

ENVIRONMENTAL VARIABILITY AND GENOTYPIC CONFLICTS  
DURING REPRODUCTION IN FAMILIES OF OSPREYS

by

Lyle Scott Forbes

B.Sc. (Zoology), University of British Columbia, 1981

M.Sc. (Zoology), University of Manitoba, 1985

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

© Lyle Scott Forbes 1989

SIMON FRASER UNIVERSITY

September, 1989

All rights reserved. This work may not be reproduced in  
whole or in part, by photocopy or other means, without  
permission of the author

APPROVAL

Name: Lyle Scott Forbes  
Degree: Doctor of Philosophy

Title of Thesis:

ENVIRONMENTAL VARIABILITY AND GENOTYPIC CONFLICTS DURING REPRODUCTION IN  
FAMILIES OF OSPREYS

Examining Committee:

Chairman: Dr. R. C. Brooke

Dr. R.C. Ydenberg, ~~Assistant Professor,~~  
Senior Supervisor

---

Dr. B.D. Roitberg, Associate Professor

---

Dr. W.T. Munro, ~~B.C. Fish and Wildlife Branch,~~  
Supervisor

---

Dr. L. Dill, ~~Professor~~ Public Examiner

---

Dr. C. Crawford, ~~Professor~~ Psychology  
Public Examiner

---

Dr. D.W. Mock, Associate Professor, Zoology,  
University of Oklahoma, U.S.A.,  
External Examiner

Date Approved 15 September 1989

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

ENVIRONMENTAL VARIABILITY AND GENOTYPIC CONFLICTS DURING REPRODUCTION

IN FAMILIES OF OSPREYS

---

---

---

Author:

(signature)

LYLE SCOTT FORBES

---

(name)

(date)

15 Sept. 89

## ABSTRACT

In this thesis I examine how environmental variability and genotypic conflicts of interest affect the behaviour of ospreys (Pandion haliaetus) during reproduction. Field studies reported here were carried out in the Creston Valley of southeastern British Columbia between 1981 and 1988. In a year when parents had to travel farther to gather food for the young, the provisioning rate to broods of two declined, and brood reduction occurred. With broods of one, however, males worked harder to maintain the same provisioning rate as in other years. The fledging success of ospreys was lower in wet, cool years. However the chick provisioning rate did not decline when it rained. The relationship between inter-annual variability in parental provisioning and siblicide is examined theoretically. Due to the diminishing fitness returns of additional nestlings, senior sibs should be risk averse (i.e., siblicide may be obligatory even when food is sufficient to rear an additional sib in most years). A simulation model of chick feeding according to an absolute dominance hierarchy is used to examine how parents might affect resource allocation among offspring without preferentially feeding junior sibs. Parents may skew resources to junior sibs by increasing the rate of delivery, and/or the size of prey, or by temporally clumping feedings. All can serve to satiate the senior sibs

more often, allowing junior sibs to feed. In a field test of the hierarchy model, parents with broods of artificially exaggerated asynchronous hatching temporally clumped their feeds, resulting in more food going to junior sibs.

Parent-offspring conflict in siblicidal birds was examined using a game-theoretical model. The model predicted reduced phenotypic conflict over brood size when (i) parental costs of reproduction were considered, and (ii) when parental resources were allocated according to the brood's dominance hierarchy, rather than being evenly apportioned.

TABLE OF CONTENTS	PAGE
APPROVAL .....	ii
ABSTRACT .....	iii
TABLE OF CONTENTS .....	iv
LIST OF TABLES .....	vii
LIST OF FIGURES .....	x
ACKNOWLEDGEMENTS .....	xiv
I. GENERAL INTRODUCTION .....	1
II. RESOURCE VARIABILITY AND THE PROVISIONING BEHAVIOUR OF OSPREYS .....	16
STUDY AREA .....	18
METHODS .....	20
RESULTS .....	24
DISCUSSION .....	35
III. WEATHER AND REPRODUCTION IN OSPREYS .....	39
METHODS .....	41
RESULTS .....	45
DISCUSSION .....	60
IV. SIBLICIDE IN A VARIABLE ENVIRONMENT .....	63
THE MODEL .....	65
THE EFFECT OF A VARIABLE ENVIRONMENT .....	68
TRACKING THE ENVIRONMENT .....	71
TRACKING COSTS .....	75
DISCUSSION .....	78

TABLE OF CONTENTS (cont.)

V. RESOURCE ALLOCATION IN OSPREY FAMILIES .....	84
SECTION 1: THE HIERARCHY MODEL .....	87
MODEL RESULTS AND DISCUSSION .....	92
SECTION 2: FIELD STUDIES .....	98
METHODS .....	99
RESULTS .....	101
DISCUSSION .....	112
VI. SIBLICIDE, REPRODUCTIVE COSTS, AND PARENT-OFFSPRING CONFLICT OVER BROOD SIZE .....	117
THE GAME .....	119
MODEL RESULTS AND DISCUSSION .....	134
VII. GENERAL CONCLUSIONS .....	142
SOME ISSUES IN OSPREY MANAGEMENT.....	151
LITERATURE CITED .....	155

Tab. 2.1.	Mean number (n) and biomass (g) of bullhead, perch, and pumpkinseed per 2-hr gill-net set at Corn Creek Marsh before (CCM before) and after the drawdown (CCM after), and at Leach Lake (LL) .....	29
Tab. 2.2.	Fish delivered to nests at Corn Creek Marsh before, during, and after the drawdown .....	30
Tab. 2.3.	Comparison of lengths (mm) of black bullhead, yellow perch, and pumpkinseed from collections of skeletal remains of fish at nests at Corn Creek Marsh before, during, and after the drawdown .	33
Tab. 2.4.	Percent of time males and females (fem) spent on or near the nest during weeks 1-6 of brood-rearing before, during, and after the drawdown .....	33
Tab. 3.1.	Comparison of fledging survey methods. From 1981-85, visual surveys were used. From 1986-88, nests were climbed .....	44
Tab. 3.2.	Reproductive success of ospreys in the Creston Valley of southeastern British Columbia from 1981 to 1988 .....	46
Tab. 3.3.	Correlations between breeding parameters (mean number of young/successful nest, and percent of occupied nests that are successful) with mean temperature and rainfall. For all correlations, n=8 .....	47
Tab. 3.4.	Correlations between number of days with measurable precipitation (days with rain) and mean monthly temperature, total monthly rainfall (mm) and mean monthly wind velocity (km/h), at Creston, British Columbia, for April-July 1969-1988 (n=20 yr). Data on wind velocity only available for 1983-1987 (n=18 mo), therefore data for the months April through July were pooled .....	50



Tab. 3.5.	Serial correlations between residuals from monthly means for temperature (mean monthly temp.) and days (d) with rain for different pairs of months. For all correlations n=20. A positive correlation indicates that within a year, weather in one month tends to resemble that in another month (e.g., a wet May tends to be followed by a wet June). If weather in one month is independent of that in another, a zero correlation is expected .....	51
Tab. 3.6.	Effect of rain on the frequency of prey deliveries (percent of observation hours with delivery) during incubation and brood-rearing, 1981-86 .....	53
Tab. 3.7.	Frequency of different masses of prey delivered to nests during hours with and without rain, during brood-rearing, 1981-86 .....	54
Tab. 3.8.	Effect of rain on the proportion of time male and female ospreys spent at or near the nest during incubation and brood-rearing, 1981-86 .	56
Tab. 3.9.	Number of partially eaten fish delivered to nest by male and female at nests at Corn Creek Marsh during hours with and without rain in 1986 ...	58
Tab. 4.1.	Posterior probabilities that year i is a 'good' year after sampling for t periods with j prey deliveries ( $Pr(U_{ij} j,t)$ ). Probability that year i is a 'bad' year is simply 1-(probability of a good year). Prior probabilities of good and bad years are 0.5 .....	76
Tab. 5.1.	Frequency of aggression (physical aggression and threat displays) at feeds in normal broods ...	103
Tab. 5.2.	Number of feeds with and without aggression in relation to the number of bites eaten by the A-chick in the last 3 h in normal broods .....	103
Tab. 5.3.	Feeding frequency for normal and asynchronous broods .....	107
Tab. 5.4.	Proportion (%) of bites to female and chicks in normal and asynchronous broods .....	111
Tab. 6.1.	Definitions of variables and parameters in the model .....	121

Tab. 6.2. Optimal proportion of  $M$  ( $p^*$ ) taken by sibs in broods of one to four.  $A$  is the most senior sib,  $D$  is the most junior ..... 132

Tab. 7.1. A simple binomial model of chick survival. A brood of five chicks begins the day. The chicks are fed sequentially according to a dominance hierarchy  $A$  first,  $B$  second and so on. If a chick feeds during the day, it survives - if not it dies. A day consists of  $n$  discrete periods of length  $t$  (for an osprey,  $t$  might correspond to the minimum amount of time required for a complete hunt) and prey are delivered to the nest according to a stochastic process. The probability that a prey item is captured and delivered to the brood during any  $t$ , is  $P$ . I assume that a maximum of one prey item is delivered during any one  $t$ , that all prey are the same size, and that one prey item is eaten by one chick. Now by specifying  $n$  ( $n=10$ ) and  $P$  (0.1 to 0.5) I can calculate the probability of  $B$  ( $= 0$  to 5) chicks surviving a given day,  $Pr(B|n,P)$ , using the binomial expansion. At  $P=0.5$ , the probability of a brood of five surviving (i.e., the probability of five or more prey items being returned to the nest during the day) is 62.3% whereas at  $P=0.1$  it is 0.01% ..... 148

LIST OF FIGURES	PAGE
Fig. 1.1. The Creston Valley of southeastern British Columbia. Dots indicate locations of osprey nests occupied between 1981 and 1988 .....	10
Fig. 2.1. The study area. The locations of Corn Creek Marsh, Leach Lake and the old channel of the Kootenay River are shown. Black squares indicate locations of osprey nests .....	19
Fig. 2.2. Percent of number and biomass of fish in the gill-net catch at Corn Creek Marsh (CCM) before and after the drawdown (dd), Leach Lake (LL) and the old channel of the Kootenay River (OCKR). Fish taxa are: (i) black bullhead, (ii) yellow perch, (iii) pumpkinseed, (iv) largemouth bass, (v) catostomids, (vi) cyprinids, and (vii) salmonids .....	25
Fig. 2.3. Length-frequency distributions of black bullhead, yellow perch, and pumpkinseed in the gill-net catch at Corn Creek Marsh (CCM) before (bef) and after (aft) the drawdown and at Leach Lake (LL). Too few pumpkinseed were caught in Corn Creek Marsh after the drawdown for comparison .....	26
Fig. 2.4. Rates of delivery of prey (g, and kJ of fish/h) to nests with one and two chicks at Corn Creek Marsh during weeks 1-6 of brood-rearing before, during, and after the drawdown .....	34
Fig. 3.1. Correlation between the number of days with measurable precipitation, April to July (Rain days, April-July) from 1981 to 1988 and the mean number of young fledged per successful nest (young per succ. nest) .....	48
Fig. 4.1. Relationship between $M$ and $\lambda$ in broods of one and two. Below $M_{MIN}$ (=1.0) no chicks are viable therefore the fitness of the senior sib is zero. Below $M=2.4$ , the junior sib is not viable. At $M_{CRIT}$ (=3.8, the siblicide threshold), the fitness of the senior sib in broods of one and two is equivalent, and the senior sib favours retaining the junior sib .....	69

Fig. 4.2. Variability in M and the asymmetry of fitness costs and benefits (ben) of obligate and non-siblicide at levels of M above and below M <sub>CRIT</sub> .....	72
Fig. 5.1. Flow chart of simulation model .....	89
Fig. 5.2. Relationship between chick hunger level (H) and time since chick was last fed to satiation (T). H reaches a maximum (max) at 2 h .....	90
Fig. 5.3a. Results of the Even simulation. P <sub>A</sub> is the proportion of an individual prey item that chick A takes. Percent frequency distributions of P <sub>A</sub> are shown for small (S <sub>x</sub> =100) and large (S <sub>x</sub> =200) prey at rates of prey delivery of 100, 50 and 25 g/h. Maximum meal size is 100 g .....	93
Fig. 5.3b. Same as 5.3a, except maximum meal size (M <sub>MAX</sub> ) is now 150 g .....	94
Fig. 5.4a. Results of the Random simulation. P <sub>A</sub> is the proportion of an individual prey item that chick A takes. Percent frequency distributions of P <sub>A</sub> are shown for small (S <sub>x</sub> =100) and large (S <sub>x</sub> =200) prey at rates of prey delivery of 100, 50 and 25 g/h. Maximum meal size (M <sub>MAX</sub> ) is 100 g .....	95
Fig. 5.4b. Same as 5.3a, except maximum meal size (M <sub>MAX</sub> ) is now 150 g .....	96
Fig. 5.5. Frequency distribution of the proportion of bites (P <sub>A</sub> ) the A-chick ate at feeds with and without aggression. A-chicks took greater than 50% of the bites significantly more often at feeds with aggression than without (G <sub>1,1</sub> =5.8, p<0.05) .....	105
Fig. 5.6. Frequency of different sizes of feeds (No. of bites) to (A) female & chicks and (B) female alone in normal (Norm) and asynchronous (Asyn) broods .....	108
Fig. 5.7. Frequency distribution (Freq.) of observed intervals between feeds (0.5 h increments) in normal (Norm) and asynchronous (Asyn) broods .....	110

Fig. 5.8. Frequency of different sizes of meals (Bites per feed) eaten (A) by sib-A and (B) sib-B at feeds to normal (Norm) and asynchronous (Asyn) broods .....	113
Fig. 6.1. Relationship between present reproductive effort, $\underline{M}$ , and future reproductive success, $\underline{K}(\underline{M})$ at differing levels of $\underline{N}$ .....	123
Fig. 6.2a. Fitness value of current brood to parents at brood sizes of 1, 2 and 3 at different values of $\underline{M}$ under Even allocation .....	127
Fig. 6.2b. Fitness value of current brood to senior sib at brood sizes of 1, 2 and 3 at different values of $\underline{M}$ under Even allocation .....	127
Fig. 6.3a. Fitness value of current brood to parents at brood sizes of 1, 2 and 3 at different values of $\underline{M}$ under Despotic allocation .....	131
Fig. 6.3b. Fitness value of current brood to senior sib at brood sizes of 1, 2 and 3 at different values of $\underline{M}$ under Despotic allocation .....	131
Fig. 6.4 Numerical results of the model under Even allocation. The initial optimum brood size for parents (square in upper right hand corner of each cell) is shown for each combination of $\underline{N}$ (varied from 1 to 4), $k_{\text{MAX}}$ (varied from 1 to 6), and $M_{\text{MAX}}$ (varied from 7.5 to 15). Shaded cells indicate combinations of parameter values where offspring perform siblicide in opposition to parental interests. Cross-hatched areas indicate combinations where offspring initially favour siblicide but are constrained from doing so by the prospect of parental readjustment. Open cells indicate combinations where parents and offspring initially agree over brood size .	135

Fig. 6.5 Numerical results of the model under Despotic allocation. The initial optimum brood size for parents (square in upper right hand corner of each cell) is shown for each combination of  $N$  (varied from 1 to 4),  $k_{\max}$  (varied from 1 to 6), and  $M_{\max}$  (varied from 7.5 to 15). Shaded cells indicate combinations of parameter values where offspring perform siblicide in opposition to parental interests. Cross-hatched areas indicate combinations where offspring initially favour siblicide but are constrained from doing so by the prospect of parental readjustment. Open cells indicate combinations where parents and offspring initially agree over brood size . 136

## ACKNOWLEDGEMENTS

I would like to begin by thanking my senior thesis supervisor, Ron Ydenberg. More than anything, Ron challenged me to think about problems in different ways and I have benefitted greatly from that experience. Without Ron's efforts (and perseverance), this thesis wouldn't have been possible. The other behavioural ecologists in the department, in particular Larry Dill, Bernie Roitberg, and (the late) Mart Gross, also affected my thinking considerably. Larry, by the way, is a frightening clean-up batter on the Gouger softball team (for both his teammates and the opposition). I am grateful to Doug Mock for serving as the external examiner, for making the long trek from Oklahoma, for miscellaneous advice rendered over the last couple of years, and for writing a series of interesting papers on siblicide.

I owe a special debt of gratitude to the many people in Creston who aided my research in countless ways. These include the staff of the Creston Valley Wildlife Management Authority, and the Canadian Wildlife Service. In particular I would like to thank Brian Stushnoff, Dwight and Roz Moore, Sandra Hopcraft, Harold Casemore, Santo and Carmen Wood, Ken, Kim and Scott Haskell, Rob Butler, Bob Purdy, Don and Molra Flook, Ed McMackin, Monty Eben, Terry Sullivan, Larry Schalla, Lisa Needhams, Nell Hills, Hans Esselink, Betty Chapman-Mosher, Penny Ohanjanian and Margaret, Sylvia and

Jack Mitchell. Over the years, members of the B.C. Fish and Wildlife Branch have also helped in many ways. These include Bill Munro (who while serving on the thesis committee added his considerable expertise with raptors), Harvey Andrusak, and Tom Wood.

The most enjoyable time I spent as a graduate student was as a member of the Association of Serious Scientists for Holistic and Organismal Landmark Ecological Studies. The members of this association formed what might best be described as an extended family. I am amazed at how Mark Abrahams can be such a good fish biologist and such a bad fishing biologist. I attribute this to Mark's deeply felt conservation ethic. Robin Baird is a late arrival, but he has already made a big splash. Doug Bertram was a lot of fun (he's a fish biologist now). If I was Doug I would check into DNA fingerprinting - 'Hef' seemed terribly pleased with himself for quite a long time. I think Doug's future lies in the study of chaotic systems. Isaac Newton once remarked that "if I can see further than other men, it is only because I stand upon the shoulders of giants", or something like that. Old Isaac never met Ralf Cartar. I thank Ralf for the concept of the Cartarian unit. My thesis is testimonial to its central principle: never waste your time collecting too much data when a little bit will do. Zeke Houtman has been a stimulating addition to the group. A colour-blind individual studying colour preference in fish



would normally seem a bit odd. However, this is hardly unusual in the Dill lab. Any person crazy enough to work on ospreys is worth knowing. Marlene Machmer is one of these. Her remarks about Ralf's gait were quite amusing. Guy Martell has a passionate love for the Montreal Canadiens (and, we suspect, for ducks although this is not yet proven), thus I feel badly that I cheered when Lanny McDonald scored the goal that sunk the Habs. Peter Nonacs is the only scientist I know in the Tupperware hall of fame. Pete's evil little grin, the one he got after a couple of beers in the pub, is unforgettable. By the way, did they ever catch the Green River killer? Karen Price didn't start to say anything for almost a year after she arrived. For the last year we couldn't get her to stop. Clive Welham. Even the name is overwhelming. Clive served as the intellectual father for Zeke's polygyny threshold model. Clive has many interests but is particularly fond of curling. Any activity where it is a requirement to hold a beer in one hand and a smoke in the other is Clive's kind of sport. Chris Steeger is an illegitimate member of the Association. Chris is the first of us to apply the theory of behavioural ecology to the real world (offspring are more valuable early in the year). Chris's approach to potential dog-offspring conflict also seems quite innovative. I await eagerly the results of this study. Finally, I save special thanks for Maggie - she knows why. Hi Ho.

CHAPTER ONE

GENERAL INTRODUCTION

In this thesis I present studies of the reproductive behaviour of ospreys (Pandion haliaetus), large, fish-eating hawks of the family Accipitridae, which exhibit facultative brood reduction. The goal of this work is to understand the roles of environmental variability and genotypic conflict among relatives in shaping the reproductive decisions of both parents and offspring. The present work involves empirical and theoretical aspects.

Parents make two sets of reproductive decisions simultaneously: how much total effort to expend on current reproduction (a present-future trade-off), and how much of the total effort to allocate to individual offspring (a quantity-quality trade-off). Parents draw upon a finite pool of resources and therefore are forced to make compromises among offspring, both present and future (Williams 1966a,b). Osprey parents must decide what size of brood to rear, and how to allocate resources among brood members.

Nestling ospreys depend upon their parents for food, and have two ways to garner more resources for themselves. Such offspring can either take food from contemporary sibs (by outcompeting or eliminating them), or they can induce parents to bring more food, which may result in fewer future sibs if such behaviour lowers the parent's expectation of future survival or fecundity.

## ROLE OF ENVIRONMENTAL VARIABILITY

Both parents and offspring are faced with the prospect of environmental uncertainty. In proposing the original brood-reduction hypothesis, David Lack (1947) recognized the importance of resource variability to parents. According to Lack parents initiate clutches larger than they normally expect to rear and, if food is insufficient, allow brood size to be reduced to match prevailing food conditions. Although the literature on avian brood reduction is vast (see Mock and Parker, in prep., for a review), only Magrath (1989) has presented a thorough experimental evaluation (by both manipulating food supplies and following offspring until they were recruited into the breeding population) of Lack's hypothesis (which was verified). Furthermore, the effects of resource variability on the behaviour of offspring are just beginning to be explored (Mock 1984a,b, 1985, Mock et al. 1987a,b). And even though resource variability is central to Lack's brood reduction argument, it is rarely measured directly. Our knowledge of variation of food supplies within and between seasons remains scant.

Nestlings require a regular supply of food for growth and maintenance. Very young chicks, for example, may be unable to go without food for more than a few hours. During incubation and much of the nestling period, offspring are vulnerable to hypo- or hyperthermia and require the

attention of a brooding parent to buffer them from the effects of thermal fluctuations.

Both thermal and resource variability are affected by weather. Metabolic costs of thermoregulation increase at very low or high temperatures, and wind and rain affect the rate of heat loss, especially for nestlings. Ospreys plunge-dive for their fish prey and inclement weather depresses hunting success (Grubb 1977, Machmer and Ydenberg, 1989). A primary responsibility of parents, then, is to buffer offspring from the inimical effects of environmental variability.

Chapters Two and Three examine the effects of environmental variability on osprey reproduction at two different levels. In Chapter Two I investigate the effects of long-term (inter-annual) variability in food supplies; Chapter Three examines the short- (day-to-day variation) and long-term effects of weather on reproduction. In Chapter Four I investigate theoretically the effects of interannual variation in food on the brood reduction decisions of offspring.

#### ROLE OF GENOTYPIC CONFLICT AMONG RELATIVES

Hamilton (1964) presented the current conceptual framework with which to examine the behaviour of relatives toward one another, which can be distilled to Hamilton's rule:  $rB-C > 0$ . In order for an action to evolve, it must provide a benefit

(B) to the recipient (increased number of offspring) exceeding the cost (C) to the donor (decreased number of offspring), discounted by the coefficient of relationship (the probability of sharing an allele by descent). Building upon this framework, Trivers (1974) established that genotypic conflict should exist between parents and offspring; each should be more selfish than the other desires. The behavioural consequences of parent-offspring conflict and sibling rivalry have been much explored in a theoretical context (MacNair and Parker 1978, 1979, Parker and MacNair 1978, 1979, Stamps et al. 1978, Stamps and Metcalf 1980, Parker 1985, Mock 1987, Parker et al. 1989). The general conclusion of this work is that, over evolutionary time, a pro rata compromise solution between the interests of both parents and offspring is to be expected.

In Chapter Five I examine resource allocation among contemporary sibs in relation to parental provisioning behaviour. In Chapter Six I investigate theoretically the consequences of reproductive costs for parents on parent-offspring conflict over brood size.

The parents are of course not related and throughout the thesis I have treated them as though they were a fully co-operating unit. In fact, osprey parents perform different roles during breeding (see below) and there are reasons to suspect that there will be conflict between them

over aspects of breeding. This aspect of their biology is not considered here.

### Parent-offspring conflict in siblicidal birds

In siblicidal birds, parents establish competitive asymmetries among offspring at hatch, and in doing so, appear to relinquish control over (i) how resources are shared among offspring, and (ii) brood size. Senior siblings through size and motor-skill advantages and the use of aggression command a disproportionate share of parental resources, and are capable of eliminating junior siblings. Due to the differing genetic interests of parent and offspring, we expect evolutionary conflict over resource allocation and brood size. Yet behavioural evidence of such conflict in siblicidal birds is slim. Parents rarely intervene in sibling aggression, and generally do not feed junior sibs preferentially, although some exceptions exist (see Mock 1984a, 1987; Drummond et al. 1986).

Mock (1987) proposed two alternatives to resolve this seeming paradox. First, significant parent-offspring conflict exists and the offspring are "winning"; but if this is the case, two further questions arise: Why has natural selection not favoured opposing parental behaviour, and why do parents establish the initial competitive asymmetries (e.g., via hatch asynchrony) among offspring (Mock 1987)?

Mock's second alternative is that no significant evolutionary conflict exists: offspring perform siblicide according to their own selfish interests, and this behaviour also serves the parent's interests; parents create the initial asymmetries among offspring, but do not intervene further. Such a "laissez-faire" policy (sensu Mock 1987), where resources are shared unequally among offspring, may be favoured if it allows parents to adjust brood size to reflect variation in the environmental yield of resources. Drummond et al. (1986) have described such congruency between parent and offspring interests as 'parent-offspring' cooperation.

#### Patterns of siblicide

Siblicide (infanticide carried out by full or half sibs, sensu Mock 1984a) occurs in a variety of forms that can be divided for convenience into two broad categories: obligate and facultative siblicide. (Here I follow the terminology of Mock (1984a)) Obligate siblicide is best known in various eagles, boobies, and pelicans. All lay two eggs, hatching is asynchronous, and usually the elder sib kills its younger sib soon after hatch. From the parent's perspective, the second egg/chick serves as insurance against the unexpected failure of the first (Cash and Evans 1986). Interestingly, obligate siblicide seems to be independent of the prevailing level of food at the time of



the junior sibling's demise. This is graphically illustrated in Gargett's (1978) oft cited description of a four-day-old black eagle (Agulla verreauxi) chick, weighing 163 g, pummeling its newly hatched sib (which died) while more than 5 kg of prey remained uneaten in the nest. Stinson (1979) proposed the 'pending competition' hypothesis to explain this paradoxical behaviour. Simply, food may not be limiting at the time of the junior sib's demise, but may become so later on. Pre-emptive siblicide may therefore be favoured.

Facultative siblicide, where the survival of the junior sibling is conditional (at least in part) upon the prevailing levels of food, can be further subdivided into two broad categories: conditional and probabilistic facultative siblicide. The former is distinguished by a proximate link between food, hunger, and sibling aggression. Chicks seem to obey the simple behavioural rule 'fight if hungry.' Food shortage triggers aggression resulting in the demise of the junior-most member(s) of the brood hierarchy.

Under probabilistic facultative siblicide, sibling aggression is obligatory, but chick survival depends upon prevailing food levels. When food is abundant, junior sibs remain sufficiently strong to withstand the beatings from their senior sibs and survive to fledge, whereas if food is short, junior sibs weaken and die.

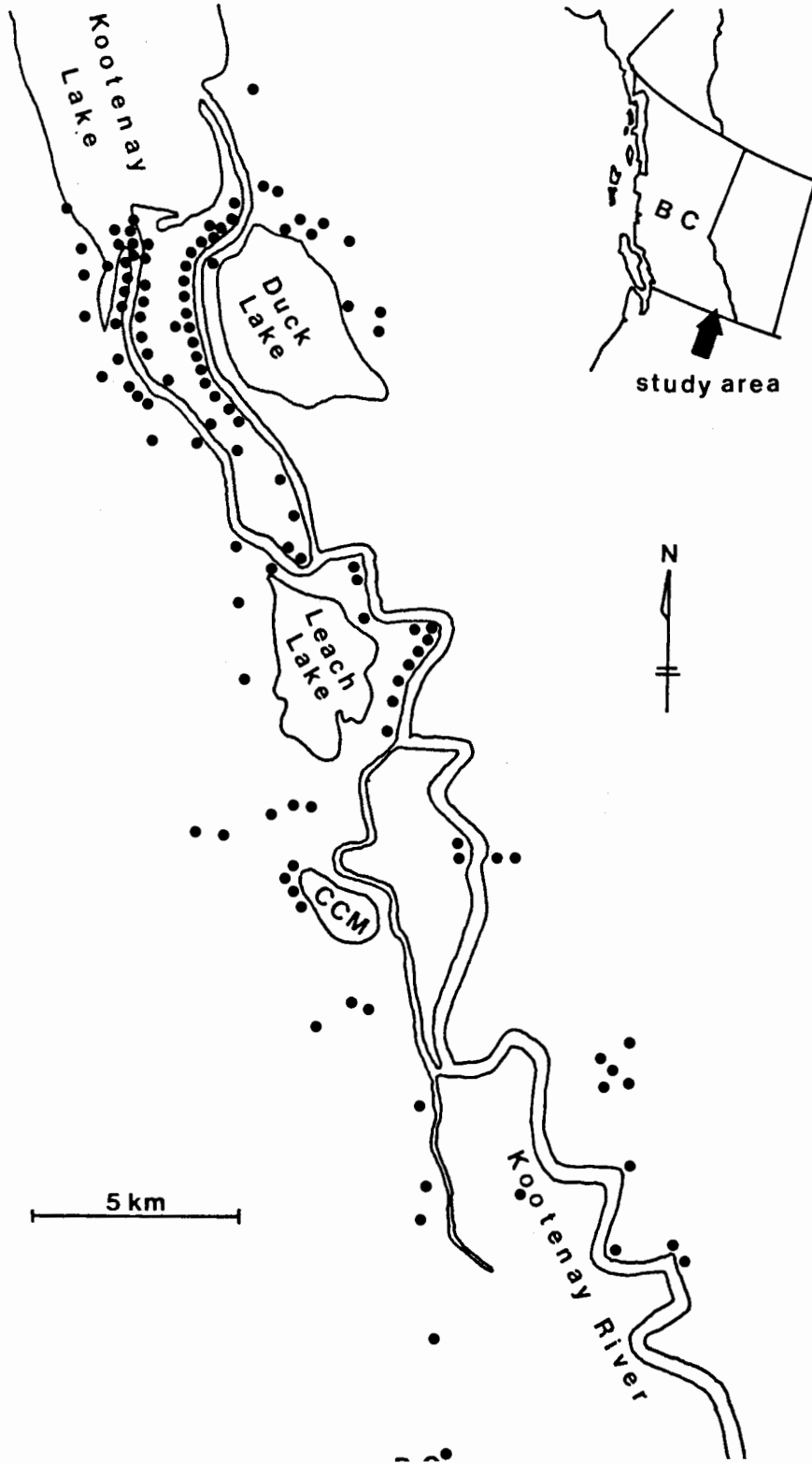
The key difference between conditional and probabilistic facultative siblicide appears to be within-season variation in food availability (Mock et al. 1987a). When food varies in a predictable manner (i.e., what a chick receives today is a reliable indicator of what it will receive tomorrow), facultative aggression may be favoured. Under such conditions chick hunger accurately portends pending food shortages, thus triggers aggression appropriately. Similarly if food is plentiful and likely to remain so, then aggression is superfluous. However, where food is unpredictable (i.e., what a chick receives today is not a reliable indicator of what it will get tomorrow), obligatory aggression may be favoured; senior sibs guarantee priority access to parental resources, such that if an unpredictable food shortage does occur, junior sibs are burdened with the shortfall.

To summarize, on a behavioural continuum, obligate siblicide lies at one extreme, conditional facultative siblicide lies at the other, and probabilistic facultative siblicide lies in between.

#### CRESTON AND ITS OSPREYS

I studied ospreys in the the Creston Valley in southeastern British Columbia from 1981-88. The valley extends 32 km from the Canada-USA boundary on the south to the shores of Kootenay Lake on the north (Fig. 1.1). The

Figure 1.1. The Creston Valley of southeastern British Columbia. Dots indicate locations of osprey nests occupied between 1981 and 1988.



valley is oriented north-south and is bounded on the east and west by the Selkirk and Purcell ranges, respectively. The valley floor is broad and flat (elevation=530 m), and is comprised primarily of the alluvial flood-plain of the Kootenay River. The Kootenay River winds its way north through the valley to its confluence with Kootenay Lake.

Extensive wetlands occur throughout the valley, and nearly all (83% of area) are contained behind dykes (Butler et al. 1986). Northern black cottonwood (Populus trichocarpa) line the numerous watercourses in the valley. The hillsides are forested primarily with conifers including Douglas fir (Pseudotsuga menziesii), western larch (Larix occidentalis), lodgepole (Pinus contorta) and ponderosa pine (P. ponderosa), western red cedar (Thuja plicata), and western hemlock (Tsuga heterophylla).

Approximately sixty breeding pairs of ospreys and an unknown number of non-breeders occupy the valley each year. This population has remained stable since my study began in 1981 (The smaller number of occupied nests (37) reported in Flook and Forbes (1983) is due to the fact that not all nests were surveyed in the early stages (1981-82) of the study.) The present population is about twice the size of that which occupied the valley in the 1940-60's. Flook and Forbes (1983) attributed this population increase to the extensive dyking of the late 1960's and 1970's, which created many permanent wetland areas. Prior to the creation

of these impoundments and the construction of the Libby dam upstream on the Kootenay River, water levels in the valley fluctuated at least 4 m, from a high during the June freshet to a late summer low. With water levels stabilized, the impoundments were colonized by four introduced fish species [black bullhead (Ictalurus melas), yellow perch (Perca flavescens), pumpkinseed (Lepomis gibbosus), largemouth bass (Micropterus salmoides)], creating large, stable prey populations for ospreys. Native cyprinids, catostomids, and salmonids still predominate the fish fauna in the Kootenay River and its various side-channels and tributaries. These fish, too, are taken by ospreys.

Most osprey nests in the Creston Valley are located in northern black cottonwoods along channels of the Kootenay River. Near the mouth of the Kootenay River, several nests (5-6) occur on man-made structures (railway trestle, pilings). A few nests are located on the hillsides in conifers or on man-made structures (power poles, nest platforms). Flook and Forbes (1983) mapped the locations of nests in the Creston Valley in 1981; although more nests have been located since then, the general distribution is still similar, with most nests occurring in the northern half of the valley, where most wetland areas are present (Fig. 1.1).

### Breeding chronology

Ospreys arrive in the valley from late March to mid-April, and initiate clutches of one to four eggs (usually three) from late April to mid-May. Hatching, which occurs from late May through June, is asynchronous, with the first and second eggs usually hatching 0-1 d apart; the interval between the second and third eggs is longer, usually 1-4 d (Steeger 1989). The chicks begin flying at seven to eight weeks of age in late July and August, and by early October all ospreys have left the valley. Ospreys from northern Idaho (and presumably Creston) winter in the Pacific coastal areas of Central America (Melquist et al. 1978, Melquist and Johnson 1984).

### Osprey natural history

The following information is derived from Henny (1988) except where noted. Ospreys are sexually dimorphic, with female body mass exceeding that of males by about 10%. During breeding the roles of males and females differ greatly; females are primarily responsible for incubation and brooding of the young, whereas males are responsible for provisioning the female and chicks. Late in the nestling period and during the post-fledging period, the female aids the male in provisioning the brood.

The annual rate of adult mortality is 15-20% per annum; juvenile mortality is much higher at 41 to 57%. Juvenile

ospreys remain on the wintering grounds for 16-18 months, not returning north to breeding areas until at least their third calendar year. Most ospreys begin breeding at age three or later.

### Sibling rivalry in nestling ospreys

The following is derived from my own observations of ospreys at Creston and I shall elaborate further upon much of this in the body of the thesis. Among osprey nestlings, a stable dominance hierarchy based on size and age differences among the chicks is usually established soon after hatch. Sibling aggression is manifested in two ways: physical abuse (biting, pecking) and threat displays. Physical aggression appears to be replaced largely by threat displays as the chicks grow older. In some broods, there is no evidence of any aggression, either physical or threat. During a feed, the female parent tears fish into bite-sized pieces which she holds out for the chicks to grab. In most cases aggression occurs during feeds, when chicks jockey for position directly in front of the female. Dominant chicks generally stand immediately in front of the female as she distributes bites of fish to the brood. When chicks are not aggressive, two or more may stand in front of the female and feed simultaneously. The parent female appears to play a passive role in chick feeding, not favouring one chick over the others in any obvious way, and never intervening in

sibling aggression. When aggressive, dominant chicks may prevent others from feeding; in extreme cases intimidated chicks may cower in the corner of the nest while the more senior sibs feed. Often the begging of a junior sib elicits an aggressive response from a senior sib.

Nestling aggression is probably proximally linked to food. In ospreys, as hungrier chicks seem to fight more often (Chapter Five). Once satiated, dominant chicks allow subordinates to feed. Very young chicks may even be physically incapable of preventing their nest-mates from feeding as their loaded crops appear to be so heavy.

I have occasionally observed siblicidal aggression among nestlings. In these cases, senior sibs beat a junior sib relentlessly, even between feeds and the junior sib disappeared from the nest soon after. More frequently, chicks succumbed to starvation. In most cases, nestlings perish when less than three weeks of age, when food demands are low and the parents would easily be able to provision the entire brood.



CHAPTER TWO

RESOURCE VARIABILITY  
AND THE PROVISIONING  
BEHAVIOUR OF OSPREYS

## INTRODUCTION

Unpredictable variation in the availability of resources is a fact of life for many organisms. For dependent offspring this may be manifested in unpredictable levels of provisioning by their parents. By adjusting their effort, however, parents can potentially buffer offspring from the effects of resource variation. Parental behaviour in the face of environmental variability thus will be an important element of reproductive behaviour.

From the onset of incubation until late in the nestling period, the male osprey conducts nearly all of the foraging (Stinson 1978, Levenson 1979, Jamieson et al. 1982), capturing and delivering prey - almost exclusively fish - singly to the nest (Henny 1988, Poole 1989). Thus the brood depends upon the foraging effort of the male for its provisioning.

From 1981 to 1986, three to five pairs of ospreys nested near Corn Creek Marsh (Fig. 2.1). Prior to 1984 ospreys foraged primarily at Corn Creek Marsh, but in 1984 the marsh was drained (drawn down) by the management authority, forcing ospreys to forage at more distant sites, primarily Leach Lake about 3 km away, but at Summit Creek and the old channel of the Kootenay River as well. In the following year, the marsh was reflooded but fish populations were depressed from previous levels; furthermore, a portion of Leach Lake was drawn down. The distance between foraging

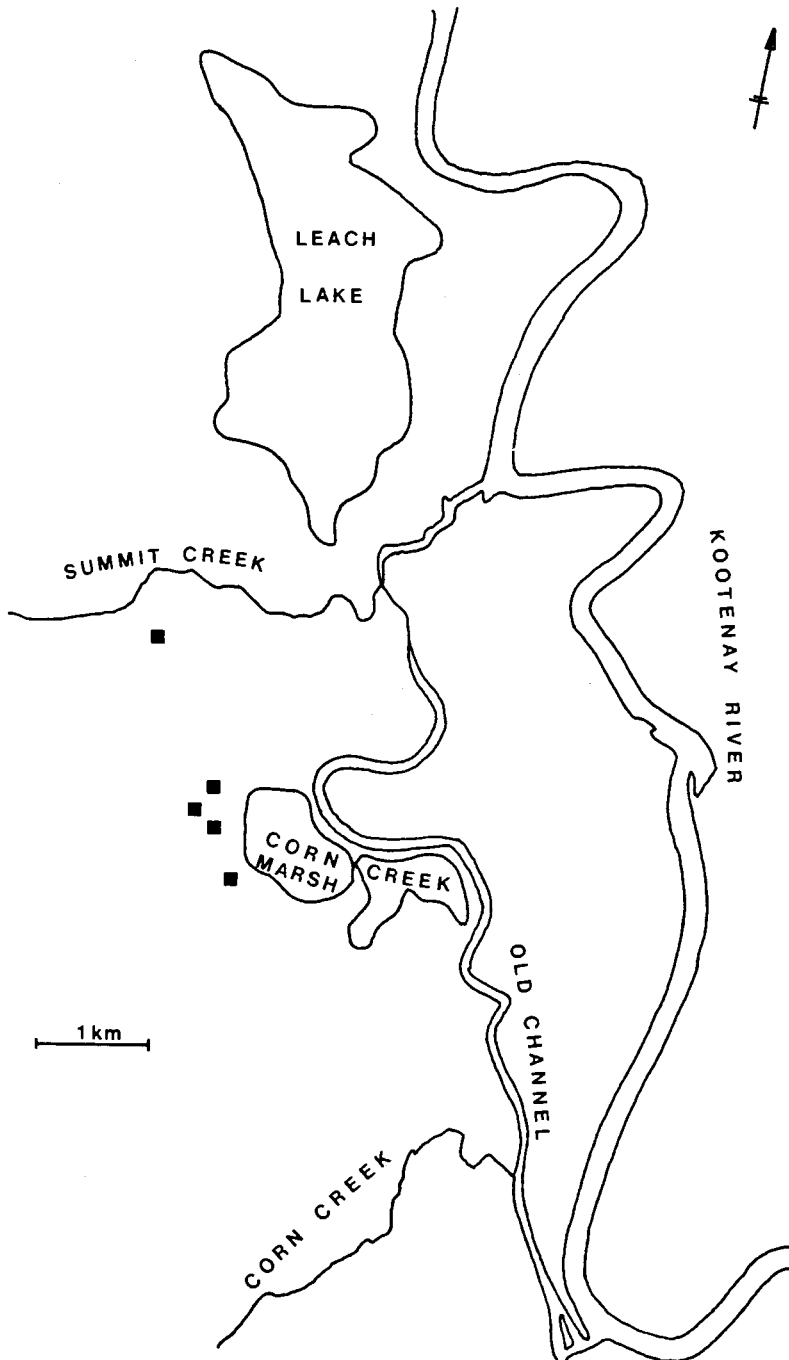
areas and the nest seems likely to affect the rate of prey delivery, and this sequence of events therefore allowed me to address questions about the foraging effort of ospreys in response to unanticipated changes in food availability. I measured the abundance of prey at the different foraging sites in order to establish the effect of the drawdown, and measured the provisioning behaviour of ospreys by observing their nests.

#### STUDY AREA

The study was conducted at Corn Creek Marsh on the Creston Valley Wildlife Management Area (CVWMA) in the Creston Valley of southeastern British Columbia. A small number of ospreys nested near the marsh (Fig. 2.1) and hunted there, except in 1984 when the marsh was drained.

Corn Creek Marsh is a shallow, eutrophic marsh, less than 1.5 m deep over most of its area. Where an old creek channel runs through the marsh and in ditches beside dykes the water may be as deep as 3 m. The periphery of the marsh is dyked and water levels are controlled by the Management Authority. Extensive emergents and submergents occur throughout the marsh. Leach Lake is similar in most respects to Corn Creek Marsh, being shallow and eutrophic. Vegetation is also similar. Leach Lake is divided into compartments by dykes (Fig. 2.1).

Figure 2.1. The study area. The locations of Corn Creek Marsh, Leach Lake and the old channel of the Kootenay River are shown. Black squares indicate locations of osprey nests.



The old channel of the Kootenay River ranges from 2 to 6 m in depth. It is connected to the main channel of the Kootenay River and its water level fluctuates with that of the Kootenay River, but water flow within the old channel is minimal; it is essentially a long slough. Summit Creek is a moderate-sized mountain stream inhabited primarily by various salmonids including rainbow trout (Oncorhynchus mykiss, formerly Salmo gairdneri).

#### METHODS

Nest watches were conducted at nests surrounding Corn Creek Marsh from May to August 1981-1984 and 1986. At four of the five nests the observer sat above or level with the nest. Observations were made with the aid of a spotting telescope between 0400 and 1900 h PST. Most observations were made 50 to 100 m from the nest without the use of a blind. No difference in behaviour was noted when a blind was or was not used. Observation sessions lasted from 1 to 14 h. During observations, the presence or absence of the male and female at the nest or a perch near the nest, the number and age of young, the timing of fish deliveries to the nest, and the size and species of fish were recorded. Nearly all fish could be identified by their characteristic shapes and colours. The size of the fish was estimated as a proportion of the tarsus, tail, or body length of the osprey, accurate to about 5 cm (Stinson 1978). Ospreys were

sexed by differences in body size and by the presence of streaking on the breast of the female (Macnamara 1977). Time spent at the nest by both males and females was used as an index of hunting effort, reasoning that individuals hunting longer would be at the nest less. Observations of fish delivered to nests were used to quantify the rate of prey delivery with respect to the stage of the drawdown.

The observations reported here were made when the chicks were one to six weeks old. The distribution of observation effort with respect to chick age was similar across years, minimizing potential biases due to differences in chick age.

Male ospreys usually eat the anterior portion of a fish at a habitual perch near the nest prior to delivery. Hard parts of the fish (e.g., opercula, cleithrum, spines, etc.) are dropped beneath these perches, and can be used to determine the size and species of fish eaten. Each year I collected fish bones beneath the nests and associated perches around Corn Creek Marsh. I obtained a reference collection of skeletal elements from fish sampled from local populations. From this I obtained bone-fish length and bone-fish mass regressions. For each sample of bones collected at perches and nests, I used the most abundant bone for each species. In order to ensure that bones from one fish were not counted twice, I chose either right side or left side bones, whichever was more abundant. Estimates of the mean sizes of black bullhead, yellow perch, and

pumpkinseed, the three most common prey species, were obtained from the collections of fish remains, and were used as estimates of the size of these fish returned to nests in preference to observational estimates of the length of fish.

The energetic equivalents for different prey species were obtained from Watt and Merrill (1975). Where values for a particular species did not exist, the value for the most closely related species was used (e.g., the value for white sucker (Catostomus commersoni) was used for largescale (C. macrochellus) and longnose sucker (C. catostomus)).

Gill-nets were used to estimate the species and size composition, and relative abundance of fish at the different foraging sites of the ospreys. Sampling sites at Corn Creek Marsh and Leach Lake, the two primary foraging areas for ospreys, were nearly identical with respect to water depth, turbidity, and vegetation characteristics. Gill-nets were used for fish sampling during 1981-83, and 1986. The gill-net consisted of five gangs of mesh (25, 38, 51, 63, and 76 mm) each 10 m by 2.5 m. Diurnal gill-net sets were one or two hours long; nocturnal sets were 12 hours. Captured fish were measured to the nearest millimeter and weighed with hand-held spring balances. Fish under 100 g were measured to the nearest gram and fish over 100 g measured to the nearest 5 g. Fish weights reported throughout the thesis refer to wet weights. Fish were released after measurement. Gill-netting at Corn Creek

Marsh was conducted bi-weekly from May to August; gill-netting at Leach Lake and the old channel of the Kootenay River was conducted at monthly intervals.

### Statistical Analyses

The small number of nests in the study population necessitated pooling data across nests. No significant differences were found between individuals in various behavioural measures, however due to small sample sizes, the statistical power of such analyses is low (<10% in most cases). Thus I can not be confident that no differences existed between individuals. If such differences exist, but are small relative to the effect of the variable being measured (in this case the drawdown), then their importance statistically is small. Nevertheless, when interpreting the results of this and subsequent chapters, the reader must be cognizant of the fact that the behaviour of a small number of individuals was being measured.

Overall, behavioural data collected before and during the drawdown were from four nests, and after the drawdown were from five nests. In some cases brood reduction occurred at nests with two chicks during the course of observations. Data collected from those nests on foraging rates sometimes occurs in both the one (after brood reduction occurred) and two chick categories (before brood reduction occurred). The



number of nests in each category in a given year ranged from one to four.

## RESULTS

### Composition of fish species in the gill-net catch

The species composition differed among sites (Corn Creek Marsh before and after the drawdown, Leach Lake and the old channel of the Kootenay River, Fig. 2.2:  $G_{(2)}=732$ ,  $p < 0.001$ ). Leach Lake and Corn Creek Marsh contained a marsh fauna, predominated by black bullhead, yellow perch and pumpkinseed (Fig. 2.2), whereas the old channel of the Kootenay River contained a river fauna, predominated by northern squawfish (Ptychocheilus oregonensis), peamouth (Mylocheilus caurinus), largescale and longnose suckers, and largemouth bass (Micropterus salmoides) (Fig. 2.2).

The drawdown had a large effect on fish populations in Corn Creek Marsh; the proportion of yellow perch increased, and the proportion of black bullhead decreased after the drawdown (Fig. 2.2:  $G_{(2)}=47.1$ ,  $p < 0.001$ ). However, the yellow perch were much smaller after the drawdown (see below) and so the proportional biomass of perch and bullheads did not change.

### Size distributions of fish in the gill-net catch

There were no significant differences between the size distributions of black bullhead or yellow perch in the gill-net catch at Leach Lake and Corn Creek Marsh before the

Figure 2.2. Percent of number and biomass of fish in the gill-net catch at Corn Creek Marsh (CCM) before and after the drawdown (dd), Leach Lake (LL) and the old channel of the Kootenay River (OCKR). Fish taxa are: (i) black bullhead, (ii) yellow perch, (iii) pumpkinseed, (iv) largemouth bass, (v) catostomids, (vi) cyprinids, and (vii) salmonids.

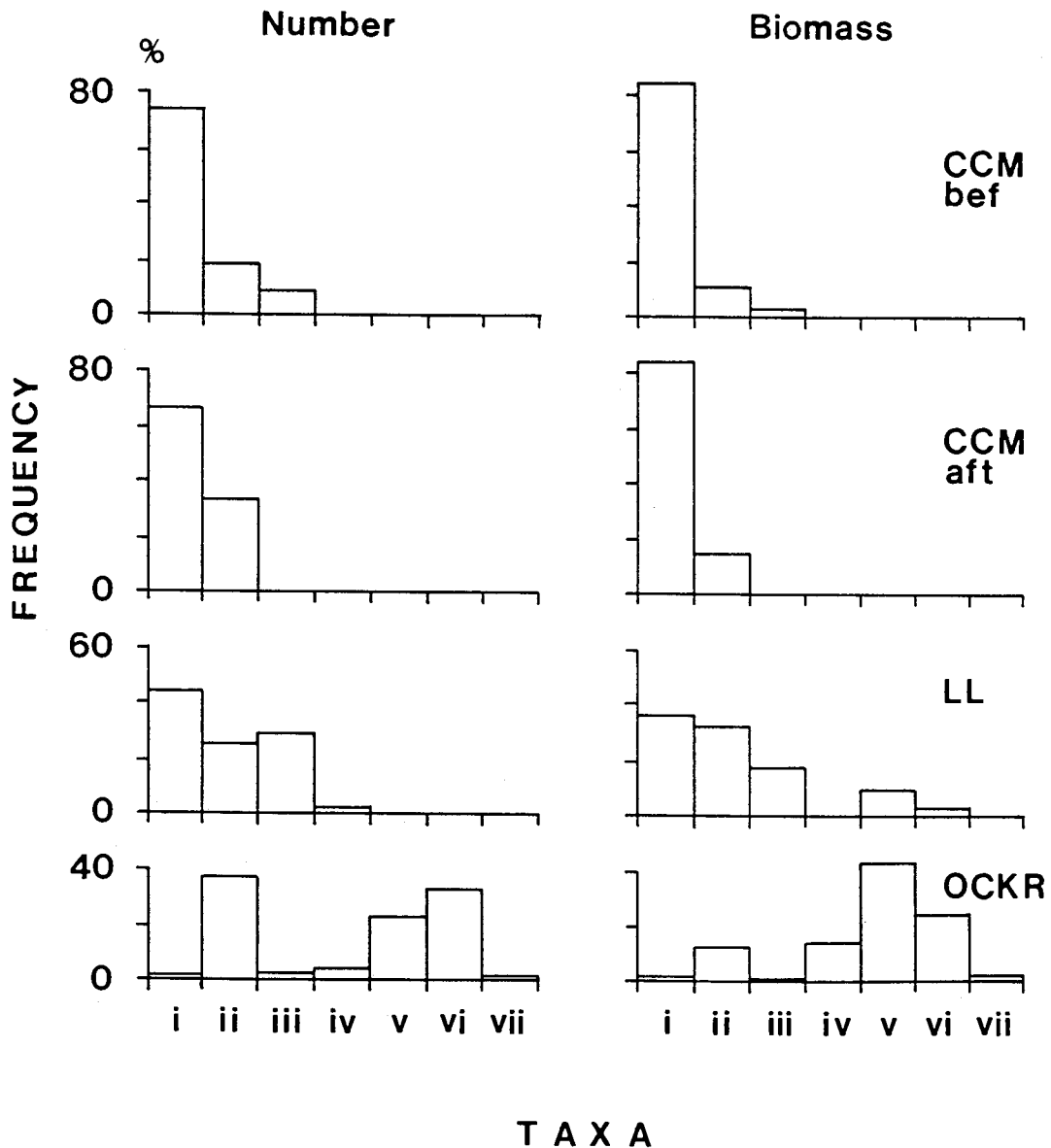
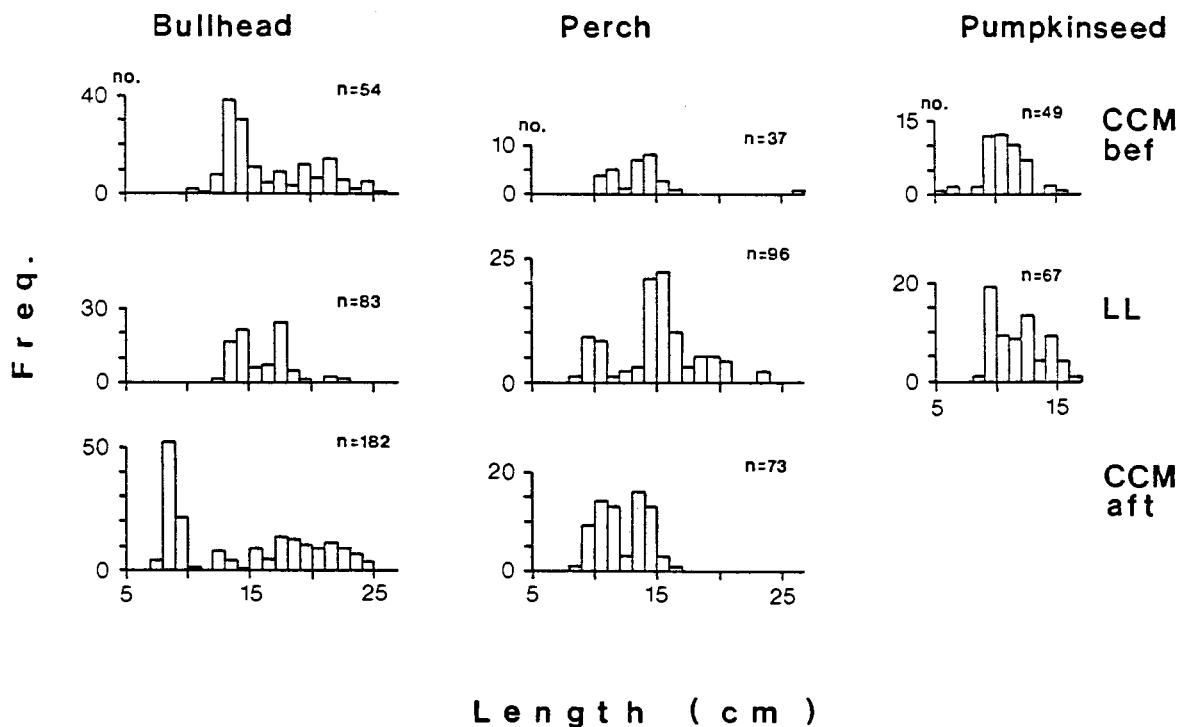


Figure 2.3. Length-frequency distributions of black bullhead, yellow perch, and pumpkinseed in the gill-net catch at Corn Creek Marsh (CCM) before (bef) and after (aft) the drawdown and at Leach Lake (LL). Too few pumpkinseed were caught in Corn Creek Marsh after the drawdown for comparison.



drawdown (Fig. 2.3; black bullhead: Mann-Whitney U-test,  $z=0.126$ ,  $p=0.45$ ; yellow perch,  $z=0.972$ ,  $p=0.167$ ).

Pumpkinseed at Leach Lake were, however, larger than those at Corn Creek Marsh before the drawdown ( $z=1.696$ ,  $p=0.045$ , Fig. 2.3).

After the drawdown, however, fish at Corn Creek Marsh were smaller than before (Fig. 2.3; black bullhead: Mann-Whitney U-test,  $U=10622$ ,  $p=0.0001$ ; yellow perch,  $U=502.5$ ,  $p<0.0001$ ); too few pumpkinseed were taken at Corn Creek Marsh after the drawdown to make a formal comparison.

Fish in old channel of the Kootenay River were much larger than fish in Corn Creek Marsh or Leach Lake (e.g., mean mass in gill-net catch at old channel of the Kootenay River: longnose sucker,  $\bar{x} = 330$  g, range = 47-670; largescale sucker,  $\bar{x} = 212$  g, range = 57-540; peamouth,  $\bar{x} = 81$  g, range = 22-210; mean mass in gill-net catch at Corn Creek Marsh in 1981-82: black bullhead,  $\bar{x} = 97$  g, range = 10-300; yellow perch,  $\bar{x} = 52$  g, range = 10-240; pumpkinseed,  $\bar{x} = 37$  g, range = 8-150).

#### Abundance and size of fish in the gill-net catch

Compared to Leach Lake, the biomass of black bullhead, but not the number, was greater at Corn Creek Marsh before the drawdown (Table 2.1, biomass:  $U=7$ ,  $p<0.05$ , number:  $U=18.5$ ,  $p>0.05$ ). However, the size and abundance of yellow perch and pumpkinseed at Leach Lake was greater than at Corn Creek

Marsh before the drawdown (Table 2.1; yellow perch, biomass:  $U=29$ ,  $p<0.05$ , number:  $U=29$ ,  $p<0.05$ ; pumpkinseed, biomass:  $U=5$ ,  $p<0.05$ , number:  $U=3$ ,  $p<0.05$ ).

The abundance and size of black bullhead, yellow perch and pumpkinseed in the gill-net catch in Corn Creek Marsh declined following the drawdown (Table 2.1, Mann-Whitney U-test, black bullhead, biomass:  $U=2$ ,  $p<0.001$ ), number:  $U=2.5$ ,  $p<0.001$ ; yellow perch, biomass:  $U=29$ ,  $p<0.05$ , number:  $U=29$ ,  $p<0.05$ ; pumpkinseed, biomass:  $U=5$ ,  $p<0.05$ , number:  $U=0$ ,  $p<0.001$ ).

#### Prey Returned to Nests

Significant differences in the species composition of prey returned to nests occurred among years. The proportion of pumpkinseed (captured at Leach Lake) taken was significantly higher during the drawdown (Table 2.2). Before the drawdown black bullhead and yellow perch, captured primarily at Corn Creek Marsh, predominated in the diet (Table 2.2). After the drawdown, black bullhead, captured primarily at Corn Creek Marsh, once again were the predominant prey, but suckers caught at the old channel of the Kootenay River, and rainbow trout, caught at Summit Creek, were taken more frequently than in previous years.

Table 2.1. Mean number (n) and biomass (g) of bullhead, perch, and pumpkinseed per 2-hr gill-net set at Corn Creek Marsh before (CCM before) and after the drawdown (CCM after), and at Leach Lake (LL).

Location	bullhead		perch		pumpkinseed		sets
	n/set	g/set	n/set	g/set	n/set	g/set	
CCM before	21.3	1985.3	5.3	204.5	2.3	83.3	8
CCM after	0.7	62.7	1.7	79.0	0	0	20
LL	21.0	983.5	12.8	843.5	14.3	457.5	4

Table 2.2. Fish delivered to nests at Corn Creek Marsh before, during, and after the drawdown<sup>1</sup>.

---

Fish	Before	During	After
black bullhead	8	3	38
yellow perch	11	1	3
pumpkinseed	5	39	0
rainbow trout	0	0	3
sucker sp.	2	2	8
other <sup>2</sup>	2	3	4
	28	48	56

---

1. Comparison of species taken before, during, and after the drawdown:  $G_{(2)}=117$ ,  $p<0.01$  (suckers, trout and other fish grouped in analysis).
2. Includes kokanee, northern squawfish, largemouth bass and unidentified fish.

### Prey Size

There were no differences in the size of black bullhead recovered in collections of fish skeletal remains before, during, and after the drawdown (Table 2.3; ANOVA,  $f=0.58$ ,  $df=2,190$ ,  $p>0.05$ ). Also, there were no differences in the sizes of yellow perch and pumpkinseed in the skeletal remains before and during the drawdown (Table 2.3; yellow perch:  $t=0.07$ ,  $df=38$ ,  $p>0.05$ ; pumpkinseed:  $t=0.32$ ,  $df=29$ ,  $p>0.05$ ).

### Time At The Nest

Males spent less time away from nests before the drawdown than either during or after the drawdown (Table 2.4). Females were never absent before the drawdown but spent a small amount of time away from the nest during and after the drawdown. These data suggest that before the drawdown both males and females spent less time foraging than during or after the drawdown.

### Rates of Delivery of Fish to Nests

In all years the delivery rates of fish biomass and energy to broods of one were similar, but the number of fish delivered per hour was more variable. During the drawdown, ospreys took more and smaller fish, primarily pumpkinseed captured at Leach Lake (Table 2.2). After the drawdown, ospreys took fewer, larger fish, primarily black bullhead,



trout and suckers (Table 2.2), captured at the old channel of the Kootenay River and Summit Creek.

Before and after the drawdown, the rate of delivery (g/h) to broods of two was substantially higher than to broods of one (Fig. 2.4). During the drawdown, however, the rate of delivery to broods of two was lower, and similar to that of broods of one. During that year brood reduction occurred at the two nests with two chicks. The pattern of delivery to broods of two was different than that to broods of one. The mass and energetic value of fish delivered to broods of two was much lower during the drawdown. As observations necessarily were made before the younger chick was killed, the lower delivery rate to broods of two may be due in part to the younger age of those broods. During the drawdown, ospreys brought more of the small and energetically less valuable pumpkinseed (Table 2.2). After the drawdown ospreys brought larger and energetically more valuable fish to the brood (Fig. 2.4). The mass of fish delivered was similar before and after the drawdown (Fig. 2.4), but the energetic value of fish taken after the drawdown tended to be higher.

#### Female Foraging

Before and during the drawdown, females caught only 1 of 77 (1.3%) fish delivered to the nest. After the drawdown,

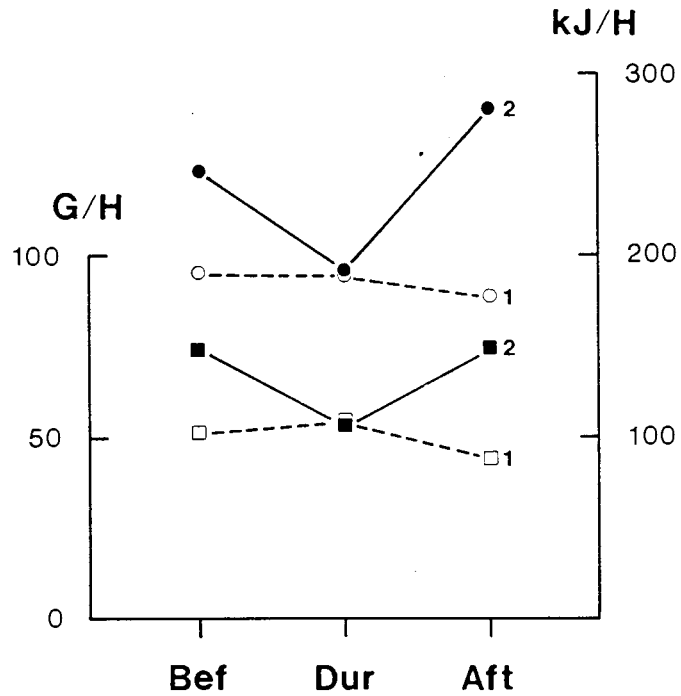
Table 2.3. Comparison of lengths (mm) of black bullhead, yellow perch, and pumpkinseed from collections of skeletal remains of fish at nests at Corn Creek Marsh before, during, and after the drawdown.

Fish species	before			during			after		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
bullhead	209.5	28.4	63	206.5	23.2	85	211.2	24.3	45
perch	217.5	30.6	13	230.7	35.2	27	-	-	-
pumpkinseed	151.3	9.4	8	149.8	11.7	23	-	-	-

Table 2.4. Percent of time males and females (fem) spent on or near the nest during weeks 1-6 of brood-rearing before, during, and after the drawdown.

	Percent of time								
	before			during			after		
	male	fem	h	male	fem	h	male	fem	h
one chick	41	100	17	21	99	50	12	98	56
two chicks	26	100	34	22	94	55	27	98	96

Figure 2.4. Rates of delivery of prey (g and kJ of fish/h to nests with one (open squares) and two chicks (solid squares) at Corn Creek Marsh during weeks 1-6 of brood-rearing before, during, and after the drawdown.



however, 10 of 56 fish (18%) delivered to the nest were caught by females, significantly more than before and during the drawdown ( $G_{1,1} = 12.7, p < 0.01$ ). Females caught all of their fish at Corn Creek Marsh.

## DISCUSSION

The drawdown in Corn Creek Marsh affected the availability of prey for ospreys in two ways. First, the ospreys were forced to travel to Leach Lake, a round trip of about 6 km. Following the drawdown, not only was the abundance of fish at Corn Creek Marsh lowered, but a large portion of Leach Lake was drawn down, reducing the availability of prey at this alternative foraging site. Consequently, prey were less available to the ospreys during and after the drawdown than before. This affected where the ospreys foraged and consequently what they took, since prey species differed among sites. Before and after the drawdown, most foraging occurred at Corn Creek Marsh, and black bullhead, the predominant fish there, were the primary prey. However, after the drawdown, more foraging occurred away from Corn Creek Marsh (although Corn Creek Marsh was still the most important foraging site), very likely due to the lower abundance of fish there, and more trout and suckers were taken.

During the drawdown direct observations showed that most foraging took place at Leach Lake and pumpkinseed were the

predominant prey. This shift to pumpkinseed was consistent with differences in the abundance of fish between Leach Lake and Corn Creek Marsh: pumpkinseed were more abundant and bullhead were less abundant at Leach Lake than at Corn Creek Marsh. Because pumpkinseed were on average much smaller than the other fish species, the diet shift to pumpkinseed apparently forced ospreys to make more foraging trips in compensation.

The sizes of fish taken by the ospreys reflected the sizes present at different sites. There were no differences detected in the sizes of yellow perch and black bullhead taken before, during and after the drawdown, nor were there differences in the sizes present before and after the drawdown at Corn Creek Marsh and in Leach Lake. Larger fish were taken from the old channel of the Kootenay River, a more distant feeding site, but larger fish occurred there.

The drawdown of Corn Creek Marsh apparently made it more difficult for ospreys to obtain fish. Thus, for a given brood size, ospreys seemed to work harder to provision chicks. Males spent more time away from nests, presumably hunting. However, in all years the provisioning rates for one-chick broods were similar. The same was true for ospreys with broods of two before and after the drawdown. During the drawdown, however, males were away from nests longer, but the provisioning rate was lower than either before or after the drawdown: at both nests with two young,

brood reduction occurred. Evidently, under these conditions even elevated male effort may not have been sufficient to rear two chicks. Similarly, Hagan (1986) noted high rates of brood reduction in a population of ospreys where males had to travel long distances (26 km round trip) to gather food, and rates of food delivery to nests were low.

That females engaged in foraging after the drawdown was unexpected. In other populations studied, males conducted virtually all of the foraging until just prior to fledging (e.g., males captured 98% of the fish, Stinson 1978; 96-100%, Levenson 1979; 93%, Jamieson et al. 1982). Female foraging was presumably a response to lower food deliveries by their mates. With the additional foraging effort of the females, pairs delivered fish to the nest at the same rate as prior to the drawdown when males alone foraged. Similarly, female sparrowhawks (Accipiter nisus) hunt more when provisioning rates of males are low (Moss 1979).

Why do females not normally forage during brood-rearing? The answer may lie in the risk of leaving the chicks and/or nest unprotected (e.g., nestlings may be exposed to predators or inclement weather). Female hunts occurred only when the male was away from the nest. As well, the nest may be vulnerable to 'prospecting' ospreys (non-breeders attempting to procure nest-sites). Females on nests were frequently harassed by apparent prospectors, and often responded by chasing the intruders from the nest.

Why then did females forage after but not during the drawdown? During the drawdown, the female would have had to travel to distant sites, leaving chicks untended for extended periods. After the drawdown, though, females foraged at Corn Creek Marsh, where the hunts were short (2-15 min), and the nest remained in sight, minimizing potential risks. Hartwick (1976) similarly found that in black oystercatchers (Haematopus bachmani), one adult would feed in richer but more distant patches, whereas the other fed in poorer but nearby patches, allowing the latter to both guard and feed the chicks.

Although the drawdown examined here was an artificial manipulation, it is not dissimilar to the natural cycle of flooding and drying that occurred historically in the Kootenay River system; water levels fluctuated widely from year to year (Flook and Forbes 1983) and undoubtedly generated differing levels of prey availability.

In this study, both male and female ospreys exhibited flexibility in their foraging effort. That they were able to elevate their foraging effort during and after the drawdown indicates that they normally work at less than maximal levels (i.e., they may withhold parental investment), and thus may be able, at least partially, to buffer offspring from declines in the abundance of food in the environment.

CHAPTER THREE

WEATHER AND REPRODUCTION IN OSPREYS



## INTRODUCTION

The previous chapter showed how unanticipated changes in prey availability affected the provisioning behaviour of ospreys. Weather is another important source of environmental variability for breeding raptors. It affects foraging success (Grubb 1977, Machmer and Ydenberg 1989) and therefore the effort required to provision the family. It also affects adults and nestlings directly: rain and cool temperatures elevate metabolic costs (Stalmaster and Gessaman 1984) and hypothermia may result in the death of offspring (Balfour 1957, Reese 1977, Mearns and Newton 1988).

During breeding parents must buffer offspring from the inimical effects of environmental variability. For reproduction to be successful, the male parent must provide nestlings with a steady supply of food, and the female parent must ensure a stable thermal environment for eggs and nestlings.

In this chapter I examine the effects of weather on the reproductive behaviour of ospreys. First, I investigate interannual variation in the reproductive success of ospreys in the Creston Valley of southeastern British Columbia. If weather is an important determinant of reproductive success, then there should be significant correlations between fledging success and weather variables. I then examine the provisioning, brooding, and feeding behaviour of males,

females, and nestlings in relation to rainfall. My expectation was that inclement weather should affect the foraging and brooding behaviour of parents.

## METHODS

### Reproductive surveys

The reproductive success of ospreys in the Creston Valley was monitored from 1981 to 1988. Nests were surveyed between the Canada-U.S.A. boundary to the south end of Kootenay Lake, a distance of 32 km. The terminology and criteria for determining nest occupancy follow Postupalsky (1977). A nest was deemed to be occupied if there was evidence of a mated pair (e.g., a pair at a nest, incubating female, eggs, young). Each nest was surveyed at least twice (and usually more often): during incubation to determine the number of territorial pairs, and again late in the nestling period, when chicks were six to eight weeks of age, to determine fledging success. From 1981 to 1985, nests were surveyed using binoculars and a spotting telescope. Nests were inspected from elevated sites when possible. For nests along the Kootenay River, however, this was not generally possible, and these nests were observed through a telescope at distances of 75 to 250 m. Fledgling surveys were conducted during the middle of the day to maximize the probability that all nestlings were seen. At this time chicks were most likely to be standing on the nest panting,

and hence were most visible. Care was taken when approaching occupied nests not to alarm parents; if neither parent called alarm (which caused the chicks to lie still on the floor of the nest) the nest was inspected for 10-20 min, longer if chicks were sitting low. If parents called alarm, the nest was observed until a fish was delivered (at which time chicks were most visible), or until offspring resumed normal behaviour (standing, moving about on nest): Sometimes this required more than two hours. Where uncertainty existed over the number of chicks, the nest was resurveyed on another day. Some of these, and some inaccessible nests, were checked by staff of the Creston Valley Wildlife Management Authority in fixed wing or ultra-lite aircraft. From 1986 to 1988, nearly all occupied nests were climbed to determine the number of chicks.

To check for biases between the methods, I compared the survey data from 1981-85 to that collected from 1986-88. No significant differences were found in the proportion of successful nests (occupied nests that fledged young) with one, two, and three chicks (Table 3.1), the proportion of occupied nests that were successful (Table 3.1), and the overall proportion of occupied nests with zero, one, two, and three chicks (Table 3.1). I conclude therefore that any differences between the survey methods were small.

Meteorological data from a weather station in Creston were obtained from Environment Canada, Atmospheric Environment

Service. Weather data from 1969-1988 were used to examine the correlations among weather variables. Data on average wind velocity were available only for 1983-1987. Due to large intermonthly differences among the means for total precipitation and average temperature from April to July (April for example is on average much cooler and wetter than July), the correlations between temperature and rainfall were determined for each month. Due to small sample sizes, wind data were pooled for all months.

#### Behavioural observations at the nest

The behavioural procedures are the same as used in Chapter Two (see the note in Chapter Two about pooling of data across nests). Observations reported here were made from May-July 1981-87, from incubation until the chicks were eight weeks of age. Corn Creek Marsh, the primary foraging area for ospreys on which behavioural observations were made, was drawn down in 1984. This drawdown affected the prey species taken and the rates at which prey were delivered to nests, particularly during the nestling period, less so during incubation. Thus behavioural data are analyzed here with respect to the stage of the drawdown: before (1981-1983), during (1984), and after (1985-1987). The drawdown affected only 3-5 local nests and hence probably had only a small impact on overall nesting success in the whole population.

Table 3.1. Comparison of fledging survey methods. From 1981-85, visual surveys were used. From 1986-88, nests were climbed.

No. of fledged young	1981-85		1986-88	
	no. of nests	%	no. of nests	%
zero	60	26	49	34
one	52	22	31	22
two	85	37	39	27
three	35	15	23	16

- A, B, C
- A. The proportion of successful nests with one, two, and three fledglings did not differ significantly between 1981-85 and 1986-88:  $G_{(2)}=1.44$ ,  $p>0.05$ .
- B. The proportion of occupied nests that were successful did not differ significantly between 1981-85 and 1986-88:  $G_{(1)}=3.15$ ,  $p>0.05$ .
- C. The proportion of occupied nests with zero, one, two, and three fledglings did not differ significantly between 1981-85 and 1986-88:  $G_{(3)}=1.44$ ,  $p>0.05$ .

## RESULTS

### Weather and fledging success

There was large and significant interannual variation in osprey reproductive success. The number of chicks fledged in both occupied and successful nests varied among years (Table 3.2). The proportion of occupied nests that were successful did not, however, differ significantly among years (Table 3.2).

The relationships between weather variables (April-July; spanning the period from clutch initiation to fledging) and reproductive success were examined using meteorological data as shown in Table 3.3. My expectation was that reproductive success should be correlated positively with mean temperature and negatively with rainfall. Both correlations are in the predicted direction (Table 3.3) but only the correlation between rainfall and the mean number of young per successful nest was significant (Fig. 3.1). No significant relationship was found between the proportion of successful nests and any weather variable, although the correlations were in the expected direction. With a sample size of eight years the power of the analysis is low.

### Correlations among rain, wind, and temperature

The number of days with measurable precipitation was negatively correlated with mean monthly temperature and positively correlated with mean monthly wind velocity (Table

Table 3.2. Reproductive success of ospreys in the Creston Valley of southeastern British Columbia from 1981 to 1988.

Year	Occupied nests surveyed	Fledged young				Mean no. fledged/		Prop. of succ. nests <sup>c</sup> (%)
		0	1	2	3	occ. <sup>a</sup> nest	succ. <sup>b</sup> nest	
1981	39	15	9	13	2	1.1	1.7	61
1982	39	9	4	17	9	1.7	2.2	77
1983	49	13	14	10	12	1.4	1.9	73
1984	53	10	18	20	5	1.4	1.7	81
1985	52	13	7	25	7	1.5	2.0	75
1986	54	23	13	12	6	1.0	1.8	57
1987	42	9	9	14	10	1.6	2.0	79
1988	46	17	9	13	7	1.2	1.9	63

- A. The occurrence of 0,1,2 & 3 fledglings in occupied nests differs significantly among years:  $G_{(2,1)}=39.1$ ,  $p<0.01$ .
- B. The occurrence of 1,2 & 3 fledglings in successful nests differs significantly among years:  $G_{(1,4)}=26.2$ ,  $p<0.05$ .
- C. The proportion of occupied nests that were successful did not differ significantly among years:  $G_{(7)}=12.8$ ,  $p>0.05$ .

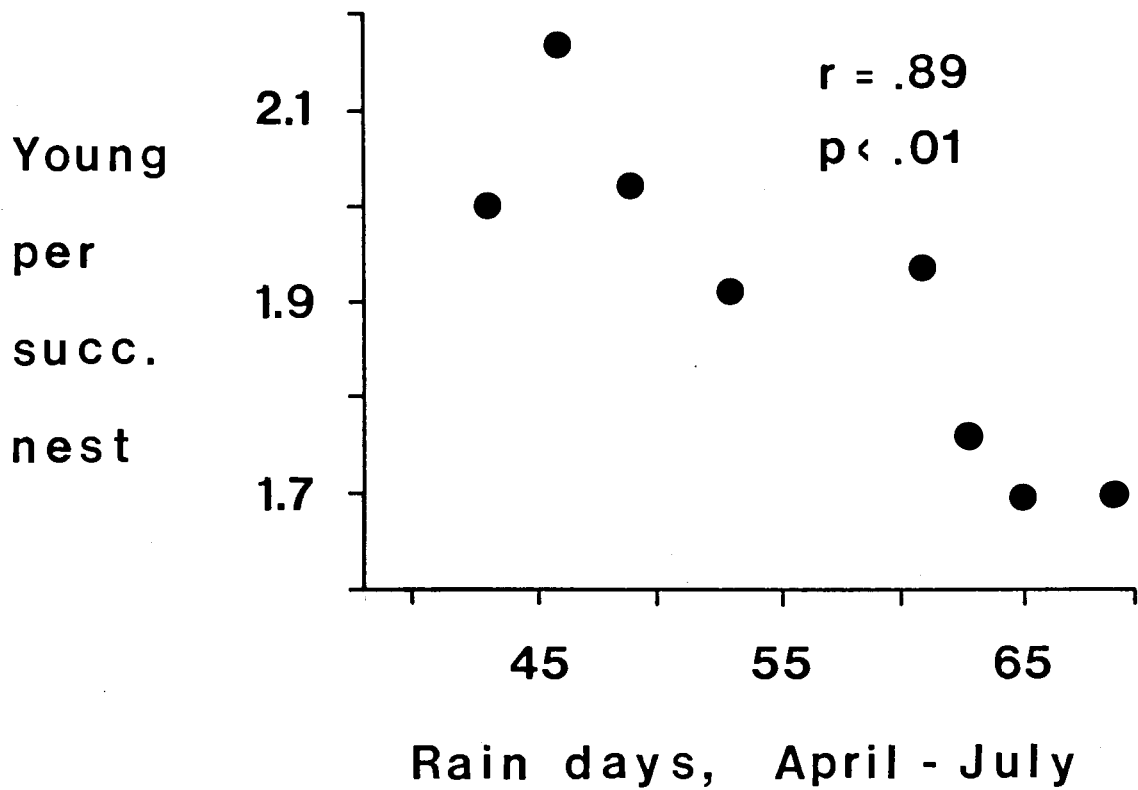
Table 3.3. Correlations between breeding parameters (mean number of young/successful nest, and percent of occupied nests that are successful) with mean temperature and rainfall. For all correlations, n=8.

Correlation	r	P
Mean Number of Young Per Successful Nest vs:		
d with rain, April-July	-0.886	<0.01
mean temperature, April-July	0.513	>0.05
Percent Successful Nests vs:		
d with rain, April-July	-0.404	>0.05
mean temperature, April-July	0.260	>0.05

A. Arcsin (Y)<sup>1/2</sup> transformed.



Figure 3.1. Correlation between the number of days with measurable precipitation, April to July (Rain days, April-July) from 1981 to 1988 and the mean number of young fledged per successful nest (young per succ. nest).



3.4). As expected, the number of days with rain was highly correlated with total monthly rainfall (Table 3.4). In short, rain was associated with cool, windy weather.

#### Correlations among rain and temperature within a year

Since a link between weather and reproductive success has been demonstrated, an interesting question now emerges: is weather early in a breeding season a good predictor of weather later on? If so, parents and offspring might use such information in their various behavioural decisions (e.g., how hard to work to provision offspring, whether to commit siblicide).

To address this question I examined the serial correlations of temperature and rainfall (there were insufficient wind data available for analysis) between months within a year (residuals from monthly mean values: Table 3.5). For example, if in a given year a dry May is followed by a dry June, then the residuals from the monthly means would be positively correlated.

No significant correlations either negative or positive, were found (Table 3.5). Thus it appears unlikely that current weather conditions could have been useful predictors of seasonal trends in weather for ospreys.

Table 3.4. Correlations between number of days with measurable precipitation (days with rain) and mean monthly temperature, total monthly rainfall (mm) and mean monthly wind velocity (km/h), at Creston, British Columbia, for April-July 1969-1988 (n=20 yr). Data on wind velocity were only available for 1983-1987 (n=18 mo), therefore data for all months (April to July) were pooled.

Correlation	r	P
Days with rain vs mean temperature:		
April	-0.216	>0.05
May	-0.585	<0.05
June	-0.684	<0.01
July	-0.783	<0.01
Days with rain vs mean total rainfall:		
April	0.469	<0.05
May	0.773	<0.01
June	0.681	<0.01
July	0.850	<0.01
Days with rain vs mean wind velocity:		
April-July	0.526	<0.05

Table 3.5. Serial correlations between residuals from monthly means for temperature (mean monthly temp.) and days (d) with rain for different pairs of months. For all correlations  $n=20$ . A positive correlation indicates that within a year, weather in one month tends to resemble that in another month (e.g., a wet May tends to be followed by a wet June). If weather in one month is independent of that in another, a zero correlation is expected.

Months	Correlation (r)	
	Mean monthly temp.	Days with rain
April-May	+0.160	+0.381
April-June	-0.002	+0.333
April-July	-0.026	+0.126
May-June	-0.061	+0.086
May-July	-0.023	+0.246
June-July	-0.066	+0.084

A. For all correlations,  $p > 0.05$ .

### Effect of rain on parental behaviour

In both the analysis of the frequency of prey deliveries and the time males and females spent at the nest, significant inter-year differences occurred, attributable in large part to the differing stages of the drawdown (see Chapter Two). In order to partition the effect of rain from this inter-annual variation, I performed a three-dimensional contingency analysis (weather-year-behaviour) (Fienberg 1970, Bishop et al. 1975); below I report the significance of the weather-behaviour interaction isolated from the year effects.

#### Frequency of prey deliveries and prey size

Rain did not significantly affect the frequency of prey deliveries either during incubation ( $G_{1,1}=0.71$ ,  $p>0.05$ ) or brood-rearing ( $G_{1,1}=0.24$ ,  $p>0.05$ ; Table 3.6). Neither was there evidence that the size of prey taken changed during rain (Table 3.7), although sufficient data for analysis were available only for brood-rearing in 1984 and 1986 (prey delivered to the nest during hours with rain vs hours with no rain, 1984: Mann-Whitney U-test,  $z=-0.67$ ,  $p=0.51$ ; 1986:  $z=-0.10$ ,  $p=0.57$ ).

#### Time at the nest

Rain affected the time males and females spent at the nests both during incubation and brood-rearing (Table 3.8).

Table 3.6. Effect of rain on the frequency of prey deliveries (percent of observation hours with delivery) during incubation and brood-rearing, 1981-86.

	Percent of hours with prey deliveries		Hours of observation	
	rain	no rain	rain	no rain
<b>Incubation</b>				
1981-83	33	21	6	29
1984	33	28	21	36
<b>Brood-rearing</b>				
1981-83	25	41	8	53
1984	37	55	19	82
1986	50	28	32	135

Table 3.7. Frequency of different masses of prey delivered to nests during hours with and without rain, during brood-rearing, 1981-86.

	Mass of prey (g)		
	<100	100-199	>200
-----			
1981-83			
rain	4	13	2
no rain	0	2	0
1984			
rain	40	11	4
no rain	7	5	0
1986			
rain	1	33	16
no rain	1	13	3
-----			

During all periods females spent more time at the nest when it rained, reflecting their role. Females are primarily responsible for incubation and brooding of small chicks (Stinson 1978, Levenson 1979, Jamieson et al. 1982) and during rain, the risk of chilling increases. The behaviour of males was more complex, apparently differing with the stage of the drawdown at Corn Creek Marsh. During 1984, when the marsh was drained, males spent more time away from the nest when it rained, but before (1981-83) and after (1986) the drawdown, males spent less time away from the nest when it rained. Before and after the drawdown, males foraged primarily at Corn Creek Marsh where black bullhead were the primary prey. Bullhead are a nocturnal species, and become more active under overcast conditions (Wydoski and Whitney, 1979), as would occur during rain. During the drawdown, males hunted primarily at Leach Lake, where pumpkinseed, a diurnal species (Scott and Crossman 1973) were the primary prey. Thus differences in the time males spent away from nests may, at least in part, be attributable to differences in prey behaviour.



Table 3.8. Effect of rain on the proportion of time male and female ospreys spent at or near the nest during incubation and brood-rearing, 1981-86.

	Percent of time at nest				Hours of observation	
	male		female		rain	no rain
	rain	no rain	rain	no rain		
<b>Incubation</b>						
1981-83	18	33	92	88	6	29
1984	30	31	84	78	21	71
<b>Brood-rearing</b>						
1981-83	46	19	100	99	6	53
1984	9	21	100	93	19	62
1986	35	17	99	97	32	135

Males sometimes eat the head of a fish before delivering it to the nest, a behaviour which can be time consuming (15 min->1 h), accounting for a considerable amount of time males spend away from the nest. Females always delivered whole fish to the nest (Table 3.9), and never delivered fish when it rained. These results suggest that females minimized time spent away from the brood.

In sum, there is no evidence that rain impaired the ability of males to provision nests, and in some years, prey may have been easier to find when it rained.

#### Effect of storms on chick survival

The effects of a prolonged rainstorm were clear at one closely observed nest with two chicks on the bridge at the mouth of the Kootenay River. On 13 July 1987 the senior (sib-A) and junior sib (sib-B) were nearly identical in mass (1205 vs 1180 g), and at feeds both received nearly identical portions of food. A three-day rainstorm accompanied by strong winds began on 16 July, during which time no observations could be made at the nest. Observations resumed on 19 July, when the storm had abated. At 1008 h the male delivered a 20 cm bullhead that the female fed to the chicks. Although no aggression occurred, sib-A received 65 (78%) of the 87 bites. It was evident

Table 3.9. Number of partially eaten fish delivered to nest by male and female at nests at Corn Creek Marsh during hours with and without rain in 1986.

	Male		A	Female	
	partially eaten	uneaten		partially eaten	uneaten
Rain	6	11		0	0
No rain	13	18		0	10

- A. The proportion of partially eaten fish delivered by males and females differed significantly:  $G_{(1,1)}=8.9$ ,  $p<0.01$ .
- B. The proportion of partially eaten fish delivered by male during hours with and without rain did not differ significantly:  $G_{(1,1)}=0.2$ ,  $p>0.6$ .

that sib-B was greatly weakened, and by 1305 h was lying on its back making only feeble movements. At that time, the brooding female left the nest and flew toward a male from an adjacent nest with a still live 40 cm largescale sucker (estimated mass 600 g). The female grabbed the sucker and after a prolonged struggle with the male, took the fish to a site about 300 m north (and was attacked in flight by the male). She fed continuously for the next 45 min (number of bites not determined). At 1351 h she returned to the nest with the fish, and over the next 2 h and 27 min, at two feeds, fed sib-A 544 bites. The 472 bites sib-A ate at the first of these feeds exceeded by a factor of two the amount fed to any chick at Creston in 184 other observed feeds: in only one did a single chick eat more than 200 bites (225), and in only 26 (14%) did a single chick eat more than 100 bites. While sib-A fed, sib-B became weaker and by 1600 h had died; at no time during these feeds did the female offer food to it. The carcass of sib-B was recovered and found to be severely emaciated (mass = 915 g, a decline of 265 g from 13 July). There were no indications of physical abuse (bite or scratch marks, damaged plumage), although Poole (1979) noted that he observed physical aggression in Florida ospreys without detecting injuries when he visited nests.

Thus the extended rainstorm appeared to have a profound effect on the behaviour of both the nestlings and parent female.

## DISCUSSION

### Weather and fledging success

Because rain, low temperatures and wind all tend to occur together, the strong correlation (accounting for 78.5% of the variation) between the mean number of young fledged per successful nest and rainfall is likely a product of the joint effect of these three weather variables on egg and chick survival. Reese (1977) noted that osprey fledging success was higher in years when fair weather predominated during the nestling period, and speculated that this was due to enhanced hunting performance of adults, and a reduced rate of offspring failure due to chilling. Odsjo and Sondrell (1976) similarly noted that fledging success of ospreys in southern Sweden was unusually low in 1971, a year with a cold, wet June.

The weaker (non-significant) relationship between the proportion of successful nests (as opposed to the mean number of young fledged per successful nest) and weather at Creston likely reflects greater variability in the factors resulting in breeding failure. Weather effects (starvation, hypothermia) most likely result in partial loss of the clutch or brood (facilitated by competitive asymmetries among chicks), whereas complete failure may more often be attributable to other factors such as disease, nest destruction, or death of a parent (Reese 1977). Moreover,

some 'failed' pairs lay no eggs, and thus would be unaffected by factors relating to egg or chick survival.

That monthly temperatures and rainfall were not strongly correlated within a year likely means that weather conditions at the beginning of a season provide little useful information about conditions later in the brood-rearing period.

#### Rain and chick survival

In this study rain did not impair the foraging success of males sufficiently to depress the rate of prey delivery to the nest. Stinson (1978) and Stinson et al. (1987), in studies of ospreys nesting in Virginia and Washington respectively, similarly reported no effect of weather conditions on parental provisioning behaviour; hunt lengths and the number of fish delivered did not change or changed only slightly during inclement weather. Yet at Creston poor fledging success was strongly correlated with wet weather, and previous studies have shown that osprey hunting success declines during poor weather (Grubb 1977, Machmer and Ydenberg 1989). How do we reconcile these apparent contradictions? Two possibilities seem likely.

First, wet weather may elevate the thermoregulatory metabolism of the chicks or female, raising their energetic demands. Simply maintaining the same delivery rate when it rains as during fair weather may not be sufficient to ensure

chick survival. More food may be necessary. In bald eagles (Haliaeetus leucocephalus) heavy rain reduces the insulative properties of the plumage, which can increase energy loss over short periods (Stalmaster and Gessaman 1984).

Alternatively, males may work harder to provision the brood when it rains, but may be unable to sustain this effort for longer periods (e.g., the length of a prolonged storm). As a result, short periods of inclement weather may have little detectable effect upon a male's provisioning behaviour, but longer periods may.

In addition to the effects of variation in prey availability, weather imposes significant variability in osprey breeding success. This appears to be a truly random effect in that ospreys are unable to predict the weather in any given year.

CHAPTER FOUR

SIBLICIDE IN A VARIABLE ENVIRONMENT



## INTRODUCTION

Siblicide occurs in an array of forms (reviewed in Mock 1984a). In most species it is facultative and proximally regulated by food (Mock et al. 1987a). At the extreme, siblicide is obligatory (or nearly so) and independent of prevailing levels of food (e.g., some pelicans, eagles, boobies). Here I define a third category, non-siblicide, in which siblicide never occurs. Only one of these three types of siblicide, facultative, is a conditional strategy. An obvious advantage of facultative siblicide is that it allows a nestling to incorporate information about the state of the environment into the decision to perform siblicide. Ideally, an individual would track variation in the environmental yield of resources, allowing a junior sib to survive when food is abundant, but eliminating it when food is short. Obligate siblicide clearly precludes the use of such information.

The previous two chapters have demonstrated two important sources of environmental variation for breeding ospreys: inter-annual differences in the availability of food, and weather (which may affect both resource availability and resource requirements). A chick with information about the state of the environment clearly might derive a benefit by incorporating it into its decision of whether to perform siblicide. But in order to gain information about the state of the environment, a senior sib must allow a junior sib to

remain alive. During this period of clemency a senior sib invests time and energy in aggression, shares some of the total food and may risk future injury or a dominance reversal (Mock 1984a, Ploger and Mock 1986) in doing so (Gargett 1978, Hahn 1981, Mock 1984a, Fujloka 1985). As well, the junior sib is consuming food that might otherwise go to the senior sib (see Chapter Six).

The objectives of this chapter are three-fold. First, I develop a simple model to examine inter-annual variation in the environmental yield of resources and the costs of acquiring information (i.e., delaying siblicide) in relation to strategies of siblicide. Second, I outline how offspring might use acquired information to update a priori expectations of resource yield and concomitant parental provisioning. Third, I discuss what types of information offspring might use to evaluate resource yield.

## THE MODEL

### Environmental yield of resources and parental provisioning

I begin by defining the environmental yield of resources in a given year as a discrete random variable,  $Y$ . I assume that within a year,  $Y$  is constant. I also assume that  $M$ , the resources gathered by the parents and delivered to the brood over the period of parental care, is proportional to  $Y$  such that:

$$(1) \quad M = h Y$$

where  $h$ , the harvesting efficiency of parents, is a positive constant. For simplicity,  $h$ , is set to unity such that:

$$(2) \quad M = Y$$

### An inclusive fitness model

In this section I loosely follow the protocol and terminology of Macnair and Parker (1979) and Parker et al. (1989). I begin by assuming that the fitness (survival to breeding) of an offspring is an increasing function,  $f$ , of the resources (e.g. food),  $m$ , it consumes. It is convenient here to think of  $m$  as the total provisioning obtained by an offspring over the entire period of parental care, so the sum of  $m$  to all offspring is  $M$ . The function  $f(m)$  is zero up to an arbitrary minimum,  $m_{MIN}$ , above which it decelerates to some asymptote such that  $f(m)$  shows diminishing returns above  $m_{MIN}$ .

Now consider two sibs ( $A$  and  $B$ ) together in a nest. Sib  $A$  is older and larger than sib  $B$ , is dominant, and can take any proportion,  $p$ , of parental resources,  $M$ , it desires. Now consider the fate of a rare mutant allele that causes  $A$  to take proportion  $p'$  of  $M$ . Assuming that  $A$  and  $B$  are full sibs, there is a probability of 0.5 that  $B$  also carries the mutant allele. The replication rate of the mutant allele,  $\lambda$ , is thus equal to:

$$(3) \quad \lambda = f(Mp') + 0.5 f([1 - p'] M).$$

From the perspective of  $\underline{A}$ , the optimal value  $p_*$  is found by setting  $d\lambda/dp' = 0$ . At the optimum:

$$(4) \quad f'(Mp_*) = -0.5 f'([1 - p_*] M).$$

That is,  $\underline{A}$  should take an additional unit of  $M$  (i.e.,  $p_*$  increases) when the benefit it derives is greater than half the benefit  $\underline{B}$  would derive from the same unit of  $M$ , in accordance with Hamilton (1964).

I now define an explicit function for  $f(m)$ :

$$(5) \quad f(m) = \begin{cases} k (m - m_{\text{MIN}}) / m & \text{if } m > m_{\text{MIN}} \\ 0 & \text{otherwise,} \end{cases}$$

where  $k$ , a positive constant, is the asymptotic value of  $f(m)$  ( $f(m)$  converges to  $k$  as  $m \rightarrow \infty$ ). For simplicity I shall set both  $k$  and  $m_{\text{MIN}}$  equal to unity so that (5) simplifies to:

$$(6) \quad f(m) = \begin{cases} (m - 1) / m & \text{if } m > 1 \\ 0 & \text{otherwise.} \end{cases}$$

Substituting (6) into (3) gives:

$$(7) \quad \lambda = \frac{Mp' - 1}{Mp'} + 0.5 \left[ \frac{M [1 - p'] - 1}{M [1 - p']} \right]$$

Differentiating with respect to  $p'$  and setting  $d\lambda/dp' = 0$  gives:

$$(8) \quad \frac{d\lambda}{dp} \frac{Mp_* - 1}{Mp_*} = \frac{d\lambda}{dp} 0.5 \frac{M [1 - p_*] - 1}{M [1 - p_*]}$$

This simplifies to:

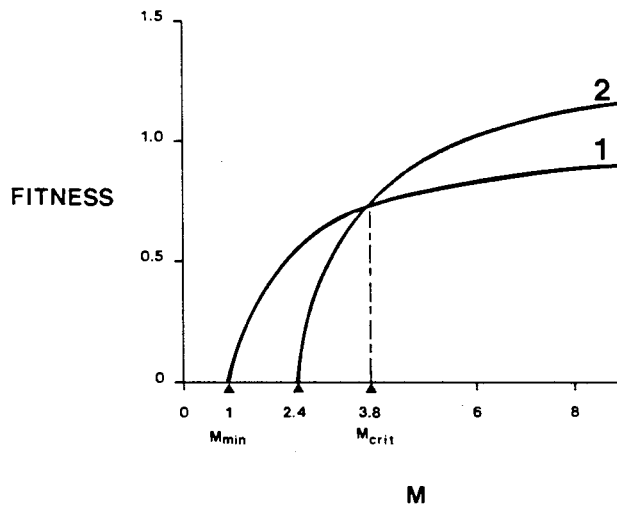
$$(9) \quad 4p_* - 2 = p_*^2$$

so  $p_* = 0.58$ . Thus  $1 - p_*$ , the share of  $M$  to  $B$ , is 0.42. As noted in (6), however, this is only true where  $m > 1$ . When  $m (=Mp)$  is less than 1,  $f(m) = 0$ . Sib  $B$  does not receive any resources until  $M$  exceeds 3.8 at which point its allocation becomes 0.42.

#### THE EFFECT OF A VARIABLE ENVIRONMENT

The strategy of siblicide favoured by natural selection will be that which maximizes mean fitness across all years; where variation in reproductive success results from stochastic temporal fluctuations in the environment, natural selection favours the strategy maximizing geometric mean fitness (Gillespie 1977). The fitness functions for obligate siblicide,  $E[\ln \lambda_O]$ , and non-siblicide,  $E[\ln \lambda_N]$  can now be written as:

Figure 4.1. Relationship between  $M$  and  $\lambda$  in broods of one and two. Below  $M_{\text{MIN}}$  ( $=1.0$ ) no chicks are viable therefore the fitness of the senior sib is zero. Below  $M=2.4$ , the junior sib is not viable. At  $M_{\text{CRIT}}$  ( $=3.8$ , the siblicide threshold), the fitness,  $\lambda$ , of the senior sib in broods of one and two is equivalent, and beyond that point the senior sib favours retaining the junior sib.



$$(10) \quad E[\ln \lambda_{\text{O}}] = \sum_{M_{\text{MIN}}} \ln \left[ \frac{M-1}{M} \Pr(M) \right]$$

$$(11) \quad E[\ln \lambda_{\text{N}}] = \sum_{M_{\text{MIN}}} \ln \left[ \frac{Mp-1}{Mp} + 0.5 \frac{M(1-p)-1}{M(1-p)} \right] \Pr(M)$$

where  $E$  denotes mathematical expectation,  $\Pr(M)$  is the probability that  $M$  is equivalent to some discrete value of  $M$ , and where  $M > M_{\text{MIN}}$ . Obligate siblicide will be favoured over non-siblicide when:

$$(12) \quad E[\ln \lambda_{\text{O}}] > E[\ln \lambda_{\text{N}}].$$

Consider the situation now, where  $A$  possesses perfect information about the current state of  $M$ . Siblicide will be favoured in those years when  $M < M_{\text{CRIT}}$ , whereas sib  $A$  should allow  $B$  to live when  $M > M_{\text{CRIT}}$  (Fig. 4.1). It is clear that if  $M$  never exceeds  $M_{\text{CRIT}}$ , obligate siblicide will be favoured, since  $E[\ln \lambda_{\text{O}}]$  will always exceed  $E[\ln \lambda_{\text{N}}]$ . Conversely, if  $M$  never falls below  $M_{\text{CRIT}}$ , siblicide will never be favoured. It seems unlikely, though that either case will ever be satisfied. Rather, variability in  $M$  will result in  $M > M_{\text{CRIT}}$  in some years, and  $M < M_{\text{CRIT}}$  in others. The threshold for a policy of obligate siblicide vs non-siblicide,  $M_{\text{T}}$ , is not only a function of the mean level of  $M$ , but of the variance in  $M$  as well.  $M_{\text{T}}$  will be less than  $M_{\text{CRIT}}$  when  $M$  varies from year to year. Mathematically,

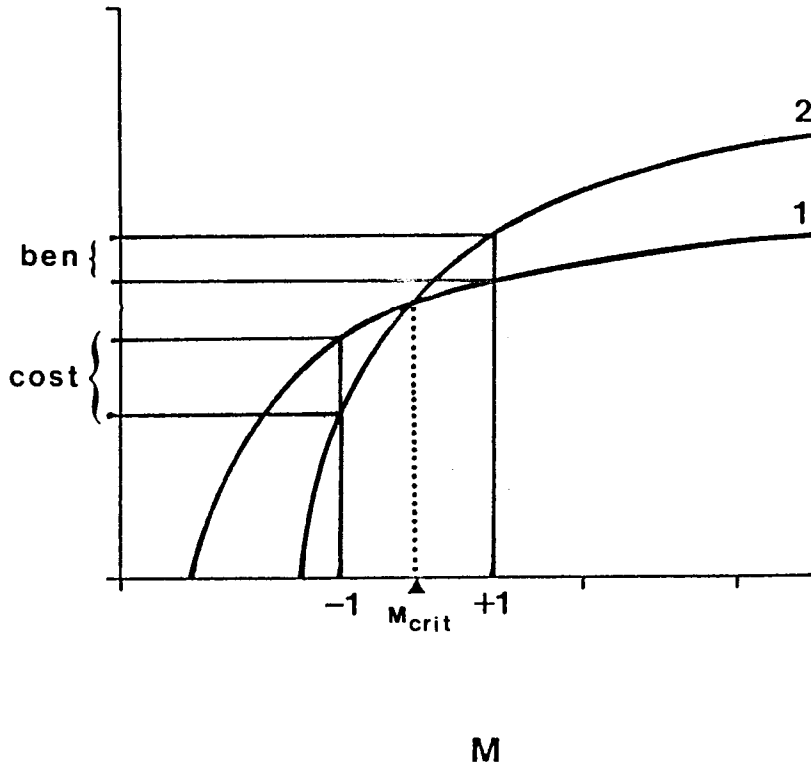
this is because the geometric mean is less than the arithmetic mean. Biologically, this is because of the diminishing fitness returns for non-siblicide at levels of  $M$  greater than  $M_{CRIT}$ ; quite simply, the fitness benefit of a unit increase in  $M$  above  $M_{CRIT}$  for an individual practicing non-siblicide is less than the fitness cost of a unit decrease in  $M$  below  $M_{CRIT}$  (Fig. 4.2). That is, the fitness risks associated with erring on the side of clemency outweigh the fitness gains for judging correctly that clemency is best. Because of this asymmetry in fitness costs and benefits, the threshold for obligate siblicide lies below  $M_{CRIT}$ . Furthermore, since the geometric mean becomes smaller as variance increases,  $M_T$  will decrease as variability in  $M$  increases. This is completely analogous to the concept of risk-aversion in foraging theory (Stephens and Krebs 1986).

#### TRACKING THE ENVIRONMENT

So far I have considered policies of obligate siblicide and non-siblicide. What about facultative siblicide? If the senior sib has perfect information about  $M$ , it would seem that facultative siblicide is the best policy. For a chick, the goal of tracking will be to estimate whether  $M$  is greater than  $M_{CRIT}$ , i.e., whether, from  $A$ 's perspective, there is sufficient food for one or two chicks. Four outcomes are possible: (i) siblicide occurs when there is



Figure 4.2. Variability in  $M$  and the asymmetry of fitness costs and benefits (ben) of obligate and non-siblicide at levels of  $M$  above and below  $M_{\text{CRIT}}$ .



sufficient food for only one chick; (ii) siblicide does not occur when there is sufficient food for two chicks; (iii) siblicide does not occur when there is sufficient food for only one; (iv) siblicide occurs when there is sufficient food for two. Outcomes (i) and (ii) are correct decisions given the current state of the environment, whereas (iii) and (iv) are incorrect decisions.

Presumably a chick will assess the state of the environment through the pattern of food deliveries it receives at the nest. Consider the situation where prey arrive at the nest according to a binomial process with mean  $Y$  and probability distribution:

$$(13) \quad \Pr(j;t,Y) = \binom{t}{j} Y^j (1-Y)^{t-j}$$

where  $j$  is the number of prey delivered in  $t$  sampling intervals. Within a season,  $Y$  is constant, but between years varies as a discrete random variable. That is, when food is scarce ( $Y$  is low), the mean rate of food delivery ( $M$ ) is also low, such that the probability distribution of  $Y$  is equivalent to the probability distribution of  $M$  (i.e.,  $\Pr[Y=Y_k] = \Pr[M=M_k]$ ).

Now consider the situation where sib  $A$  is born with some prior expectation of the rate of prey delivery with mean  $Y'$  and probability distribution  $x_k = \Pr(Y' = Y'_k)$  (the prior probability distribution). Bayes' theorem provides a simple

and logical method for updating prior probabilities with information derived from sampling (Mangel and Clark 1988), stating that for any  $k$ , the conditional probability of  $U_k$  given  $V$  is defined by:

$$(14) \quad \Pr(U_k | V) = \frac{\Pr(U_k) \Pr(V | U_k)}{\Pr(V)}$$

Now let  $U_k$  be the event  $Y' = Y'_k$  and  $V$  be the event  $j$  prey arrivals over  $t$  sampling intervals. Then:

$$(15) \quad \Pr(U_k) = x_k$$

$$(16) \quad \Pr(V) = \Pr(j, t, Y'_k) \Pr(Y' = Y'_k)$$

$$(17) \quad \Pr(V | U_k) = \Pr(j; t, Y'_k)$$

Substituting these into (14) gives:

$$(18) \quad \Pr(Y'_k | j, t) = \frac{x_k \Pr(j; t, Y'_k)}{\Pr(j, t, Y'_k) \Pr(Y' = Y'_k)}$$

This formula proscribes the probability distribution of the updated arrival rate in terms of the sampling data  $j$  and  $t$ , and the prior information,  $Y'$  and  $x_k$ . This posterior distribution has an important property: as sampling continues (i.e.,  $j$  increases and the variance of the sample declines), the estimate becomes weighted more heavily toward the sampling information.

A simple example illustrates this point. Consider the situation where there are only two types of years: good and bad (denoted by the subscripts g and b respectively). In a good year, sufficient food is delivered to the nest (from  $\Delta$ 's perspective) for two chicks; in a bad year, there is only sufficient food for one chick. Good and bad years occur with equal frequency ( $\Pr(U_g) = \Pr(U_b) = 0.5$ ), and in a good year the probability,  $Y'_g$ , of a food item being delivered during any sampling period,  $t$ , is 0.7; in a bad year the corresponding probability,  $Y_b$  is 0.3.

At hatch, sib  $\Delta$  must determine from the rate of food delivery whether it is a good or bad food year. At  $t=0$ , its expectation of a good year is 0.5, but as sampling periods (e.g., days) pass and prey deliveries occur,  $\Delta$ 's expectation of a good year is continually updated (Table 4.1). If for example a prey delivery occurs on the first day,  $\Delta$ 's expectation of a good year changes from 0.5 to 0.7; the corresponding expectation of a bad year changes from 0.5 to 0.3. If two prey deliveries occur in two days, the corresponding probability is 0.845. Conversely, if no deliveries occur in the first two days, the probability of a good year is 0.155.

### Tracking costs

For a senior sib to use information gained about the current state of M, it must allow the junior sib to survive.

Table 4.1. Posterior probabilities that year  $i$  is a 'good' year after sampling for  $t$  periods with  $j$  prey deliveries ( $\Pr(U_{gi}|j,t)$ ). Probability that year  $i$  is a 'bad' year is simply  $1 - (\text{probability of a good year})$ . Prior probabilities of good and bad years are 0.5.

j	t					
	0	1	2	3	4	5
0	0.500	0.300	0.155	0.073	0.033	0.014
1	-	0.700	0.500	0.300	0.155	0.073
2	-	-	0.845	0.700	0.500	0.300
3	-	-	-	0.927	0.845	0.700
4	-	-	-	-	0.967	0.927
5	-	-	-	-	-	0.986

In doing so, the senior sib is giving up some share of parental resources it might otherwise have had. Moreover, as a junior sib grows older, it becomes larger and stronger, and may become more difficult to kill. Thus the cost of allowing the junior sib to live if  $M < M_{CRIT}$  will increase the longer a senior sib allows the junior sib to live. If the primary cost lies in lost growth opportunity, the expense should reflect the shape of the nestling growth curve (sigmoidal). A small cost very early on will be followed by steeply increasing costs during the period of rapid growth, eventually changing into a negligible cost late in the growth period when  $A$  is essentially safe from sibling competition.

#### How long to track?

It is clear that the length of the tracking period will depend on the tracking costs when  $M < M_{CRIT}$ , and the inclusive fitness benefit of having a junior sib when  $M > M_{CRIT}$ , each discounted by its probability of occurrence. Thus sib  $A$  should continue tracking until:

$$(19) \quad C(t) > \Pr(M > M_{CRIT} | j, t) \sum_{i=M_{CRIT}}^{+} \ln[\lambda_N - \lambda_0]$$

In words, the senior sib should allow the junior sib to live until the cost,  $C(t)$ , exceeds the benefit

$(E(\ln \lambda_N) - E(\ln \lambda_D))$  of two sibs when  $M > M_{CRIT}$  for all  $M_k > M_{CRIT}$  discounted by the probability  $M > M_{CRIT}$  given  $j$  prey deliveries in  $t$  days. Sib A can therefore 'purchase' better information about the state of  $M$  at the cost of letting sib B live longer in years when  $M < M_{CRIT}$ : essentially it buys time.

## DISCUSSION

There are three possible strategies of siblicide: obligate, facultative, and non-siblicide. From sib A's perspective, should the level of provisioning ( $M$ ) never exceed the minimum required to sustain two chicks ( $M_{CRIT}$ ) obligate siblicide will always be favoured. Conversely, if  $M$  always exceeds  $M_{CRIT}$  siblicide will never be favoured. If  $M$  varies above and below  $M_{CRIT}$  and if  $M$  can be tracked perfectly and at no cost, then facultative siblicide will be favoured.

In most cases, interannual variation in food availability will result in levels of  $M$  both above and below  $M_{CRIT}$ . A relevant case was illustrated in Chapter Two, in which the degree of brood reduction differed with the availability of food. As well, estimates of food availability will be imperfect, and tracking costs inevitable (junior sibs must survive during sampling). Thus the relative costs and benefits of each strategy will determine which will be used. The primary cost of obligate siblicide will be the loss of

the junior sib when the level of provisioning is sufficient to rear two chicks, whereas the primary cost of non-siblicide will be the loss in growth opportunity when insufficient food exists to rear two chicks.

The primary cost of facultative siblicide will lie in the tracking costs. Two tracking costs are apparent: (i) the cost of allowing the junior sib to survive during the sampling period in years when  $M < M_{CRIT}$ , and (ii), the cost of incorrect decisions (i.e., letting the junior sib live/die in years when insufficient/sufficient food exists for two chicks). The magnitude of the tracking costs will be a function of the relationship between mean rate of food delivery and  $M$ : if variability in food deliveries is low, and the correlation between food deliveries and  $M$  is high,  $\Delta$ 's estimate of  $M$  will be reliable (incorrect decisions will be rare) and the sampling period will be short, diminishing the cost of sampling. Conversely, if the correlation between food deliveries and  $M$  is low, and variability in food deliveries is high, the estimate of  $M$  will be inaccurate (incorrect decisions will be frequent) and sampling periods will be long (sampling costs in years when  $M < M_{CRIT}$  will be high).

If tracking does not provide a reliable estimate of  $M$ , or if the cost of tracking is high, an inflexible strategy (obligate or non-siblicide) will be favoured. The decision to perform siblicide will be based upon some expectation of



resource availability. When obligate siblicide is favoured, it should occur as soon as possible, to minimize the possible costs of allowing the Junior sib to live. In general then, siblicide is most likely to occur early in the nestling period. Note that it is irrelevant whether food is abundant at the time of the Junior sib's demise, or even whether sufficient food exists over the entire season to support two chicks. All that is necessary for obligate siblicide to be favoured is that individuals that always eliminate Junior sibs do better on average than individuals that do not. This is similar to, but not the same as the 'pending competition hypothesis' of Stinson (1979). He suggests that although food may not be limiting at the time of the demise of the junior sib, it may become so later in the nestling period. Moreover, in a variable environment, one expects a threshold for obligate siblicide below  $M_{CRIT}$ : thus obligate siblicide can be favoured even if  $M$  is greater than  $M_{CRIT}$  in most years. It is important to note, that although the argument here has been developed with a two-chick-model, exactly the same logic applies to larger brood sizes: we should expect senior siblings to be risk averse when making decisions regarding siblicide.

#### Type of information used during sampling

Sampling can provide a senior sib with information about future food deliveries and whether or not it should perform

siblicide. Exactly which information a sib might use is unclear but clues that relate to the rate of food delivery are likely candidates. A chick might sample the number of deliveries or quantity of food it receives over some interval (e.g., a day). Other proximate cues of food availability might be used (e.g., early growth rate, proportion of time crop is full, etc.). Even the size or species composition of the diet alone could provide useful information about the state of the environment and the corresponding parental behaviour (in 'good' food years a particular type of prey might be prevalent). Species such as the Peruvian guanay cormorants (Phalacrocorax bougainvilli), piqueros (Sula variegata), and brown pelicans (Pelecanus occidentalis), which rear chicks primarily on Peruvian anchovetta (Engraulis ringens), the presence of many non-anchovetta prey in the diet might reliably indicate to chicks a failure of the anchovetta (e.g., an El Niño event), and hence a 'bad' food year. Thus a simple decision rule, independent of the rate of prey delivery might be favoured: perform siblicide if diet not primary prey (anchovetta), do not perform siblicide if diet primary prey. This type of information is less likely to be important for species with more catholic diets, and hence is unlikely to apply to ospreys.

Similarly, other cues not directly related to food abundance may influence the decisions of offspring regarding

siblicide. Hatching date (which might be judged by photoperiod) could provide an offspring with useful information about its future prospects for several reasons. Post-fledging survival of late-hatched chicks is often lower than early-hatched chicks (Perrins 1963, 1970, Birkhead and Nettleship 1982, Røskaft and Slagsvold 1985, Poole 1989), thus appropriating more resources from parents at the expense of junior sibs may become more important. Hatching date and parental quality are negatively correlated in many species (Askenmo and Unger 1986) (young breeders nest later in the season), thus offspring could expect a lower rate of parental provisioning; once again obligate siblicide may be increasingly favoured.

#### Timing of brood reduction

O'Connor (1978: his Table 5) noted that brood reduction most often occurs early in the nestling period. This is also true in ospreys: most chicks die when less than three weeks old (Hagan 1986, Poole 1989, Steeger 1989). Food limitation seems unlikely to be the proximate cause when the chicks are small and food demands are low relative to later in the nestling period; parents should be easily able to provision offspring. Yet sibling aggression in ospreys is proximally related to food. Parents have had a greater opportunity to sample the environment than chicks, and may 'decide' to withhold parental investment early in the

nestling period to induce brood reduction when they deem  $M$  to be insufficient to rear a full brood. Such a pattern is consistent with a reduction of the cost of sibling competition,  $C(t)$ . Based on the information at hand, senior sibs 'decide' to eliminate junior sibs, avoiding more costly sibling conflict later on, a behaviour also favoured by parents. I investigate this idea further in Chapter Six.

CHAPTER FIVE

RESOURCE ALLOCATION  
IN OSPREY FAMILIES

## INTRODUCTION

In siblicidal birds parents create competitive asymmetries among their offspring, usually through hatching asynchrony and/or differences in egg size, in order to facilitate adaptive brood reduction (reviews in O'Connor 1978, Mock 1984a). In doing so the parents appear to relinquish at least partial control over how resources are shared among contemporary sibs, leaving that for the sibs to 'decide' (Mock 1987). Thus, through their size and motor-skill advantages, senior sibs can command a disproportionate share of parental resources at the expense of junior sibs. Due to the differing genetic interests of parents and offspring, we expect evolutionary conflict to exist between parents and offspring over the division of resources (Trivers 1974): each sib may desire a greater share than parents desire it to have. If such genetic conflicts truly exist, the parental trait of establishing competitive asymmetries among contemporary sibs is rather puzzling. Furthermore, in various siblicidal species, parents generally do not attempt to intervene in sibling aggression, nor do they feed junior sibs preferentially (reviewed in Mock 1987).

There may be alternative mechanisms by which parents are able to influence resource allocation in the brood even after creating within-brood competitive asymmetries. Sibling aggression is an important determinant of access to parental resources, but even in species such as egrets where

the incidence of aggression is not proximally regulated by food amount, junior sibs are able to feed more after senior sibs have been satiated (Mock et al. 1987a). This raises the possibility that parents might work through the sibling dominance hierarchy to influence resource allocation. Parents could bring more food to the brood, thereby satiating senior sibs more often. Alternatively, parents could deliver very large prey (or large amounts of food), or temporally clump smaller deliveries of prey, so as to satiate the senior sib(s), and thus allow the junior sib(s) to feed more often, an idea first suggested by Mock 1987a.

This chapter is divided into two sections. In the first, I develop a simple model of chick feeding, referred to as the hierarchy model, to explore the consequences of changing (i) the long-term average rate of food delivery, (ii) the size of prey, (iii) the temporal pattern of deliveries, and (iv) the ability of senior siblings to monopolize individual prey items, on food allocation among sibs within an absolute feeding hierarchy.

In the second section I present a field-test of the hierarchy model on families of ospreys. I first explore whether food allocation is proximately related to hunger in osprey nestlings. I then present the results of an experimental manipulation designed to examine whether parents can work through the dominance hierarchy to affect food allocation among offspring.

## SECTION I: THE HIERARCHY MODEL

### Model description

The present model examines the effects of variation in (i) the rate of prey delivery, (ii) the size of prey, (iii) the temporal pattern of prey deliveries, and (iv) the maximum meal size for a chick (which determines the degree to which a dominant sibling can monopolize an individual prey delivery through exploitation competition), on the allocation of food between siblings when an absolute dominance hierarchy exists. The model described here is run as a Monte Carlo simulation (format outlined in Figure 5.1). Two chicks, A and B share a nest to which parents deliver single prey items that can be divided between A and B. The model proceeds in 0.2 h time periods, with either zero or one prey being delivered to the brood during each unit,  $t$ . A completely dominates B, such that A feeds until it is replete, before B can feed. The amount of a prey item that a chick eats depends on (i) its rank, (ii) its hunger level,  $H(t)$ , and (iii) its gut capacity (maximum amount of food it can eat),  $M_{max}$ . Presumably  $M_{max}$  is related to the size of chick (big chicks can eat more than small chicks), however in the present model  $M_{max}$  is fixed and is the same for A and B so that the effects observed in the model results are attributable only to the dominance hierarchy, prey size, and schedule of food deliveries.



Hunger diminishes with feeding, the amount determined by the proportion of the maximum meal size a chick eats:

$$H(t+1) = H(t) - \frac{F}{M_{\max}} \quad H(t) > 0: F < M_{\max} \quad (1)$$

where  $F$  is the amount of food a chick eats during a meal. If a chick feeds to satiation, hunger declines to zero; if a chick does not feed during period  $t$ , its hunger increases according to the linear function:

$$H(t+1) = \begin{cases} H(t) + 0.1 & H(t) < 0.9 \\ 1.0 & \text{otherwise} \end{cases} \quad (2)$$

That is, a chick's hunger increases from 0 to maximal in 2 h (Fig. 5.2). If the size of a prey item exceeds the amount  $A$  and  $B$  can eat together, both  $A$  and  $B$  feed to satiation and the remainder of the prey item is divided evenly between them.

Two types of simulation were run, differing in the pattern of deliveries of prey items to the brood. In the first, the Even simulation, prey are delivered at fixed intervals, ranging from 1 prey/h to 1 prey/8 h. In the second, the Random simulation prey are delivered at the same mean intervals as in the Even simulation, but the pattern of deliveries is determined with a random number generator drawing from a uniform distribution. Thus some intervals between deliveries are shorter, and others longer in the

Figure 5.1. Flow chart of simulation model.

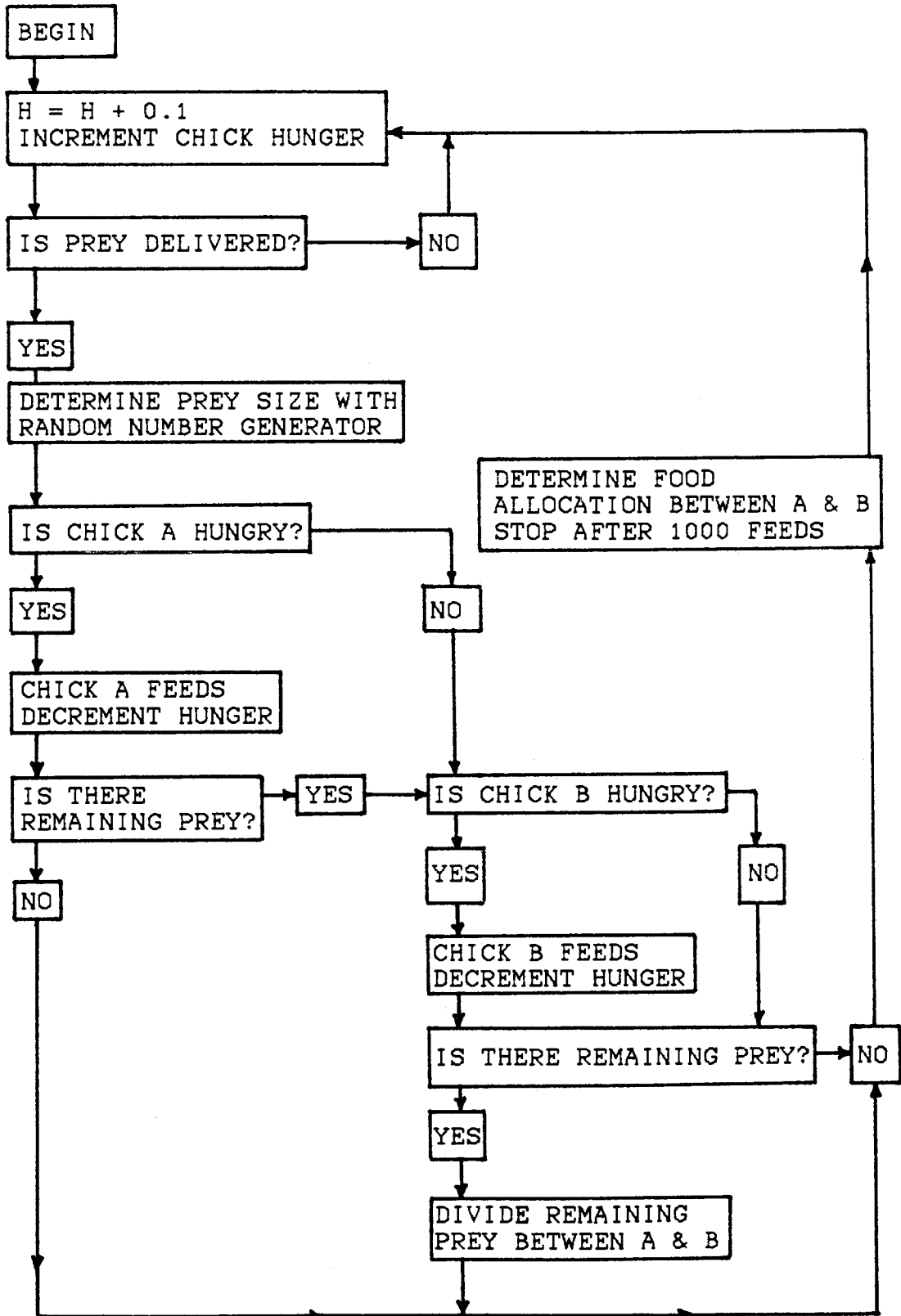
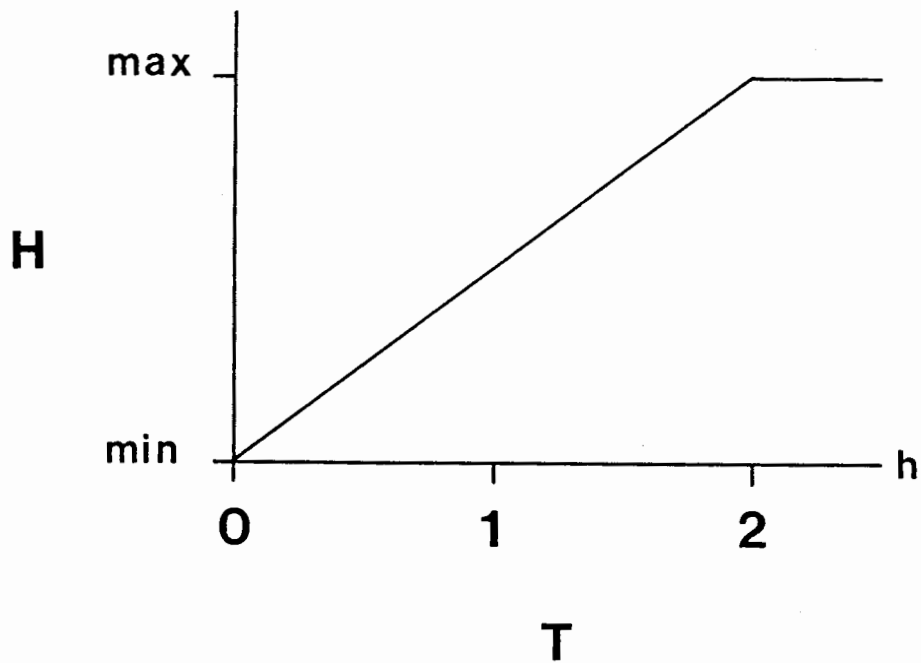


Figure 5.2. Relationship between chick hunger level (H) and time since chick was last fed to satiation (T). H reaches a maximum (max) at 2 h.



Random simulation than in the Even simulation, although the means are identical.

Two sizes of prey are used in the Even and Random simulations: small ( $S_x=100$  g; range=50-150 g) and large ( $S_x=200$  g; range=100-300). Prey sizes were drawn randomly from a uniform distribution. Prey were delivered to the brood at three rates in both the Even and Random simulations: 25, 50 and 100 g/h. For small prey the three rates corresponded to 1 prey/4 h, 1 prey/2 h and 1 prey/h respectively. For large prey the corresponding rates were 1 prey/8 h, 1 prey/4 h, and 1 prey/2 h.

Two levels of  $M_{MAX}$  were used in the model: 100 and 150 g. The first is equal to the mean size of small prey (100 g). The second is larger than the mean size of small prey and smaller than the mean size of large prey.

In each simulation run, chicks began at the maximum hunger level, and prey were delivered to the brood according to one of the schedules described above. Each simulation terminated when 1000 prey items had been delivered to the brood. For each prey item, the portions eaten by A ( $P_A$ ) and B ( $P_B$ ) were determined and these data were used to generate the frequency distributions in Figures 5.3 and 5.4. A value of  $P_A$  close to 1 indicates that the senior sib monopolized a prey item, whereas a value of  $P_A$  near 0.5 indicates that A and B ate nearly equal portions of a prey item.

### Model results and discussion

Four main points can be derived from the results summarized in Figures 5.3 and 5.4. First, increasing the rate of prey delivery produces a more even distribution of food between A and B ( $P_A$  is closer to 0.5). The reason for this is simple. When more prey are delivered to the brood, A is hungry less often and thus B can feed more often.

Second,  $P_A$  was higher in the Even simulation than in the Random simulation. The reason for this is more subtle. In the Even simulation the interval between feeds was constant, whereas in the Random simulation, both short and long intervals occurred, although the mean interval length was the same. As the interval between feeds decreases,  $P_B$  tends to increase since A is less likely to be hungry when a prey is delivered. However, very long intervals (>2 h) between feeds have little effect on the model results, since A's hunger rises from zero to maximal in 2 h if no food is delivered. Longer intervals (>2 h) have no further effect on A's hunger level.

Third, increasing prey size results in a more even distribution of food between A and B. Once again, the reason for this is simple. With large prey, A is satiated more often than with small prey, allowing B to feed more often. In the present model, only random and even intervals between prey deliveries were examined. The reason for this is that temporal clumping of deliveries would have

Figure 5.3a. Results of the Even simulation.  $P_A$  is the proportion of an individual prey item that chick  $\Delta$  takes. Frequency distributions (%) of  $P_A$  are shown for small ( $S_x=100$ ) and large ( $S_x=200$ ) prey at rates of prey delivery of 100, 50 and 25 g/h. Maximum meal size ( $M_{max}$ ) is 100g.

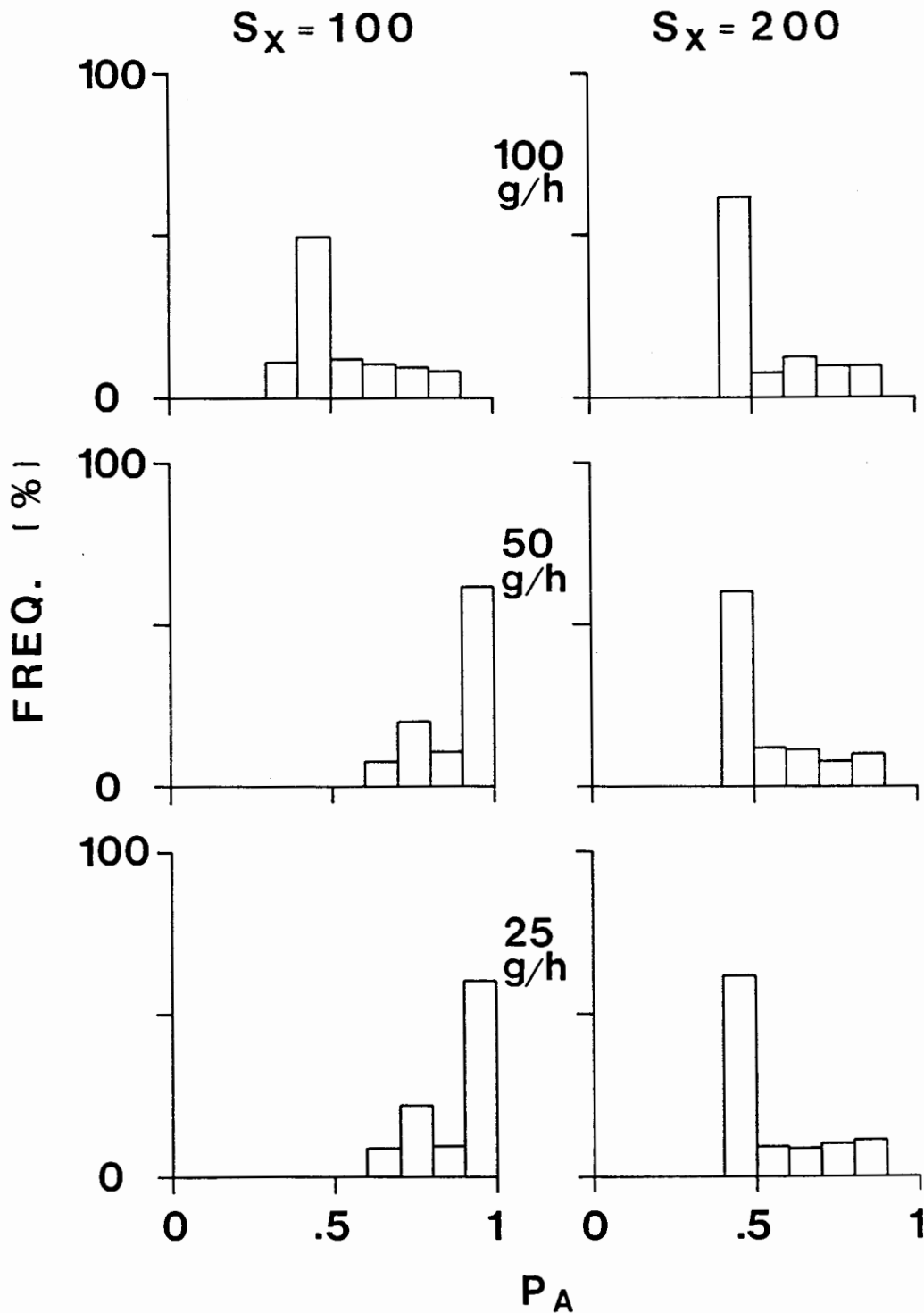


Figure 5.3b. Same as 5.3a, except maximum meal size ( $M_{MAX}$ ) is now 150g.

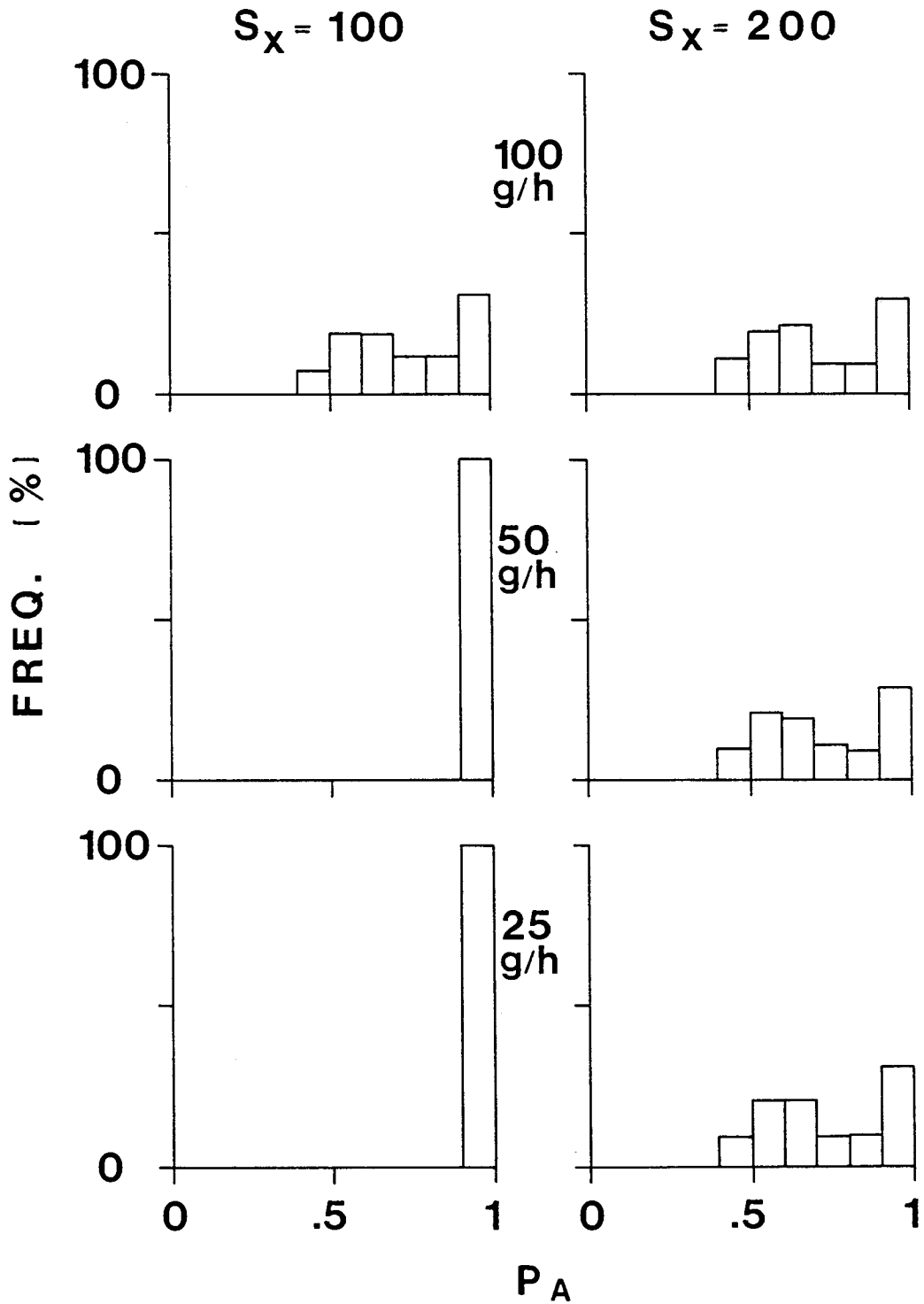


Figure 5.4a. Results of the Random simulation.  $P_A$  is the proportion of an individual prey item that chick A takes. Frequency distributions (%) of  $P_A$  are shown for small ( $S_x=100$ ) and large ( $S_x=200$ ) prey at rates of prey delivery of 100, 50 and 25 g/h. Maximum meal size is 100 g.

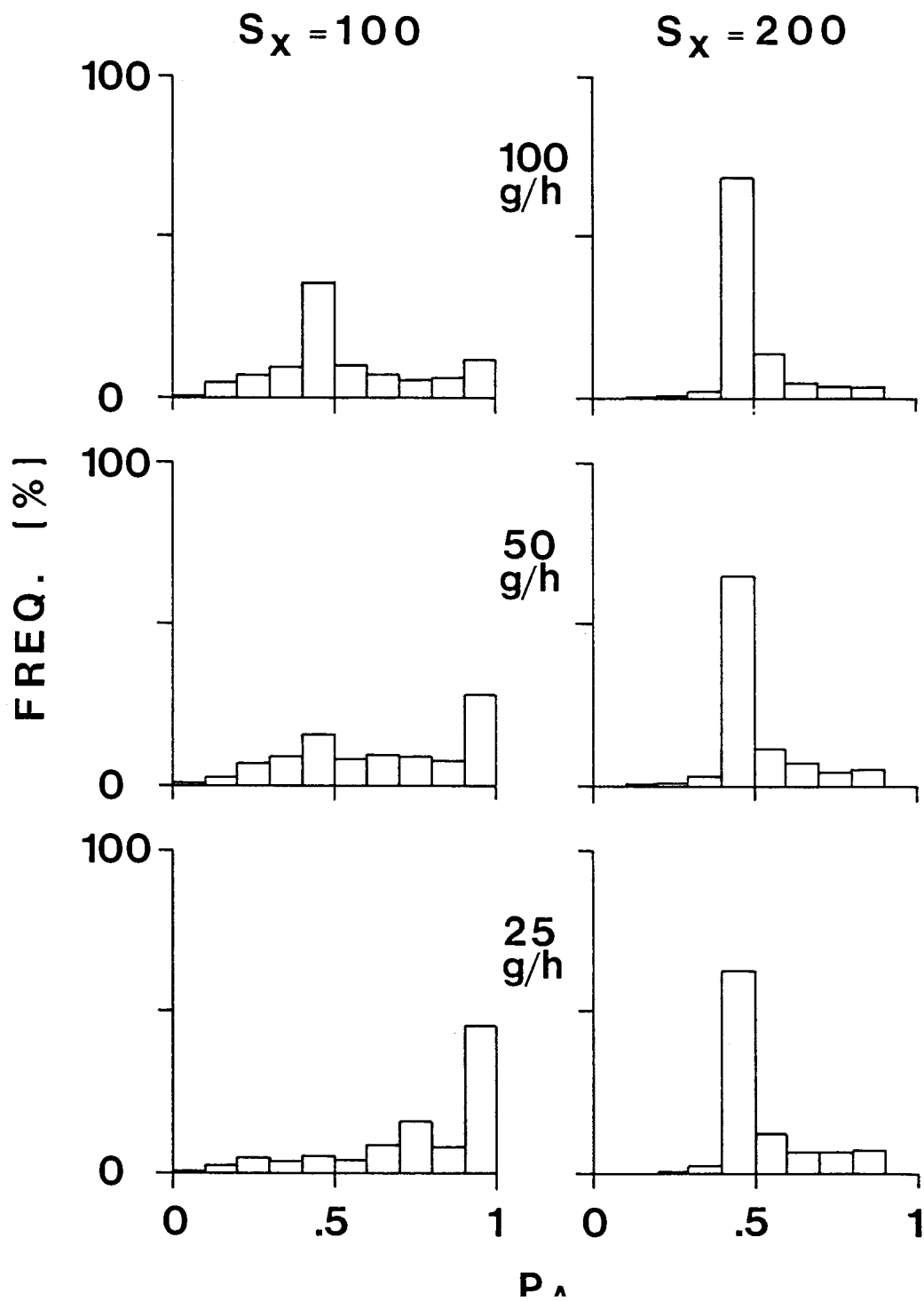
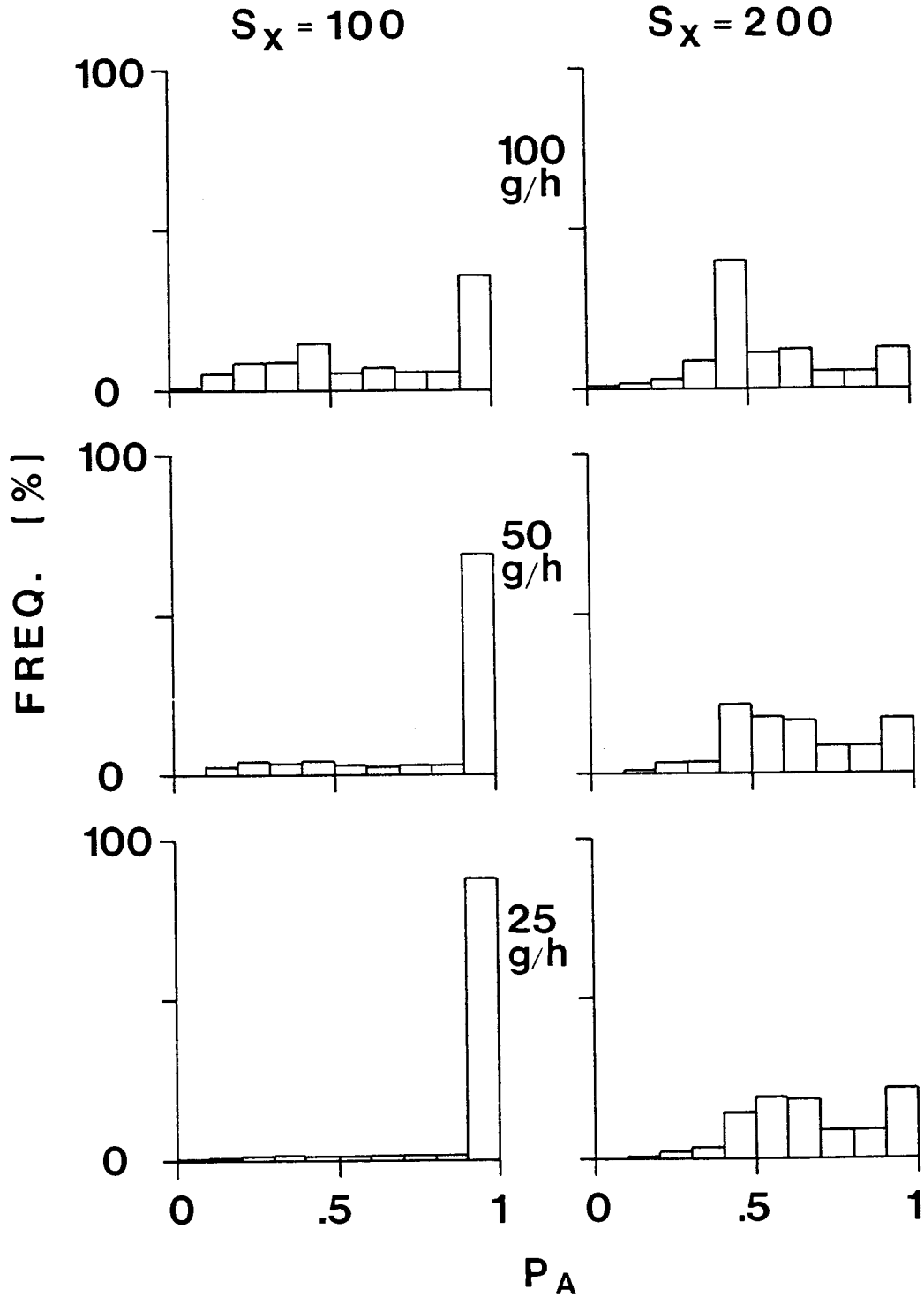




Figure 5.4b. Same as 5.4a, except maximum meal size ( $M_{MAX}$ ) is now 150g.



the same effect as increasing prey size; bringing two small prey to the brood close in time has, in this model, the same effect as bringing one large prey (i.e., the senior sib is sated more often).

Fourth, as gut capacity increases, A's ability to monopolize prey increases. The senior sib takes more food before it is satiated, leaving less for the junior sib. It follows that if parents desire to distribute food equally among chicks, parents should reduce size asymmetries between chicks.

The model results illustrate a simple but important point. Under an absolute dominance hierarchy, marked differences in food allocation can occur as a function of differences in (a) the temporal pattern of provisioning, and (b) prey size. A mechanism therefore exists for parents to work through an absolute dominance hierarchy to influence allocation of food among sibs without necessarily changing the rate of prey delivery. By satiating senior sibs, parents create a window of opportunity to feed junior sibs. This window can be created either by bringing more or larger prey at a single feeding than can be eaten by a senior sib, or by temporally clumping feedings such that junior sibs are fed while senior sibs are still sated.

The relative growth of chicks may also be important in food allocation among nestlings. By virtue of their dominant status, senior sibs take more food and grow faster

(Bortolotti 1989) resulting in a further size advantage, effectively generating a positive feedback loop. Such an effect is likely most important during the early nestling period when growth is fastest and most chick mortality occurs (Hagan 1986, Poole 1989).

## SECTION II: FIELD STUDIES

In this section I present a field test of the hierarchy model on families of ospreys. First I examine food allocation in ospreys in relation to hunger to validate the key assumptions of the hierarchy model: that aggression and more importantly, food allocation, are related to the hunger level of the senior sibling. I then present the results of an experiment where I created artificially asynchronous broods of two osprey chicks. My expectation was that parents should be sensitive to resource allocation among brood members (e.g., parents do not want brood reduction to occur if food is abundant), and moreover, parents should attempt to skew resources toward the junior sib in order to reduce the competitive asymmetry between the chicks, or at least prevent the asymmetry from growing larger. Moreover, I predicted that parents should work through the feeding hierarchy to direct resources to the junior sib, using one of the mechanisms (larger or more prey, or temporal clumping of deliveries) examined in the model. I then examine the effects on resource allocation between the senior and junior

siblings to determine if indeed resources were skewed to the junior sib. I begin with a description of the feeding behaviour of nestling ospreys.

### Methods

Nest-watches were carried out at four nests in 1986 and a further four manipulated nests (see below) in 1987. Individual nest-watches varied from seven to 14 h in length. Nests were observed with the aid of binoculars and spotting telescope from blinds 30 to 100 m from nests. A tape recorder was used to record data during feed sequences. Observations were carried out from the late stages of incubation until the chicks were six weeks of age.

Parent females butchered fish and gave bite-sized pieces to the chicks. The sequence and number of pieces eaten by individual chicks and the female were recorded. Individual chicks were identified by differences in size or plumage markings; in some cases the bills of chicks were marked with paint to aid recognition.

Prey were identified by their characteristic shapes, sizes and colours. Prey length was estimated as a proportion of different body parts of the adult osprey (tarsus, tail, total body length). Estimates of prey size were checked by placing a metre rule on one nest.

In 1987 I created four artificially asynchronous two-chick broods by moving the B-chick from two three-chick broods to

two one-chick broods. In the two enlarged broods, the fostered chick became the Junior sib. In all four broods, the moves created age disparities of four to six days between the junior and senior sibs, where the normal hatching interval between A and B chicks in the Creston population is at most two and usually one day (Steeger 1989). The moves were made when the senior-most chicks in all four broods were 17 to 21 d old. Both chicks were readily adopted by their foster parents and survived to fledging. Hereafter I shall refer to these four manipulated broods from 1987 as *asynchronous* broods and four unmanipulated broods from 1986 as *normal* broods. Unfortunately, a paucity of observable nests precluded me from running a proper control, i.e., exchanging chicks of the same age. However, ospreys readily accept foster chicks (Spitzer 1978, Poole 1989, pers. obs.); indeed at one of the experimental nests, parents began feeding the foster chick within minutes of its arrival. Observations of normal and *asynchronous* broods were collected on broods of similar age (Table 5.3). Behavioural data were pooled across broods for analysis due to small sample sizes (see description of this in Chapter Two).

## Results

### Feeding behaviour

Two kinds of feeds occurred. One began with the delivery of a new fish, the other resumed from a fish remaining on the nest. These were not differentiated in analyses. Multiple feeds occurred with some very large fish (e.g., suckers, northern squawfish, rainbow trout). Smaller fish such as black bullhead, yellow perch and peamouth were usually consumed at a single feed. A feed normally ended when either the fish was consumed entirely, or when the brood and the female were satiated. Some feeds were interrupted by disturbance (human, avian intruders); if feeding resumed when the disturbance ceased, I considered this to be part of the original feed. Usually disturbance events were short-lived and feeding resumed within a few minutes. If feeding was not resumed within 15 min, the feed was considered to have ended.

The general pattern of a feed was as follows. A male would return to the nest with a fish, which was then taken by the female. (Females occasionally caught fish - see Chapter Two). The female then began to tear bites from the anterior portion of the fish (discarding hard parts such as spines, opercula, and mandibles and either eating them herself or holding them out to be grabbed by chicks in front of her). On most occasions a single chick occupied the position directly in front of the female and received most

of the bites. Alternatively, both chicks might sit side by side, each reaching out to grab bites presented by the female. Chicks continued to feed until apparently satiated (as indicated by a full crop and disinterest in the food), whereupon they turned away from the female. The mother showed no obvious favoritism, usually holding bites in front of her to be grabbed by any chick. Occasionally satiated chicks remained in front of the female, whereupon she reached over them to feed a begging chick, or she moved to another position on the nest, and the hungry chick followed her. The mother continued to feed the chicks until bites were rejected. The female ate the greatest share of her food after the chicks were satiated. The tail was usually eaten by the female, but sometimes by a large chick. The female then picked up any bits of flesh from the nest floor, eating them, or feeding them to a begging chick, and finally, she rearranged sticks or nest lining.

#### Sibling aggression

Nearly all aggression among nestlings occurred during feeds. Aggression took two forms: physical abuse (biting, striking with the bill), and threat displays (Table 5.1). In the latter, a chick stretched its head and neck upward, and oriented toward its sibling. Most often the chick closest to the female distributing bites would attack or threaten another nest-mate that was attempting to move

Table 5.1. Frequency of aggression (physical aggression and threat displays) at feeds in normal broods.

Aggressor	Number of feeds		
	Physical attack	Threat display	Feeds with aggression
A-chick	8	11	11
B-chick	2	1	2

Table 5.2. Number of feeds with and without aggression in relation to the number of bites eaten by the A-chick in the last 3 hr in normal broods.

Bites eaten by A-chick in last 3 h	Number of Feeds	
	With Aggression	Without Aggression
<50	8	16
>50	2	19

A. Aggression occurred more frequently at feeds when the A-chick had eaten <50 bites in the previous 3 h:  $G=3.9$ ,  $p<0.05$ .



closer to the female. An aggressive interaction usually ended when one chick moved away or assumed a submissive posture (crouched against the floor of the nest), or both. Intimidated chicks usually moved away from the female and dominant chick, and waited until the dominant chick was satiated before attempting to feed.

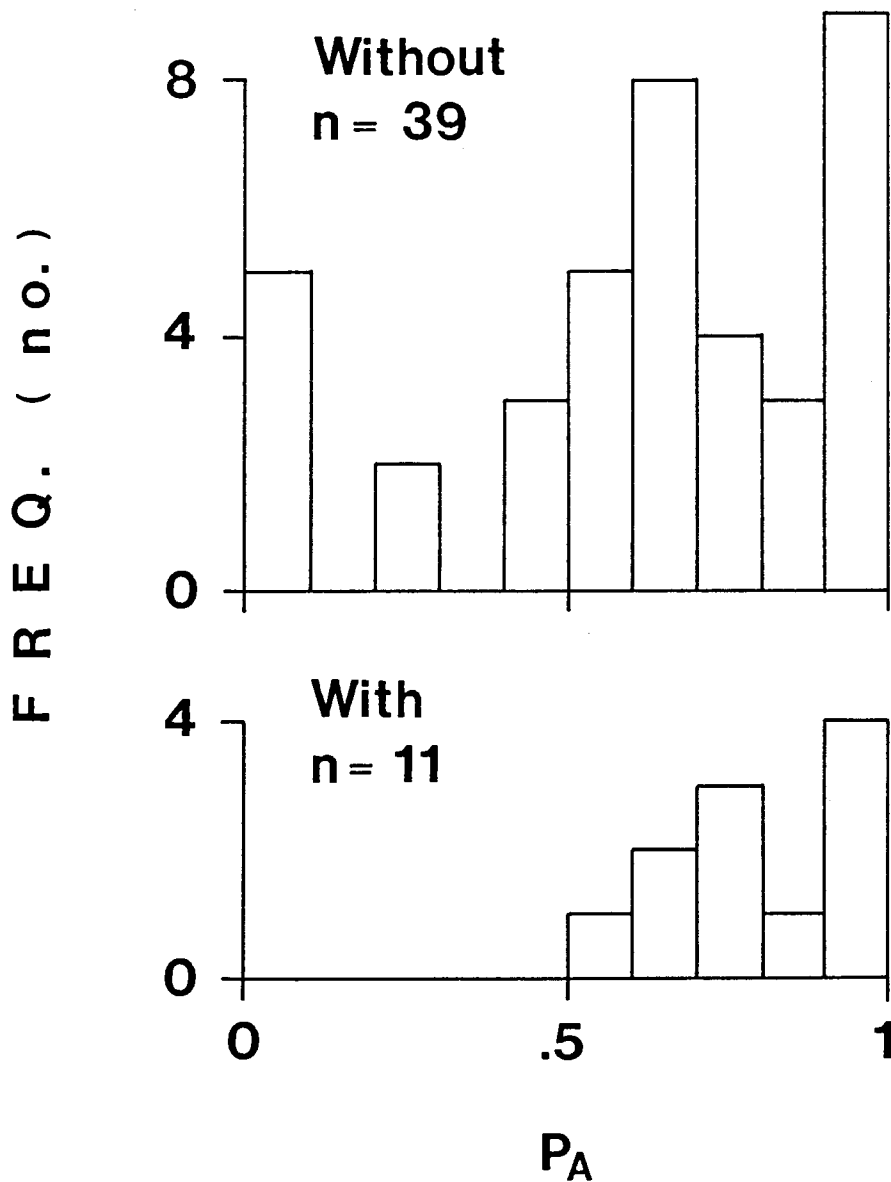
Parents never intervened in sibling aggression, although the female was present at the nest during virtually all such episodes. The A-chick was the aggressor most often and threat displays were used more frequently than physical aggression (Table 5.1).

#### A. Hunger and food allocation in osprey nestlings

If food allocation in osprey nestlings is proximally related to hunger and mediated by aggression, then we should expect the senior sibling to (1) be more aggressive, and (2) to take a larger share of available food, when hungry. The data support these predictions.

First, aggression was rare once the A-chick was satiated. When the A-chick had had fewer than 50 bites in the previous three h (about half the length of time it took a chick to empty the contents of a full crop, pers. obs.), aggression was more frequent (Table 5.2). Fifty bites was chosen because it was the median amount that A-chicks had eaten in the previous 3 h.

Figure 5.5. Frequency distribution of the proportion of bites ( $P_A$ ) the A-chick ate at feeds with and without aggression. A-chicks took greater than 50% of the bites significantly more often at feeds with aggression than without ( $G_{1,38}=5.8$ ,  $p<0.05$ ).



Second, the A-chick took a greater share of food during feeds in which it used aggression (Fig. 5.5). When the A-chick had had fewer than 50 bites in the previous 3 h, it took greater than 90% of the bites at 10 of 22 feeds (45%); when it had had greater than 50 bites in the previous 3 h, it took greater than 90% of the food at only 3 of 22 feeds (14%), a significant difference ( $G=5.6$ ,  $p<0.05$ ).

#### B. Testing the hierarchy model

The results so far are consistent with the idea that aggression and resource allocation in nestling ospreys are proximally related to hunger. I now turn to an experimental test of the hierarchy model. In the artificially asynchronous broods, my expectation was that parents should attempt to narrow this exaggerated competitive asymmetry by skewing resources to the junior sib by one or more of the three mechanisms described in the model: (i) bringing more food to the brood, (ii) temporal clumping of prey deliveries, or (iii) bringing larger prey.

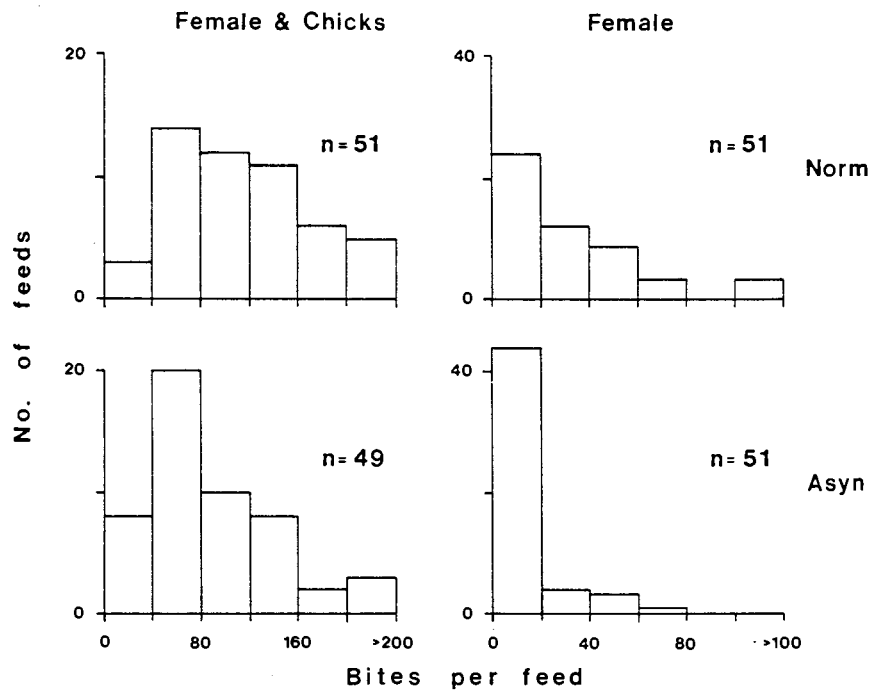
Parents did not bring more or larger prey to asynchronous broods. The frequency of feeds did not differ significantly between normal and asynchronous broods (Table 5.3), and the size of feeds (no. of bites to the female and brood) was actually smaller in asynchronous than in normal broods (Fig. 5.6: Mann-Whitney U-test:  $z=-2.61$ ,  $p=0.009$ ).

Table 5.3. Feeding frequency for normal and asynchronous broods.

	Brood ages (d)	20 min blocks		Total observation time (h)
		with feed	without feed	
normal	21-41	102	554	219
asynchronous	17-37	53	271	108

A. The frequency of feeds did not differ significantly between normal and asynchronous broods:  $G_{(1)} = 0.1$ ,  $p > 0.65$ .

Figure 5.6. Frequency of different sizes of feeds (No. of bites) to (A) female & chicks and (B) female alone in normal (Norm) and asynchronous (Asyn) broods.



The pattern of intervals between chick feeds differed significantly between normal and asynchronous broods (Fig. 5.7:  $G=11.7$ ,  $df=4$ ,  $p=0.02$ ); many more feeds occurred close together in time ( $<0.5$  h apart) in asynchronous than in the normal broods. Thus parents did clump feedings at asynchronous broods.

Did clumped feedings result in a more even distribution of food between the A and B chicks in asynchronous than in normal broods? To examine this question it is necessary to account for the behaviour of the parent female since she is an active participant in chick feedings, and could alter her own feeding behaviour; for example, Poole (1989) noted that osprey females with artificially enlarged broods ate less food.

B-chicks received a substantially larger a share of food in asynchronous broods than in normal broods (Table 5.4), opposite to the pattern expected based on size differences of the chicks alone (i.e., because the size disparity is larger in asynchronous broods, the A-chick would be expected to take a greater share in these broods). A-chicks received a slightly smaller share of food in asynchronous broods than in normal broods, but females ate a substantially smaller portion of food in asynchronous broods (Table 5.4).

Figure 5.7. Frequency distribution (Freq.) of observed intervals between feeds (0.5 hr increments) in normal (Norm) and asynchronous (Asyn) broods.

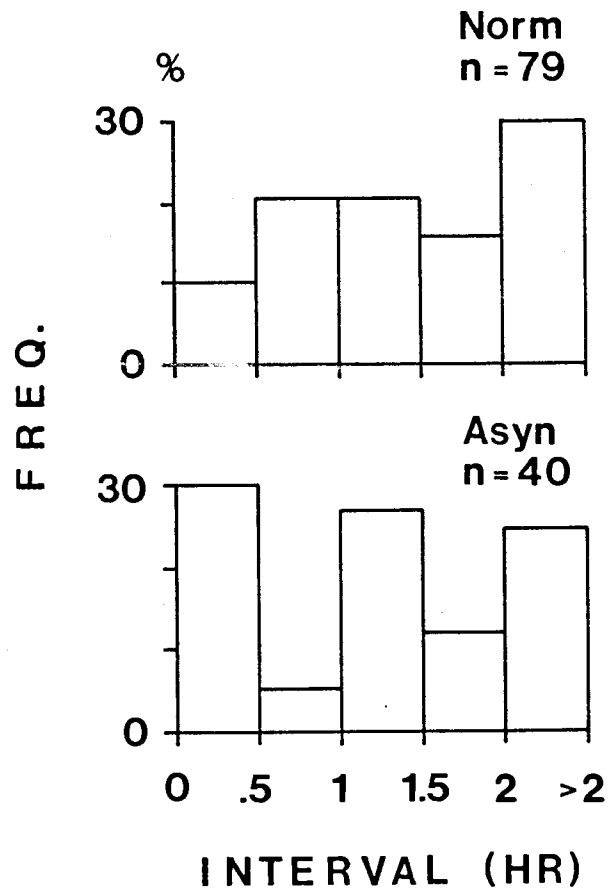


Table 5.4. Proportion (%) of bites to female and chicks in normal and asynchronous broods.

	Female	Chick		n (bites)
		A	B	
normal	27.7	47.4	24.9	5939
asynchronous	14.3	44.9	40.8	4444

A. The A chick ate a smaller share and the B chick ate a larger share of bites to the brood (excludes bites to the female) in asynchronous than in normal broods:  $G_{(1)}=146$ ,  $df=1$ ,  $p < 0.001$ .



In terms of bites to the brood only, A and B received 66% vs 34% of the bites respectively in normal broods but 52% vs 48% of bites respectively in asynchronous broods (Table 5.4), a significant difference ( $G_{1,15}=146$ ,  $p < 0.001$ ).

On a per-feed basis, females ate fewer bites in asynchronous than in normal broods (Mann-Whitney U-test:  $z = -3.79$ ,  $p < 0.001$ , Fig. 5.6) as was the case for A-chicks ( $z = -2.66$ ,  $p = 0.007$ , Fig. 5.8). B-chicks took slightly more bites per feed in asynchronous than in normal broods (Fig. 5.8:  $z = -1.55$ ,  $p = 0.117$ ).

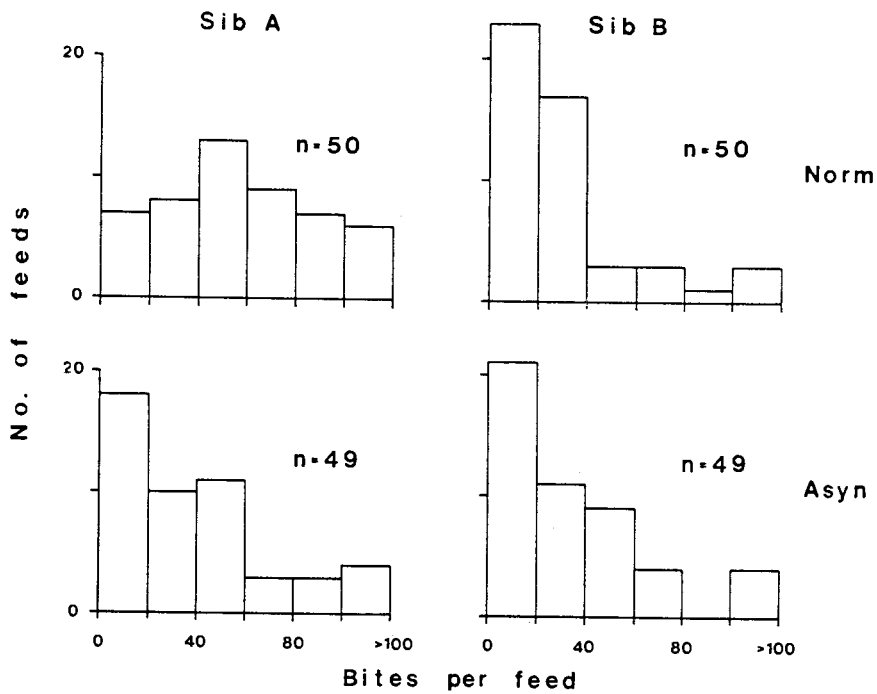
Aggression occurred at 11 of 51 feeds (22%) in normal broods but was absent in all 51 feeds at asynchronous nests, a significant difference ( $G = 16.4$ ,  $p < 0.001$ ).

Overall, in asynchronous broods a greater proportion of the food eaten by the family (female and chicks) was available for the chicks since the female ate less, and of this, the B-chick ate a greater share than in normal broods.

## DISCUSSION

Resource allocation decisions among family members of siblicidal birds may be considerably more complex than previously suspected. Although on the surface parents seem to leave resource allocation decisions to the offspring, this may be misleading. Parents may play an active but

Figure 5.8. Frequency of different sizes of meals (Bites per feed) eaten by sib-A and sib-B at feeds to normal (Norm) and asynchronous (Asyn) broods.



subtle role in the division of resources among offspring. In the asynchrony experiment, parents of asynchronous broods temporally clumped feeds and a greater share of food went to the chicks (the female, by eating less, effectively elevated the rate of food delivery to the brood). And of the food that went to the chicks, a greater share went to the junior sib. Poole (1989) also noted that when broods were artificially enlarged females ate less of the fish delivered to the nest. It must be borne in mind that the results of my study are based on data pooled across broods.

#### The evolutionary limits of parental favoritism

Parents might under some circumstances choose to feed junior sibs preferentially. This would seem to be a more effective mechanism for parents to control resource allocation among sibs than by working through the dominance hierarchy, but they may be constrained from doing so by the prospect of evolutionary retaliation by the sibs (Parker and MacNair 1979, Drummond 1989). Senior sibs enjoy priority access to food and hence superior prospects for growth and survival, and would be selected to oppose preferential feeding of junior sibs since this might upset the status quo (i.e., junior sibs may displace senior sibs in the hierarchy, Ploger and Mock 1986). As well junior sibs may take resources that might otherwise go to the senior sib. In order to minimize these risks, senior sibs might

eliminate junior sibs before they could become a threat (obligate siblicide), thereby eliminating the benefits of a system of facultative brood reduction for parents.

The net effect of sib-swamping tactics by the parents is a more equal division of resources among offspring. As with preferential feeding, parent-offspring conflict over resource allocation is still possible, and senior siblings still hold the threat of siblicide. How far parents can impose their will upon senior sibs will depend upon where the threshold for siblicide lies. By swamping senior sibs, however, its needs are less likely to be disaffected than if parents feed junior sibs preferentially. Senior siblings maintain priority access to food at individual feeds and presumably can take their desired share of food. This enables senior sibs to maintain a size and growth advantage over juniors which minimizes the risk of a dominance reversal.

#### Working harder vs clumping deliveries

In order to bring more food to the brood, parents (in ospreys primarily the male) must work harder and may diminish their expectation of future reproduction if there exist reproductive costs (Williams 1966a,b, Charnov and Krebs 1973, Sargent and Gross 1986, Reid 1987). By temporally clumping feeds to chicks, or by bringing larger prey, parents may be able to avoid these costs while

achieving the same goal: diverting a greater share of resources to the junior sib.

CHAPTER SIX

SIBLICIDE, REPRODUCTIVE  
COSTS, AND PARENT-OFFSPRING  
CONFLICT OVER BROOD SIZE

## INTRODUCTION

A number of models of parent-offspring conflict now exist (e.g., Stamps et al. 1978, Parker and MacNair 1978, 1979, MacNair and Parker 1978, 1979, Parker 1985), but none investigate the dynamics of reproductive costs for parents. For example, in the models of Parker and MacNair, a parent is assumed to possess a fixed quantity of resources to expend on reproduction during its lifetime, and all offspring are assumed to be equally costly. But this is not likely to be true. Parents must decide how to allocate effort between present and future reproduction (Williams 1966a,b, Charnov and Krebs 1974, Goodman 1974, Reid 1987, Dijkstra 1988, Gustafsson and Sutherland 1988), and at the optimum, increases or decreases in present reproductive effort diminishes lifetime reproductive success. Thus the rate at which reproductive effort is expended will itself be a determinant of the lifetime reproductive effort available (Winkler and Wallin 1987, Clark and Ydenberg 1989).

In this chapter I develop a model relating parental investment to the value of present and future reproduction in order to examine brood reduction decisions of both parents and offspring. I do not differentiate here between brood reduction by starvation and brood reduction by direct acts of violence (e.g. siblicide): although the proximate mechanisms differ, the fitness consequences for parents and offspring in the context of the model are identical. I

shall show (i) that the parental trade-off between present and future reproduction may constrain the brood reduction decisions of offspring, and (ii) that phenotypic conflict between parents and offspring is less likely to occur if the offspring themselves 'decide' how parental resources are to be shared.

#### THE GAME

The game modelled here consists of four sequential decisions, taken alternately by parents and offspring. First, parents establish an initial brood size and level of investment according to the value of present and future broods, such that they maximize expected lifetime reproductive success (i.e., in accordance with Williams' principle, Williams 1966a,b, Sargent and Gross 1986). Second, senior siblings assess their current inclusive fitness and decide whether they would be better off reducing the size of the brood, given that parental investment remains constant. Third, if brood reduction occurs, parents reassess the value of their current brood, and may re-adjust their allocation of investment between current and future broods accordingly. And fourth, senior siblings reassess their fitness after the corresponding parental response. Only if the senior sib's inclusive fitness turns out to be higher after parental readjustment than initially, will brood reduction be favoured. Clearly, this sequence of



events represents an evolutionary game, in that the behaviour of both parties depends upon the actions of the other.

In this chapter I shall consider two types of food allocation among members of the current brood. In the first (Even), parents distribute food equally to all brood members. In the second case (Despotic), parents allow the offspring to distribute resources among themselves. I begin by considering Even allocation, the simpler of the two cases. I then outline the consequences of Despotic allocation for parent and offspring decisions, and in the following section, present a numerical analysis of the model. In Table 6.1, I list the variables and parameters used in the model, and their definitions.

## EVEN ALLOCATION

### Future reproductive success of parents

Following Williams' principle, increasing parental investment in present reproduction decreases the potential for investment in future reproduction. Let present reproductive success be some increasing function,  $J$ , of the quantity of resources (primarily food),  $M$ , that parents expend on the present brood and let future reproductive success be some monotonically decreasing function,  $K(M)$ . At the highest attainable value of  $M$ ,  $M_{max}$ , the effort a parent

Table 6.1. Definitions of variables and parameters in the model.

---

Variables

$M$	parental investment in present brood
$M^*$	optimal level of investment in present brood
$M_{before}$	parental investment before siblicide
$M_{after}$	parental investment after siblicide
$J(M)$	present reproductive success of parents
$K(M)$	future reproductive success of parents
$L(M)$	lifetime reproductive success of parents
$f(m)$	fitness of an individual chick
$s$	brood size
$p_i$	proportion of $M$ given to sib $i$
$\lambda$	replication rate of mutant allele

Parameters

$M_{max}$	maximum parental investment in current brood
$K_{max}$	maximum future reproductive success of parents
$N$	shape constant
$M_{min}$	minimum level of investment of parental resources, below which chick fitness is zero

---

expends in gathering resources will be so great that the parent dies, whereupon  $K(M)$  will be zero. Conversely, when  $M=0$ , (parents forego present reproduction), future reproductive success will reach some maximum level,  $K_{MAX}$ , since all parental effort will be devoted to future reproduction. I now define an explicit function for  $K(M)$  satisfying these requirements:

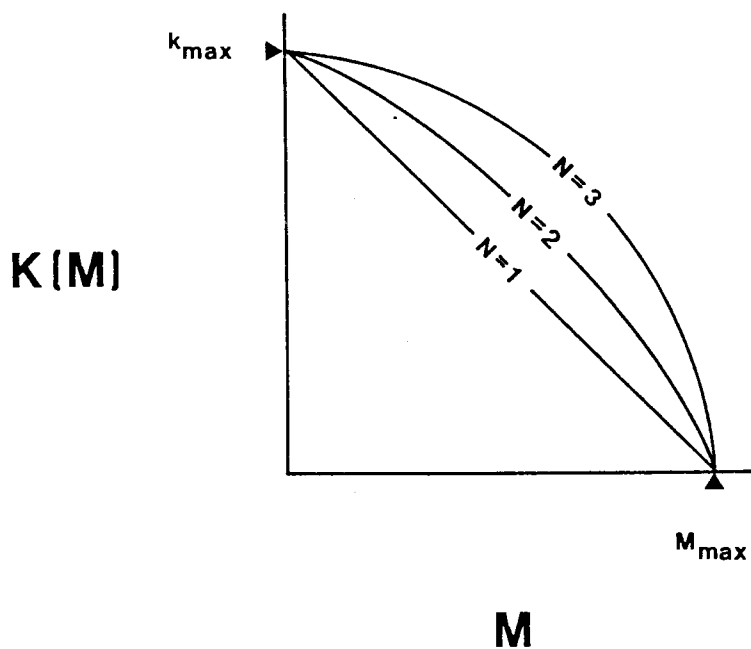
$$(1) \quad K(M) = K_{MAX} (1 - ([M / M_{MAX}]^N)),$$

where  $N$  is a positive shape constant. An advantage of this function is that it allows for a variety of potential relationships between  $K(M)$  and  $M$ ; when  $N > 1$ ,  $K(M)$  is concave downward (Fig.6.1) and when  $N=1$ ,  $K(M)$  is linear.

#### Present reproductive success

In this section I begin by defining a function for the fitness of individual chicks in terms of the parental resources received. I loosely follow the protocol and terminology of MacNair and Parker (1979) and Parker et al. (1989). I begin by assuming that the fitness (=survival to breeding) of an offspring is an increasing function  $f$  of the amount of resources,  $m$ , it obtains. It is convenient here to think of  $m$  as the total provisioning received by an offspring over the entire period of parental care, and is some proportion of  $M$ , the total quantity of resources parents invest in the current brood. The function  $f(m)$  is zero up to an arbitrary minimum,  $m_{MIN}$ , above which it

Figure 6.1. Relationship between present reproductive effort,  $M$ , and future reproductive success,  $K(M)$  at differing levels of  $N$ .



decelerates to an asymptote. I now define an explicit function for  $f(m)$  satisfying these requirements:

$$(2) \quad f(m) = \begin{cases} E_{\text{MAX}} (m - m_{\text{MIN}}) / m & \text{if } m > m_{\text{MIN}} \\ 0 & \text{otherwise} \end{cases}$$

where  $E_{\text{MAX}}$ , a positive constant, is the asymptotic value of  $f(m)$  [ $f(m)$  converges to  $E_{\text{MAX}}$  as  $m \rightarrow \infty$ ]. For simplicity I shall set both  $E_{\text{MAX}}$  and  $m_{\text{MIN}}$  equal to unity such that (2) simplifies to:

$$(3) \quad f(m) = \begin{cases} (m - 1) / m & \text{if } m > 1 \\ 0 & \text{otherwise} \end{cases}$$

Where resources are divided equally among members of the current brood (Even allocation),  $m$  will be equivalent to  $M/s$  where  $s$  is the brood size, such that:

$$(4) \quad f(m) = \begin{cases} ([M/s] - 1) / (M/s) & \text{if } M/s > 1 \\ 0 & \text{otherwise} \end{cases}$$

(Fig. 6.2a.).  $J(M)$  thus will be:

$$(5) \quad J(M) = s \left( (M/s - 1) / (M/s) \right).$$

#### Optimal effort and brood size

The optimal level of investment in the current brood,  $M^*$ , and the optimal brood size,  $s^*$ , must be solved iteratively. The simplest method is to solve for the optimal effort at each brood size. The optimal effort for a given brood size

will be that which maximizes  $L(M)$ , the sum of present and future reproductive success:

$$(6) \quad L(M) = J(M) + K(M),$$

Substituting (5) and (1) into (6) gives:

$$(7) \quad L(M) = s((M/s - 1)/(M/s)) + k_{max}(1 - ([M/M_{max}]^N))$$

$M_*$  can be found using standard optimization techniques, i.e., setting  $dL(M)/dM = 0$  and solving for  $M$ , which gives:

$$(8) \quad M_* = [ \{ (M_{max})^N s^2 \} / \{ k_{max} N \} ]^{1/(N+1)}.$$

The optimal brood size,  $s^*$ , thus, will be:

$$(9) \quad s^* = \max_s L(M_*)$$

In sum, for each brood size there is an optimal effort that maximizes  $L(M)$ ,  $M_*$ ; given that for each brood size,  $s$ , parents expend  $M_*$  effort, the optimal brood size will be that which maximizes  $L(M)$  across all brood sizes.

### The offspring's decision

Assuming that parents initially choose  $s^*$  and  $M_*$  so as to maximize  $L(M)$ , the offspring must now decide whether siblicide is favoured. I shall carry out this analysis from the perspective of the senior sib since the degree of parent-offspring conflict is potentially greatest for this

member of the brood (O'Connor 1978). I assume throughout that all offspring are full sibs.

I reiterate here the argument developed in Chapter Four. Consider two sibs (A and B) together in a nest. A is older and larger than B, such that it is possible for A to kill B, but not the reverse. Now consider the fate of a rare mutant allele that causes A to kill B. There is a probability of 0.5 that B also carries the mutant allele. Following Hamilton's rule, siblicide will be favoured when:

$$(10) \quad f(M) > f(M/2) + 0.5 f(M/2)$$

That is A should kill B whenever the benefit it derives from appropriating that quantity of M that B would have had is greater than half the benefit B would derive from the same quantity of M (Hamilton 1964). More generally, siblicide will be favoured when:

$$(11) \quad f(M/(s-1) + 0.5 ((s-2) f(M/[s-1]))) > \\ f(M/s) + 0.5 ((s-1) f(M/s)).$$

(Figure 6.2b illustrates the fitness of the senior sib in broods of one to three in relation to M.) The assumption here is that M is constant. Thus if  $s=2$ , and A kills B, A expects to receive that share of M that B would have received. It is important to note that a senior sib's 'fitness interests' would also include future sibs if its actions affect the future reproductive success of its

Figure 6.2a. Fitness value of current brood to parents at brood sizes of 1, 2 and 3 at different values of  $\underline{M}$  under Even allocation.

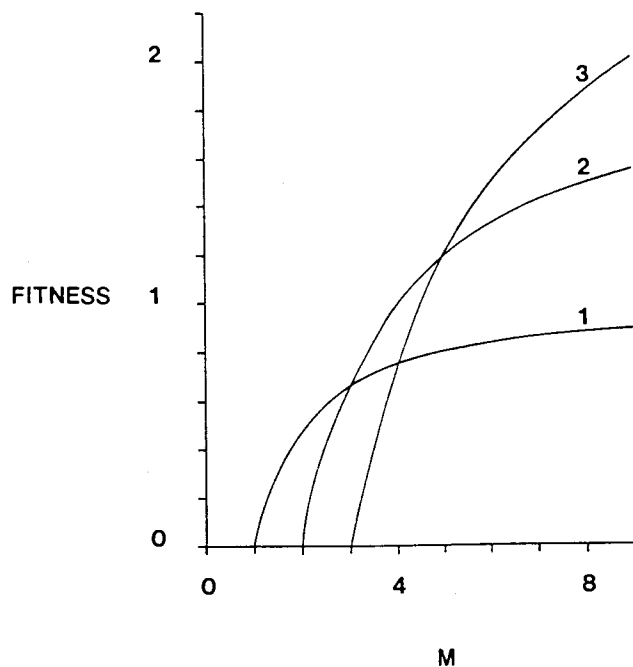
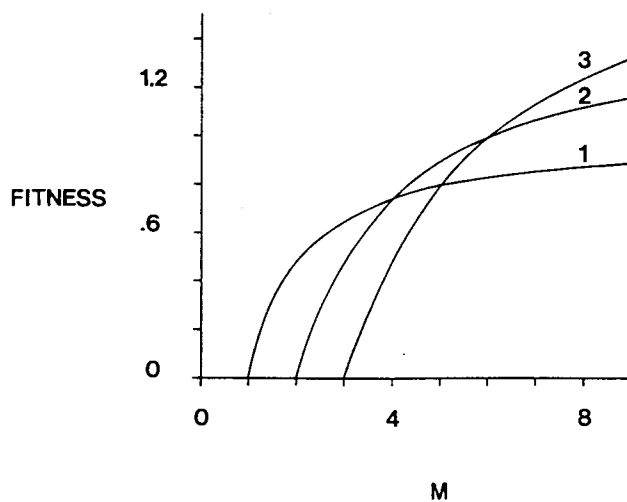


Figure 6.2b. Fitness value of current brood to senior sib at brood sizes of 1, 2 and 3 at different values of  $\underline{M}$  under Even allocation.





parents (i.e., if  $M$  changes). In the next section, I consider whether parents should adjust  $M$  (withhold parental investment) in the face of potential siblicide.

### Parental readjustment of $M$

If at this point siblicide is not favoured the game is terminated: both parents and offspring agree about the size of the current brood. If siblicide occurs, however, then the value of the current brood to the parents declines. The new question of interest from the parent's perspective is what value of  $M$  now maximizes  $L(M)$  given that  $s$  has fallen to  $s-1$ . From (8) it is clear that  $M^*$  will decrease with  $s$ . For the senior sib, this has two effects. Resources available for the current brood diminish, but resources for future sibs effectively increase (indirectly through increased parental survival). Thus siblicide will be favoured if:

$$(12) \quad f(M_{a+t}/(s-1)) + 0.5 ((s-2) f(M_{a+t}/[s-1]) + k(M_{a+t})) > \\ f(M_{b+t}/s) + 0.5 ((s-1) f(M_{b+t}/s) + k(M_{b+t}))$$

where  $M_{b+t}$  and  $M_{a+t}$  are the levels of  $M$  before and after siblicide respectively, and where  $k(M_{b+t})$  and  $k(M_{a+t})$  represent the expected number of future sibs before and after siblicide respectively.

## DESPOTIC ALLOCATION: SELFISH SIBS

In Despotic allocation, as in Even, the parents choose their initial level of investment in the current brood, but here the dominance hierarchy governs resources among the brood members. I assume the existence of a linear dominance hierarchy such that elder sibs are completely dominant to junior sibs, i.e., sib A can take its desired portion of M before sib B; sib B takes its desired portion of the remaining M before sib C receives any M and so on.

Before the value of the present brood to parents can be determined, it is necessary to establish how M will be shared among sibs. In other words, how selfish should senior sibs be? Parker et al. (1989) have dealt with this question at length, and I follow their general argument.

Unlike Even allocation, sibs do not receive equal shares of M, therefore I replace the term  $\underline{M}/\underline{s}$  in equations (4) and (5) with  $\underline{M}p_i$ , where  $p_i$  is the proportion of M sib i receives, such that  $\sum p_i = 1$  and

$$(13) \quad \underline{f}(\underline{m}_i) = \begin{cases} (\underline{M}p_i - 1) / \underline{M}p_i & \text{where } \underline{M}p_i > 1 \\ 0 & \text{otherwise} \end{cases}$$

As before, for a given level of M, the optimal brood size for parents will be that maximizing  $\underline{L}(\underline{M})$  or:

$$(14) \quad \underline{s}^* = \max_s \sum_1^s f(m_i) + K(M)$$

Now how should sibs share  $M$  (i.e., what is  $p_i$ ?)? I begin with the case where  $\underline{s}=2$ . Consider the fate of a rare mutant allele that causes  $A$  to take proportion  $p_A'$  of  $M$ . The replication rate of the mutant allele,  $\underline{\lambda}$ , is thus:

$$(15) \quad \underline{\lambda} = f(M p_A') + 0.5 f((1 - p_A')M).$$

From the perspective of  $A$ , the optimal value  $p^*$  is found by setting  $d\underline{\lambda}/dp$  equal to zero, which gives  $p^*=0.58$  and  $1-p^*$  (the share of  $M$  to  $B$ ) = 0.42 (see Chapter Four).

Knowing now how a brood of two divides  $M$ , one can determine what share of  $M$  sib  $A$  should take in a brood of 3. Given that  $A$ 's share is  $p_A$ , then the total share of  $M$  that sibs  $B$  and  $C$  will receive will be  $1-p_A$ . Therefore the replication rate of the mutant allele will be:

$$(16) \quad \underline{\lambda} = f(M p_A) + 0.5 ( f(M 0.58 [1-p_A]) \\ + f(M 0.42 [1-p_A]) )$$

Once again, using standard optimization techniques we find that  $p_A=0.50$ , therefore the proportion of  $M$  that  $B$  and  $C$  will receive will be  $1-0.50=0.50$ . The share  $B$  receives will be  $0.50 \cdot 0.58=0.29$ , and the remaining share  $C$  receives will be  $0.50 \cdot 0.42 = 0.21$ . Following the same procedures, one can determine the optimal policies of resource allocation

Figure 6.3a. Fitness value of current brood to parents at brood sizes of 1, 2 and 3 at different values of  $M$  under Despotic allocation.

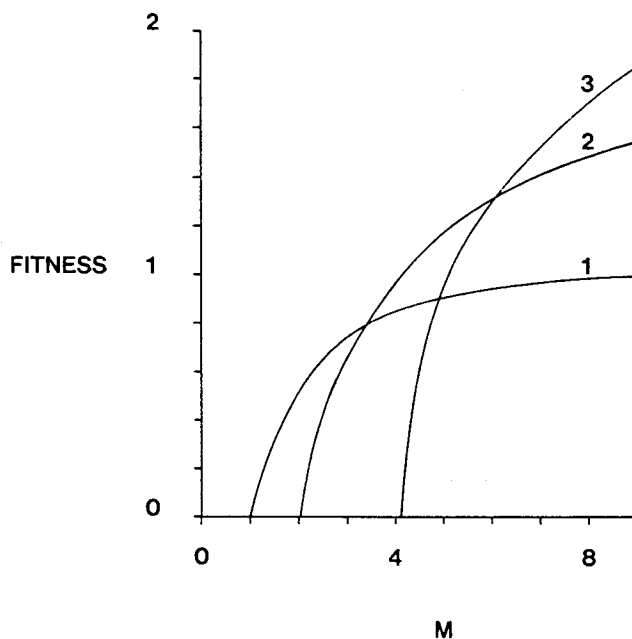


Figure 6.3b. Fitness value of current brood to senior sib at brood sizes of 1, 2 and 3 at different values of  $M$  under Despotic allocation.

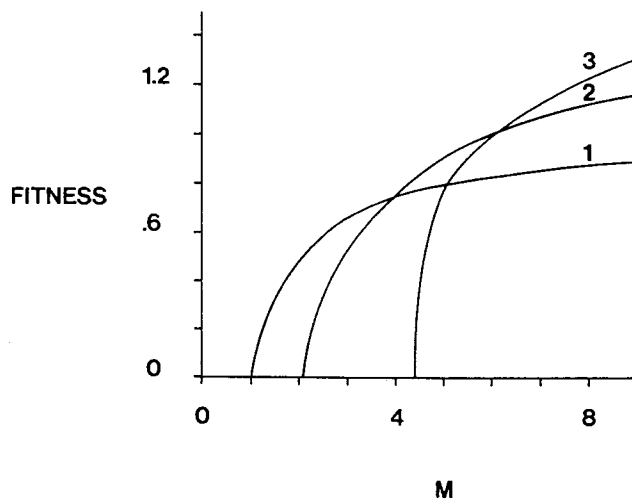


Table 6.2. Optimal proportion of  $M$  ( $p^*$ ) taken by sibs in broods of one to four.  $A$  is the most senior sib,  $D$  is the most junior.

$n$	Sib			
	A	B	C	D
1	1.00	-	-	-
2	0.58	0.42	-	-
3	0.50	0.29	0.21	-
4	0.39	0.31	0.18	0.13

for broods of four (Table 6.2) and, in principle, for larger broods of any size. Figures 6.3a & b illustrate the fitness value of broods of one to three to parents and to senior sibs, respectively, under Despotic allocation.

The steps of the game are the same as in the Even situation. First, parents choose an initial brood size,  $\underline{s}$ , and investment of resource,  $\underline{M}$ , that maximizes lifetime reproductive success. Second, senior sibs evaluate whether, at a given level of  $\underline{M}$ , they will profit by eliminating a junior sib and appropriating that sib's share of  $\underline{M}$ . Third, if siblicide occurs, parents readjust their level of investment in the current brood, usually downward, and fourth, senior sibs determine whether they are now better off than before siblicide occurred. If they are not siblicide is not favoured and parents and offspring 'agree' over the initial brood size. The only difference between the Even and Despotic situations is the allocation of resources among sibs. As a result, in the Despotic situation, not all sibs are equally valuable to parents and senior sibs (see Mock 1987 for a discussion of a related point).

In the analysis of the model, the optimal values of  $\underline{s}$  and  $\underline{M}$  were solved numerically (on a computer) for Despotic allocation.

## MODEL RESULTS AND DISCUSSION

The parameters  $M_{MAX}$ ,  $N$ , and  $k_{MAX}$  were varied broadly in a sensitivity analysis of the model (Figs. 6.4 & 6.5). The biological implications for changes in parameter values are as follows. As  $k_{MAX}$  increases,  $K(M)$  (future reproduction) increases relative to  $J(M)$  (present reproduction). As  $M_{MAX}$  increases, the maximum amount of resources that parents can provide to the current brood increases, making the present brood potentially more valuable. As  $N$  increases, the relationship between  $K(M)$  and  $M$  becomes increasingly concave (Fig. 6.1). That is, at high values of  $N$ , future reproduction is diminished only slightly at low values of  $M$ , but drops sharply at high values of  $M$ .

Several trends were evident in the numerical analysis for both the Even and Despotic simulations. First, lifetime reproductive success,  $L(M)$ , increased with  $M_{MAX}$ , the upper limit on investment in the current brood. Second, brood size,  $\underline{s}$ , tended to increase with  $M_{MAX}$ . Third,  $\underline{s}$  increased as the upper limit on the value of future reproduction,  $k_{MAX}$ , increased. Fourth,  $\underline{s}$  increased with  $N$ , the shape parameter in the function for future reproductive success, and fifth,  $L(M)$  increased with  $N$ .

### Conflict over brood size

Two main results can be derived from the numerical analysis of the model in Figures 6.4 and 6.5. First,

Figure 6.4. Numerical results of the model under Even allocation. The initial optimal brood size for parents (square in upper right hand corner of each cell) is shown for each combination of  $N$  (varied from 1 to 4),  $k_{MAX}$  (varied from 1 to 6), and  $M_{MAX}$  (varied from 7.5 to 15). Shaded cells indicate combinations of parameter values where offspring perform siblicide in opposition to parental interests. Cross-hatched areas indicate combinations where offspring initially favour siblicide but are constrained from doing so by the prospect of parental readjustment. Open cells indicate combinations where parents and offspring initially agree over brood size.

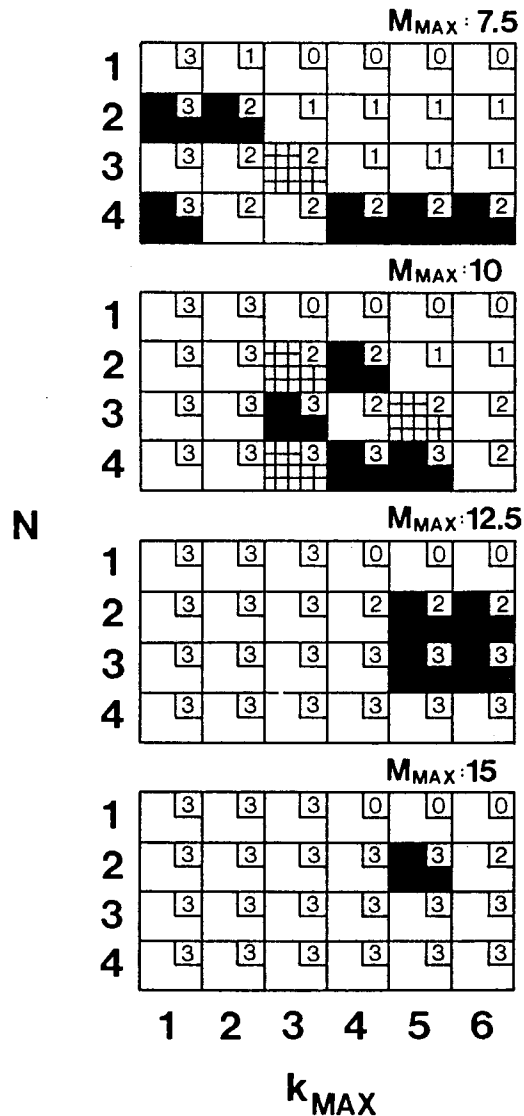
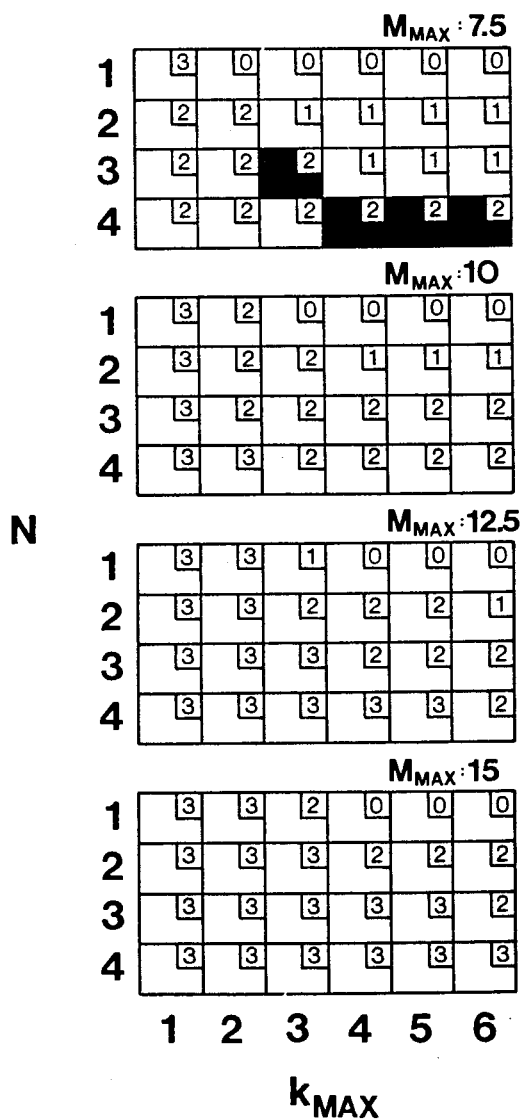




Figure 6.5. Numerical results of the model under Despotic allocation. The initial optimal brood size for parents (square in upper right hand corner of each cell) is shown for each combination of  $N$  (varied from 1 to 4),  $k_{MAX}$  (varied from 1 to 4),  $k_{MAX}$  (varied from 1 to 6), and  $M_{MAX}$  (varied from 7.5 to 15). Shaded cells indicate combinations of parameter values where offspring perform siblicide in opposition to parental interests. Cross-hatched areas indicate combinations where offspring initially favour siblicide but are constrained from doing so by the prospect of parental readjustment. Open cells indicate combinations where parents and offspring initially agree over brood size.



conflict between parents and offspring over brood size is more likely to occur when future sibs are relatively more valuable to parents (i.e.,  $M_{MAX}$  is low and  $K_{MAX}$  is high). The reason for this is straightforward. As future offspring become increasingly valuable, there is a greater tendency for parents to withhold parental investment from the current brood. Senior sibs are therefore more likely to perform siblicide in order to garner a greater share of limited parental resources.

Second, conflict between parents and offspring over brood size is more likely to occur under Even allocation than under Despotic allocation. Once again the reason for this is straightforward. Under Despotic allocation, senior sibs can take a greater share of  $M$  than under Even allocation. Since there are diminishing returns on assimilating further parental investment, senior sibs are less likely to profit from siblicide under Despotic allocation.

O'Connor (1978), in a pioneering paper, established that siblicide should precede parental infanticide, creating parent-offspring conflict over the timing of brood reduction, and specified this should be most evident in small broods. O'Connor did not examine, however, the consequences of a reduction in parental effort. Mock and Parker (1986) developed a simple ESS model examining reproductive decisions of parents within a single breeding season and found that early in a nesting season, parents

with small broods may desert in favour of rearing a larger brood later in the season. Moreover, they suggested that the likelihood of parental desertion may constrain the selfish behaviour of offspring.

A similar logic is followed here, but in a more general case: reproductive opportunities are considered over the parent's lifetime rather than just within a breeding season. The present model also differs from previous models of parent-offspring conflict in another important respect in that it examines the effects of different parental strategies of allocating resources among sibs. Here I show that when parental costs of reproduction are incorporated, the likelihood of phenotypic parent-offspring conflict over brood size diminishes, particularly under Despotic food allocation. Parents ultimately control their allocation of resources between current and future broods and should a senior sib perform siblicide when this is not also in the parent's interests, the current brood becomes less valuable to parents. It follows that parents reduce their investment in the current brood in favour of greater investment in future broods and as a consequence, sib(s) performing siblicide may be worse off than they were initially.

#### Despotic food allocation: causes and consequences

The pattern of food allocation of most siblicidal and many non-siblicidal birds corresponds more closely with the

Despotic situation; resources tend to be skewed toward elder sibs via dominance hierarchies maintained through aggression, or size and or motor-skill advantages (e.g., Safriel 1981, Edwards and Collopy 1983, Greig-Smith 1985, Drummond et al. 1986, Mock 1987, Mock et al. 1987a, this study: Chapter Five).

For parents, Despotic food allocation bears an evolutionary cost. Given that a single phenotypic optimum for offspring exists, differential investment in offspring will result in some or all of the brood receiving too little or too much parental investment, with senior sibs being the main beneficiaries. Why then is Despotic allocation so common? One possibility is that in the face of variation in the environmental yield of resources, parents may benefit from unequal investment in brood members since this enhances the efficiency of adaptive brood reduction (Stamps and Metcalf 1980, Drummond et al. 1986, Mock 1987).

The present model suggests another but not exclusive alternative: a reduction of parent-offspring conflict over brood size. From the parent's perspective, junior sibs are less valuable, i.e., there are diminishing returns for attempting to rear additional offspring, since resources are skewed toward senior sibs. Senior sibs, on the other hand, maintain unrestricted access to parental resources and since there inevitably are diminishing returns on assimilating further parental investment, the gains from eliminating a

Junior sib are small. By allowing the offspring to control resource allocation within a brood, the interests of parents and offspring converge with regard to brood size. It follows that siblicide, when it occurs, is not an example of parent-offspring conflict, but rather a congruency of interests between parents and dominant offspring (Drummond et al. 1986).

#### Costs and benefits of even allocation

For parents in a brood-reducing species, Even food allocation (i.e., synchronous rather than asynchronous offspring) is riskier than Despotic allocation. In years when food is scarce, the fitness of all brood members may be reduced rather than just the most junior sib(s) (Hahn 1981, Fujioka 1985, Magrath 1989). Moreover, the probability of parent-offspring conflict over brood size increases with Even allocation. But the potential benefit for parents of Even allocation, a more efficient use of limited parental resources in producing offspring, is also high. We should therefore expect parents to use Even allocation whenever the risks can be minimized. Species such as coots and grebes which divide their broods (Nuechterlein 1981, Horsfall 1984) may be examples. Brood division reduces interactions among contemporary sibs, and therefore the potential for parent-offspring conflict over brood size, while allowing parents to maintain greater control of resource allocation

among brood members. Brood division is only possible, however, where young can be reared separately, usually requiring offspring mobility. Hence it occurs primarily in precocial or semi-precocial species, or after nestlings have fledged. Where offspring are confined to the vicinity of a nest, and particularly where they possess sufficient weaponry to inflict injury upon one another, parents are much less likely to maintain control over resource allocation among sibs and avoid parent-offspring conflict over brood size.

CHAPTER SEVEN

GENERAL CONCLUSIONS

In proposing the brood reduction hypothesis, David Lack (1947, 1954) recognized the importance of environmental variability. Parents lay a clutch larger than they normally expect to rear and if food is plentiful, all brood members survive. If food is scarce, one or more of the young are eliminated. Parents increasingly 'handicap' successive offspring by establishing competitive asymmetries at hatch, either through hatching asynchrony and/or differences in egg size, such that the last hatched chick is usually the first to succumb to selective starvation or siblicidal aggression or both.

Ospreys conform to this general pattern. At Creston, the typical clutch size is three, and the A and B-chicks hatch close together, often a day or less apart, whereas the C-chick generally hatches 2 or more days after the B-chick. Thus the C-chick is disadvantaged from the outset. The set of decisions concerning brood size for both parents and offspring is actually quite small: if three young hatch, will three, two, one or zero chicks survive to fledge? Clearly, the actions of both parents and offspring affect the outcome.

In Chapters Two and Three of this thesis I documented two sources of environmental variability affecting breeding ospreys: weather and food availability. Both shared the property of being essentially unpredictable, although the time scale involved differed, i.e., weather varied from day



to day, whereas food availability differed between years. Although parents demonstrated an ability to buffer offspring from these sources of environmental variation, inclement weather and low food availability resulted in lower reproductive success (i.e., a higher frequency of brood reduction).

Creation of a brood hierarchy is a prerequisite for a facultative system of brood reduction. But a brood hierarchy can have profound effects on resource allocation among offspring (see Chapter Five); senior sibs may be able to command a disproportionate share of parental resources at the expense of junior sibs. This is important since per capita investment in offspring may affect subsequent survival. On the surface, parents of siblicidal species seem disinterested in resource allocation among offspring. They do not interfere in sibling aggression, nor do they attempt to feed junior sibs preferentially. In Chapter Five I ask how can parents affect resource allocation between offspring? The answer appears to be that, by adjusting the temporal pattern of deliveries and/or the size of prey, parents may be able to direct resources to junior siblings. Such tactics take advantage of an apparent proximate link between hunger and food allocation (when senior sibs are satiated junior sibs are allowed to feed more often). By employing such tactics instead of direct preferential

feeding, parents diminish phenotypic conflict with the senior sibs over resource allocation and brood size.

I have assumed throughout that reproduction bears a cost for parents, and that some trade-off between present and future reproduction governs the allocation of effort between the two. Most models of optimal life-history are based on the concept of reproductive effort (Williams 1966a,b, Goodman 1974, Schaffer 1974, Gadgil and Bossert 1975, Ricklefs 1977, Schaffer 1979), such that increasing effort in one year diminishes that available in later years. But operational definitions of effort are elusive. What is reproductive effort in ospreys and how do we measure it? Is it the energy expended on a foraging trip, the risk of injury or predation, wear and tear on the individual, or something else? At some point, effort must be defined in relation to survival and reproductive success. For now, any definition of reproductive effort for ospreys is speculative.

Foraging is risky for ospreys as they are sometimes injured or killed. At Creston I recovered an adult female with a wing broken apparently when diving into a pool in a small stream. Ospreys may even be killed by eagles when diving for prey (LaFontaine and Fowler 1976). Hunting can be energetically expensive; hovering, a primary foraging mode of ospreys is very costly (about 12 BMR), and there may be daily limits to this activity (Drent and Daan 1980).

Foraging inevitably results in plumage wear, perhaps decreasing flight performance, and high levels of foraging activity might result in decreased physiological condition of the individual, perhaps depressing adult survival, particularly on the post-breeding migration (Poole 1989). Interestingly, Poole (1989) noted that the mass of both male and female ospreys with artificially enlarged broods declined rapidly (males worked harder to provision the brood and females ate less food).

#### Optimal clutch size and the feeding hierarchy

The chick feeding hierarchy presents an interesting and little explored facet of parental decisions regarding clutch size, since the effects of short-falls in parental provisioning are shared unequally among siblings. A simple example will help here. Imagine a brood of five chicks which are fed according to an absolute dominance hierarchy. If a chick feeds during the day (it eats a maximum of one prey item) it lives; if not, it dies. Now assume that the maximum number of hunts parents can make in a day,  $n$ , is fixed, and that hunt success varies randomly. For any mean rate of hunt success, there will be a probability distribution for the number of prey deliveries during a day from 0 to  $n$ . In Table 7.1 I outline a simple example. (The details of the model are less important than the overall pattern.) As the mean rate of hunt success declines, the

probability that the Junior-most (sib E) chicks survive declines sharply. As well, as the brood size approaches the maximum number of hunts during the day, the probability that sib E survives also declines sharply. In effect, there are strongly diminishing returns for creating additional chicks when foraging success varies stochastically, even when the average rate of provisioning is sufficient to rear all chicks (in the example in Table 7.1 this would correspond to  $P=0.5$ , or 5 prey items per day). Recall that I am considering survival only over a single day. Over the entire span of the nestling period, the probability that sib E survives becomes vanishingly small. For example, at  $P=0.5$  the probability of daily survival for sib E is 62.3% (Table 7.1), whereas the probability of sib E surviving 10 days is less than 1% (the corresponding probability of survival for sib A for 10 days is greater than 99%).

If there is no cost to creating and provisioning offspring, then the probability of offspring survival is irrelevant: parents should create a brood of the maximum size possible on the small chance that all young will survive. However, if there is any fitness cost for producing offspring, the probability of offspring survival becomes an important consideration. And from the simple model outlined above, it is clear that costs will soon exceed benefits as brood size increases.

Table 7.1. A simple binomial model of chick survival. A brood of five chicks begins the day. The chicks are fed sequentially according to a dominance hierarchy A first, B second and so on. If a chick feeds during the day, it survives - if not it dies. A day consists of  $n$  discrete periods of length  $t$  (for an osprey,  $t$  might correspond to the minimum amount of time required for a complete hunt) and prey are delivered to the nest according to a stochastic process. The probability that a prey item is captured and delivered to the brood during any  $t$ , is  $P$ . I assume that a maximum of one prey item is delivered during any one  $t$ , that all prey are the same size, and that one prey item is eaten by one chick. Now by specifying  $n$  ( $n=10$ ) and  $P$  (0.1 to 0.5) I can calculate the probability of  $B$  ( $= 0$  to 5) chicks surviving a given day,  $Pr(B|n,P)$ , using the binomial expansion. At  $P=0.5$ , the probability of a brood of five surviving (i.e., the probability of five or more prey items being returned to the nest during the day) is 62.3% whereas at  $P=0.1$  it is 0.01%.

---

Number of chicks, $B$	Probability of $B$ chicks surviving day				
	Mean rate of hunt success, $P$				
	0.1	0.2	0.3	0.4	0.5
0	0.349	0.107	0.028	0.006	0.001
1	0.387	0.268	0.121	0.040	0.010
2	0.194	0.302	0.234	0.121	0.044
3	0.057	0.201	0.267	0.215	0.117
4	0.011	0.088	0.200	0.251	0.205
5	0.001	0.032	0.150	0.367	0.623

---

I suggest that this simple model may apply to ospreys. In this thesis I have shown that environmental variability, particularly that related to weather, is an important determinant of the reproductive success of ospreys. Weather affects both male foraging performance (Grubb 1977, Machmer and Ydenberg 1989), and the metabolic state of the offspring. For offspring to survive to fledging age and maintain a reasonable expectation of survival thereafter, nestlings require a regular supply of food. Chicks starved for periods perhaps as short as one or two days early in the nestling period will probably die. Under ideal weather conditions, a single male might be able to gather sufficient food for broods much larger than three chicks. However, as weather conditions deteriorate, male foraging success declines and the food needs of chicks may increase. It follows that it will be increasingly difficult for males to maintain sufficient provisioning of the entire brood. And since during periods of inclement weather the female must attend the brood closely, she is unable to assist the male with foraging duties. As the rate of food delivery declines relative to chick needs (it need not decline in an absolute sense), we would expect senior chicks to monopolize food increasingly. Thus under ideal conditions, a male osprey might be able to provision a brood of perhaps six or seven chicks. But, because of the feeding hierarchy, the junior-most sibs in this hypothetical brood would be

unlikely to survive to fledging age. And if resources that junior sibs receive, which from the parent's perspective are unlikely to pay reproductive dividends, might otherwise have gone to more senior sibs, and enhanced their survival, then there is an opportunity cost to creating these marginal offspring. As well, senior sibs which kill junior sibs may expend energy and risk injury in doing so (Gargett 1978, Mock 1984a, Gerrard and Bortolotti 1988: 82-83).

Moreover, peak food demands for the brood do not occur until well into the nestling period (4-6 weeks). Presumably it would be at this time that the male osprey would experience the greatest difficulty in maintaining regular food deliveries to a large brood. Thus, by the time a 'crunch' is likely to occur, a male with a brood of five will already have made a substantial investment in chicks D and E, an investment unlikely to reap reproductive dividends. Thus appearances may be deceiving. Ospreys males often remain inactive for much of the day, giving the impression that they could easily forage longer and rear a larger brood. Such male inactivity may simply represent a foraging schedule designed to accommodate peak food requirements of offspring and stochastic availability of food (Sutherland and Moss 1985).

## SOME ISSUES IN OSPREY MANAGEMENT

Our experience at Creston has taught us that fish management is an integral component of osprey management. Ospreys require a stable and accessible supply of food for successful breeding. For marsh managers, this involves creating conditions conducive for fish spawning and survival. Here avoidance of both winter and summer fish-kills is important. Summer-kills occur when marsh waters become anoxic, an effect most pronounced in areas with aquatic emergents. Maintaining areas of open, deep water provides refuge (e.g., deep channels beside dykes) for fish avoiding anoxic conditions and thus will enhance survival. Winter-kill occurs under thick ice cover and is also a function of anoxia; the presence of deep water may minimize its impact.

Stable water levels are the primary determinant of fish spawning success. Most fish spawn in spring and early summer although the chronology for individual species may vary considerably. At Creston, three of the four primary marsh fish (black bullhead, pumpkinseed, largemouth bass) spawn between mid-May and the beginning of July; rapid increases or decreases in water levels at this time will result in fluctuating oxygen and thermal conditions, and may expose nests built in shallow water. All will result in diminished spawning success. As well, rapid temperature changes (as might occur when filling a marsh with water from



a cooler source) may result in year-class failure of larval fish. Marsh managers should be cognizant of such effects when adjusting spring water levels in impoundments.

Marsh draw-downs are a necessary element of marsh management, but as my experience at Corn Creek Marsh indicates, have drastic effects on fish survival. There are techniques to cushion the negative impacts, however. Fish do not do well when they pass through mechanical pumps; thus when possible, using gravity to move water through culverts is the best option, for transferring fish from one body of water to another. As well, when draining an impoundment, it is useful if fish from that site can be deposited in an adjacent impoundment for future recolonization. For example, at Creston some marshes are drained directly into the Kootenay River. Those marsh fish transferred out of the impoundment are effectively lost for the purposes of future recolonization. Moreover, when the marsh is refilled, also from the Kootenay River, few fish enter the marsh, and are generally species less suitable (various cyprinids and salmonids) than the dominant marsh fish (however this strategy takes advantage of fluctuations in the level of the Kootenay River to drain and flood a marsh without having to pump water). Recolonization of a marsh following a drawdown is facilitated if marsh fish are available in an adjacent impoundment. Returning a stock of adult fish to a marsh following a drawdown will accelerate recolonization by fish;

if few fish enter an impoundment when it is being filled (e.g., if it is being filled using mechanical pumps), managers might consider seining fish from nearby impoundments and depositing them in the refilled marsh.

Conversely, managers may want to prevent fish (and hence discourage ospreys from breeding) from colonizing a marsh since fish may compete with waterfowl for invertebrate forage. One can take measures to do so by enhancing water level fluctuations over the course of the year (e.g., allowing marshes to dry over winter).

### Nestling Transfers

Nestling transfers are a frequently used management tool for re-introducing birds where local populations have been extirpated. Our experience with ospreys, and more generally, the experience of researchers studying brood-reducing species, provides information potentially valuable for managers. Perhaps most importantly, many chicks are essentially surplus to the parent's needs. In ospreys at Creston, only a small proportion (about 20%) of broods fledged three chicks even though nearly all ospreys laid clutches of three eggs. The last hatched chick seems to serve primarily as insurance against the accidental failure of an egg or small chick, or as 'insurance' against years of abundant food. From a population standpoint, the removal of one of the chicks has little impact upon

reproductive success. In nearly all brood-reducing species, it is the last-hatched chick that is most likely to die; however, removal experiments have shown that when any of the brood members is removed early in the nestling period, survival of the last hatched chick increases dramatically. Thus, it makes little difference for subsequent success of the donor brood which chick is selected for removal; if the A-chick (senior sib) is removed from a brood of three, we would expect the B and C chicks to survive as well as the A and B chicks in the original brood. Since the elder A-chick is likely to be larger and more vigorous at the time of removal, it makes the best candidate for the inevitable stress of handling during transfer.

## LITERATURE CITED

- ASKENMO, C. and U. UNGER. 1986. How to be double-brooded: trends and timing of breeding performance in the Rock Pipit. *Ornis Scand.* 17: 237-244.
- BALFOUR, E. 1957. Observations on the breeding biology of the hen harrier in Orkney. *Bird Notes* 27: 177-183, 216-224.
- BIRKHEAD, T. R. and D. N. NETTLESHIP. 1982. The adaptive significance of egg-size and laying date in thick-billed murrees (*Uria lomvia*). *Ecology* 63: 300-306.
- BISHOP, Y. M. M., S. E. FIENBERG and P. W. HOLLAND. 1975. *Discrete multivariate analysis: Theory and practice*. MIT Press, Cambridge, Mass.
- BORTOLOTTI, G. R. 1989. Factors influencing the growth of bald eagles in north central Saskatchewan. *Can. J. Zool.* 67: 606-611.
- BUTLER, R. W., B. G. STUSHNOFF, and E. McMACKIN. 1986. *The birds of the Creston Valley and southeastern British Columbia*. Can. Wild. Serv. Occ. Pap. No. 58.
- CARLANDER, K. D. 1977. *Handbook of freshwater fishery biology*. Vol. 2. Iowa State University Press, Ames, Iowa.
- CASH, K. J. and R. M. EVANS. 1986. Brood reduction in the American white pelican. *Behav. Ecol. Sociobiol.* 18: 413-418.

- CHARNOV, E. and J. KREBS. 1974. On clutch size and fitness. *Ibis* 116: 217-219.
- CLARK, C. W. and R. C. YDENBERG. In press. The risks of parenthood. I. General theory and applications. *Evol. Ecol.*
- DIJKSTRA, C. 1988. Reproductive tactics in the Kestrel, Falco tinnunculus: a study in evolutionary biology. Ph.D Thesis, Univ. of Groningen, Groningen, The Netherlands.
- DRENT, R. H. and S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- DRUMMOND, H. 1989. Parent-offspring conflict and brood reduction in boobies. *Proc. XIX Int. Ornithol. Congr.*
- DRUMMOND, H., E. GONZALEZ, and J. OSORNO. 1986. Parent-offspring cooperation in the blue-footed booby (Sula nebouxi): social roles in infanticidal brood reduction. *Behav. Ecol. Sociobiol.* 19: 365-372.
- EDWARDS, T. and M. COLLOPY. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100: 630-635.
- FIENBERG, S. E. 1970. The analysis of multidimensional contingency tables. *Ecology* 51: 419-433.

- FLOOK, D. R. and L. S. FORBES. 1983. Ospreys and water management at Creston, British Columbia. pp. 281-286, In: D. M. Bird (chief ed.), Biology and Management of Bald Eagles and Ospreys, Harpell Press, Ste. Anne de Bellevue, Quebec.
- FUJIOKA, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. Behav. Ecol. Sociobiol. 17: 67-74.
- GADGIL, M. and W. H. BOSSERT. 1970. Life historical consequences of natural selection. Am. Nat. 104: 1-24.
- GARGETT, V. 1978. Sibling aggression in the black eagle in the Matopos, Rhodesia. Ostrich 49: 57-63.
- GERRARD, J. M. and G. R. BORTOLOTTI. 1988. The bald eagle. Smithsonian Inst. Press, Washington, D.C.
- GILLESPIE, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. Amer. Nat. 111: 1010-1014.
- GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. Amer. Nat. 108: 247-268.
- GREIG-SMITH, P. 1985. Weight differences, brood reduction, and sibling competition among nestling Stonechats Saxicola torquata (Aves: Turdidae). J. Zool. 205: 453-465.
- GRUBB, T. G., Jr. 1977. Weather-dependent foraging in ospreys. Auk 94: 146-149.

- GUSTAFFSON, L. and W. J. SUTHERLAND. 1988. The costs of reproduction in the collared flycatcher Ficedula albicollis. Nature 335: 813-815.
- HAGAN, J. M. 1986. Temporal patterns in pre-fledging survival and brood reduction in an osprey colony. Condor 88: 200-205.
- HAHN, D. C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. Anim. Behav. 29: 421-427.
- HAMILTON, W. D. 1964. The genetical evolution of social behaviour. I. J. Theoret. Biol. 7: 1-16.
- HARTWICK, E. B. 1976. Foraging strategy of the black oystercatcher (Haemoptopus bachmani Audubon). Can. J. Zool. 54: 142-155.
- HENNY, C. J. 1988. Osprey. pp. 73-101 In: R. S. Palmer (ed.), Handbook of North American Birds, Vol. 4, Yale Univ. Press, New Haven, Connecticut.
- HORSFALL, J. 1984. Brood reduction and brood division in coots. Anim. Behav. 32: 216-225.
- JAMIESON, I., N. SEYMOUR and R. P. BANCROFT. 1982. Time and activity budgets of Ospreys nesting in northeastern Nova Scotia. Condor 84: 439-441.
- LACK, D. 1947. The significance of clutch size. Ibis 89: 302-352.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford.

- LA FONTAINE, A. R. and J. H. FOWLER. 1976. Golden eagle preys on osprey. *Auk* 93: 390.
- LEVENSON, H. 1979. Time and activity budget of Ospreys nesting in northern California. *Condor* 81: 364-369.
- MACHMER, M. and R. C. YDENBERG. 1989. Weather and osprey foraging energetics. *Canadian Journal of Zoology*.
- MACNAIR, M. and G. A. PARKER. 1978. Models of parent-offspring conflict. II. Promiscuity. *Anim. Behav.* 26: 111-122.
- MACNAIR, M. and G. A. PARKER. 1979. Models of parent-offspring conflict. III. Intrabrood conflict. *Anim. Behav.* 27: 1202-1209.
- MACNAMARA, M. 1977. Sexing the American Osprey using secondary sexual characteristics. pp. 43-45, In: J. C. Ogden (ed.), *Trans. N. Amer. Osprey Res. Conf, U.S. Natl. Park Serv., Trans. Proc. Ser. No. 2, Washington, D.C.*
- MAGRATH, R. D. 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature* 339: 536-538.
- MANGEL, M. and C. W. CLARK. 1988. *Dynamic modelling in behavioral ecology.* Princeton Univ. Press, Princeton, NJ.
- MEARNS, R. and I. NEWTON. 1988. Factors affecting breeding success of peregrines in south Scotland. *J. Anim. Ecol.* 57: 903-916.
- MELQUIST, W. E. and D. R. JOHNSON. 1984. Additional comments on the migration of northern Idaho and eastern Washington ospreys. *J. Field. Ornithol.* 55: 483-485.



- MELQUIST, W. E., D. R. JOHNSON and W. D. CARRIER. 1978.  
Migration patterns of northern Idaho and eastern  
Washington ospreys. *Bird-banding* 49: 234-236.
- MOCK, D. W. 1984a. Infanticide, siblicide, and avian  
nestling mortality. Pp. 3-30 In: G. Hausfater and S. B.  
Hrdy (eds.), *Infanticide: comparative and evolutionary  
perspectives*. Aldine Pub. Co., New York.
- MOCK, D. W. 1984b. Siblicidal aggression and resource  
monopolization in birds. *Science* 225: 731-733.
- MOCK, D. W. 1987. Siblicide, parent-offspring conflict, and  
unequal parental investment by egrets and herons. *Behav.  
Ecol. Sociobiol.* 20: 247-256.
- MOCK, D. W., T. C. LAMEY, and B. J. PLOGER. 1987a. Proximate  
and ultimate roles of food amount in regulating egret  
sibling aggression. *Ecology* 68: 1760-1772.
- MOCK, D., T. LAMEY, C. WILLIAMS, and A. PELLETIER. 1987b.  
Flexibility in the development of heron sibling  
aggression: an intraspecific test of the prey-size  
hypothesis. *Anim. Behav.* 35: 1386-1393.
- MOCK, D. and G. A. PARKER. 1986. Advantages and  
disadvantages of egret and heron brood reduction.  
*Evolution* 40: 459-470.
- MOSS, D. 1979. Growth of nestling sparrowhawks (*Accipiter  
nisus*). *J. Zool., Lond.* 187: 297-314.
- NUECHTERLEIN, G. 1981. Asynchronous hatching and sibling  
competition in western grebes. *Can. J. Zool.* 59: 994-998.

- O'CONNOR, R. J. 1978. Brood reduction in birds: selection for infanticide, fratricide, and suicide? *Anim. Behav.* 26: 79-96.
- ODSJO, T. and J. SONDELL. 1976. Reproductive success in ospreys Pandion halliaetus in southern and central Sweden, 1971-1973. *Ornis Scand.* 7: 71-84.
- PARKER, G. A. 1985. Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. *Anim. Behav.* 33: 519-533.
- PARKER, G. A. and M. MACNAIR. 1978. Models of parent-offspring conflict. I. Monogamy. *Anim. Behav.* 26: 97-110.
- PARKER, G. A. and M. MACNAIR. 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim. Behav.* 27: 1210-1235.
- PARKER, G. A., D. W. MOCK, and T. C. LAMEY. 1989. How selfish should senior sibs be? *Amer. Nat.* 133: 846-868.
- PERRINS, C. M. 1963. Survival in the great tit Parus major. Proceedings of the International Ornithological Congress XIII: 717-728.
- PERRINS, C. M. 1970. The timing of birds' seasons. *Ibis* 112: 242-255.
- PLOGER, B. J. and D. W. MOCK. 1986. Role of sibling aggression in distribution of food to nestling cattle egrets (Bubulcus ibis). *Auk* 103: 768-776.
- POOLE, A. 1979. Sibling aggression among nestling ospreys in Florida Bay. *Auk* 96: 415-417.

- POOLE, A. F. 1989. Ospreys. Cambridge Univ. Press, NY.
- POSTUPALSKY, S. 1977. A critical review of problems in calculating osprey reproductive success. pp.1-11, In J. C. Ogden (ed.), Transactions of the North American Osprey Research Conference. U.S. Natl. Park Serv. Trans. Proc., Series 2, Williamsburg, Virginia.
- REESE, J. G. 1977. Reproductive success of ospreys in central Chesapeake Bay. Auk 94: 202-221.
- REID, W. V. 1987. The cost of reproduction in the glaucous-winged gull. Oecologia 74:458-467
- RICKLEFS, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. Am. Nat. 111: 453-478.
- RØSKAFT, E. and T. SLAGSVOLD. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. J. Anim. Ecol. 54: 261-266.
- SAFRIEL, U. 1981. Social hierarchy among siblings in broods of the oystercatcher Haematopus ostralegus. Behav. Ecol. Sociobiol. 9: 59-63.
- SARGENT, C. and M. R. GROSS. 1986. Williams' principle: an explanation of parental care in teleost fishes. pp. 275-293, In: The Behavior of Teleost Fishes, T. J. Pitcher (ed.), Croom Helm, London.
- SCHAFFER, W. M. 1974. Selection for optimal life-histories: the effects of age-structure. Ecology 55: 291-303.

- SCHAFFER, W. M. 1979. Equivalence of maximizing reproductive value and fitness in the case of reproductive strategies. *Proc. Nat. Acad. Sci.* 76: 3567-3569.
- SCOTT, W. B. and E. J. CROSSMAN. 1973. *Freshwater fishes of Canada.* Fish. Res. Bd. Canada, Bull. No. 184.
- SPITZER, P. R. 1978. Osprey egg and nestling transfers: their value as ecological experiments and as management procedures. Pp. 171-182 In: S. A. Temple (ed.), *Endangered Birds: Management Techniques for Preserving Threatened Species.* Univ. Wisconsin Press, Madison.
- STALMASTER, M. V. and J. A. GESSAMAN. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. *Ecol. Monogr.* 54: 407-428.
- STAMPS J. and R. METCALF. 1980. Parent-offspring conflict. In: Barlow, G. and J. Silverberg (eds) *Sociobiology: Beyond nature-nurture?* Westview Press, Boulder, CO, pp. 598-618.
- STAMPS J., R. METCALF and V. KRISHNAN. 1978. A genetic analysis of parent-offspring conflict. *Behav. Ecol. Sociobiol.* 3: 367-392.
- STEEGER, C. 1989. Proximate and ultimate aspects of seasonal variation in reproductive performance of ospreys. M.Sc. Thesis, Simon Fraser University, Burnaby, B.C.
- STEPHENS, D. W. and J. R. KREBS. 1986. *Foraging theory.* Princeton Univ. Press, Princeton, NJ.

- STINSON, C. 1978. The influence of environmental conditions on aspects of the time budgets of breeding Ospreys. *Oecologia* 36: 127-139.
- STINSON, C. H. 1979. On the selective advantage of fratricide in raptors. *Evolution* 33: 1219-1225.
- STINSON, C. H., J. LAUTHNER and R. T. RAY. 1987. The effect of weather conditions on the behavior of ospreys in northwestern Washington. *Can. J. Zool.* 65: 2116-2118.
- SUTHERLAND, W. J. and D. MOSS. 1985. The inactivity of animals: influence of stochasticity and prey size. *Behaviour* 92: 1-8.
- TRIVERS, R. 1974. Parent-offspring conflict. *Am. Zool.* 14: 249-264.
- WATT, B. K. and A. L. MERRILL. 1975. Composition of foods. *Ag. Handbook No. 8, USDA, Washington, D.C.*
- WILLIAMS, G. C. 1966a. *Adaptation and natural selection.* Princeton Univ Press, Princeton, NJ.
- WILLIAMS, G. C. 1966b. Natural selection, costs of reproduction and a refinement of Lack's principle. *Amer. Nat.* 100: 687-690.
- WINKLER, D. W. and K. WALLIN 1987. Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* 129: 708-720
- WYDOSKI, R. S. and R. R. WHITNEY. 1979. *Inland fishes of Washington.* Univ. of Washington Press, Seattle, WA.