, 1991; McRae, 1995).

6.4.6 Nest Desertion

If the total energetic investment made by the host at the time of parasitism is low (i.e. few eggs have been laid and incubation not yet commenced), it would pay the host to desert the nest and lay elsewhere (Sealy, 1995). Only two nests where the host had already lain were, however, deserted following the presence of IBP egg(s) or the disturbance produced by parasitism (see also Dugger & Plums, 1999). In these cases, desertion occurred when the host female had laid 2 and 3 eggs, respectively. Rates of egg ejection and nest destruction followed similar patterns with anti-IBP tactics generally seen only when there were few host eggs in the nest (see also Jamieson *et al.*, 2000). As hosts can only detect the presence of IBP eggs in the early stages of their laying period, IBPs would benefit from laying parasitically after the host had accumulated at least three eggs (section 6.4.5). Over 84% of IBP eggs were accepted into host's nests on the day they were laid. Furthermore, the vast majority were laid when a minimum of 3 host eggs were already present in the host nest (see also Lyon & Everding, 1996; Robertson, 1998; Yamaguchi, 2000).

Moorhen hosts are likely to be aware they have been parasitised (McRae, 1996b). Hosts may still be able discriminate against suspect eggs within their clutch by preferentially transferring suspect eggs to the periphery of the nest where incubation temperatures are cooler (Drent, 1975). Hosts could thus reduce the hatchability of suspect eggs whilst maintaining their current investment in the rest of the clutch (McRae, 1995; Sorenson, 1997a). Despite the theoretical benefits of this behaviour to hosts, evidence from a number of wildfowl species suggests that, once laid and

accepted, IBP eggs are incubated to the same degree as the host's own eggs. This has been seen in Canvasbacks (Sorenson 1997), Common pochard *Aythya ferina* and Tufted ducks *Aythya fuligula* (Dugger *et al.*, 1999). Once IBP and host eggs are present in the nest together, Moorhens cannot distinguish them, a feature likely to facilitate the selection and success of IBP this species (McRae, 1994; 1995).

6.4.7 Host Response to IBP: Host Clutch Size Adaption

Parents of many avian species are able to successfully raise broods greater in size than they actually lay (e.g. Nur, 1984b; Finke *et al.*, 1987; Mock & Ploger, 1987; Dijkstra *et al.*, 1990 but see Högstead, 1980). Furthermore, increased parental effort can affect the future reproductive success and survival of individuals (Lessells, 1991 and see also section 1.5.1). If the parental effort is increased by IBP, this may affect the lifetime fitness of hosts (e.g. Brown & Brown, 1998). Hosts may benefit by reducing their own clutch size in anticipation of the future possibility of IBP, particularly if this is extremely prevalent within a population (Powers *et al.*, 1989; Lyon, 1998). Both Goldeneye ducks (Andersson & Eriksson, 1982) and European starlings (Powers *et al.*, 1989) reportedly do this. In contrast, there was no evidence to suggest that Moorhen reduced their average clutch size in response to the threat of IBP (see also Lyon, 1998). Moreover, there are many more plausible factors explaining clutch size variation in birds (see Rothstein, 1990b; Petrie & Møller, 1991).

6.4.8 Laying Synchronicity: The Importance of Timing in IBP

Similar numbers of eggs were laid parasitically during and after the host had laid (see sections 6.3.3-6.3.8). Approximately 11% of eggs were, however, laid

parasitically in a host's empty nest, suggesting a low IBP-host laying synchronicity. Such eggs were abandoned, ejected or destroyed by the host group. Similar host behaviour to the presence of IBP eggs in their empty nest has been observed in a number of other studies (see Emlen & Wage, 1986; Gibbons, 1986; Møller, 1987; Stouffer *et al.*, 1987; Brown & Brown, 1989; Bischoff & Murphy, 1993; McRae, 1995; McRae & Burke, 1996). Hosts recognise the presence of foreign egg(s) in their empty nests and subsequently abandon their laying attempt (see also section 6.4.5).

As host responses to the presence of IBP eggs in their empty nests guarantees its failure, selection towards IBP-host laying synchronicity should occur. Why then, are eggs laid parasitically in empty nests when more viable host nests may be available in neighbouring territories (McRae, 1994)? Several explanations can be given to explain these seemingly "wasted" IBP efforts. As Moorhens often construct several potential nests prior to laying (Wood, 1974; McRae, 1994; pers.obs), IBPs may lay in the right territory but the wrong nest. Host aggressive behaviour during the laying event may result in IBPs "dumping" eggs in empty nests (see McRae, 1996b). Females in the process of producing eggs may also "dump" their eggs in the first available nest they locate if their partner(s) are unable or unwilling to commence nesting (Gibbons, 1985).

6.4.9 Host Nest Monitoring and Viability

A strong relationship between synchronizations of IBP and host laying and the eventual success of eggs laid parasitically is evident in a number of IBP species (e.g. Gibbons, 1986; Bischoff & Murphy, 1993; Lyon, 1993b; McRae, 1995; Lyon & Everding, 1996; Yamaguchi, 2000). Clearly, in order for parasitism to be successful, good parasite-host synchronicity is necessary (McRae, 1995). For example, eggs

added parasitically to Lesser snow geese nests two, four and five days after incubation commenced had respectively 37%, 29% and 0% chances of hatching (Davies & Cooke, 1983). As the majority of eggs laid parasitically are not evenly distributed within the hosts laying period, IBPs of some species appear to be able to closely monitor potential host nests (see Møller, 1987; Brown & Brown, 1989; Petrie & Møller, 1991; Lyon & Everding, 1996; Robertson, 1998 but see also Yamaguchi, 2000).

In addition to monitoring favourable host nests, IBPs may also access the viability of “active” host nests located (i.e. nests already with eggs). In particular, as the timing of Shiny cowbird *Molothrus bonariensis* parasitism was related to the degree by which host Yellow-winged blackbirds *Agelaius thilius* embryos had developed, this species appears to peck host eggs to determine the developmental stage of chick embryos (Massoni & Reboreda, 1999). Similar evidence has been described by Petrie & Møller (1991) in Moorhens. In the current study, several host eggs in certain nests appeared to have been pecked but not removed from the host’s nest (pers.obs). Similar damage was not evident in IBP eggs laid in these nests. This indicates that some Moorhen IBPs may also assess the development of host eggs by pecking them. This behaviour may also cause embryo mortality encouraging hosts to lay in a way more favourable to the IBP’s own laying sequence (Petrie & Møller, 1991). This behaviour, in conjunction with laying parasitically, may facilitate the eventual success of each IBP egg by reducing future intra-brood competition (see Soler & Martinez, 2000). This phenomenon is, however, rare suggesting it is simply a non-functional consequence of egg damage during IBP events.

6.5 Conclusions

1. Host groups were almost exclusively the immediate neighbours of IBP groups.

This feature of Moorhen IBP is likely to facilitate IBPs identification of potential host nests although it may not guarantee successful IBP-host laying synchronicity.

2. The overall success of IBP within the population was poor. Only one quarter of all IBP eggs hatched. A lack of IBP-host laying synchronicity in most cases is likely to be the ultimate cause of this poor success.

3. IBPs laid eggs at all stages of the hosts laying sequence, although the majority of these eggs were laid parasitically either during or after hosts had laid. IBP eggs laid parasitically before host females laid or after they had ceased laying were usually abandoned.

4. In the majority of IBP events, host groups usually accepted eggs laid parasitically in their nests. Host groups, however, were able to respond to the presence of IBP eggs in the early stages of their laying. This behaviour was conditional to the number of host eggs present in the nest and involved ejection of eggs or the abandonment/ destruction of the suspect clutch.

CHAPTER 7

BREEDING STRATEGIES AND REPRODUCTIVE SUCCESS

“Looking after your children is one way of looking after yourself”
Ian McEwen (Black Dogs, 1999, Anchor Books, London)

7.1 Introduction

Parents must be successful in raising young as the survival and subsequent reproductive performance of offspring account for relative differences in parental fitness (Tinbergen & Daan, 1990; Daan *et al.*, 1990). As the costs of reproduction can affect an individual's survival and future ability to reproduce, parents should adjust their reproductive effort or adopt breeding strategies that promote their own fitness (Trivers, 1972; Drent & Daan, 1980; Lessells, 1991). Moorhens breed using a variety of different mating systems (sections 2.2 & 3.3.3). It is unclear, however, whether individuals always benefit reproductively from these partnerships. By assessing the intra-population reproductive performance and success of different breeder types, it may be possible to partially determine the selective forces behind the adoption of specific breeding behaviours.

In addition to the reproductive success gained through the rearing of their own broods, female Moorhens can also increase their fitness by laying opportunistically in the nests of conspecifics (section 1.4.2). The success of this additional strategy is, however, conditional on critical timing and the identification of suitable host nests (Lyon, 1993b; Yamaguchi, 2000). Despite these limitations, it is generally considered that IBPs have greater reproductive success and fitness than females not using the strategy (Petrie & Møller, 1991). In contrast, host groups are expected to suffer

reduced reproductive success through increased parental expenditure during the parental care process.

7.2 Aims

This chapter aimed to:

1. Describe, assess and compare the reproductive performance and success of the four breeder types found at WWT Llanelli.
2. Determine the reproductive success of IBP.
3. Investigate the influence of IBP on various aspects of host group reproductive performance.

7.3 Results

7.3.1 Group Reproductive Success

An analysis was conducted on the reproductive success over the three years of the four different breeder types found at the study site (see table 7.1 page 139). Polygynandrous groups were generally excluded from the subsequent analysis, as these were rare. In one monogamous group from 1997, the female was found dead on the nest. The male succeeded in acquiring another mate and continued to breed successfully but the data from this group was also excluded from the analysis.

The breeder types laid significantly different numbers of eggs over the three years (one-way ANOVA: $F_{2,102}=5.385$, $p=0.006$). Interestingly, there were no significant differences in terms between the breeder types of the mean number of chicks hatched (one-way ANOVA: $F_{2,102}=0.958$, N.S.) and chick survivorship after 5 days per group (one-way ANOVA: $F_{2,102}=1.316$, N.S.). All three breeder types raised similar numbers of chicks to 45 days of age (one-way ANOVA: $F_{2,102}=0.853$, N.S.).

Monogamous, polyandrous and polygynous groups initiated their first clutch attempt broadly at the same time of year (one-way ANOVA: $F_{2,102}=0.608$, N.S.).

Breeder type	N	Eggs laid	Chicks hatched	Chicks surviving after 5 days	Chick surviving at 45days	Week first laid
Monogamous	88	13.86±0.82	9.11±0.68	6.28±0.49	4.10±0.34	8.86±0.37
Polyandrous *	6	14.33±3.20	6.17±3.32	4.17±4.80	3.17±1.22	9.83±1.14
Polygynous °	9	23.00±3.55	11.11±3.48	8.33±2.68	5.33±1.58	7.89±1.18
Polygynandrous †	1	33.00±0.00	6.00±0.00	4.00±0.00	1.00±0.00	3.00±0.00

*all polyandrous groups in this data were comprised of 2 males and 1 female

°all polygynous groups were comprised of 1 male and 2 females

† the only polygynandrous group in this data comprised of 2 males and 3 females

Table 7.1. The mean (\pm S.E.) numbers of eggs laid, chicks hatched, survivorship of chicks after 5 and 45 days and the week when all four-breeder types commenced laying in the different breeder types over the duration of the study.

Notably of the four breeder types, the polygynandrous group had the poorest success with fewer than 19% of eggs laid hatching (see table 7.1 above). This results may, however, be atypical. In contrast, monogamous groups were the most successful in terms of the proportion of eggs laid subsequently hatching. Both polyandrous and polygynous groups hatched similar proportions of chicks. The proportion of chicks that survived 5 days post-hatch was greatest for polygynous groups.

7.3.2 A Comparison of the Reproductive Performance of IBP and Non-IBP Groups

Non-IBP and IBP groups had the same mean success per group and over the duration of the study began laying at the same time of the year (table 7.2 below). Of the 63 known IBP eggs over the three years only 19.05% (12 eggs) hatched. In contrast, over 60% of non-parasitic eggs hatched successfully (945/1546 eggs). Of the IBP chicks that hatched, 58.33% (7/12 eggs) survived to 45 days of age and in total, IBP groups produced an additional 0.27 ± 0.12 ($n=63$) chicks per group than non-IBP groups. The mean (\pm S.E.) total of chicks produced by IBP groups surviving to 45 days (including those from IBP events), was not significantly different from that produced by non-IBP groups (T-test assuming equal variance: $t=-0.0052$, $p=0.099$, $df=102$).

Nature of Groups	N	Mean (\pm S.E.)	Mean (\pm S.E.)	Mean (\pm S.E.)	Mean (\pm S.E.)
		Number of eggs	Survival of chicks	Survival of chicks	Week first
		hatched	after 5 days	at 45 days	laid
Non-IBP groups	79	9.16 \pm 0.73	6.41 \pm 0.55	4.08 \pm 0.38	8.96 \pm 0.41
IBP groups [†]	25	8.84 \pm 1.55	6.04 \pm 0.06	4.00 \pm 0.62	8.20 \pm 0.48
't' Test statistic		0.21	0.32	0.099	1.72
P		0.84	0.72	0.921	0.24

[†] the analysis of IBP groups excludes data from the success of eggs laid parasitically

Table 7.2. A comparison of the reproductive success of IBP and non-IBP groups and associated t-test output

7.3.3 Incubation Analysis

A total of 87 non-parasitised clutches (n=591 eggs) and 34 parasitised clutches (n=313 eggs) were used in the incubation analysis and the data for the three years research was pooled. Correlations were performed using pooled data from all breeder types but excluding those nests in which eggs were laid parasitically. Insufficient data was available to perform this analysis on the polygynandrous category, and results shown in table 7.3 (below) represent data from the complete clutches of 72 monogamous, 9 polyandrous and 6 polygynous breeding groups. Total clutch volume (cm³), mean incubation duration (days) and the number of eggs present in the nest when incubation commenced were significantly correlated with clutch size (see table 7.3 below). In contrast, the number of eggs present when incubation commenced was not significantly correlated with final clutch size. Clutch size was significantly correlated with clutch volume (Pearson's correlation coefficient: $r=0.92$, $p=0.0001$).

Interaction	Pearson's product moment	<i>p</i>
Clutch size vs number of eggs present in nest when incubation commences	$r=0.37$	0.0004
Clutch size vs incubation duration	$r=0.37$	0.0004
Number of eggs present in nest when incubation commences vs incubation duration	$r=0.02$	0.86

Table 7.3. Correlation Coefficients between various parameters of clutch size and incubation duration

7.3.4 The Incubation Duration of Different Breeder Types

Table 7.4 (below) summarises the mean clutch size, incubation duration and number of eggs present in nest when incubation commenced for the three breeder types used in the analysis. Polygynous groups clearly had the greatest mean total clutch size, incubation duration and number of eggs present in the nest when incubation was initiated. Monogamous and polyandrous groups were similar on these parameters. Mean incubation duration showed significant variance (one-way ANOVA: $F_{2,84}=12.05$, $p<0.0001$) but the number of eggs present in the nest when incubation commenced did not vary (one-way ANOVA: $F_{2,84}=1.63$, N.S.) between the three different breeder types. Polygynous groups, however, commenced incubation earlier into their laying sequence than either monogamous or polyandrous groups (one-way ANOVA: $F_{2,84}=3.495$, $p=0.035$ see table 7.5 page 143).

Breeder Type	Clutch size (eggs)	Incubation duration (days)	Number of eggs in nest when incubation commenced
Monogamous	6.50±0.23	22.25±0.20	4.44±0.14
Polyandrous	6.78±0.36	23.43±0.30	4.22±0.32
Polygynous	10.33±1.71	25.65±0.99	5.33±0.96

Table 7.4. The mean (\pm S.E.) clutch size, incubation duration and number of eggs present in nest when incubation commenced in monogamous, polyandrous and polygynous groups

Breeder type	Number of clutches	Number of days into laying that incubation commenced
Monogamous	72	4.44±0.14
Polyandrous	9	4.22±0.32
Polygynous	6	3.17±0.48

Table 7.5 The mean (\pm S.E.) number of days into laying the clutch when different breeder types commenced full incubation.

7.3.5 IBP and Host Incubation

The median number of IBP eggs laid per parasitised clutch was 1 (range 1-9 eggs) in the present analysis. Parasitised clutches were significantly larger and were incubated for longer than non-parasitised counterparts (see Table 7.6 below).

Variable	Non-parasitised clutches	Parasitised clutches*	t-test result	<i>P</i>
Clutch size	6.79±0.24	9.21±0.61	-3.02	0.0036
Incubation duration	22.61±0.21	23.76±0.32	-2.98	0.0034

*The data from parasitised clutches includes all nests that were parasitised during all stages of the host's laying period (df=119)

Table 7.6. The mean (\pm S.E.) clutch size and incubation duration of non-parasitised and parasitised nests

7.3.6 Hatch Period Analysis

124 non-parasitised clutches (n=842 eggs) and 36 parasitised clutches (n= 329 eggs) were used in the analysis of HP. HP data from the three years of research, excluding

those from parasitised nests, were pooled (Kruskall-Wallis test: $h=5.43$, N.S.) and correlation analysis performed on the data (see table 7.7 below). Both clutch size and egg volume were strongly correlated with the number of eggs hatched and HP. The number of eggs present in the nest when incubation commenced and the number of eggs hatched were only weakly correlated. Interestingly, HP significantly influenced 5-day mortality.

Variables	Spearman's correlation coefficient (r_s)	P
Clutch size vs number of eggs hatched	0.70	<0.0001
Clutch size vs HP	0.50	<0.0001
Clutch volume vs HP	0.46	<0.0001
Clutch volume vs number of eggs hatched	0.67	<0.0001
Number of eggs in nest when incubation commenced vs number of eggs hatched	0.18	0.043
HP vs 5-day mortality	0.37	<0.0001

Table 7.7. Spearman's Correlation coefficients between HP data and other hatching parameters in non-parasitised nests

7.3.7 Breeder Type Hatch Periods

A summary of the clutch size, number of eggs hatched per clutch and hatch period can be seen in table 7.8 (page 145). Polygynous groups in this data set had the greatest clutch size, greatest number of eggs hatching and longest HP.

Breeder type	Clutch size	Number of eggs hatched	HP (days)
Monogamous	6 (1-11)	6 (1-11)	3 (1-10)
Polyandrous	6 (4-9)	6 (4-9)	3 (1-6)
Polygynous	11 (5-13)	6.5 (4-11)	4 (2-8)

Table 7.8. Summary of the median (with range) clutch size, number of eggs hatched and HP of each breeder type

The breeder types laid significantly different clutch sizes (Kruskall-Wallis test: $h=7.14$, $p=0.03$) and clutch volumes (Kruskall-Wallis test: $h=8.75$, $p=0.01$). In contrast, HP duration was similar for all three breeder types (Kruskall-Wallis test: $h=2.12$, N.S.).

7.3.8 The Effect of IBP on Hatching Asynchrony

Parasitised clutches hatched slightly more host eggs and had longer HPs than non-parasitised nests (table 7.9 below). In addition, parasitised nests hatched approximately one egg per clutch more than non-parasitised clutches.

Type of Nest	N	Host eggs hatched	Total eggs hatched	HP (days)
Non-parasitised nests	124	6 (1-11)	6 (1-11)	3 (1-10)
Parasitised nests	36	5.5 (1-14)	6 (1-14)	3.5 (1-12)

Table 7.9. The median (with range) number of eggs hatched and hatch period of parasitised and non-parasitised nests

Parasitised clutches were significantly larger than non-parasitised counterparts (Mann-Whitney U-test: $U=3235.5$, $p<0.0001$). The clutch size of host groups was, however, not significantly different from that in non-parasitised nests (Mann-Whitney U-test: $U=2347.5$, N.S.). The number of host eggs hatched were similar in these two treatment groups (Mann-Whitney U-test: $U=2261.5$, N.S.), as was HP (Mann-Whitney U-test: $U=2453.5$, N.S.). A similar total number of eggs from parasitised and non-parasitised nests also hatched (Mann-Whitney U-test: $U=2629$, N.S.).

7.3.9 Hatching Mortality and Chick Survival Analysis

In total, 178 non-parasitised clutches ($n=1189$ eggs) and 47 parasitised clutches ($n=420$ eggs) were used in the analysis of hatching mortality and chick survival. Of these 178 non-parasitised clutches, 146 were monogamous, 17 were polyandrous, 12 were polygynous and 3 were polygynandrous clutches. Table 7.10 (page 147) summarises the hatching success and 5-day survivorship in each of the three years of research. Hatching success did not differ significantly from year to year (one-way ANOVA: $F_{2,161}=0.211$, N.S.). In contrast, 5-day mortality between years varied considerably (one-way ANOVA: $F_{2,161}=4.658$, $p=0.011$), with 1998 having the greatest survivorship and 1997 the least.

A seasonal decline between 5-day survivorship and time of hatching was only found in 1998 (Pearson's Product Moment Correlation coefficient: $r=-0.35$, $p=0.003$). Despite the yearly discrepancies between the variance of 5-day survivorship, it was thought necessary to pool the data over the 3 years to provide a baseline level of 5-day survivorship for each breeder type.

Year	Number of clutches	Number of eggs hatched per clutch	Chick survivorship per clutch after 5-days
1997	22	5.40±0.25	3.00±0.43
1998	69	5.67±0.26	4.48±0.24
1999	87	5.72±0.28	4.06±0.24

Table 7.10. The mean (\pm S.E.) number of eggs hatched and chick survivorship per clutch after 5-days in each of the 3 years of study

Analysis of the data on an annual basis is precluded by small sample sizes of individual breeder types clutch numbers. A summary of the mean number of eggs hatched and the survivorship of 146 monogamous, 17 polyandrous, 12 polygynous and 3 polygynandrous clutches can be seen in table 7.11 (below). Significant variances in the mean clutch size (one-way ANOVA: $F_{3,174}=29.21$, $p<0.0001$), number of eggs hatched (one-way ANOVA: $F_{3,174}=4.49$, $p=0.0046$) and 5-day survivorship per clutch (one-way ANOVA: $F_{3,174}=4.10$, $p=0.0076$) were found between the four breeder types.

Breeder type	Clutch size	Number of eggs hatched per clutch	5-day survivorship per clutch
Monogamous	6.36±0.16	5.43±0.16	3.90±0.15
Polyandrous	6.29±0.29	5.65±0.32	3.76±0.60
Polygynous	10.00±1.08	7.67±1.00	5.92±0.72
Polygynandrous	11.00±4.00	5.00±1.00	3.67±0.33

Table 7.11. The mean (\pm S.E.) clutch size, number of eggs hatched and chick 5-day survivorship per successful clutch of the four breeder types

Multi-female groups (polygynous and polygynandrous) had mean clutch sizes almost double those of single female groups (monogamous and polyandrous). Interestingly, polygynandrous groups hatched fewer eggs and had lower chick survivorship per clutch than any other breeder type. Polygynous groups hatched the most eggs and had greater chick survivorship after 5-days post hatch than both monogamous and polyandrous groups. Although mean polyandrous clutch sizes were greater than monogamous clutches both the number of eggs and 5-day survivorship were less than that recorded for monogamous clutches.

7.3.10 IBP and Host Chick Survivorship

Clutch and early survivorship data for parasitised and non-parasitised clutches is present in table 7.12 (below). The total clutch size of parasitised nests was, as expected significantly greater in than that of non-parasitised nests (Mann-Whitney U-test: $U=4694$, N.S.). Chick survivorship at 5-days was however, similar for both treatment groups (Mann-Whitney U-test: $U=3910$, N.S.).

Variable	Non-parasitised clutches	Parasitised clutches
Host clutch size	6 (1-15)	7 (3-16)
Total clutch size	6 (1-15)	8 (4-17)
5-day survivorship	4 (0-10)	4 (0-9)

Table 7.12. Median (with range) of host clutch size, total clutch size and chick 5-day survivorship of parasitised and non-parasitised nests

7.4. Discussion

7.4.1 Communal Breeding and Conflict at the Nest

The occurrence, stability and relative reproductive success of different mating systems in this Moorhen population illustrates the wide spectrum of male and female life history strategies. Whether individuals breed communally or monogamously and whom they breed with, is determined by many social, reproductive and environmental factors (Verner & Willson, 1966; Emlen & Oring, 1977). Individuals within each breeding group, strive to maximise their current and future reproductive success. This can, however, result in conflicts of interest within groups between breeders of the same sex (Davies & Houston, 1982; Mumme *et al.*, 1983, McRae, 1994). In particular, females and males in polygynous and polyandrous groups respectively compete for a greater share of reproduction to maximise their fitness. The outcome of such “game play” over reproduction may determine the relative stability and cohesion of these groups for future reproductive efforts.

The significant variability in the reproductive success of different breeder types per clutch attempt in the current study suggests that individuals may benefit from adopting specific mating systems. As breeding territories of male and female Dunnocks and Alpine accentors *Prunella collaris* overlap, mate sharing arises through conflicts of interest between individual (Davies & Houston, 1982; Davies *et al.*, 1995). In such conflict-driven mating systems dominant individuals do not benefit from sharing mates (Davies *et al.*, 1995) and therefore mating patterns do not influence breeding success (Davies & Houston, 1982). In contrast, Moorhen communal mating systems are unlikely to arise through such competition and conflict. As Moorhens pairs defend exclusive territories, communal breeding occurs by mutual

cost-benefit decision making by consenting members of the group (see also Goldizen *et al.*, 1998).

7.4.2 Mating Systems and the Reproductive Success of Individuals and Groups

In communally breeding Tasmanian native hens, group composition does not affect the number of young surviving. Hatching success and clutch size, however, increased with group size and female number in a manner similar to that found in the present study (Goldizen *et al.*, 1998). The overall number of Moorhen young produced to independence per group was not influenced by group size. Group composition, however, may promote (e.g. through greater parental care) and reduce (e.g. through reproductive conflict and inbreeding) reproductive success in certain breeder types. Major differences in the overall reproductive success per sex for each communal group type, raises the question of the adaptive benefits to each member of these breeding systems.

Over the duration of the study, females breeding in multi-female and males in polyandrous groups (assuming an equal share of reproduction- see section 7.4.3) produced fewer young to independence per individual than they would if they had bred monogamously. As such, the pattern of intra-sex reproductive success per breeder type is similar to that found in communally breeding Dunnocks (Davies & Houston, 1982) and Pied flycatchers *Ficedula hypoleuca* (Lubjuhn *et al.*, 2000). Females breeding in polyandrous groups, however, produced fewer young to independence than if they had bred monogamously, which contrasts with what has been found in Dunnocks. Such within group intra-sex reductions in reproductive success are unlikely to be sufficient to cause the disbanding of the communally-breeding group in current (and possibly) future years. This is especially so if the risks

of dispersal are high and the probability of finding a mate(s) is low as is the case in the present population (see sections 3.4.3 & 3.4.5). Nevertheless, it was observed that in one monogamous and one polygamous group, extended nest failure (through predation) appeared to cause these groups to suffer permanent 'divorce'. This suggests that high reproductive failure can affect breeding group stability. The social structure of Tasmanian native hen breeding groups can also be unstable during population crashes in which the reproductive success of the entire population is continually poor (Goldizen *et al.*, 1993).

The numbers of young hatching and surviving to independence per clutch per female and mating system over the duration of the study were lowest for multi-female groups. Conflict was evident over the share of reproduction that each female contributed in polygynous groups, regardless of relatedness. Successful communal clutches generally occurred only when all females within the group laid synchronously (sections 4.4.5-4.4.8). Partnerships between mothers and daughters were characterised by egg destruction and possible social suppression by the senior (mother) female. The daughter's chicks that hatch are, however, as likely to survive as their mother's (McRae, 1996a). It seems therefore, that female conflict over reproductive sharing does not extend to chick discrimination (both kin and non-kin based) and infanticide as has been described in other communally breeding species (e.g. Guira cuckoos Macedo & Bianchi, 1997b).

In addition to natural clutch losses through predation, mutual egg destruction and competition by individual females may affect the reproductive success and fitness of not only each female within the group but the group as a whole (Davies, 1986 but see Mumme *et al.*, 1983). This reproductive conflict reduces the number of successful clutch attempts achieved over the breeding season and probably accounts for the

observed frequency of synchronous laying in polygynous groups. The success of communal clutches can be lowered both by the loss of eggs from the communal clutch and reduced egg hatchability (Macedo & Bianchi, 1997b; Fernandez & Reboreda, 1998). Indeed, polygynous and polygynandrous groups hatched the lowest proportion of eggs per clutch attempt (see also section 7.3.7). Nevertheless, these costs incurred by female conflict are likely to be less than the potential lifetime benefits of group living (Mumme *et al.*, 1983). The reproductive success of males was greatest for those that bred polygamously (see also Soukup & Thompson, 1998; Lubjuhn *et al.*, 2000). Males may attempt, however, to inhibit the potentially costly female activity of egg destruction to maximise their reproductive success and fitness in the current breeding season (see section 7.4.7).

7.4.3 Multi-male Groups and Reproductive Sharing

Unrelated primate males in polyandrous Golden-lion tamarins *Leontopithecus rosalia* gain differing amounts of reproductive success depending on their social rank (Baker *et al.*, 1993). This occurs despite both males caring for the young. Dominant male Dunnocks rely on help (provisioning) given by subordinate males. Because of this, dominant males do not prevent subordinate male from mating (Davies, 1986; Davies & Houston, 1986 and see also Gowaty, 1981). It was impossible to determine (without the aid of genetic analysis) the paternity of polyandrous clutches. The exact reproductive success per male breeding in such groups is, therefore, uncertain. Moorhen males in polyandrous groups were observed, however, to copulate with the group female and assist with chick rearing. Pukeko and Tasmanian native hen males breeding in multi-male groups equally share copulation and help rear offspring

(Jamieson *et al.*, 1994; Goldizen *et al.*, 2000). It is likely that a similar egalitarian mating system occurs in Moorhen polyandrous groups.

Male body mass and resource holding potential (RHP) may determine the ability of males to access certain resources or territory size (Petrie, 1984). For example, larger male polyandrous Bronze-winged jacanas *Metopidius indicus* and Moorhens, defend larger territories (Petrie, 1984; Gibbons, 1985; Butchart *et al.*, 1999). The benefits to co-males breeding in polyandrous systems may, therefore, include the ability to successfully defend good quality territories from larger conspecifics (see also section 7.4.4). Females in polyandrous groups would then have access to higher quality territories and would benefit from two males assisting in chick rearing and predator defence. Reproductive success per female in this breeding system was, however, slightly less than females in monogamous systems. It is possible, however, that communal living increases the survivorship of individuals (see Mumme *et al.*, 1983). Females in stable polyandrous groups may consequently have a greater lifetime reproductive success than their monogamous counterparts.

7.4.4 Group Living, Territory Quality and Reproductive Success

Differences in the seasonal reproductive success within and between breeder types may arise through variability in female fecundity as expressed by egg size and/or quality (French & Tullet, 1991) as well as clutch size. It may also occur because of variability in male quality and RHP (Petrie, 1983; Gibbons, 1985) as well as seasonal environmental changes in territory quality and food supply (Davies, 1986; Wiggins *et al.*, 1994). Territory quality affects the reproductive success of specific breeding groups in Moorhens (Gibbons, 1985). Pairs with larger territories had greater

seasonal reproductive success, began breeding earlier and, consequently, had more broods per year than those pairs on small territories (op. cit.).

The adoption of a group living style is based upon the intrinsic characteristics of sociality that increase both survival and lifetime reproductive success (Macedo & Bianchi, 1997). By breeding communally, individuals can not only share existing territories but also retain the location in the current and future year(s) (Goldizen *et al.*, 1998; Butchart *et al.*, 1999). The retention of territories may greatly benefit all members of the communal group. For example, communally breeding Acorn woodpeckers have increased survivorship and are able to retain quality territories from year to year. This increases their individual lifetime reproductive success compared to that of monogamously breeding woodpeckers (Mumme *et al.*, 1983; Koenig & Mumme, 1987).

Moorhen territory size in the present study did not differ significantly between breeder types over the 3 years. Nest predation was strongly influenced by nest exposure and vegetation height surrounding the structure suggesting the importance of vegetative cover in Moorhen nesting success. In general, communal groups defended territories that had substantial amounts of layered vegetative cover (grass, herb and shrub), easy access to water and were relatively undisturbed by humans. It was not, however, established whether communal group territories were of better quality (e.g. nest site availability and food supply/quality) and suffered less predation than territories of monogamous birds. The decision to breed communally in Great reed warblers *Acrocephalus arundinaceus* appears related to levels of nest predation (Hansson *et al.*, 2000). Future research examining relationships between territory/individual quality, nest predation and breeder type may improve our

understanding of this interesting aspect of communal breeding formation in Moorhens.

7.4.5 Chick Survivorship

The length of the breeding season varied considerably between groups. The majority began breeding at the same time of year, perhaps reflecting a synchronizing response to environmental stimuli (e.g. increasing ambient temperatures, day-length and food quality/abundance). Many multi-brooded species often breed under sub-optimal conditions where limiting resources may hinder an individual's reproductive success (Davies, 1992). Consequently, Moorhen reproductive effort and success varies seasonally (see Gibbons, 1985). In particular, the reproductive success of groups in this study was generally extremely poor at the extremities of the breeding season (i.e. prior to March or after August).

Over the duration of the study, the breeding group types raised similar numbers of young to independence (45 days) despite significant disparities in the clutch sizes and numbers of eggs laid (see also sections 4.4.4 & 7.3.1). The number of eggs laid and hatched per breeding group is directly related to the number of breeding females present in the group (see also Goldizen *et al.*, 1998). Because of this, polygynandrous groups comprising three females and two males produced the greatest number of eggs per breeder type. There was no evidence of clutch reduction or adaptation in response to breeding communally in Moorhens (see also Koenig & Pitelka, 1979; Craig, 1980; McRae, 1994; Goldizen *et al.*, 1998). Such adaptation would be advantageous in terms of the energy expended in parental care and the relatively poorer hatching success of multi-female groups. Group stability and success, may be maintained, however, by all members of the breeding group contributing directly to the group's

reproductive effort (Vehrencamp, 1983; Keller & Reeve, 1994; Davies, 1986; Jamieson *et al.*, 1994). Infanticide can occur if such provisions for reproductive equality are not met in reproductive sharing (Macedo & Bianchi, 1997b).

Polygynous groups reared more chicks to independence than did monogamous pairs. Polyandrous groups, however, raised slightly more chicks to independence than polygynous counterparts (52% of chicks produced that survived compared to less than 47%). A female paired with two males therefore, benefit reproductively. Polygynandrous groups were largely excluded from the detailed analysis because of their rarity. It is important, however, to recognise the low success of this particular breeding system at WWT Llanelli. The breeder types attempted similar numbers of clutches, although polygynous groups attempted the greatest number per year. Polygynous and polygynandrous (and, to a lesser extent, polyandrous groups) were often comprised of parents and offspring from the previous breeding season(s) (see section 3.4.5). Incestuous mating may account for the relatively low reproductive success of these groups (section 7.4.6). In particular, the only polygynandrous group recorded in 1999 was comprised of parents, two daughters and one son from the previous year. This group raised only one chick to independence, despite laying 33 eggs over the entire breeding season. Most of the eggs laid by the daughters in this group failed to hatch and were abandoned after the mother's eggs had hatched. Post-hatch survival of chicks from this group (in particular those of the daughters) was also poor in comparison to neighbouring groups. Interestingly, despite its low reproductive success of this group, weekly visits to the study site in the year following the studies' completion, revealed that this group was comprised of the same individuals and occupied the same territory.

Factors other than incest may be responsible for the low reproductive success of polygynandrous groups. For example, the 1999 polygynandrous group's territory was located close to a well-used path and was consequently prone to frequent human disturbance. Observations of this group revealed, that during incubation, adults regularly left the nest for considerable periods of time. Periodic cooling of eggs during incubation may affect their subsequent hatchability and chick weight at hatching, as well as increasing the cost of incubation to the parents (Booth & Rahn, 1991; Suarez *et al.*, 1996). Such affects on polygynandrous clutches (which were often greater than 15 eggs), may result in greater hatch losses through reduced fitness of hatched chicks (Fernandez & Reboreda, 1998).

7.4.6 Incest and Communal Breeding

Strong natal philopatry and short-distance dispersal in co-operatively breeding species (such as the Moorhen) can increase the probability of within-group incest (Koenig & Pitelka, 1979; Craig & Jamieson, 1988). Pukekos breed incestuously and often results in a low survivorship of chicks (Craig & Jamieson, 1988). It is possible that selection for inbreeding avoidance mechanisms can only evolve if incest results in severely reduced fitness of offspring produced (McRae, 1994). Low survivorship of offspring from Moorhen inbreeding suggests that inbreeding can allow the expression of deleterious genotypes (McRae & Burke, 1996). The prevalence of inbreeding within communally groups at WWT Llanelli suggest that inbreeding avoidance mechanisms (such as those described in Acorn woodpeckers by Koenig *et al.*, 1998) have not yet fully evolved or that incest is the best available option under certain circumstances in Moorhens.

7.4.7 Incubation and Hatching Patterns in Moorhens Breeding Systems

Incubation is costly in Moorhens (Siegfried & Frost, 1976) and its duration is strongly related to clutch size (section 7.3.3). A greater energetic input, therefore, may be required per individual in multi-female clutches than in single clutch groups due to the presence of many eggs (Fernandez & Rebores, 1998). As clutch size increases, it is more likely that incubating individuals will have to rotate eggs more frequently to ensure adequate incubation of the whole clutch. Such increased egg jostling may increase in a greater probability of accidental loss of eggs from the nest (Macedo & Bianchi, 1997b). Indeed, the probability of accidental egg loss from multi-female nests during incubation was greater than from single clutch nests in the present study. The energetic demand of longer incubation and increased nest attentiveness in double clutches may also be greater than for single female clutches. By sharing incubation more equally between all members of the breeding group (which is not the case in monogamous pairs Siegfried & Frost, 1976), these costs can be reduced in communal breeding. It is not yet known, however, whether this actually occurs in polygynous groups.

There was a strong relationship between clutch size and HP. Consequently, clutches laid by polygynous groups had longer (but not significantly so) HPs than either polyandrous or monogamous groups. An increased HP may benefit the breeding group by distributing the energetic demands of the newly hatched chicks over several days. This is consistent with both the peak load (Hussell, 1972) and sibling rivalry (Hamilton, 1964; Hahn, 1981) hypotheses of hatching asynchrony.

The demands of the larger number of chicks from polygynous clutches are likely to exceed those of single clutch groups. It might, therefore, pay polygynous groups to commence incubation earlier to promote HA. In agreement with this prediction,

polygynous groups initiated full incubation almost a day earlier than monogamous and polyandrous groups (section 7.3.2). This occurred despite there being at least one egg more in these nests than in those of single female clutches at the onset of incubation.

Initiating incubation earlier in communal groups may also be an adaptive mechanism reducing or even preventing female conflict over reproductive sharing (see also sections 4.4.5-4.4.7). Communal laying is often associated with the slightly asynchronous production of eggs (particularly in mother-daughter partnerships) and mutual egg destruction. Incubation in Moorhens may be initiated by males, who predominately incubates in monogamous pairs (Siegfried & Frost, 1976, see plate 7.1, page 158). By commencing incubation earlier, a male might prevent females from aborting a laying attempt through mutual egg destruction. As males stand to lose fitness in female-female conflict, this may be a counter strategy.

Polyandrous and monogamous groups commenced incubation when similar numbers of eggs were present in the nest. This is unsurprising since these groups have similar clutch sizes. It suggests that expected clutch size rather than group size influences the incubation behaviour and subsequent hatching pattern in Moorhens. The presence of two males (who may perform the majority of incubation) in polyandrous groups may allow significant energy savings to female, promoting her current and lifetime fitness.

7.4.8 Incubation Behaviour: The Risks of Predation and IBP

In all breeder types, eggs were often ‘warmed’ before clutch completion and before full incubation occurred. In several cases, egg warming took place on first laid eggs. Eggs warmed prior to the commencement of full incubation show improved



Plate 7.1. Male Moorhen incubating a monogamous clutch.

hatchability (Wilson, 1991 but see Persson & Göransson, 1999). In addition, eggs that are not incubated show declining viability, thus promoting the strategy of early warming of eggs (R.Edwards, pers.comm; Arnold *et al.*, 1987). The initiation of incubation before clutch completion may be adaptive in areas of high predation risk by reducing the exposure of eggs to potential predators (Persson & Göransson, 1999).

Many species increase their time spent on nests as the laying sequence progresses (Craig, 1980; Grenier & Beissinger, 1999; Persson & Göransson, 1999). This may be a defense of the investment in the face of potential predation, as well as a means of improving egg hatchability. Moorhens were often observed provisioning their mates on the nest, a factor strongly associated with nest attentiveness and perceived predation risk (Martin & Ghalambor, 1999). Interestingly, after disturbance, it was often the male who returned to the nest (see also Craig, 1980). Adult male Moorhens are larger than females (Wood, 1974; Petrie, 1983; Cramp & Simmons, 1980; Gibbons, 1985) and are thus more suited to nest defence against predators than the smaller, less tenacious females (Forman *et al.*, 1998).

Since IBP's are able to lay eggs even when the host is on the nest, the early commencement of incubation observed in many Moorhen clutch attempts is unlikely to be a counter-measure against the risk of parasitism (McRae, 1996b). IBP's successfully laid eggs during and after the host had begun incubation (see section 6.3.3). There was no correlation between the density of female Ring-necked pheasants around nests (and hence parasitism risk) and when females initiated incubation suggesting that the increasing risk of IBP is not countered by earlier commencement of incubation in this species (Persson & Görensson, 1999).

7.4.9 Hatching Asynchrony

Several studies have reported inter-female variation in the incubation pattern used by individual females similar to that reported in this study (e.g. Wiebe & Bortolotti, 1994; Wiebe *et al.*, 1998; Grenier & Beissinger, 1999; Persson & Göransson, 1999). Females may be able to adapt hatching patterns to suit environmental conditions (e.g. food supply). They may also change incubation patterns to reflect their own body condition (Wiebe & Bortolotti, 1994; Persson & Göransson, 1999). For example, Eurasian kestrels *Falco tinnunculus* females with poor body conditions were characterised by ‘pulsed’ and exaggerated hatching patterns (Wiebe & Bortolotti, 1994). This suggests that HA, rather than being adaptive in some species or individuals, may simply be a consequence of the particular incubation behaviour employed by females with different energy budgets. Research is needed to examine the different types of incubation patterns exhibited by Moorhen females in different breeding types, to determine the roles of mating system and group/individual body condition on hatching asynchrony.

7.4.10 Chick Mortality

Commencing incubation during the laying phase results in the majority of Moorhen clutches hatching asynchronously, with some larger clutches hatching over 8 days (see also Gibbons 1985). There may, however, be a cost to this hatching pattern, as chick 5-day post hatch mortality was significantly correlated with HP duration. First hatched chicks often remained within the egg nest. After the majority of eggs had hatched, chicks were often led to brood nests constructed some time before the clutch hatched (see Wood, 1974). Many first hatched chicks were found dead in the egg nest. Although the cause of death was generally unknown (but see Horsfall, 1984;

Skagen, 1988; Slagsvold, 1997), some chicks appeared to have been crushed by parents assisting the subsequent hatching of the rest of the clutch. Chick survival may have also been affected during extended HPs as the amount of parental and chick activity at these nests may have attracted potential predators.

The average 5-day mortality of chicks per clutch differed between years at the study site, although chick survivorship declined seasonally only in one year of the study (c.f. Gibbons, 1985). This yearly trend appeared to mirror the local abundance of predators (namely Grey herons, Carrion crows, Jackdaws and rats) and the climatic conditions in each year of the study. The study site is located on the edge of the Loughor estuary and is prone to strong winds and high rainfall during the summer months (G.Williams, pers.comm.). It is likely that poor weather (especially cold spells with heavy rainfall and strong winds) killed many chicks (particularly at the extreme ends of the breeding season) by exposure in certain years. The greatest loss of chicks per clutch per week occurred in 1997, a year in which rat and corvid numbers were very high throughout the breeding season and the weather was frequently poor. In contrast, chick survivorship was greatest in 1998 when predator numbers were controlled and the weather was less harsh. Respiratory diseases and avian TB were prevalent in certain areas of the study site, which may also account for a significant proportion of chick losses in each year.

7.4.11 IBP and Host Group Reproductive Performance

Few studies have been able to determine the potential lifetime reproductive and associated fitness costs of IBP on host group (but see Brown & Brown, 1998). Moorhen IBP had no significant effect on the reproductive success of host groups. Indeed, host groups raised as many chicks to independence as did individuals with

non-parasitised nests (see also Gibbons, 1985; McRae, 1994). Host groups appear to be able to acutely absorb (i.e. within the current breeding season) the costs of IBP with little discernible affect on their reproductive performance. In comparison, host clutch size and the subsequent survivorship of ducklings from parasitised nests are negatively affected by inter- and intra-specific brood parasitism in the precocial Canvasback duck, *Aythya valisineria* (Sorenson, 1997).

IBP eggs laid early in the host's laying period occasionally caused that individual to abandon or destroy their clutch (see section 6.3.7). As Moorhens are multiple-clutched indeterminate layers the loss of a few eggs at the start of laying may not be a serious drain on female resources. Indeed, host females in these instances often re-nested a few days after aborted laying attempts, without any observable affect in clutch size. Host eggs may be lost accidentally during the laying of parasitic eggs (Lyon & Everding, 1996; Sorenson, 1997). The displacement of host eggs by IBPs in this study, however, was rarely recorded at greater frequencies than in unparasitised nests.

Moorhen chicks require considerable parental care during the dependence stage of development (section 7.4.1) confirming the findings of Gibbons (1985). The rearing of additional chicks within the brood may prove to be extremely costly to hosts although these costs (e.g. increased vigilance, provisioning and brooding) have yet to be assessed in Moorhens. Many IBP attempts were poorly timed with respect to the hosts own laying sequence (see sections 6.3.5 & 6.4.3). Consequently, few parasitic eggs hatched. It was, therefore, rare for host groups to incur any cost of rearing parasitic chicks.

Host parents should reduce their parental investment as a response to IBP (Owens, 1993; Westneat & Sherman, 1993). As parasitised clutches showed equal or even

higher survival of parasitised clutches in which IBP eggs hatched there appears to be no parental discrimination between host's and parasitic chicks within IBP species (e.g. Canvass back ducks, Sorenson, 1997; American coots, Lyon, 1991a; 1991b). Furthermore, there was no evidence of kin-discrimination by host parents between their own offspring and parasitic chicks in Moorhens (e.g. McRae, 1997a). Indeed, successful temporary and permanent adoption has been observed in this species, in which adopted chicks from neighbouring groups were reared to fledging (Gibbons, 1985; pers.obs). The high probability that neighbouring Moorhen groups are related (McRae, 1994), means that kin-altruistic adoption, such as that recorded in Common gulls (Bukacinski *et al.*, 2000), cannot be ruled out as facilitating this behaviour. Any differential mortality of host and IBP chicks seems likely to be due to phenotypic differences than parental care (McRae, 1997a).

As incubation is significantly correlated with clutch size, it is unsurprising that parasitised nests (being significantly greater in size) were incubated for longer than non-parasitised nests. Similar increases in the incubation duration of parasitised nests have also been found in Pied avocets *Recurvirostra avocetta* (Hotker, 2000). Gibbons (1985) calculated that IBP increased the incubation duration of Moorhen host clutches at a rate of 0.5 days per parasitic egg laid. The costs of incubation in Moorhens are known to be high, particularly to males (Siegfried & Frost, 1976). The presence of additional eggs in a nest might consequently affect his fitness (and, to a lesser extent, the female of the group) by increasing the overall energetic cost of incubating. Even if IBP eggs fail to hatch, this cost is incurred.

Very few incubated clutches were abandoned by hosts when parasitised. As the investment in the clutch is high, it is likely that parents are forced to absorb the cost of accepting and incubating IBP egg(s) (section 6.4.5). Parasitised clutches often

exhibited slightly greater HA than non-parasitised counterparts. This difference was not significant and is likely to be a feature of the greater size of parasitised clutches. IBP did not appear to reduce the current host's ability to hatch and rear their own offspring. Nevertheless, it is impossible to determine whether a host's lifetime reproductive success and fitness were affected by IBP in this species as in Cliff swallows (Brown & Brown, 1998).

Gibbons (1986) noted that IBP predominately occurred towards the start of the breeding season (see also Hotker, 2000). IBP in the current Moorhen population was mainly influenced by opportunity and not factors such as seasonality. It should be noted, however, that environmental factors (e.g. predation or sub-optimal breeding conditions) may affect the relative frequency and success of this strategy (McRae, 1994; 1997a; Jamieson *et al.*, 2000). Since the reproductive success of individuals varies seasonally (Gibbons, 1985), Moorhen IBPs would benefit from parasitising at times when conditions are favourable for chick survival (Yamaguchi, 2000). In the current study, IBPs laid parasitically throughout the year. They did not wait for optimal conditions (e.g. favourable weather, good quality hosts) that may promote the survival of IBP eggs/chicks before attempting to lay parasitically. In contrast, Pied avocet females predominantly laid parasitically in high density breeding colonies where breeding success was enhanced, thus adopting a parasitic strategy that increased its success (Hotker, 2000).

A female could maximise the success of IBP eggs by spreading the laying of over several nests (Petrie & Møller, 1991). Only a small minority of female Moorhens laid, however, parasitically in several host nests concurrently, perhaps reflecting the constraint of host availability. The ability of host groups to care for parasitically-enlarged clutches may restrict the number of IBP eggs laid in any one nest. The

increased energetic load of incubating and rearing a large number of parasitic eggs/chicks in addition their own, may decrease the host parent's ability to care for all (kin and parasitic) chicks. Indeed, many hatching variables including chick mortality were strongly associated with clutch size (this study) indicating some energetic ceiling for parental care with respect to brood size (see also Royama, 1966; Drent & Daan, 1980; Tinbergen & Verhulst, 2000). It is perhaps unsurprising that most IBPs laid only one egg per host nest, although up to 9 eggs were recorded as being laid parasitically in a single host nest by the same female (but see also section 1.3.2).

7.4.12 Reproductive Success of IBPs

It has been claimed that the majority of IBPs are in poor condition and are consequently unable to successfully raise their own broods (Yom-Tov, 1980; Petrie & Møller, 1991). Many studies, however, have concluded that IBPs have equal or greater reproductive success than non-IBPs (e.g. Møller, 1987; Lyon, 1991a; McRae, 1994; Brown & Brown, 1998; Hotker, 2000). Female Moorhens employing a dual strategy of IBP and parental care had similar fecundity, clutch sizes (sections 5.3.5 & 5.3.6) and reared the same number of young to independence as females that laid only in their own nests (section 7.3.2). Females that use IBP may have an evolutionary edge over those females that do not, as they are able to potentially increase their lifetime fitness through the occasional success of IBP (e.g. Brown & Brown, 1998).

Despite the obvious potential benefits of IBP to the parasitic female (and indirectly her mate), IBP's did not produce significantly more young per group than non-parasitic groups. IBP groups, however, showed greater variance of reproductive success (chicks produced to independence) than non-parasitic groups consistent with previous findings in a similar Moorhen population (McRae, 1994). For some

individual females, IBP resulted in a net increase indirect fitness. Since, however, the majority of IBP eggs laid were poorly timed in relation to the host's laying sequence, few chicks hatched from parasitic eggs.

7.5 Conclusions

1. The four breeder types had similar reproductive success (number of offspring raised to 45 days) over the duration of the study, despite significant differences in the number of eggs and chicks hatched between groups. In particular, polygynandrous groups produced the fewest chicks to 45 days.
2. Polygynous clutches were incubated for longer and had extended HPs than any other breeder types. There were significant variations between the hatching success of each breeder type per clutch attempt, with polygynous groups producing the greatest number of young to 45 days of age.
3. When the success of eggs laid parasitically is excluded, both IBP and non-IBP groups produced similar numbers of young to independence. When the success of IBP eggs was taken into account IBPs did not have greater reproductive success than non-IBPs.
4. IBP significantly increased host clutch size. This resulted in an increased incubation and hatch period of affected clutches. The number of hosts eggs hatched in nests in which eggs had been laid parasitically was no different to that recorded in identical but unparasitised nests. IBP, therefore failed to impose excessive costs on hosts.

CHAPTER 8

MOORHEN FAMILY LIFE AND PARENT-OFFSPRING INTERACTIONS

“What anxious parents those old moorhens were, and how they fussed after their brood”

Frances Pitt (Waterside Creatures, 1925, George Allen & Unwin Ltd, London)

“One parent is enough to spoil you but discipline takes two”

Clive James (Unreliable Memoirs, 1980, Chatto & Windus, London)

8.1 Introduction

The young of semi-precocial species (e.g. American coots and Moorhens) are partially dependent on their parents for food provisioning. This is particularly apparent in the early phase of post-hatch brood development, where poor motor coordination skills and foraging efficiency limit the ability of young to obtain their own food. These skills improve with age and provisioning behaviour is costly to parents, so one would expect that offspring would be encouraged to independently fulfil their own nutritional requirements as quickly as possible. During this transitional process, offspring may be in “conflict” with parents over the amount of care provided and the timing of their independence (Trivers, 1972; 1974).

The clutches of many avian species hatch asynchronously, creating brood size hierarchies (see sections 1.3.9 & 1.5.4). In order to maximise their current investment in the brood, parents must prevent the monopolisation of care by larger offspring, feed smaller offspring at greater rates or facilitate brood reduction (section 1.5.2). In addition, parents of sexually dimorphic species are forced to adjust their level of care to each offspring sex to avoid a biased mortality favouring the larger sex.

8.2 Aims

The aims of this chapter were to look at the effects of the following variables on chick size and sex:

1. Food provisioning behaviour of parents.
2. Chick self-provisioning rates.
3. Parent-offspring interaction by both sexes.

8.3 Database

The mean clutch size (\pm S.E.) of the behavioural study broods was 8.05 ± 0.76 eggs per clutch ($n=177$ eggs). The mean (\pm S.E.) number of chicks hatched per study brood was 6.23 ± 0.46 per brood ($n=137$ chicks). The mean (\pm S.E.) survival of young at 60 days was 3.64 ± 0.24 young per brood ($n=80$ chicks).

8.4 Results

8.4.1 Parental Feeding

Parents were observed for a total duration of 26017 minutes over the three years (for 13035 and 12982 minutes male and female parents, respectively). Parents were similarly observed for a total duration of 16154 minutes in the study of sexed chicks (for 8118 and 8036 minutes male and female parents, respectively). The high frequency of 0 feeds per minute recorded for all chick categories, resulted in summarising the mean parental feed rates per minute to large and small chicks rather than the respective medians and ranges (table 8.1 page 171). Parental feed rates per minute decreased significantly with increasing chick age for both large (Spearman's Rank Correlation coefficient: $r_s=-0.49$, $p<0.0001$) and small chicks (Spearman's Rank

Correlation coefficient: $r_s = -0.52$, $p < 0.0001$). Figure 8.1 (page 172) illustrates the decline in feeds given by both parents to large and small chicks, respectively.

There was no difference between the rate that male and female parents fed large chicks (Mann-Whitney U-test: $U = 8068593$, N.S.). Similarly, male and female parents fed small chicks at a similar rate (Mann-Whitney U-test: $U = 8143139$, N.S.).

Parent	Chick	N (minutes)	Parental feed rate per minute
Male	Large	6515	1.52±0.041
	Small	6520	1.71±0.044
female	Large	6466	1.57±0.044
	Small	6516	1.67±0.045

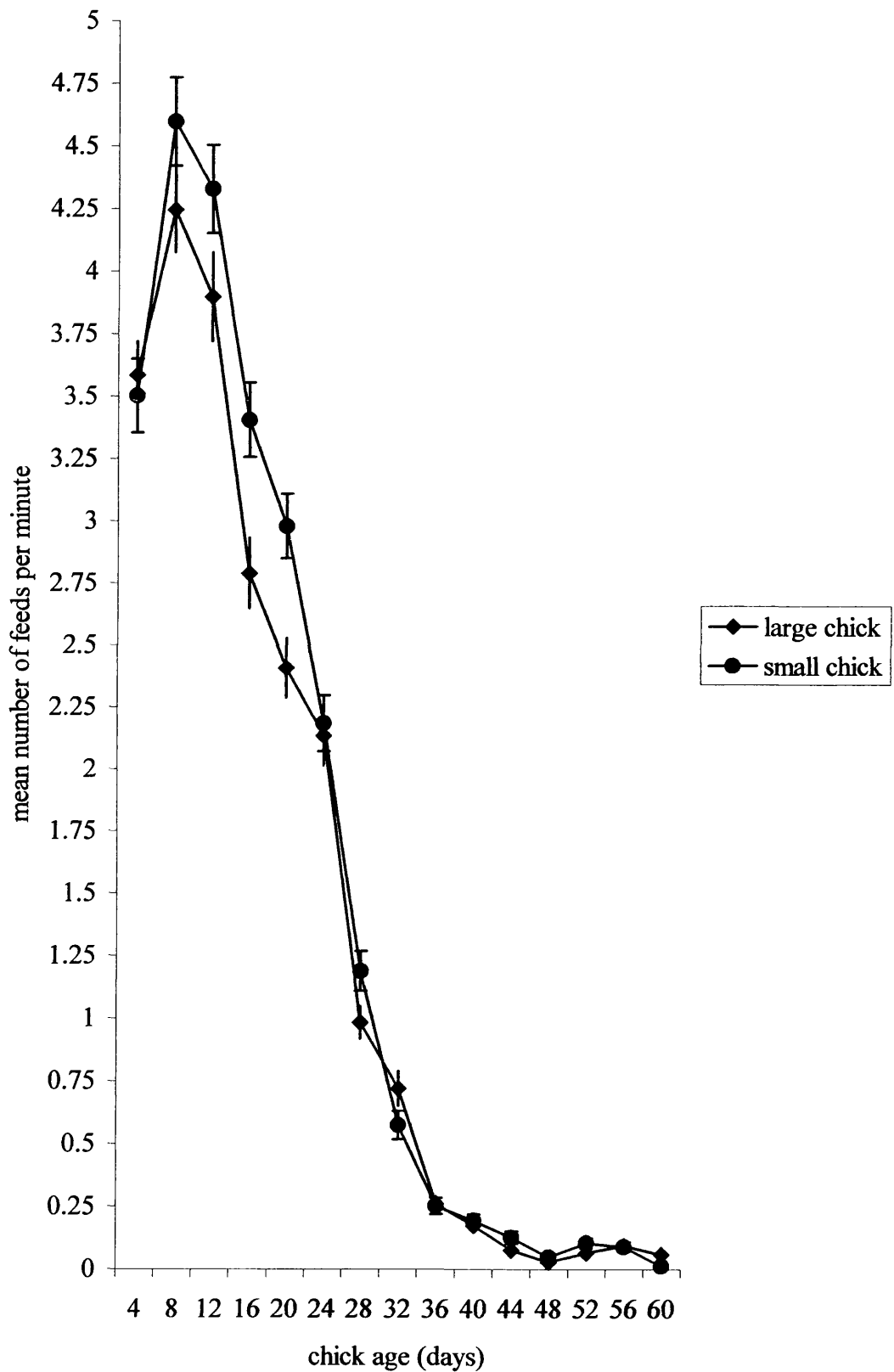
Table 8.1. The mean (\pm S.E.) parental feed rate per minute to large and small chicks by male and female parents

The feeding data was consequently pooled for both parental sexes. Small chicks were fed significantly more per minute than large chicks by parents of both sexes (Mann-Whitney U-test: $U = 86809237$, $p < 0.0001$).

8.4.2 Parental Feeding and Chick Sex

The median number of parental feeds to each chick category was 0. Table 8.2 (page 173) summarises, therefore, the mean feed rates per minute to each category of chick size and sex by male and female parents (see also section 8.3.1). Both male and female parents fed male chicks (both large and small) at the same rate per minute throughout the 60 day observation period (Mann-Whitney U-test: $U = 11041589$, N.S.). Male parents, however, fed female chicks (both large and small) at a significantly

Figure 8.1 Mean parental feed rate per minute to large and small chicks of differing age



greater rate per minute than female parents (Mann-Whitney U-test: $U=5532028.5$, $p=0.0009$).

Adult sex	Chick sex	Chick size	N (minutes)	Parental feed rate per minute
	Male	Large	2357	1.61±0.072
		Small	2474	1.69±0.071
Male	Female	Large	1598	1.48±0.077
		Small	1689	1.72±0.085
	Male	Large	2115	1.70±0.078
		Small	2476	1.72±0.073
Female	Female	Large	1910	1.52±0.082
		Small	1585	1.69±0.097

Table 8.2. The mean (\pm S.E.) feed rates per minute by male and female parents to large and small chicks of each sex

In order to ascertain whether there is any sexual bias exists in the feeding behaviour of Moorhen parents, individual analyses were performed between each type of parent and chick size and sex (table 8.3 page 174). Male parents fed small female chicks at a significantly greater rate per minute than female parents (test 4). Female parents fed large and small male chicks at rates significantly greater than their female siblings (tests 7 and 8). Female parents also fed male chicks at a significantly greater rate per minute than to female chicks (test 10). Male parents provisioned male and female chicks at similar rates per minute (tests 5,6 and 9).

Test	Variable 1		Variable 2		Mann-Whitney Test output		
	Parent	Chick size and sex	Parent	Chick size and sex	N	U-score	<i>p</i>
1	Male	Large male	Female	Large male	4472	2523596.5	0.36
2		Small male		Small male	4900	3002826	0.96
3		Large female		Large female	3508	1485718.5	0.083
4		Small female		Small female	3274	1278039	0.0052
5		Large male	Male	Large female	3955	18921995	0.74
6		Small male		Small female	4163	2122536.5	0.28
7	Female	Small male	Female	Small female	4011	1864899.5	0.042
8		Large male		Large female	4025	1952395.5	0.019
9	Male	Male	Male	Female	8118	8023351.5	0.31
10	Female	Male	Female	Female	8036	7677134.5	0.0015

Table 8.3. The results of Mann Whitney *U*-tests between feed rates per minute recorded to large and small chicks of each sex by male and female parents.

8.4.3 Chick Self-Feeding

Chicks were observed for a total of 12709 minutes over the three years (large and small chicks 6457 and 6252 minutes, respectively). Sexed chicks were observed for a total of 7985 minutes. Male chicks were observed for 4470 minutes (large and small chicks 2218 and 2252 minutes, respectively). Female chicks were observed for 3515 minutes (large and small female chicks 1812 and 1703 minutes, respectively). Large chicks fed themselves at a significantly (Students t-test: $t=6.078$, $p<0.0001$) greater mean (\pm S.E.) rate per minute than small chicks (32.32 ± 0.25 cf. 30.17 ± 0.25 feeds per minute).

8.4.4 Self-Feeding and Chick Sex

Male and female chick self-feed rates per minute (see table 8.4 below) were positively correlated with age (Spearman's Correlation coefficient: $r_s = 0.79$, $p < 0.0001$; see figure 8.2 page 176).

Chick sex	Chick size	N	Self-feeds per minute
Male	Large	2218	32 (0-107)
	Small	2252	33 (0-101)
Female	Large	1812	31 (0-106)
	Small	1703	28 (0-101)

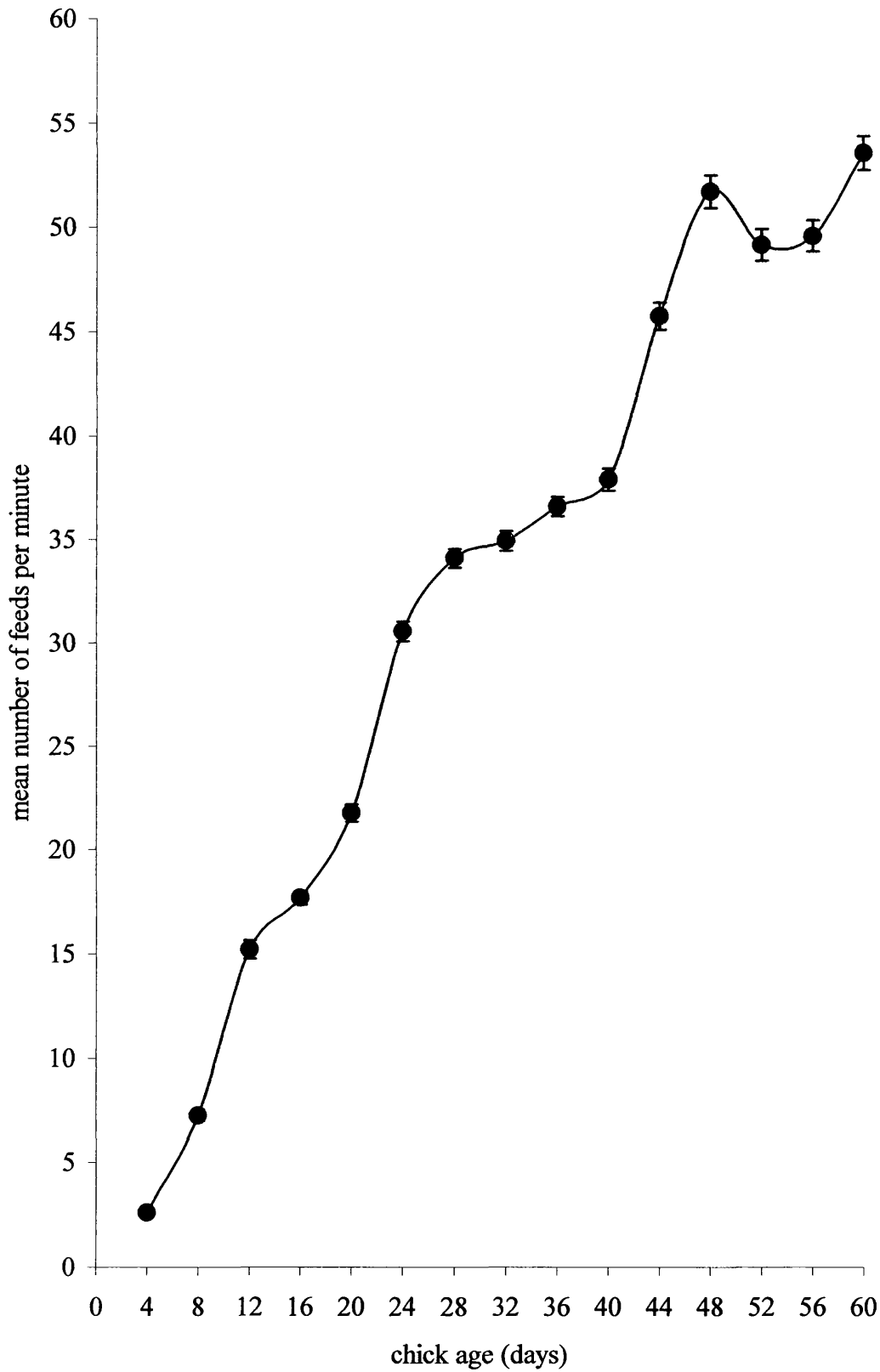
Table 8.4. The median (with range) self-feed rates per minute (4-60 days of age) for chicks of different size and sex

The median chick self-feed rates per minute of both sexes (pooling large and small chicks) were not significantly different (Mann-Whitney U-test: $U = 7714557$, N.S.). The median self-feed rate of large male chicks was, however, significantly less than that of their female counterparts (Mann-Whitney U-test: $U = 2088823$, $p = 0.03$). In contrast, small male chicks fed themselves at a greater rate per minute than female counterparts (Mann-Whitney U-test: $U = 1768549.5$, $p < 0.0001$).

8.4.5 Parent-Offspring Conflict: Touse Frequencies

Parents were observed for a total duration of 25280 minutes (12670 and 12610 minutes for male and female parents, respectively). A total of 977 touses were recorded (604 and 373 to large and small chicks, respectively). In the analysis of sexed chicks, male and female parents were observed for 7689 and 7660 minutes,

Figure 8.2 The increase in mean self-feeding rate per minute of chicks with increasing age



respectively and 542 touselles were recorded. Of these touselles, 266 were directed to male chicks (176 and 90 large and small chicks, respectively) and 276 to female chicks (137 and 139 to large and small chicks, respectively). During the observation period, male and female parents touselled chicks of each size and sex at similar frequencies (G-Test: $G=3.02$, N.S.). Interestingly, female parents touselled small female chicks more frequently than large female counterparts, although as with male parents, large male chicks were touselled more frequently than small counterparts (see figure 8.3a & b pages 178 & 179, respectively).

8.4.6 Chick Behaviour Before Touseling Events

The behaviour of large and small chicks before touselles (begging, self-feeding or resting) was similar (G-Test: $G=0.56$, N.S.). Begging was the most common chick behaviour prior to a tousel. Large and small chicks begged in 87.31% ($n=461$) and 87.74% ($n=322$) of instances, respectively. Age-related differences in chick behaviour prior to a tousel event occurring can be seen in figures 8.4a & b (pages 180 & 181, respectively). Large and small chicks were more frequently recorded feeding themselves or resting prior to a tousel occurring with increasing age.

8.4.7 The Behaviour of Sexed Chicks Before Touseling Events

The analysis of chick sex and behaviour confirmed the above (section 8.4.6). Prior to a tousel, begging was the most common chick behaviour (see table 8.5, page 182). Interestingly, small male chicks were least likely to be begging before an attack, being more likely to be feeding themselves than the other three chick categories.

Figure 8.3a The proportion of tousles given by male parents to chicks of different size and sex

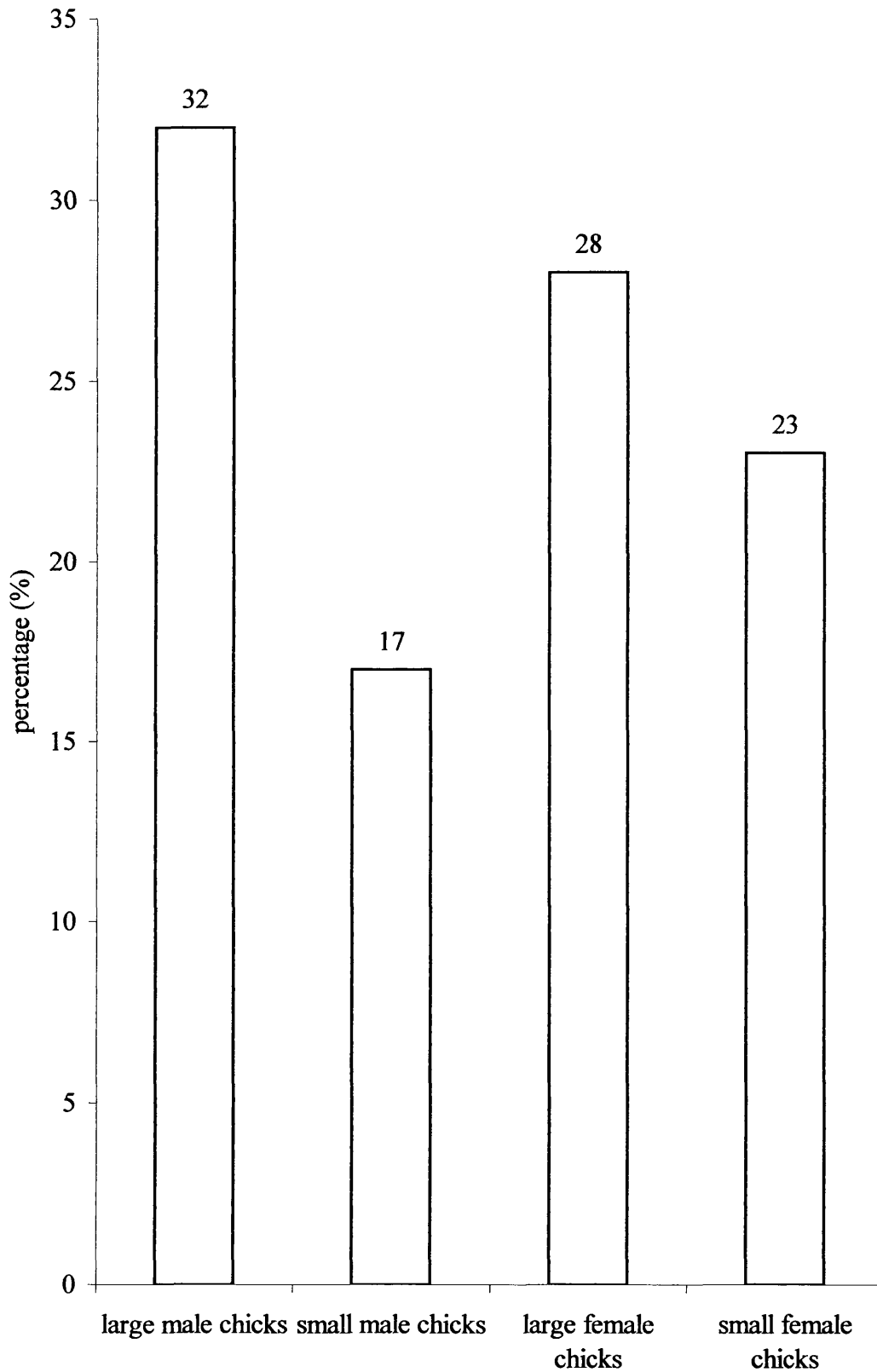


Figure 8.3b The proportion of tousles given by female parents to chicks of different size and sex

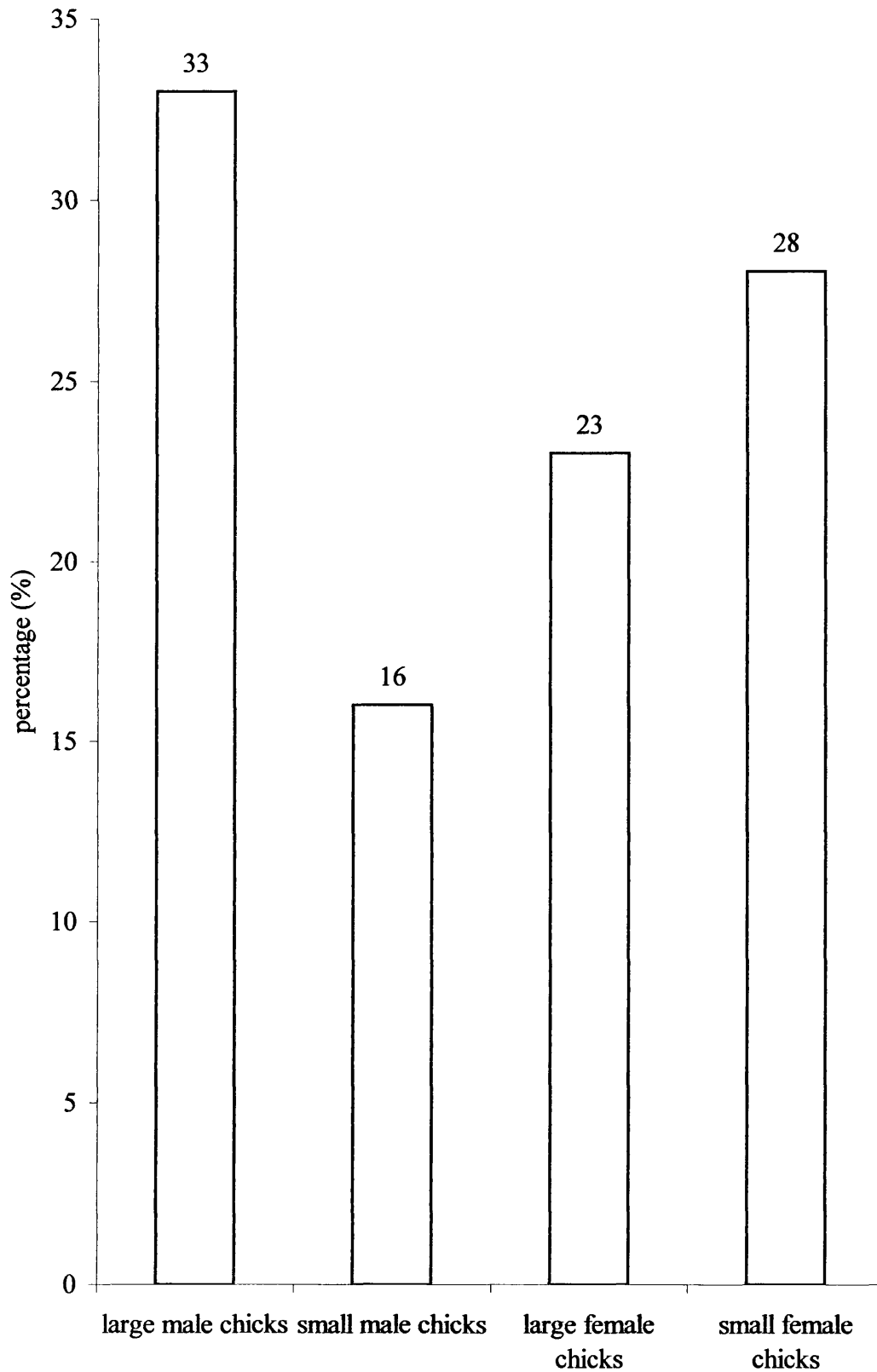


Figure 8.4a Behaviour of large chicks prior to parental tousing with increasing age

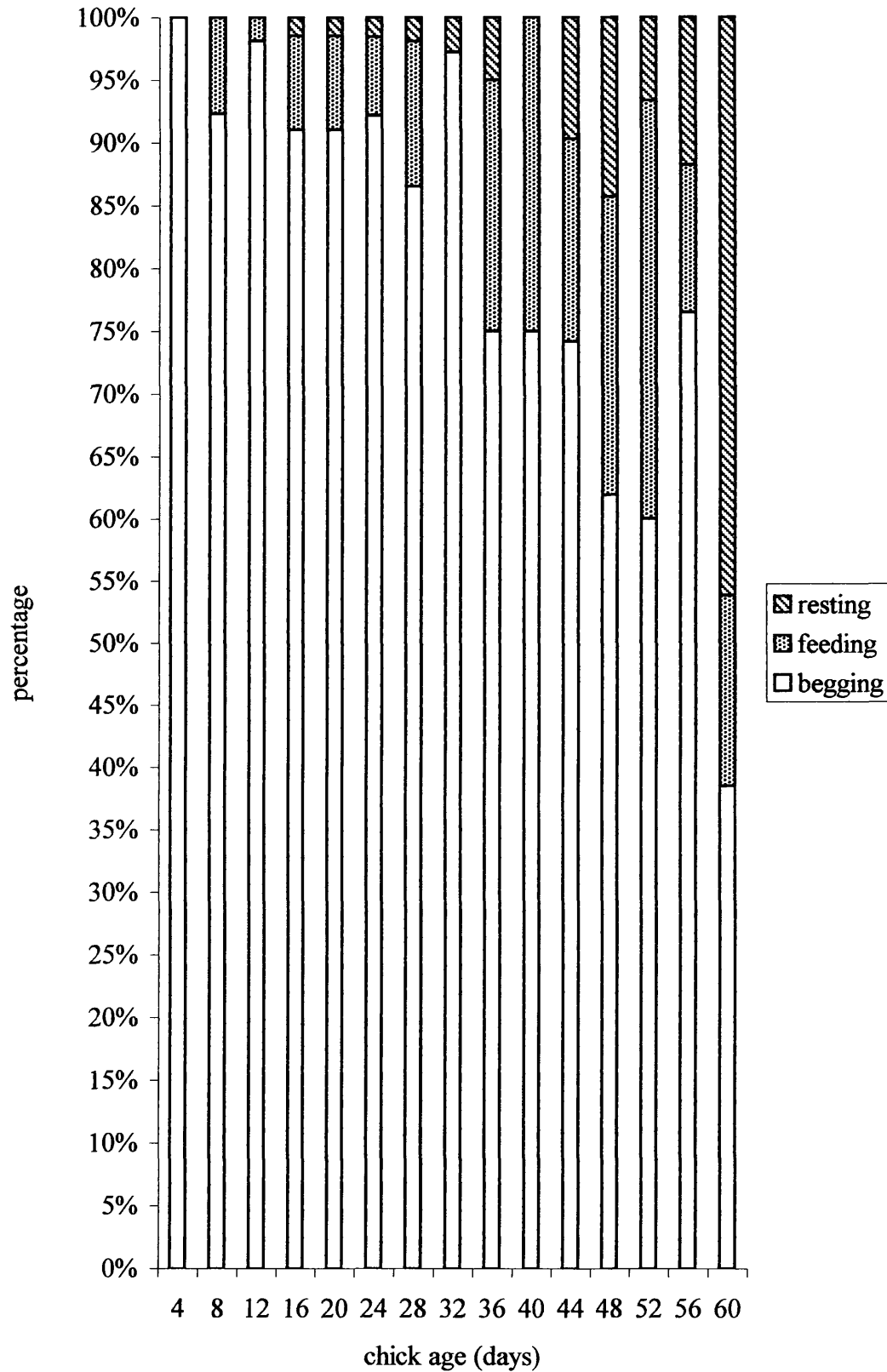
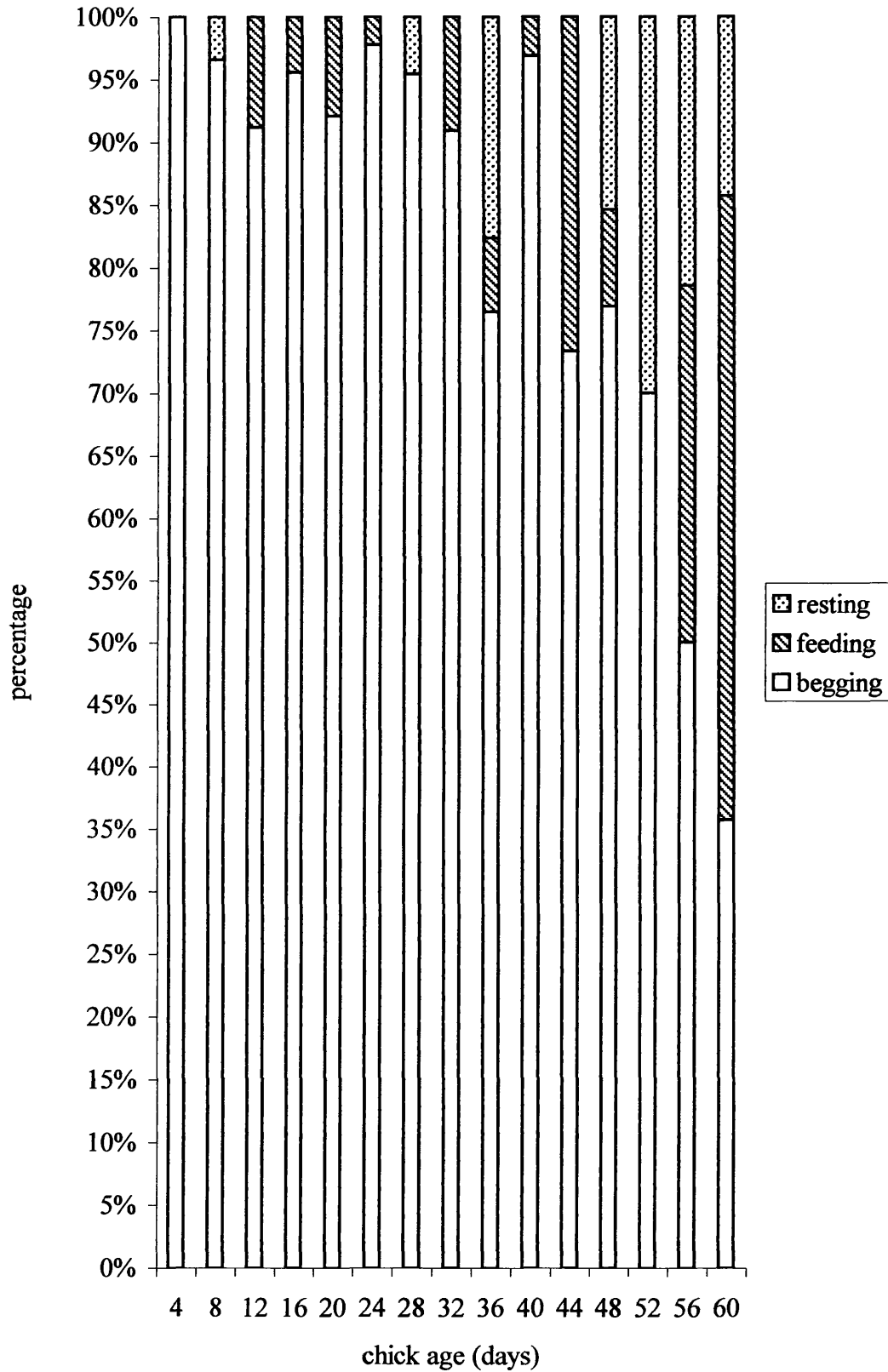


Figure 8.4b Behaviour of small chicks prior to parental tousing with increasing age



Chick sex	Chick size	% Chick behaviour prior to event		
		Begging	Self-Feeding	Resting
Male	large	90.91	6.25	2.84
	small	78.89	14.44	6.67
Female	large	87.59	6.57	5.84
	small	91.37	6.47	2.16

Table 8.5. The relative proportions of chick behaviour recorded before parental touselles in chicks of different sex or size

8.4.8 Parental Tousel Rates

Median tousel rates to all chick categories were 0. Mean (\pm S.E.) values are given, therefore, to illustrate the differences in tousel rate to large and small chicks (see table 8.6 below). Male and female parents showed similar rates of tousel behaviour towards both large and small chicks (Mann-Whitney U-test: male and female parents touselles to large chicks $U=19957776.5$, N.S.; male and female touselles to small chicks $U=19928943.5$, N.S.). Large chicks were, however, touselled more than small chicks during the observation period (Mann-Whitney U-test: $U=4614802$, $p=0.007$).

Chick size	N	Tousel rate per minute
Large	12650	0.048 \pm 0.003
Small	12630	0.030 \pm 0.002

Table 8.6. The mean (\pm S.E.) parental tousel rate per minute to large and small chicks

8.4.9 Chick Sex and Parental Touse Rates

As in section 8.4.8, median touse rates to each chick sex were zero. The mean touse rate per minute for each chick size and sex per male and female parent are, therefore, shown in table 8.7 (below). Male and female parents toused both male and female chicks at similar rates per minute (Kruskall-Wallis test: $h=8.32$, N.S.). Clearly, small chicks were toused less than their larger counterparts by both male and female parents.

Adult sex	Chick sex	Chick size	N	Touse rate per minute
Male	Male	Large	2238	0.037±0.007
		Small	1918	0.024±0.006
	Female	Large	1623	0.046±0.008
		Small	1910	0.033±0.006
Female	Male	Large	2230	0.042±0.007
		Small	1910	0.023±0.004
	Female	Large	1600	0.039±0.007
		Small	1920	0.032±0.007

Table 8.7. The mean (\pm S.E.) touse rates per minute by male and female parents to each chick size and sex

8.4.10 Touse Type

Figures 8.5a & b (pages 184 & 185, respectively) illustrate the proportions of different touse type to large and small chicks with increasing age. Overall, pecks were the most frequent type of touse to both large and small chicks and peck-chases were least common. The proportions of each touse type altered with increasing chick age.

Figure 8.5a The proportion of each tousel type received by large chicks from male and female parents with increasing chick age

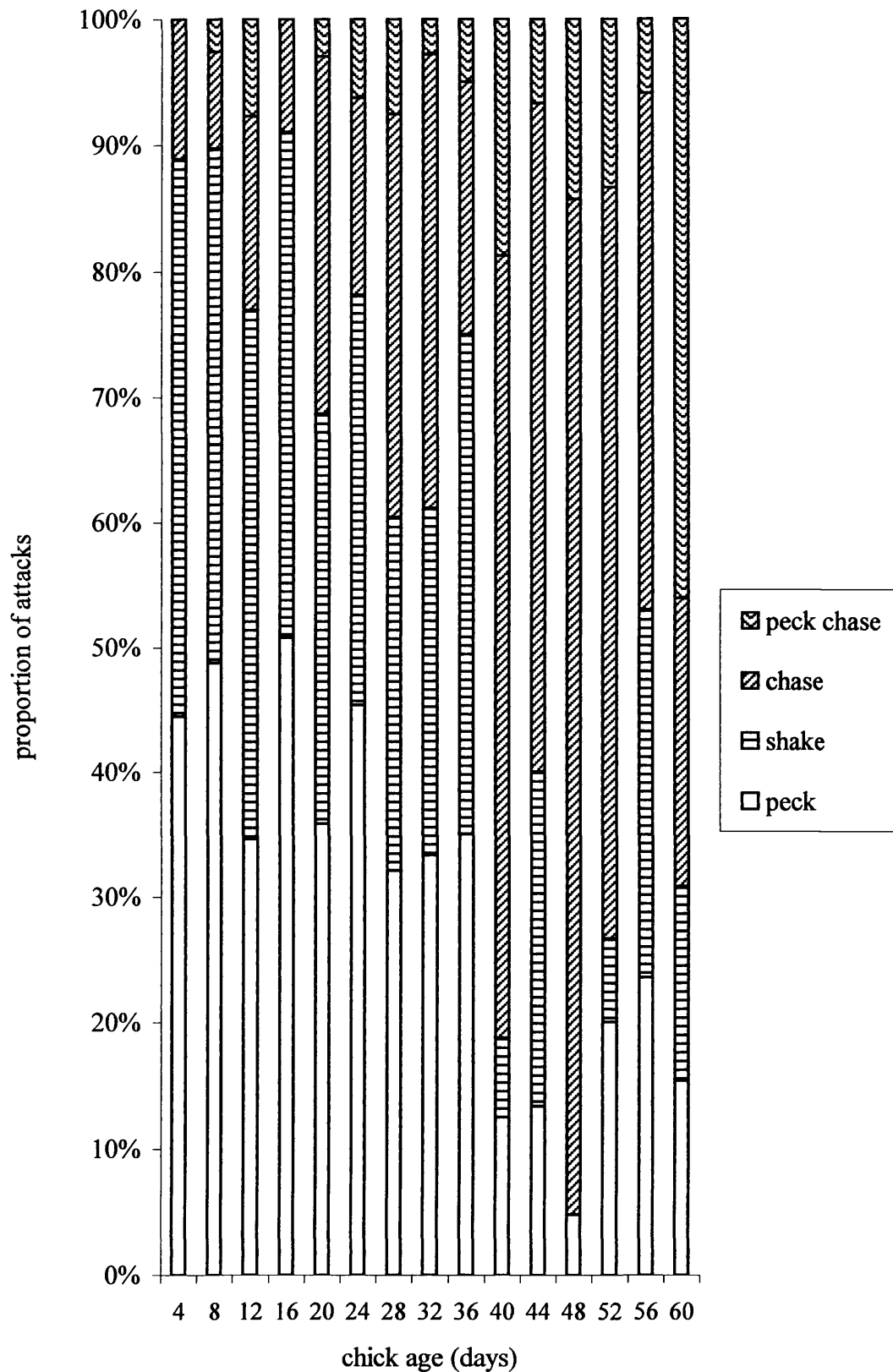
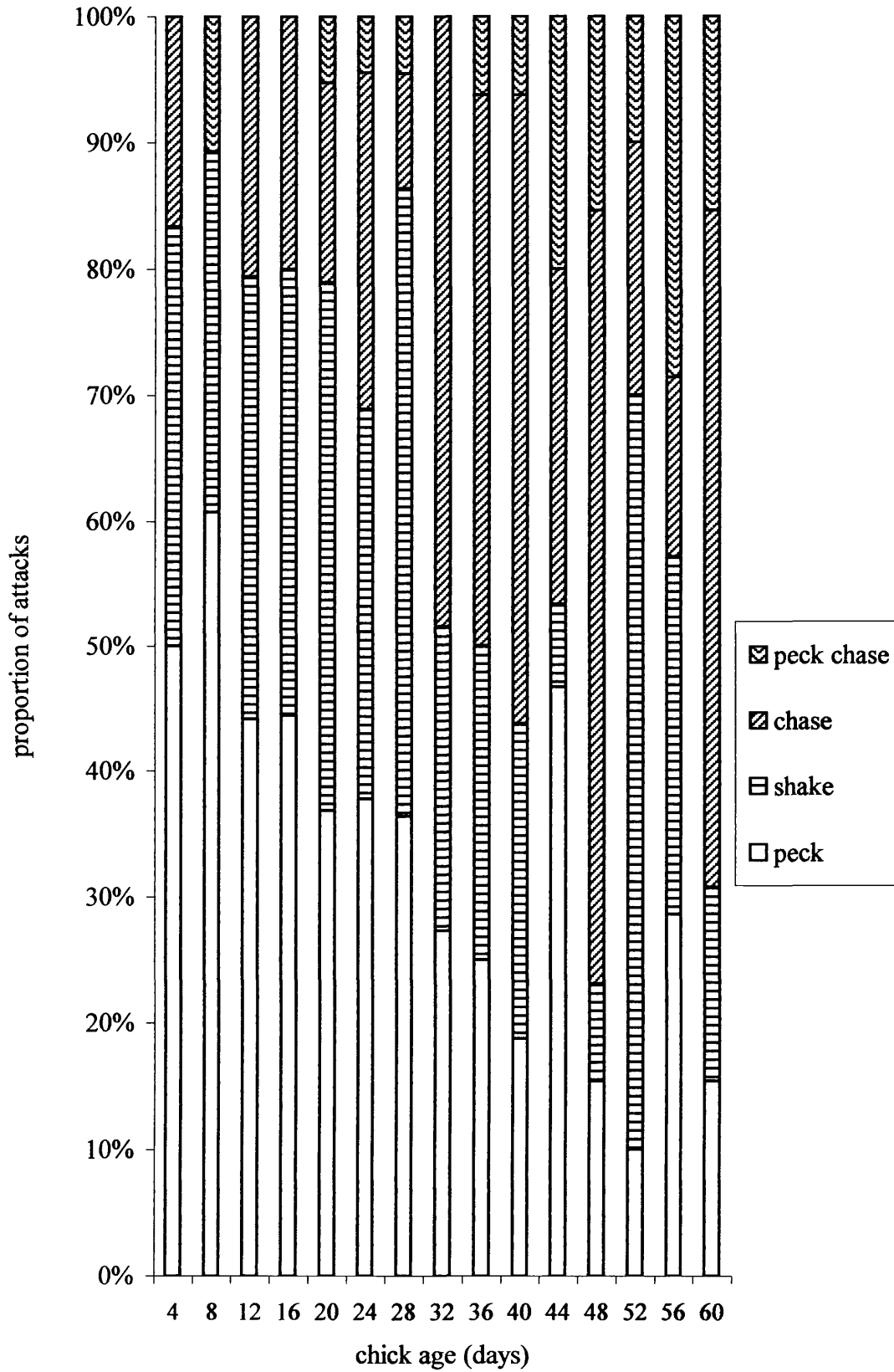


Figure 8.5b The proportion of each touse type recieved by small chicks from male and female parents with increasing chick age



There were significant differences in the proportions of each tousle type given by both parents to large and small chicks (G-Test: $G=31.14$, $p<0.01$). There were also significant differences between the proportions of each tousle type given by parents to large chicks (G-Test: large chicks $G_{adj}=65.23$, $p<0.01$) and small chicks (G-Test: $G_{adj}=41.48$, $p<0.01$).

8.4.11 Tousle Type and Sex Analysis

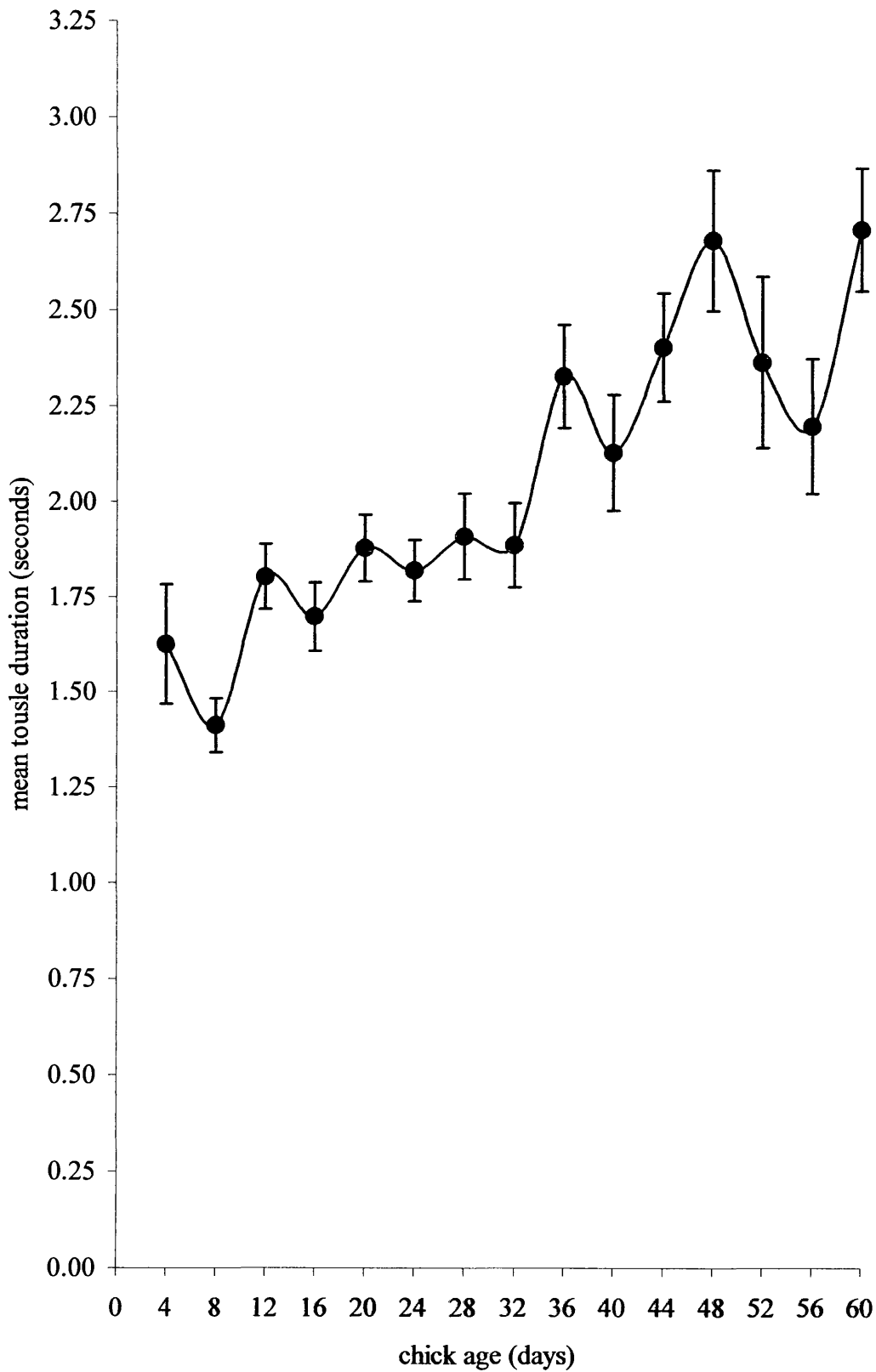
Figure 8.6 (page 187) illustrates the proportion of different tousle types per parent received by each size and sex of chick. The proportion of different tousle types given by male and female to each chick category did not differ significantly (G-Test: $G=16.41$, N.S.). Small females received the greatest proportion of peck tousles by female parents (52.05%, $n=47$ pecks). In contrast, large males were pecked more frequently by male parents (46.53%, $n=41$ pecks) although small female chicks were also pecked substantially (39.68%, $n=25$ pecks). In addition, both male and female parents peck-chased small female chicks more frequently than any other chick size and sex. Interestingly, large female chicks were chased more frequently by both parents.

8.4.12 Tousle Duration

Tousle duration was positively correlated with chick age (Spearman's Rank Correlation coefficient: $r_s=0.30$, $p<0.0001$; see figure 8.7 page 188). Large and small chicks were tousled for similar durations (Mann-Whitney U-test: $U= 95137$, N.S.).

The median (with range) duration of tousles to male and female chicks (large and small chicks pooled) by parents is shown in table 8.9 (page 189).

Figure 8.7 Increase of the mean tousel duration of chicks by both parents with increasing chick age



Female parents tousled male chicks (both large and small chicks pooled) for significantly shorter durations than male parents did (Mann-Whitney U-test: $U=11128.5$, $p=0.043$). In comparison, female chicks (both large and small pooled) were tousled for similar durations by male and female parents (Mann-Whitney U-Test: $U= 8773.5$, N.S.).

Parent sex	Chick sex	N	Tousle duration (seconds)	
Male	Male	134	1 (1-4)	1.77±0.08
Male	Female	133	2 (1-4)	1.81±0.07
Female	Male	147	2 (1-6)	1.97±0.07
Female	Female	135	2 (1-4)	1.77±0.07

Table 8.9. The median (with range) and mean (\pm S.E.) tousle duration (seconds) received by chicks of each sex from male and female parents

A large number of Mann-Whitney U-test comparisons were made. These tests revealed that male and female parents tousled small and large chicks for similar durations. Similarly, male and female parents did not discriminate between chicks of different sex and size in terms of tousle duration. Female parents did, however, tousle small male chicks for significantly longer than small females (Mann-Whitney U-test: $U=1226$, $p=0.008$).

8.4.13 Chick Position Before and After Parental Tousling

Significant differences were found in the position of the parent in relation to both large and small chicks before and after tousle events (table 8.10, page 190).

Unremarkably, both large and small chicks tended to be <1m of a parent before a touse and >1m away after the event.

Chick Size	Chick position	Frequency		G-Test Output	
		<1m of parent	>1m away from parent	G_{adj}	p
Large	before touse	367	161	42.27	<0.01
	after touse	179	349	28.86	<0.01
Small	before touse	265	102	38.49	<0.01
	after touse	136	231	12.47	<0.01

*all tests df=1

Table 8.10. Frequency of chick position before and after touses for chicks of different size with associated G-tests

There was a tendency for large and small chicks to >1m away from a parent before a touse with increasing chick age (see figures 8.8a, b, c & d pages 191, 192, 193 & 194, respectively). Small and large chicks were as likely to be within 1m of a parent as they were to be further away than 1m before a touse after 28 and 32 days of age, respectively. Similarly, after a touse both small and large chicks were as likely to be within 1m of a parent as they were to be further away up to the age of 28 and 32 days, respectively. Subsequently, large and small chicks predominately remained more than 1m away from a parent after a touse.

Figure 8.8a The proportion of large chicks within 1 metre of parents with increasing age before receiving a touse

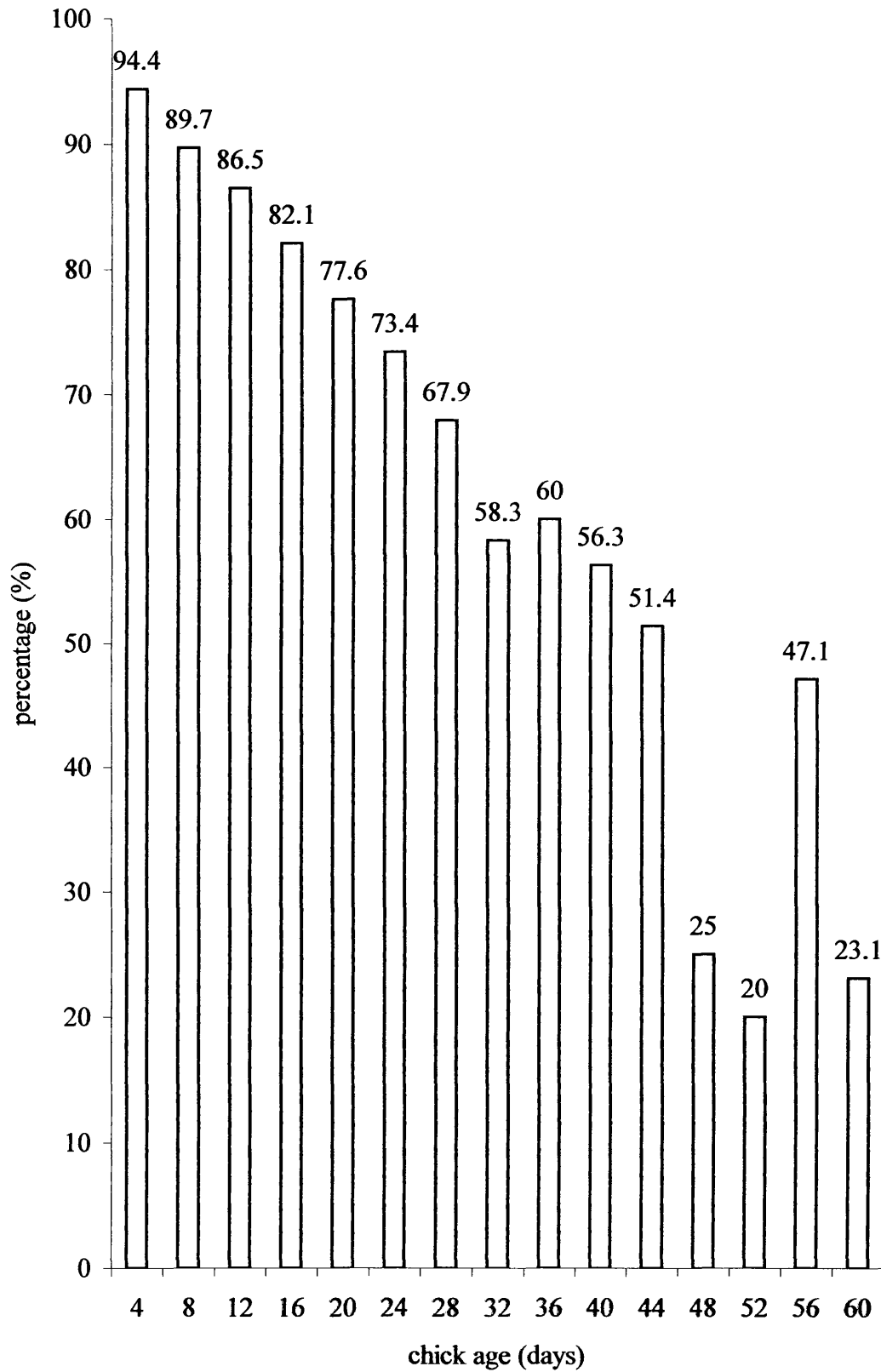


Figure 8.8b The proportion of large chicks within 1 metre of parents with increasing age after receiving a tousle

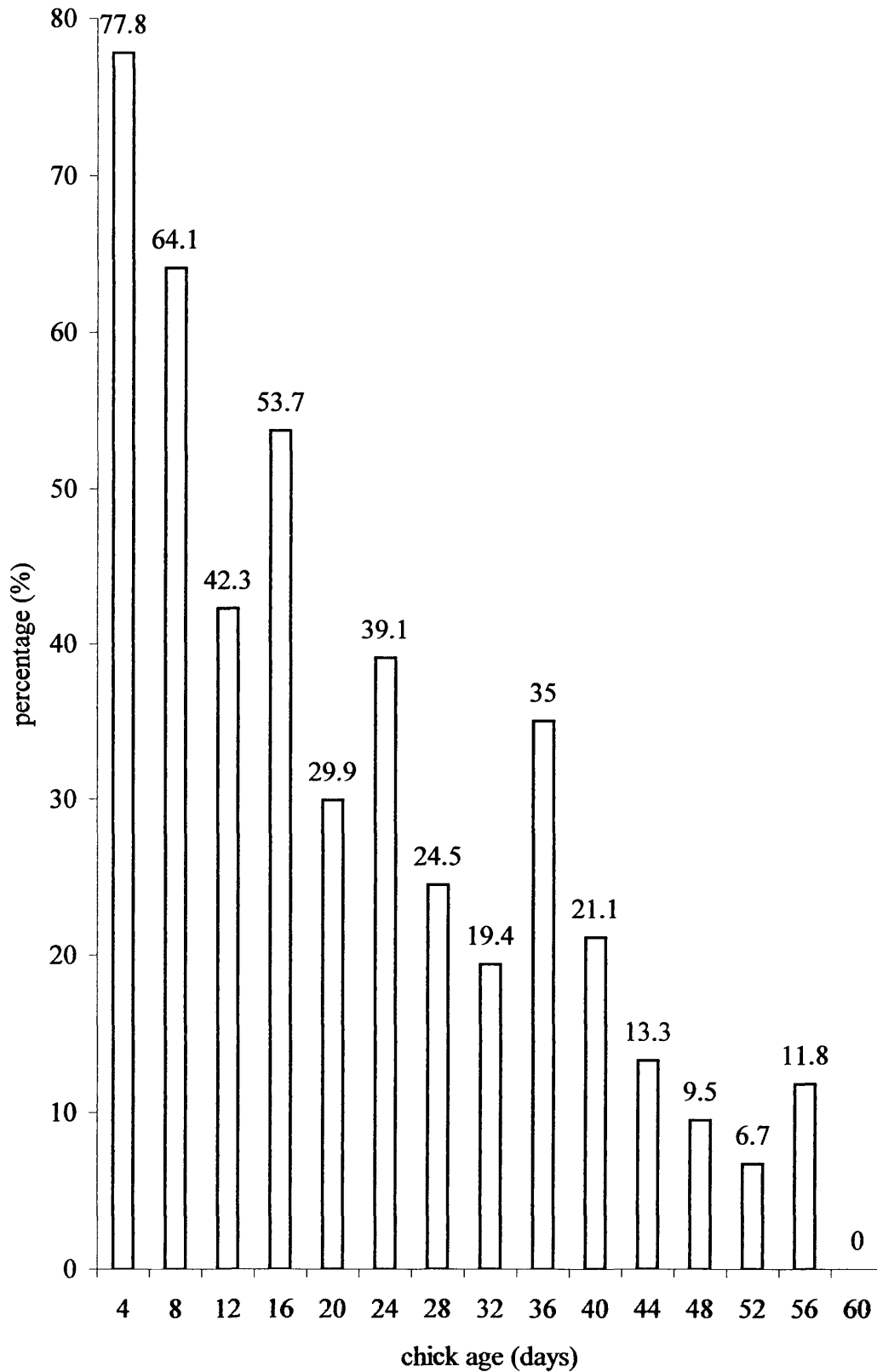


Figure 8.8c The proportion of small chicks within 1 metre of parents with increasing age before receiving a touse

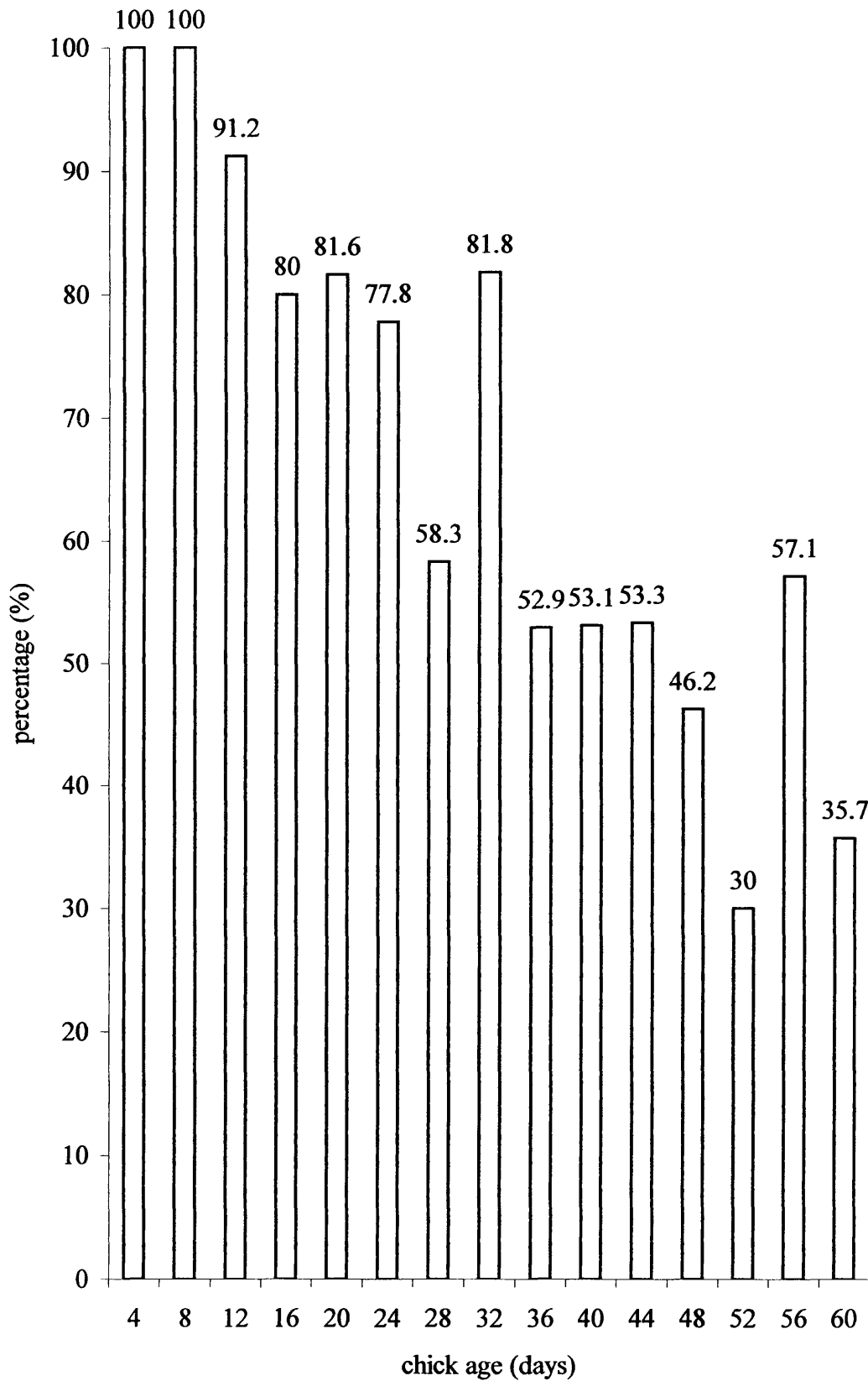
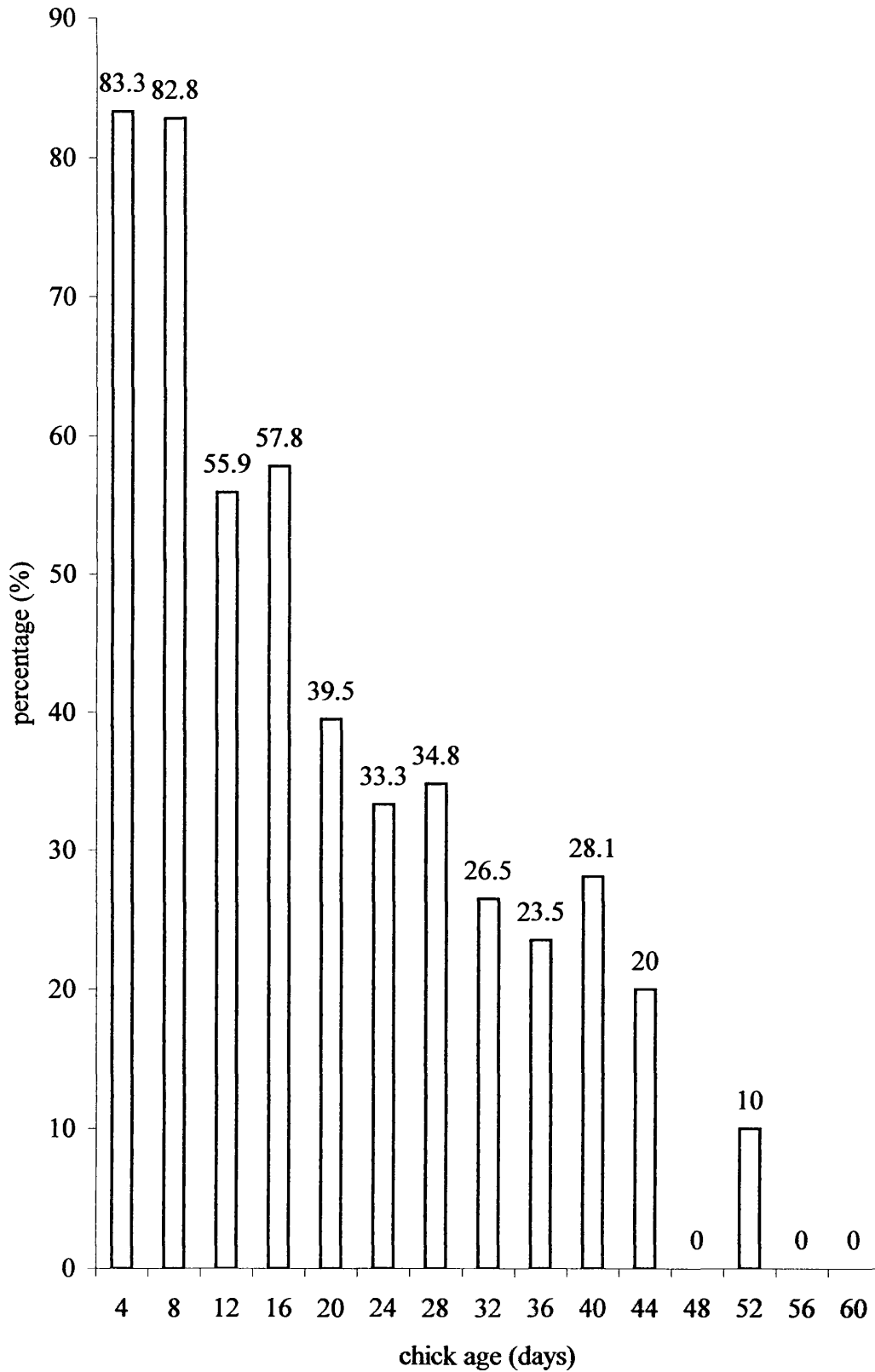


Figure 8.8d The proportion of small chicks within 1 metre of parents with increasing age after a receiving a touse



8.5 Discussion

8.5.1 HA and Sibling Conflict

Severe intra-brood conflict over parental care exists between dependent siblings of many species (Horsfall, 1984; Mock, 1987; Skagen, 1988; Mock *et al.*, 1990; Slagsvold, 1997). As Moorhen clutches predominately hatch asynchronously, a distinct brood size hierarchy (based on chick age) is produced (see section 7.4.9; see plate 8.1 page 196). Within broods of many HA species, older larger chicks are more competitive than their smaller younger siblings (Safriel, 1981; Mock, 1984a; Gibbons, 1985). These older chicks are consequently, more able to physically monopolise parental care (Horsfall, 1984; Mock, 1984b; 1987; Skagen, 1988; McRae *et al.*, 1993; Nilsson, 1995; Slagsvold, 1997; Cotton *et al.*, 1999; Krebs *et al.*, 1999). Since Moorhen parents feed chicks with discrete items of food (Wood, 1974; Cramp & Simmons, 1980; Leonard *et al.*, 1988), food provisioning can easily be monopolised by dominant larger chicks during the dependence stage of parental care. Due to their relatively large size and gait, older chicks were able to reach foraging parents before smaller counterparts. Larger chicks also generally obtained the first of the food offered by parents when foraging (pers.obs and see Leonard *et al.*, 1988). Despite the frequent occurrence of intra-brood competition over parental provisioning, physical aggression was rarely observed between large and small chicks within each study brood.

HA may establish stable dominance hierarchies within broods by reducing the amount of sibling-sibling conflict over parental care between chicks of a similar competitive ability (Hamilton, 1964; Hahn, 1981; Slagsvold, 1997). Chicks waste less energy on competitive interactions under these conditions.



Plate 8.1. Hatching asynchrony in a monogamous Moorhen clutch.

Consequently, a lower parental feed rate is required, reducing parental expenditure (Mock & Ploger, 1987; Leonard *et al.*, 1988; Wiebe & Bortolotti, 1994). Considerable energy savings in provisioning costs can, therefore, be made by parents with HA broods compared to that of synchronously hatching broods, particularly over critical (peak) times of chick energy demand e.g. in American kestrels (Wiebe & Bortolotti, 1994). This may be one reason for the prevalence of HA in previous Moorhen breeding studies (see Petrie, 1982; Gibbons, 1985; Leonard *et al.*, 1988; McRae, 1994).

Monopolisation of care by larger chicks can be overcome by parents ensuring that they allocate their resources between all or most members of their brood, or by attempting to reduce brood size (Trivers, 1974; O'Connor, 1978; Parker & MacNair, 1979; Horsfall, 1984). Moorhen parents controlled the behaviour and dependency of differently sized and sexed chicks within their broods during the dependency period whilst not engaging in any form of brood division or reduction cf. European coots *Fulica atra* (Horsfall, 1984). They did this firstly by feeding smaller chicks at a greater rate per minute than larger (older) chicks, ensuring that both benefited from food provision despite their relative competitive abilities (see also Trivers, 1974; Parker & MacNair, 1979). Parents also refused to provision larger chicks whilst they fed smaller, younger chicks (see Leonard *et al.*, 1988; Krebs & Magrath, 2000). The tendency of smaller chicks to remain closer to parents than larger siblings no doubt increases their chance of being fed, as chicks located closest to parents often receive food first (Leonard *et al.*, 1988). Moorhen parents were not observed to selectively locate and feed small chicks (but see Stamps *et al.*, 1985; Krebs, 1999). In contrast to the young of altricial species, Moorhen chicks are unrestricted in their ability to forage independently and provision for themselves from an early age (Wood, 1974; Gibbons,

1985). The increasing energetic cost of selectively searching out and feeding smaller chicks (rather than simply feeding the nearest chick) presumably prohibits the adoption of such behaviour in this species (Leonard *et al.*, 1988 and see Horsfall, 1984).

The second parental control strategy utilised by Moorhen parents is that of physical aggression to specific chicks within their brood (see also Slagsvold, 1997). Both male and female parents “tousle” (Horsfall, 1984) larger chicks more frequently than smaller offspring. Tousling large chicks at greater rates, would seemingly discourage them from monopolising food provisioning. Since tousling is evident from hatching (pers.obs), parents immediately counteract the effects of size-based sibling competition at a stage when it is likely to have a deleterious affect.

8.5.2 Tousling and Offspring Independence

As well as discouraging provisioning monopolisation, tousling may encourage provisioning independence in offspring (Leonard *et al.*, 1988). One would predict that larger chicks would reach foraging independence earlier than their smaller siblings. Both parental provisioning and tousle rates, however, peaked at 12 days for both large and small chicks, suggesting that the timing of chick independence is a function of age and not a consequence of discriminatory parental strategy related to the size of offspring (see also Leonard *et al.*, 1988). Despite this, it is interesting to note that, with increasing age, small chicks continued to receive significantly more feeds per minute than larger siblings (see also section 8.5.5).

8.5.3 Parental Provisioning and Chick Independence

The overall energetic requirement and costs of parental care to parents of rearing larger chicks is likely to be greater than that required to rear small chicks (Slagsvold, 1990). Adult Moorhens primarily forage randomly for food (Cramp & Simmon, 1980; Sutherland *et al.*, 1986) and chicks are fed with small, discrete food items (Leonard *et al.*, 1988). It consequently seems unlikely that larger chicks are fed with higher quality food items. It is, therefore, somewhat paradoxical that parents provisioned larger chicks with fewer feeds per minute than smaller siblings. Large chicks may be forced to provide a greater proportion of their own energy budget by increasing their own food intake. Large chicks did, indeed, provision themselves at significantly greater rates than small chicks of the same age, suggesting some form of compensation for the observed difference in parental feed rates to large and small chicks (section 8.4.1). Although no detailed information is available on the growth rates of specific chicks, differential mortality was not observed between large and small chicks in each brood by the end of the observation period (but see Howe, 1976; Gibbons, 1985; Forbes, 1991; Slagsvold, 1997). Parents did not, therefore, appear to reduce provisioning to large offspring to an extent that the survival of these chicks was impaired during their residence on the natal territory. Parents have much to gain if some offspring within a brood can be encouraged to provision for themselves more regularly. Since the survival of offspring is directly related to the amount of parental care (section 1.5.3), the greater provisioning rate to small chicks is likely to promote their growth and survival, particularly in adverse conditions (Amat, 1994). This optimisation of parental expenditure during chick provisioning, by feeding different sized chicks at different rates, may also partly explain the ability of Moorhens to successfully rear several broods per year.

8.5.4 Chick Behaviour to Parental Aggression

As in Leonard *et al.* (1988), Moorhen chicks altered their behaviour in response to previous or current parental aggression. Interestingly, age-related trends were observed in the responses of large and small chicks after touse events. Young chicks (1-8 days) immediately adopted subordinate postures (see Wood, 1974) after tousel and often remained within close proximity (within 1m) of the touseling parent although their begging rates decreased. After this age, chicks responded to parental aggression by moving rapidly away from the touseling parent whilst adopting submissive postures. More importantly (and with increasing age), chicks were often located more than 1m away from the touseling parent both before and after a touse event. This suggests that Moorhen chicks have the capacity to “learn” from past aggressive encounters with their parents and adapt their behaviour accordingly.

Larger chicks were the first within the brood to decrease their proximity to parents before and after tousel with increasing age (see section 8.4.13). This is consistent with larger chicks being touselled more frequently. Although chick independence occurs at the same age for both large and small chicks (see section 8.5.2), larger offspring begin to forage further away from parents earlier than small chicks. Large chicks are likely to be more independent than smaller younger chicks of the same age, facilitating parental care of smaller chicks within the brood (see Slagsvold, 1997).

As all chicks become more independent with age (due to their increased foraging efficiency and increasingly limited parental provisioning), they spend more time foraging away from parents. The frequency of parental touseling to all chicks, increased significantly with chick age. As young passerines become independent, their foraging efficiency increases and begging profitability decreases (Davies, 1978). Moorhen chick self-provisioning rates were strongly correlated with age and juveniles

have been recorded as becoming increasingly more efficient foragers with age (Sutherland *et al.*, 1988). This is also true of American coots (Desrochers & Ankey, 1986). Parents respond to the increasing foraging efficiency of chicks by reducing their provisioning. The costs of following parents are likely to be small and such behaviour does not seriously interrupt chick self-foraging efficiency so the profitability of begging is unlikely to decrease significantly with chick age in this species (Leonard *et al.*, 1988). In order to resolve the conflict over the timing of chick independence, parents reduce chick dependence by continued tousling behaviour throughout the entire period of parental care. In contrast, older European coot chicks are tousled less frequently and these parents use different strategies to control both sibling competition and the timing of brood independence (Horsfall, 1984).

Chick behaviour recorded prior to tousle events strongly indicates that begging is a primary stimulus inciting this behaviour (see Wood, 1974 for a detailed description of begging behaviour). Older Moorhen chicks following foraging parents were noted to be frequently begging and harassing parents, despite their ability to forage independently. As the costs of begging in this species are likely to be low (section 8.5.4) it is, perhaps, unsurprising that chicks begged even when they were distant from their parents. It is plausible that these chicks were responding to the visual cue of the red culmen and bill of parents, inciting a begging response (see Kear, 1965; Weidmann, 1965).

Independent Moorhen chicks were increasingly tousled by parents when not engaged in food soliciting behaviour. Such behaviour might simply represent factors within the family group other than a parent-offspring conflict (e.g. “squabbling” Mock & Forbes, 1992). It is possible, however, that the selectivity and intensity of tousling

by individual parents to specific chicks has a subtle socialising function (Trivers, 1974; Leonard *et al.*, 1988; see section 8.5.5).

8.5.5 Helping Behaviour and Parental Aggression

Aggressive behaviour by parents to their own offspring is rare amongst most avian species (but see Safriel, 1981; Horsfall, 1984; Gibbons, 1985; Leonard *et al.*, 1988; 1991). In contrast to parent-offspring aggression in the related European (Horsfall, 1985) and American coot (Lyon *et al.*, 1994 but see also Desrochers & Ankey, 1986), Moorhen parents did not show any discernible brood reduction or division tactics. In specific groups, individual parents of both sexes appeared to discriminate between chicks for reasons other than size and sex (and see also sections 8.5.6 & 8.5.7). In particular, the father of one group from 1998 was observed to constantly touse his eldest son. This male dispersed soon after fledging whilst the other surviving members of the brood remained and assisted with their parents next clutch attempt (pers.obs). Similarly, both parents of a different group selectively searched out and fed the smallest female, often to the exclusion of other closer individuals. These interesting observations may reflect the wide variability of parental tolerance and preference towards specific offspring within their brood (Scott, 1980; Breitwisch, 1989; Slagsvold, 1997). Such disparities in parental allocations of food and aggression towards specific chicks may ultimately affect the social dynamics of Moorhen breeding groups.

8.5.6 Sexual Discrimination in Moorhen Parental Care

In contrast to a previous study on parent-offspring aggression in Moorhens (Leonard *et al.*, 1988), surprising and significant differences between the parental behaviour of

female and male parents to specific chick sexes were found (see section 8.5.7). Past behavioural studies on this species (e.g. Petrie, 1982; Gibbons, 1985; Leonard *et al.*, 1988 but see McRae, 1994) sexed adults and juveniles using only a discriminate function analysis (see Andersson, 1975). This technique is based on the differential morphometry of each sex and it can be highly variable in effectiveness when sexing adults (op.cit.; Cucco *et al.*, 1999). Moreover, the morphometric variables (e.g. weight and T+t) used to determine sex in independent juveniles (40-45 days) may not be as distinct between the sexes as they are in adult or mature individuals. It is, therefore, possible that the sex identification of individual chicks, undertaken at 40-45 days by Leonard *et al.* (1988), was imprecise.

Moorhens have recently been sexed using flow cytometry (Cucco *et al.*, 1999) and multilocus mini-satellite DNA fingerprinting and microsatellite analysis (McRae & Burke, 1996; van Duyse *et al.*, 1999). Such techniques are, however, time consuming and costly. In the current study, analysis was undertaken using a sexing protocol and primers designed by Griffiths *et al.*, (1998). This technique is quick, reliable and cheap. This study appears to be the first to successfully sex Moorhens using this technique.

8.5.7 Sexual Differences in Male and Female Parental Care

Male and female parents were similar in their respective provisioning and touseling behaviour to the size-based chick hierarchy (cf. Moreno *et al.*, 1995; Leonard & Horn, 1996; Slagsvold, 1997). In direct contrast, however, significant differences in provisioning rates and tousel duration were found between each parent and offspring sex (see also Stamps *et al.*, 1987; Yasukawa *et al.*, 1990; Gowaty & Droge, 1991 cf. Gibbons, 1985; Leonard *et al.*, 1988). This study clearly reveals that the behaviour of

female parents differed with respect to offspring sex and to that of male parental behaviour. Male parents, by comparison, were not observed to discriminate between male and female chicks in terms of tousing and food provisioning.

8.5.8 The Implications of Size Dimorphism on Parental Care

Sex-biased parental care has been recorded in several birds species (e.g. Gowaty & Droge, 1991). Little is understood, however, of the mechanisms that parents use to discriminate between offspring of each sex (Lessells *et al.*, 1998 but see Burley, 1986; Stamps *et al.*, 1987; Gowaty & Droge, 1991). As offspring size in Moorhens is initially determined by hatching order (age) and not sex, it is unlikely that parents use relative size as a cue.

Many hypotheses have been advanced to explain the occurrence and complexity of the different aspects of sex-biased parental care e.g. paternity (Owen, 1991; Westneat & Sherman, 1991), sexual conflict between parents (Westneat & Sargent, 1996; Lessells, 1998) and brood sex ratio (Lessells *et al.*, 1998; Albrecht, 2000). In species in which one sex is larger (therefore requiring more energy to produce), sex based differences in parental care may also evolve (Horsfall, 1984; Halliday, 1994). In particular, parents can allocate more parental resources to the larger sex (Patterson *et al.*, 1980; Fiala & Congdon, 1983; Slagsvold *et al.* 1986).

As Moorhens are sexually dimorphic in size (Wood, 1974; Andersson, 1975; Petrie, 1982) sex based mortality patterns, such as those described in the Common grackle (Howe, 1977), can be avoided by feeding male chicks more than their female conspecifics. Such parenting trends in Moorhens are supported by the observation that female parents fed theoretically “less costly” female chicks at a lesser rate than male offspring. Male parents, however, did not exhibit any provisioning differences

between chicks of the same age, apart from that related to chick size. Female parents also fed chicks at a rate determined by their size. If there was a differential cost in the production of each sex, both sexes should provision each offspring sex at a level required by their respective development costs (Howe, 1977). Moreover, since the hatching order of offspring is not sex-biased (unpub data), the costs of rearing specific young is determined by their size and not their sex. In contrast, polyandrous House wren *Troglodytes aedon* male offspring hatch first and benefit from greater parental care from their parents in comparison to their female siblings who hatched later (Albrecht, 2000). The size hierarchy resulting from HA may ensure that some high quality offspring of both sexes are raised successfully (Mock, 1987; Simmons, 1988). This may partially explain the lack of a sex bias in juvenile mortality at the age of 45 days in a sample of 18 broods taken from 1998 and 1999.

The parental costs of raising each sex of offspring may be similar, until significant size differences between the sexes become evident. Assuming that the post-hatch development of Moorhen chicks follows a similar pattern as the related European coot, sexual size asymmetry does not become apparent until 3-4 weeks of age (Visser, 1974). At this time, Moorhen chicks are no longer dependent on their parents for provisioning (Gibbons, 1985) and can fulfil the majority of their energetic requirements. For these reasons, the difference observed between female feeding rates to male and female offspring seems unrelated to their respective production costs.

8.5.9 Does Moorhen Parental Behaviour Have a Socialising Function?

Aggression may have a primitive socialising function (Trivers, 1974) and it is female parental discrimination was not limited to food provisioning but also included

aspects of parental attack (section 8.4.11). The proportion of care given by parents may be influenced by the net fitness value of a particular offspring sex (one sex may be particularly helpful or competitive) (Gowaty & Droge, 1991). Although male and female parents tousel both offspring sexes at the same rate per minute, female parents tousel male chicks for significantly less time than did male parents. There was no evidence, however, that either parent tousel female chicks for longer than male chicks and both parents tousel female chicks for similar durations. If touse duration indicates a level of aggression ‘intensity’, the results suggest that female parents are “favouring” male chicks by not reacting as aggressively to them. The female behaviour of reducing the intensity of tousel to male chicks, coupled with lesser-feed rates to female chicks may have implications for social dynamics and group formation in this species.

8.5.10 Parental Behaviour and Helper Recruitment

Moorhen cooperative groups occur frequently and the continued presence of independent juvenile offspring does not appear to hinder the ability of parents to produce and rear additional broods within the same year (Gibbons, 1987; Eden, 1987; Leonard *et al.*, 1988). It is unclear, however, whether the continued presence of Moorhen juveniles on the natal territory is actually beneficial to parents (see Gibbons, 1985; 1987 cf. Eden, 1987; Leonard *et al.*, 1989). Furthermore, the “willingness” of Moorhen juveniles to help their parents is restricted by the energetic cost of helping (Eden, 1987). Despite this, cooperative behaviour can reduce the costs of parental care (e.g. Gibbons, 1987; Legge, 2000). It may also increase the lifetime reproductive success, fitness and survival of participating individuals (Hamilton, 1964; Brown, 1987; Stacey & Ligon, 1987). Consequently, prudent parents would benefit by

encouraging offspring of the more useful sex to remain and help (see also Gaston, 1978; Emlen *et al.*, 1986).

It is difficult to ascertain conclusively which sex is the more useful in Moorhens. Male Moorhens are larger than females and are actively involved in all aspects of parental care, especially incubation (Siegfried & Frost, 1976). Males also perform the majority of territory defence. It is, therefore, plausible that they are the more helpful sex, and have a greater net fitness value to female parents (see also Trivers & Willard, 1973; Horsfall, 1984; Albrecht, 2000).

As the sex ratio of surviving offspring at 45 days did not differ significantly from unity, it can be assumed that no sex-biased mortality occurred prior to dispersal. The majority of surviving juveniles remained with their parents for variable durations after reaching independence. Female parental behaviour appeared to have no observable effect on the retention of juvenile offspring of either sex in the transitional period between independence and dispersal within the first year. Since dispersal is likely to be risky in this species (section 3.4.3), it is not surprising that juveniles remain until such time that they are physically forced out by their parents or when conditions are favourable for successful dispersal (Gaston, 1978; Scott, 1980; Gibbons, 1985; Ekman *et al.*, 1994).

The age-related touse rates recorded to independent offspring of both sex with suggests that both parents may be in conflict with offspring not only with the timing of independence but also that of dispersal. Although the majority of juveniles dispersed after approximately 72-100 days after hatching (pers.obs), a small number remained on the natal territory with their parents the following year. These individuals were generally those that hatched out during mid to late breeding season (see also Gibbons, 1985). If female parents discriminate against female offspring, it is

somewhat perplexing that over 66% of adult offspring helpers were female (section 3.3.3). Clearly, further research is required to investigate the influence of parental behaviour on the retention of offspring and the formation of kin-related cooperative and communally breeding groups.

It is possible that female parental care bias reflects some form of sexual conflict. The level of care provided by one parent is dependent on that given by their partner (Westneat & Sargent, 1996; Lessells, 1998). The exact allocation of parental care in this species is, however, currently unknown (but see Leonard *et al.*, 1988). Manipulation of brood sex ratios, in conjunction with detailed examination of parental care, may reveal the extent of such a sexual conflict in this semi-precocial species.

8.6 Conclusions

1. Moorhen broods have an extended period of parental care, although parental provisioning decreases significantly with increasing chick age.
2. HA creates a size hierarchy within the brood consistent with the Sibling Rivalry Hypothesis. In order to control brood competition, parents feed smaller chicks at greater rates than large offspring whilst tousling larger, older chicks more frequently.
3. There is strong evidence for parent-offspring conflict over offspring's timing of independence in this species. Parents use tousling in order to enforce brood independence.
4. No differences between the parental care given by male and female parents to large and small chicks were detected. In contrast, surprising differences were found in aspects of tousling and food provision to offspring of each sex by male and female parents. In particular, females fed male chicks more than female chicks of the same age and size. It is possible that such differences may be part of a primitive socialising

strategy or may represent a sexual conflict between parents of each sex over brood care. Further research is required to establish the factor(s) responsible for the observed disparity of parental care between parents in this species.

CHAPTER 9

GENERAL DISCUSSION

“Its not the end of the journey that matters, it the journey that matters in the end”

Unknown Yoga teacher

“But indeed, all moorhens are good parents”

Frances Pitt (Waterside Creatures, 1925, George Allen & Unwin Ltd, London)

9.1 The Geography of Behaviour

The Common moorhen is an extremely adaptable species and has a cosmopolitan distribution (Witherby *et al.*, 1945; Kolbe, 1979; Cramp & Simmons, 1980; Gibbons *et al.* 1993; Ritter, 1993). The adaptability of this species to different wetland environments and its ability to produce a large number of offspring over a single breeding season (Relton, 1972; Wood, 1974; Siegfried & Frost, 1976; Gibbons, 1985; McRae, 1994) has been instrumental in determining the success of this rail.

It has traditionally been assumed in ethological research, that behavioural patterns are invariant within species. Nevertheless, there is mounting evidence suggesting that observed behavioural patterns in a large range of taxa (especially aspects of reproductive behaviour), are not necessarily “species-typical” (Endler, 1992; Foster, 1999; Foster & Endler, 1999). As behavioural patterns are shaped by unique and localised environmental and ecological conditions (Verner & Wilson, 1966; Orians, 1969; Begon *et al.*, 1990), distinct or isolated Moorhen populations may exhibit significant variations in behaviour. The expression of phenotypic variation may result from the effects of different selection pressures operating within geographically-

separated populations of the same species (Arnold, 1992; Foster & Endler, 1999). As most research on this species has taken place on populations located some considerable distance from the current study site (section 1.1), it is perhaps unsurprising that significant behavioural variations in the breeding and social ecology of Moorhens were identified during this study. A future challenge lies in determining whether these behavioural differences and patterns are Evolutionary Stable Strategies (*sensu* Maynard Smith, 1982) or simply an expression of phenotypic plasticity. As there is significant genetic differentiation between closely located populations of this rail (van Duyse *et al.*, 1999), there is good reason to examine the reasons behind the selection of these specific behaviours at different locations (Foster, 1999; Foster & Endler, 1999).

9.2 Communal Groups: Conflict or Cooperation?

Communal group reproductive success per breeding attempt, their stability as well as their persistence appeared to be partly determined by the level of intra-group relatedness and individual quality (see Reeves & Ratnieks, 1993; Cant, 1998). As conflicts of interest between group members may arise over reproductive sharing, these associations are not necessarily harmonious (Trail *et al.*, 1981; Davies & Houston, 1982; Mumme *et al.* 1983; Keller & Reeve, 1994; Davies *et al.*, 1995; McRae, 1996a but see Jamieson *et al.*, 1994; Goldizen *et al.*, 1998). Observations and detailed laying information of co-breeding females indicated that matrilineal groups were characterised by dominance behaviour by mothers and a high level of reproductive skew (see also McRae, 1996a; Cunningham & Birkhead, 1997). Such behaviour appeared to limit group reproductive success by reducing the number of successful breeding events attempted. Genetic analysis of paternity and further

behavioural study is, however, necessary to determine the level of reproductive sharing and its affects on co-breeding males in polyandrous and polygynandrous Moorhen groups in a variety of locations (see Jamieson *et al.*, 1994; Jamieson, 1997).

Long term studies of communal and cooperatively breeding species indicate that group living allows individuals to share and retain good quality territories, decreases parental care costs and increases lifetime survival and reproductive success (Mumme *et al.*, 1983; Koenig & Mumme, 1987; Craig & Jamieson, 1990; Gibbs *et al.*, 1994; Goldizen *et al.*, 1998; Butchart *et al.*, 1999). Clearly, long term cohort data is needed to determine the relative and lifetime reproductive and fitness gains of breeding in different mating systems in Moorhens (see also Petrie, 1982; Gibbons, 1985; McRae, 1994). In particular, there is a need for controlled experimentation to evaluate the proximate and ultimate factors influencing individual decisions to breed communally. Further research could examine the influence of aspects of territory quality (e.g. nest site availability, vegetation cover, and predation risk) and habitat saturation on the decision to breed communally. In addition, an individual's fighting ability as well as its sex, age, RHP and relatedness to co-breeders should be assessed to determine whether physical condition, kin-selection and prior reproductive experience (partially) determine whether Moorhen individuals are willing to share resources (e.g. territory and mates).

9.3 Moorhen IBP and Behavioural Flexibility

As only one other study has documented IBPs laying parasitically after laying their own clutch (in Barn swallows by Møller, 1987), it is surprising that several Moorhen females were identified using this behaviour (cf. Gibbons, 1985; McRae, 1994). Since Moorhen eggs are laid at night (McRae, 1996b) and males predominately

incubate the clutch at this time (section 7.4.7), females may be able to use this reproductive tactic without increasing the probability that their clutch will be predated or parasitised. Behavioural flexibility in the timing of IBPs laying parasitically within their own laying sequence might even optimise their ability to lay with greater synchronicity with their hosts. Host-parasite laying synchronicity in this category was, however, consistently poor. As long as the costs of this tactic do not exceed its benefits then this behaviour will be continued to be selected. Future research is required to investigate IBP in other Moorhen populations to evaluate whether such plasticity in IBP exist elsewhere (but see Jamieson *et al.*, 2000; Post & Seals, 2000). As the frequency of Moorhen IBP appears limited by host availability, it would be prudent to investigate IBP in smaller, less densely packed populations in a variety of locations. This would allow a comparative examination of use of IBP under differing ecological conditions.

During the research, one Moorhen egg was laid parasitically in the nest of a European coot (Forman, 2001 submitted). This inter-specific brood parasitism event between Moorhens and another rail species, to the author's knowledge, is the first to be documented (see plate 9.1 page 214). Although this egg was laid during the coot female's own laying sequence and was accepted by the host group, the clutch was unfortunately predated before hatching. Additionally, several nest boxes at the study site contained eggs of Moorhens, Ringed teal, Carolina wood duck and Common shelduck. Given that these last three wildfowl species also lay parasitically and that these nest boxes were not monitored on a daily basis, it was not always possible to ascertain which species had laid parasitically. These events, however, provide an intriguing insight into the emergence of potentially new reproductive strategy in Moorhens.



Plate 9.1. Moorhen inter-specific parasitism of a Coot nest

As the success of these events is likely to be low, it is unclear whether inter-specific brood parasitism will ultimately persist in the future population of Moorhens at WWT Llanelli.

9.4 Moorhen Family Life

American and European coot parents adjust their feeding rate in response to brood size and environmental conditions (Desrochers & Ankey, 1986, Amat, 1995). Moorhen parents may behave in a similar manner. It would be interesting to examine parental feed rates in periods of increased and decreased food availability to see whether parent and chick behaviour as well as the age of chick independence is affected by differing environmental conditions. Such research should be undertaken in more “natural” settings where supplemental food is not available to parents or their offspring.

No data was collected on each parent’s exact allocation of parental care to the brood. Females may typically provide more care to younger, smaller offspring than do males in some species (Stamps *et al.*, 1987; Leonard & Horn, 1996; Slagsvold, 1997). As the respective provisioning rates to large and small chicks by male and female Moorhen parents were similar in frequency, parents appear to allocate equal amounts of parental care during the brood development period. Female parental behaviour, however, differed significantly from their partners in relation to offspring sex (see section 8.6 cf. Gibbons, 1985; Leonard *et al.*, 1988). Although the exact reason behind this difference is unclear, parents may be in conflict over the value and the consequent allocation of care to offspring of different sex (Halliday, 1994; Stamps, 1990; Yasukawa *et al.*, 1990; Westneat & Sargent, 1996). Moreover, this biased parental behaviour may serve a socialising function. It is clear that parent-

offspring associations in this species can persist for some considerable time after offspring independence (see also Gaston, 1978; Gibbons, 1985; Emlen *et al.*, 1986). Although fathers clearly did not treat male or female offspring differently up to 60 days of age, their subsequent behaviour (and that of mothers) may have an impact on offspring's decision to forgo their own attempts to breed and stay and help. As sons may exert a stronger competitive influence than daughters (Harper, 1985; Gowaty & Droge, 1991), fathers might attempt to counter tactics employed by female parents encouraging continued association with male offspring on the natal territory.

In order to assess the potential impact of continued parent-offspring associations on group formation and kin-selection, it is necessary to examine the behaviour of parents and offspring through to eventual dispersal. This would facilitate understanding of the processes and factors affecting parent and offspring's decisions to form cooperative and communal breeding groups. If possible, this research should also investigate the effect of brood size, mating systems, offspring sex ratio and territory quality on parental investment strategies (e.g. see Parker & MacNair, 1979; Desrochers & Ankey, 1986; Carey, 1990; Moreno *et al.*, 1995; Amat, 1995; Lessells *et al.*, 1998; Parish & Coulson, 1998; Albrecht, 2000).

Clearly, Moorhens are a fascinating example of a species with a rich and complex range of sexual and parental strategies. Their study is greatly facilitated by the creation of new wetlands such as those at WWT Llanelli and the detailed study of such itinerant species can be beneficial in assessing the development and health of the wetlands and the complex of species using it.

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