AN EM
ADAPTI
REDUC

i

AN EMPIRICAL AND THEORETICAL INVESTIGATION INTO THE ADAPTIVE SIGNIFICANCE OF HATCHING ASYNCHRONY AND BROOD REDUCTION IN THE TREE SWALLOW (_TACHYCINETA BICOLOR_)

By

Bryan Christopher Pijanowski

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1991

ABSTRACT

AN EMPIRICAL AND THEORETICAL INVESTIGATION INTO THE ADAPTIVE SIGNIFICANCE OF HATCHING ASYNCHRONY AND BROOD REDUCTION IN THE TREE SWALLOW (*TACHYCINETA BICOLOR*)

By

Bryan Christopher Pijanowski

This thesis investigates whether the brood reduction hypothesis can adequately explain the adaptive significance of hatching asynchrony in the tree swallow (*Tachycineta bicolor*). The first chapter discusses the major hypotheses proposed to explain the adaptive significance of hatching asynchrony in altricial birds. The second chapter presents the results of a four-year experimental study conducted in the Upper Peninsula of Michigan on the tree swallow. I established synchronous hatching and two degrees of asynchronous hatching (one of which is the most common in the population) in five nestling broods. Four levels of the brood reduction hypothesis were confirmed in tree swallows. First, several conditions favor brood

reductic
reduced
tive tac
Fourth,
that I p
chrony c
time com
My fie
food was
producti
ments tha
hatching.
The third
asynchron
with asyn
unpredict
condition
offspring
using dat
The fir
chapter.
parents b
bution of
most freq
favors an
the degree

reduction. Second, mechanisms allowing a brood to be reduced were evident. Third, survival-promoting reproductive tactics were employed prior to brood reduction. Fourth, data were consistent with four adaptive scenarios that I propose for how brood reduction and hatching asynchrony can yield the most offspring in a parent's lifetime compared synchronous hatching.

My field experiments also showed, however, that, when food was more plentiful, synchronous hatching was the most productive brood. This result, common among field experiments that have adjusted broods to simulate synchronous hatching, is viewed as maladaptive by some researchers. The third chapter presents a model showing how hatching asynchrony can be adaptive if there are costs associated with asynchronous hatching when parents breed during unpredictably good and bad food years. I discuss the conditions for which asynchronous hatching produces more offspring than synchronous hatching. I test this model using data from the second chapter.

The final chapter expands upon the model of the third chapter. I show, using computer simulations that, if parents breed in an environment where a continuous distribution of food years occur with moderate food years the most frequent, then in most cases, natural selection favors an adjustment in brood size over an adjustment in the degree of asynchronous hatching. I also use this model to show

or degre

hatching

producti

to show how adult mortality, as a function of brood size or degree of asynchronous hatching, can select for the hatching condition and brood size that yields the most productive brood in a parent's lifetime.

FOR MY PARENTS AND MY WIFE

I wou
committe
and Dona
ance. I
tutelage
He always
I came t
wisdom he
school.
ral hist
Drs. Get
respectf
versions
Their gu
scientis

I woul
the Biol
support a
Andrea Pe
much conf
Their cor

This d

ACKNOWLEDGEMENTS

I would first like to thank the members of my doctoral committee, Drs. Donald Beaver, Donald Hall, Thomas Getty, and Donald Straney for their continued patience and guidance. I was extremely fortunate to have been under the tutelage of Dr. Donald Beaver, the chair of my committee. He always knew what to say to relieve my frustrations when I came to a mental block. His good humor, patience and wisdom helped me to survive the pressures of graduate school. I know of no better scholar and teacher of natural history. He was an excellent role model.
Drs. Getty, Hall and Straney treated me politely and respectfully even after having been asked to read endless versions of model manuscripts and research proposals. Their guidance on these tasks has made me a much better scientist.

I would also like to thank all the people involved in the Biological Science Department for their continued support and guidance. I would especially like to thank Andrea Pesce, Nancy Dykema and Jan Asmann for placing so much confidence in my teaching and leadership abilities. Their confidence in me gave me confidence.

This degree would also not be possible without the

support
from Ker
skas.

The f
to keep
Rogers,
read ear
questions
and prese

For s
Palluccn
also ver
ski, hel
provided
very mis

The f
Bruce, M
hele But
valued.

Last,
gratitud
tinued s
challeng
thought
tioned

support during this last year from The Museum, especially from Ken Dewhurst, Chris Carmichael and Laura Abraczinskas.

The following fellow graduate students also helped me to keep my sanity during my tenure here: Terry Trier, Beth Rogers, Rob Morell, and Pat Lederle. Karen and Dan Cebra read earlier versions of Chapter 3 and asked difficult questions that helped me to improve modeling techniques and presentation.

For support in the field, I would like to thank Ron Palluconi, for his good humor and valued friendship. I am also very proud to boast that my father, Robert Pijanowski, helped during the last year of my field research. He provided me with much comfort and assistance during the very miserable and trying 1989 field season.

The friendship, good times and good conversation with Bruce, Mary and Keith Johnston, Nadine Wojtowicz, Michele Butterly and Jahan Eftekar are deeply cherished and valued.

Last, and of course not the least, I owe the world of gratitude to my wife, Dawn, for her love, patience, continued support and hard work, especially during these challenging last few years of my doctoral work. She always thought that my endeavors were "worldly" and never questioned why I would spend so many hours behind a computer

or livi

I wou

ported f

Sigma-X

Wallace

acknowle

System E

Tasks 5.

or living out of tents for several weeks at a time.

I would like to acknowledge that my research was supported from funds from the Department of Zoology, a Sigma-Xi Research-in-Aid Grant, and the George and Martha Wallace Endowed Scholarship Award. I would also like to acknowledge logistical support from the ELF Communications System Ecological Monitoring Program, Small Vertebrates: Tasks 5.6 and 5.12A, subcontract No. E06595-88-006.

TABLE OF CONTENTS

IV.

CHAPTER

I. I

II. T

III. R

VOLUME II

CHAPTER 3: A REVISION OF LACK'S BROOD REDUCTION HYPOTHESIS USING A GAME THEORY MODEL

CHAPTER 4: A MATHEMATICAL MODEL FOR HATCHING ASYNCHRONY AND BROOD REDUCTION

Table

Table

Table 2

Table 3A

Table 3B

Table 4.

Table 5.

Table 6.

Table 7.

LIST OF TABLES

Table

Table 9

Table 1

Table 1

LIST OF FIGURES

FI

FI

FIG

FIGU

FIGUR

FIGURE

FIGURE

FIGURE 3

FIGURE 3

FIGURE 3

FIGURE 3

FIGURE

FIGURE

FIGURE

FIGURE

FIGURE

Figure

Figure

Figure 5

F

Fi

Fig

fi
a
b
t
c
a
n
na
e
sy

res
bir
Cla
occ
ab

CHAPTER 1

INTRODUCTION TO CONCEPTS

I. DEFINITION AND POSSIBLE CAUSES OF HATCHING ASYNCHRONY

Asynchronous hatching of a clutch of eggs was rst noticed by Dunlop (1913, in Magrath 1990) as an ian reproductive pattern. He observed that in some rds, many eggs of a clutch do not hatch at the same me. Rather, a group of eggs hatch together, and e or more eggs hatch later. The obvious result of ynchronous hatching is that broods are created where stlings differ in their ages and weights. The alter- tive hatching form is synchronous hatching, where gs of a clutch hatch on same day. All nestlings in nchronous broods are the same ages.

Lack suggested that asynchronous hatching is a sult of the timing of incubation initiation. Most rds lay one egg per day (Lack 1947, 1948; Klomp 1970; ark and Wilson 1981) with the development of eggs curring once incubation raises the egg temperatures ove 25^{o} C (see Magrath 1990). If incubation

commen
those e
er. Si
tion (
those

chrony
little
1990)
geste
incub
eggs
and h
mecha
the c
obser
this
hatchi
day).
differe
asynchro

La
result o
each eg
develop
mechanis

commences before the completion of egg laying, then those eggs present when incubation begins hatch together. Since each egg requires the same amount of incubation (Drent 1975), eggs laid later will hatch after those eggs present at the start of incubation.

Alternative explanations for how hatching asynchrony is created do exist, although they have received little experimental or observational attention (Magrath 1990). Some researchers (see Magrath 1990) have suggested that asynchronous hatching results from unequal incubation temperatures applied to the clutch. Those eggs incubated at higher temperatures develop quicker and hatch earlier. Yet, it is unlikely that this mechanism could produce eggs of a clutch hatching in the order that they were laid as has been commonly observed. In addition, it is also difficult to see how this mechanism could produce complete asynchronous hatching (each egg of a clutch hatching on a different day). Incubation temperatures would have to be very different between eggs to produce complete hatching asynchrony.

Lastly, asynchronous hatching could also be the result of genetic differences in development rates for each egg of a clutch (James Asher, pers. comm.). Eggs developing faster than others will hatch first. This mechanism would be difficult to differentiate in the field

Lack (

time c

mechan

ing se

deranc

notice

handf

forme

the e

(Lack

async

all n

(1981

ines

rather

Their

include

es async

avian c

viewed a

the exce

field than the incubation initiation theory proposed by Lack (1947) because genetic differences in development time could correlate with egg laying sequence. Both mechanisms, thus, could give the same result of hatching sequence matching the laying sequence.

Lack (1947) was the first to discuss the preponderance of the asynchronous hatching in birds. He noticed that asynchronous hatching occurred only on a handful of birds, such as the Strigiformes and Falconiformes. He initially treated hatching asynchrony as the exception in hatching forms. In subsequent works (Lack 1954, 1968), Lack presented cases where hatching asynchrony was prevalent in several Orders of birds, all nonpasserines. It was not until Clark and Wilson's (1981) review of 82 species of mostly altricial passerines that hatching asynchrony became viewed as the norm rather than the exception in avian hatching strategies. Their review revealed that nearly 80% of the birds included in their literature search hatch their clutches asynchronously. If this review is represents the avian Class as a whole, hatching asynchrony should be viewed as the rule of hatching situations rather than the exception.

EXPLA

propos
ing as
review
have b
1990).
cited a
asynchr

asynchr
hierarc
of food
stronge
to die.
hierarc
all nes
broods
brood re
cially
levels c

Ha
serves t
provided

II. BRIEF PRESENTATION OF HYPOTHESES EXPLAINING THE SIGNIFICANCE OF HATCHING ASYNCHRONY IN BIRDS

To date, there have been nearly twenty hypotheses proposed to explain the adaptive significance of hatching asynchrony in altricial birds (see Magrath 1990 for review). Many of the more recently proposed hypotheses have been variations of one or more hypotheses (Magrath 1990). Below, I present seven of the most commonly cited adaptive hypotheses that explain why hatching asynchrony exists in altricial birds.

David Lack (1947, 1954) suggested that hatching asynchrony produces a beneficial competitive feeding hierarchy among nestlings within a nest. During times of food shortages, parents feed only the oldest and strongest nestlings, allowing the smallest nestling(s) to die. In synchronous broods, no competitive feeding hierarchy during periods of reduced food supply causes all nestlings in the brood to be malnourished. Entire broods risk starving. This hypothesis is called as the brood reduction hypothesis and is thought to be especially relevant for species that rely on food, future levels of which are unpredictable at egg laying.

Hahn (1981) proposed that hatching asynchrony serves to reduce sibling-sibling competition for food provided by parents. A feeding hierarchy is created by hat

themse

cordin

are ea

less f

hypoth

hypoth

(1972)

tling

sis, h

becaus

that n

require

using a

Wilson

tion, w

benefic

which a

Thus, t

exposed

creasin

S

failure

by hatching asynchrony rather than by the nestlings themselves; an energetically expensive process. According to Hahn (1981), broods hatched asynchronously are easier for parents to raise because they require less food than synchronously hatched broods. This hypothesis is called the sibling rivalry reduction hypothesis.

The peak demand reduction hypothesis of Hussell (1972) centers on the short period during which nestling growth is most rapid. According to this hypothesis, hatching asynchrony may be beneficial to parents because it staggers nestlings' maximal energy demand so that not all nestlings concurrently peak in their food requirements. Thus, parents may rear larger broods using asynchronous hatching.

The predation hypothesis (Hussell 1972, Clark and Wilson 1981) predicts that the early onset of incubation, which results in asynchronous hatching, is beneficial to parents because it advances the date for which all but the last-hatched nestling can fledge. Thus, the amount of time earlier hatched nestlings are exposed to possible predation is reduced thereby increasing the chances of producing offspring.

Similar to the predation hypothesis is the nest-failure hypothesis of Clark and Wilson (1981). The

thesis
is fa
the eg
than t
period
the mi

ferred
the eg
1962,
hatchi
occurre
the fi
hatche
all fir
tling
insuran
that ha
last-ha
the ear
nestlin
period,
The ins
pothesis
hypothes

Me

thesis of this hypothesis is that hatching asynchrony is favored when the expected nest-failure rates during the egg period (i.e. incubation period) are greater than those of the nestling period. Decreasing the egg period is accomplished by commencing incubation during the middle of egg laying.

There also exists a suite of explanations referred to as insurance hypotheses. One form, called the egg-insurance hypothesis (Ingram 1959, Dorward 1962, Mead and Morton 1985, Anderson 1990), states that hatching asynchrony benefits parents expecting a high occurrence of infertile eggs in a clutch. If one of the first-laid eggs does not hatch, then the last-hatched nestling replaces it. On the other hand, if all first laid eggs hatch, then the last-hatched nestling is selectively starved. Likewise, the young-insurance hypothesis (Nisbet and Cohen 1975) states that hatching asynchrony allows parents to starve the last-hatched nestling if all of its siblings survive the early portion of the nestling period. If one nestling dies during the first half of the nestling period, then the last-hatched nestling replaces it. The insurance hypotheses, like the nest-crowding hypothesis, is a modification of the brood reduction hypothesis.

Mead and Morton (1985) have also suggested that

hatch
cient
laying
one ho
the st
laying
last-
dramat
egg la
that t
the ch
laying
hormone
tation
starts
it. The
start i
degree
with in

Th
tion hyp
signific
(Tachyc

hatching asynchrony could be a consequence of an efficient hormonal-control mechanism that occurs during egg laying and initiation of incubation. They propose that one hormone, instead of two, regulates egg laying and the start of incubation. They cited that, during egg laying, levels of prolactin increase until the very last-laid egg is ovulated and then these levels drop dramatically. Since ovulation occurs one day before egg laying, then prolactin levels decline on the day that the penultimate egg is laid. They propose that the change in prolactin during the late phases of egg laying also is what initiates incubation. Having one hormone to control two events is a physiological adaptation and hatching asynchrony, because incubation starts before the end of egg laying, is a consequent of it. Their hypothesis predicts that most birds should start incubation on the penultimate egg and that the degree of hatching asynchrony should remain constant with increasing clutch size.

III. OVERVIEW OF CHAPTERS

This thesis investigates whether the brood reduction hypothesis can adequately explain the adaptive significance of hatching asynchrony in the tree swallow (*Tachycineta bicolor*). The second chapter discusses the m

study

The th

attemp

adapti

ductiv

years.

model

a cont

mortal

the methods and results of a four-year experimental study conducted in the Upper Peninsula of Michigan. The third chapter presents a game theory model that attempts to prove how hatching asynchrony can still be adaptive if there are costs associated with this reproductive tactic when parents breed during good food years. The forth and final chapter expands upon the model presented in the third chapter and considers how a continuous distribution of food years and adult mortality selects for hatching form and brood size.

CHAPTER 2

A TEST OF THE BROOD REDUCTION HYPOTHESIS: FIELD EXPERIMENTS ON THE TREE SWALLOW

I. INTRODUCTION

The most cited explanation for the adaptive significance of hatching asynchrony in birds is the one proposed by David Lack (1947, p. 324-326). He observed that the last-hatched nestling of a clutch frequently dies. Lack suggested that asynchronous hatching may be an adaptation to protect parents from investing in large clutches during breeding seasons where food supplies may only provide sufficient food for part of the brood. If food becomes short, the youngest chick loses in its competition with its nestmates for food and dies. On the other hand, if all nestlings were of the same age, their competitive abilities may not differ and all nestlings might starve. Lack also added that asynchronous hatching would not be disadvantageous to parents when food supplies are good because well fed nestlings become inactive when they are satiated. Thus, the smallest nestling will not experience competition and will receive food when resources are not limiting. This theory has been coined the "brood reduction hypothesis" by Ricklefs (1965).

hypot
asyncr
condit
brood
cause
shoulc
select
(1981
from
lack
nous
broo
expl

popu
shou
and
proc
hypo
the

shoul
shoul

For researchers to accept the brood reduction hypothesis as an adaptive explanation for hatching asynchrony, four conditions should be met. First, conditions that would benefit parents by reducing a brood using hatching asynchrony must be present. Because hatching asynchrony is common in a population, it should not be assumed to be a direct result of natural selection. Williams (1966b) and Gould and Lewontin (1981) have argued that a beneficial trait could result from chance rather than by natural selection. Thus, a lack of the conditions necessary to produce asynchronous hatching would result in the rejection of the brood reduction hypothesis as a satisfactory adaptive explanation for the existence of the trait.

Second, brood reduction should occur in the population by hatching asynchrony, which in turn, should produce a feeding hierarchy in a brood (Clark and Wilson 1981). If hatching asynchrony fails to produce a feeding hierarchy, then the brood reduction hypothesis is clearly not an adequate explanation for the existence of hatching asynchrony.

Third, hatching asynchrony and brood reduction should have some adaptive value. An adaptive trait should benefit individuals because it increases lifet

alter

becaus

hypoth

data s

sis (G

explan

the re

consis

ny. If

hatchi

brood

ute to

brood

levels

able w

is aff

period

being

prereq

insect

hatch

lifetime reproductive success of parents compared to alternative traits (Williams 1966a). In addition, because it is easy for researchers to fit data to a hypothesis with complex and elaborate scenarios, the data should not be forced to fit the adaptive hypothesis (Gould and Lewontin, 1981). Therefore, an adaptive explanation should only be accepted if the data provide the researcher with a reasonable explanation.

Lastly, other reproductive tactics should be consistent with brood reduction and hatching asynchrony. If another trait exists that counteracts either hatching asynchrony or brood reduction mechanisms, then brood reduction and hatching asynchrony cannot contribute toward the overall fitness of parents.

Lack hypothesized that hatching asynchrony and brood reduction should be beneficial when: (a) food levels for the upcoming nestling period are unpredictable when the eggs are laid; (b) parental performance is affected by food levels; and, (c) when nestling periods are long so that parents have increased risk of being exposed to periods of food shortage.

There is some evidence to suggest that these prerequisites do apply to a variety of birds. Many insectivores (see O'Connor 1978 for review), which hatch clutches asynchronously, rely solely on food which

has a

long

son 19

Mock a

(e.g.

also c

nestli

predat

Lastly

variet

clutch

and Hus

feeding

1975),

Quinney

T

the bro

mechani

chrony.

tlings

should

full,

food b

foragi

hungry

which is thought to be unpredictable. Brood reduction has also been frequently observed in species that have long nestling periods, such as the raptors (e.g. Stinson 1979), ciconiiformes (e.g. Evans and McMahon 1987, Mock and Parker 1986), and large-bodied passerines (e.g. Haydock and Ligon 1986). Asynchronous hatching is also common in cavity nesting birds, which have long nestling periods associated with the reduced risk of predation (see Clark and Wilson 1981 for review). Lastly, food levels have been shown to affect a wide variety of reproductive performance measures such as clutch size (see review in Quinney 1983, and Quinney and Hussell 1986), egg laying date (e.g. YomTov 1975), feeding rates (e.g. Proctor 1975, Nisbet and Cohen 1975), and nestling growth rates (e.g. Hussell and Quinney 1987), to name a few.

The second condition that must be met to accept the brood reduction hypothesis is that brood reduction mechanisms should exist and be due to hatching asynchrony. Ricklefs (1965) suggested that the older nestlings, because of their better competitive abilities, should always get fed first. Once older nestlings are full, then younger nestlings may get fed. However, if food becomes scarce, then parents will take more time foraging for food and older nestlings will become hungry by the time it is the youngest nestling's turn to ge

1984,

hatch

becau

As a

hatchi

feedin

(Clark

fueled

broods

and St

adjust

hierar

asynch

over,

nous b

Magrat

nestli

than in

searche

to faci

parents

eventua

efficie

to get fed. Several studies (Proctor 1975, Groves 1984, Forbes and Ankney 1987) have shown that last-hatched nestlings do not get fed when food is limited because their older nestmates compete better for food. As a result, the younger nestlings starve.

There is a controversy, however, over whether hatching asynchrony is necessary to establish the feeding hierarchies that facilitate brood reduction (Clark and Wilson 1981). This controversy has been fueled by experimental studies that have manipulated broods to simulate synchronous hatching (see Amundsen and Stokland 1988, for review). In most cases, broods adjusted for synchronous hatching have developed weight hierarchies that are as great as those established by asynchronous hatching (Clark and Wilson 1981). Moreover, partial brood loss was common in these synchronous broods. Many of these studies have shown (see Magrath 1990 for review), on the other hand, that nestling deaths in asynchronous broods occurred earlier than in synchronous broods, suggesting to some researchers that the function of hatching asynchrony is to facilitate the early deaths of nestlings so that parents provide less investment in nestlings that will eventually die. Thus, hatching asynchrony provides an efficient mechanism of brood reduction.

brood

an ad

recog

which

than

ies,

have

hatc

appe

for

land

be v

ple

rep

bro

bro

bro

res

bea

th

st

is

de

al

The third condition that must be met is whether brood reduction facilitated by hatching asynchrony has an adaptive value. Williams (1966) and Stearns (1976) recognized that an adaptive trait should be one in which parents produce more offspring in their lifetime than any alternative trait. However, in several studies, broods manipulated to establish hatching synchrony have been more productive than the normal degree of hatching asynchrony, especially when food did not appear to be limiting (see Amundsen and Stokland 1988, for review). Some researchers (e.g. Amundsen and Stokland 1988) have suggested that brood reduction should be viewed as maladaptive if it occurs during food plentiful conditions.

Lastly, a researcher should determine if other reproductive tactics of the parents are consistent with brood reduction. Ricklefs (1965) recognized that, if brood reduction is adaptive, then the reduction of the brood should be complimented by other strategies not resulting in nestling death. For example, when food becomes reduced, parents could attempt to increase their foraging rate rather than resort to an immediate starvation of the last-hatched nestling (Ricklefs 1965). Several researchers have also argued that decreasing egg size with laying order, common to many altricial birds (see Slagsvold et al. 1984 for review), shoul

tion

esis

be pl

of su

speci

lus),

redu

hatc

most

sear

beca

die

197

Eva

inv

ti

ti

re

di

fo

to

nes

hat

should be considered consistent with the brood reduction hypothesis because, as the brood reduction hypothesis would predict, lesser amounts of investment should be placed into the offspring that has the least chance of survival (Clark and Wilson 1981). Egg size in many species, such as the Common Grackle (*Quiscula quisculus*), increase in size with laying order (Howe 1978).

Many of the studies that have accepted the brood reduction hypothesis as an adequate explanation for hatching asynchrony in the study species have done so mostly on circumstantial evidence. Most often, researchers have accepted the brood reduction hypothesis because the last-hatched nestling either grew slower or died more frequently than its siblings (e.g. Mishaga 1974, Nisbet and Nisbet 1975, Proctor 1975, Zach 1982, Evans and McMahon 1987). There has yet to be any investigation into several aspects of the brood reduction hypothesis, and, to date, there has been no investigation that has examined all four levels of the brood reduction hypothesis. Lacking are studies on the predictability of food resources, the effects of different food years on nestling growth and development according to hatch position, the amount of food apportioned to nestlings according to hatch position and the effect of hatching asynchrony on parental behavior and inves

from
bicol
obser
that
grew
their
brood
cause
the m
of ha
swall
occur
limit
effec
brood
large
produ
chron

brood
synch
of ha
treat

investment.

This chapter reports on experiments conducted from 1986 to 1989 on the tree swallow (Tachycineta bicolor) designed to build upon the results of the observational study of Zach (1982). Zach (1982) found that the last-hatched nestling died more frequently, grew slower and reached lower asymptotic weights than their older nestmates. He cautiously concluded that brood reduction in the tree swallow was adaptive because those broods hatching more asynchronously fledged the most nestlings. However, the adaptive significance of hatching asynchrony and brood reduction for tree swallows is called into question since brood reduction occurred in Zach's study when food did not appear to be limiting. In addition, Zach could not factor out the effects of brood size on brood productivity; those broods hatching most asynchronously were from the largest clutches in the population, therefore, the high productivity associated with increased hatching asynchrony could be due solely to brood size differences.

The study reported here consists of adjusting broods, shortly after hatching, to simulate hatching synchrony (hereafter as SYNCHRONOUS), and two degrees of hatching asynchrony. One asynchronous hatching treatment contained one nestling a day younger than other

day y

their

ASYNC

to ex

inves

devel

durin

parer

atter

redu

occu

repr

also

tior

bre

cav

Per

ing

3-a

(Za

Inc

other asynchronous treatment contained one nestling one day younger and a second nestling two days younger than their older siblings (hereafter as DOUBLE ASYNCHRONOUS). I adjusted all broods to five nestlings to exclude brood size effects and followed parental investment, feeding behaviors and nestling growth and development according to hatching position, on plots during a four year study in which two years provided parents with more food than the other two years. I attempted to determine: (1) if the mechanisms of brood reduction occur; (2) whether brood reduction, if it occurs, could be viewed as adaptive; and (3) if other reproductive patterns compliment brood reduction. I also address whether the prerequisites for brood reduction exist in the tree swallow.

II. MATERIALS AND METHODS

Study Animal. The tree swallow is a monogamously breeding bird (but see Quinney 1983a) that nests in cavities and nestboxes. Tree swallows raise one brood per year (see Hussell 1983a for a case of double brooding). The most common clutch sizes are 5 and 6 (range 3-8) which are hatched over a two to four day period (Zach 1982). Only the female incubates the eggs. Incubation requires on average 14 days (Kuerzi 1941).

The r
sexes
brood
mainl
and Q
study
forag
obs.)

aroun
begin
durin
studi
first
begar
of Ju
week
dete

west
nort
year
ferr
appr
as
Aiz

The nestling period generally lasts 19-23 days. Both sexes feed and defend the nestlings. Only the female broods the non-thermoregulating young. Insects, mainly small dipterans such as nematocerans (Hussell and Quinney 1987) and occasionally tabanids (this study), are their main food source. Parents usually forage within 100 m of the nest (Holroyd 1972; pers. obs.).

Tree swallows arrive on the breeding grounds around the first of April of each year. Egg laying begins around mid-May and clutches start hatching during the first week of June. During 1986, I began my studies on May 1 and continued until the end of the first week of July. In 1987 through 1989, my studies began around June 1st and ended around the first week of July. However, I spent two-days during the second week of May each of these years checking nests to determine initial clutch sizes.

Study Sites. This study was conducted in the western portion of the Upper Peninsula of Michigan in north-central Dickinson County (Figure 1). The first year of my study, 1986, was conducted at a plot referred to as Floodwood. In 1987, I moved my study approximately 15 km to the east to a site referred to as Aimones Power Hill. Several smaller sites near Aimones were also used in 1987 to increase the number

of ne
trave
Hill.
of 3
in a
matel
the r
stand
with
Powe
tota
In
site
nes
wer
ext
nat
beg
tr
co
the
ca

of nests. In 1988, to reduce the amount of time spent traveling, I excluded the sites around Aimones Power Hill.

A total of 127 cedar nest boxes (inside dimension of 3 1/2 x 6 in.) existed in 1986 at Floodwood arranged in a 30-meter grid arrangement. The site is approximately 35 ha with several small ponds located within the nestbox grid. The area is open with scattered stands of aspen.

The Aimones Power Hill site is also very open with scattered stands of young aspen. In 1987, Aimones Power Hill and the surrounding smaller sites had a total of 40 nestboxes scattered over a 5 mile stretch. In 1988, I added 87 nestboxes to the Aimones Power Hill site to bring this area to 100 nestboxes. These 100 nestboxes were also arranged in a 30 meter grid and were used exclusively for the study in 1988 and 1989.

Natural Weight Hierarchies. To determine the extent of intra-brood weight differences established in nature by tree swallows, I visited nests every 4 hours beginning at 0800 during the hatching period of a brood. I recorded which nestlings were present, the condition of their down (wet or fluffy) and marked their toes using a nontoxic marker for later identification. In 1986, I determined that nestlings with

FIGURE 1.

Location of the study site (indicated by the star) in the Upper Peninsula of Michigan.

wet

with

visit

natur

nestl

clutc

hatch

diffe

ASYNC

conta

ment,

tion

chic

chic

as t

nes

090

wra

Tra

mir

5 c

Pos

wet down had hatched within 2 hours of the visit, those with fluffy down later than 2 hours from the nest visit. In 1988 and 1989, to determine the extent of naturally occurring weight hierarchies, I weighed all nestlings on the first noon visit after the entire clutch had hatched for those broods that had a 100% hatchability.

Experimental Manipulations. I constructed three different hatching treatments: SYNCHRONOUS, SINGLE ASYNCHRONOUS, and DOUBLE ASYNCHRONOUS. All broods contained five nestlings. Within each hatching treatment, I shall refer to nestlings by their hatch position; the oldest chicks will be referred to as 'A' chicks; those a day younger than 'A' chicks as the 'B' chicks, and those two days younger than the 'A' chicks as the 'C' chicks.

Hatching treatments were established by swapping nestlings between nests in the late morning (between 0900 and 1200 EST). During the transfer, nestlings were wrapped in polyester filling to reduce heat loss. Transfers were completed in all cases within 10 minutes. All nestlings were swapped before the age of 5 days posthatch; 83% were swapped before 2 days posthatch.

I selected nests parented only by ASY (after seco

(Hus

show

bree

selec

eggs.

menta

1986,

year

ninet

adju

'DOU

year

foll

Brie

pass

inde

dail

bio

expo

with

(IB

pass

I selected nests parented only by ASY (after second year) females using plumage characteristics (Hussell 1983b). First-year female breeders have been shown to be less productive than older, experienced breeding females (DeSteven 1978). In addition, I only selected nests whose original clutch size was 4, 5 or 6 eggs.

Fifty-three nests were selected for the experimental manipulations during the four year study. In 1986, 1987 and 1989, twelve nests were monitored each year and in 1988, 17 nests were monitored. A total of nineteen, twenty and fourteen of these nests were adjusted for 'SYNCHRONOUS', 'SINGLE ASYNCHRONOUS' and 'DOUBLE ASYNCHRONOUS' nests, respectively, for all four years.

Food Abundance. To measure insect abundances, I followed the method of Hussell and Quinney (1987). Briefly, this method entails trapping insects using a passive tow net device and obtaining an insect biomass index for the day after accounting for the effects of daily wind speeds. Johnson (1965) determined that the biomass of insects trapped in tow nests increases exponentially for windspeeds below 8 km and linearly with wind speeds above 8km. Insect biomass indices (IBI) are expressed as mg of biomass per 100 km of wind passing through the net.

cone

pole

faces

mesh

nets.

with

fly

lect

nol.

Huss

min

rea

Joh

str

co

of

ne

be

R^2

my

H

ne

e

e

The passive insect trapping device is a suspended cone net that swings freely in the wind on a vertical pole 1.5 meters above the ground so that it constantly faces the wind. The nets were constructed of 1mm vinyl mesh using the same dimensions as Hussell and Quinney's nets. The opening of each net was 30.5 cm in diameter with a cone length of 61 cm. Insects that are blown or fly toward the rear of the tow net are trapped a collecting cone that leads to jars filled with 70% ethanol. In 1988, I obtained two tow nets from David J. T. Hussell to compare the efficiency of his nets with mine. His nets differed from mine in the design of the rear collecting trap. My wind nets are similar to Johnson's (1965) original design where the net opens straight into the jar; Hussell and Quinney's nets contain a small cylindrical trap that opens to the jar of ethanol. I compared the daily insect biomass of my nets with his and found Hussell and Quinney's nets to be almost twice as efficient as mine ($y = 0.0 + 1.60x$, $R^2=0.520$, df=51, $P < 0.001$, where y= insect biomass for my nets and x = insect biomass for Hussell's nets). However, IBI measures reported throughout are from my nets. I will take into account these differences in net efficiencies when I compare my results later with the efficiency of Hussell and Quinney's nets.

The insect traps were functional from

appr
the
to t
July
one
and
198
ave

Ins
thr
otl
int
in
av
ur
sa
th
5
m
n
v

s
c
s

approxiately 0700 to 2000 EST during each day and from the day that the first hatchling at the plot appeared to the last day of the study (approximately June 5 to July 3 of each year). Of my version of wind net traps, one was erected during 1986, two each in 1987, 1988 and 1989. Two Hussell nets were erected in each of 1988 and 1989. IBI measures are expressed as the average for two nets for 1987-1989.

Daily IBI measures were obtained as follows. Insects were keyed to Order (dipterans were keyed to three further subgroups, nematocerans, tabanids and other dipterans) and placed according to body length into eight size categories. The number of individuals in each of the size-taxa groups was multiplied by the average dry weight value for each size-taxa (Beaver, unpubl.) and these were summed for each daily net sample to obtain a total insect biomass. I compared these estimated total dry weight values by regressing 50 actual dry weights against the corresponding estimated dry weights and found that these estimated values needed to be corrected by multiplying the estimated values by 2.21 ($P < 0.001$).

Wind speed measures were collected at the study sites three to ten times per day. Following the procedure of Hussell and Quinney (1987), windspeeds at the study site were used to adjust hourly wind speeds taken at K

the

where

'x' =

df=14

corre

it by

obtai

the n

net c

Howev

remov

Figure

speed

p.251)

effect

taban

hot da

steins

in the

traps

predac

is sus

at K. I. Sawyer Airforce Base approximately 45 km from the study site following this regression equation:

$$y = 1.16 + 0.435 x$$

where 'y' = the wind speeds at Aimones Power Hill and 'x' = the windspeeds at K. I. Sawyer AFB (R^2=0.723, df=149, $P < 0.001$). Wind speeds below 8 km/hr were corrected by cubing each hourly windspeed and dividing it by 64 (see Hussell and Quinney 1987). The IBIs were obtained by dividing the average dry insect biomass for the nets by the average amount of wind per day during net operation and then multiplying this value by 100. However, this procedure of Hussell's did not entirely remove the effects of wind speed from IBI measures (see Figure 2). I adjusted IBIs from the effects of wind speed using linear regression (Steele and Torrie, 1980, p.251). IBIs reported are those adjusted to remove the effects of wind speed.

After finding in 1987 that tree swallows fed tabanids to their nestlings during the afternoons of hot days, I constructed a Manitoba trap after Thorsteinson _et al._ (1965). The Manitoba trap was placed in the center of the plot in 1988 and 1989. Manitoba traps attract insects, mostly tabanids and other large predaceous dipterans, to a spherical black object that is suspended from the apex of a triangular trap. The

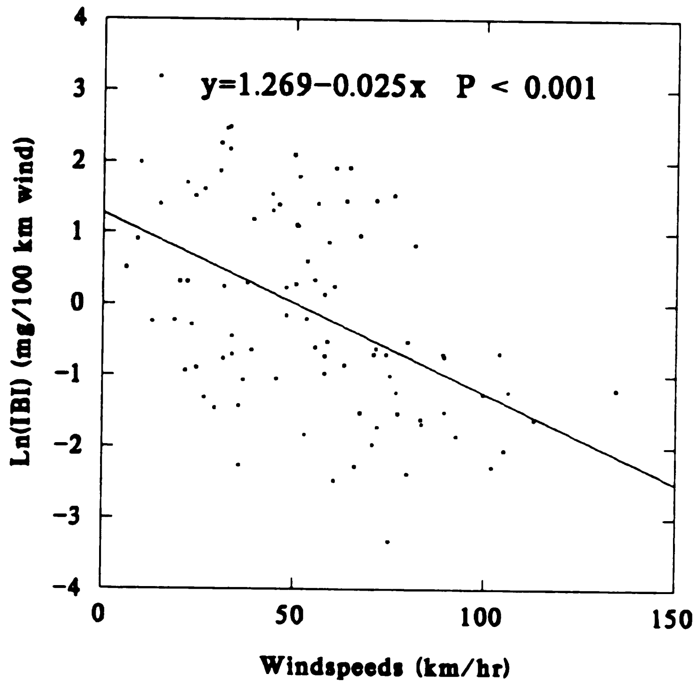


FIGURE 2.

The relationship between the natural logarithm of daily IBI measures (in mg insect/100km of wind) and daily windspeeds at the plots.

blac
flie
dipt
clea
agai
pane
jar.
Man
as
end
the
tic

mo
Ea
in
0.
we
es

n
w
l
t
w

black ball emits radiative heat that attracts the flies. After circling the black object, many of these dipterans come to rest on the inside of the three, clear plastic panels. The insects invariably then walk against gravity toward the apex of the three plastic panels where they enter a one-way funnel into a glass jar. The insects usually die within a few hours. The Manitoba traps were operational during the same periods as the Hussell nets. All insects were collected at the end of the day. I used the number of insects caught in the trap and their estimated dry weights as two additional insect abundance indices.

Egg Weights. In 1986, I weighed eggs in the morning (630-900 EST) a few hours after they were laid. Each egg was numbered for identification with India ink. I used a 5.0 gram Pesola with an accuracy of $\pm$ 0.05 grams. One hundred and seventy-four eggs were weighed from 34 clutches laid in 4, 5 and 6 egg clutches.

Nestling Growth and Development. I recorded nestling growth and development every other day, when weather permitted, in the evening hours (approximately 1600 - 2000 EST). After hatching, I marked the nestlings on their toes with a nontoxic marker. Nestlings were identified by their toe marking until age 3 days pos

DPH

A F

nes

I ob

gra

leng

accu

incr

lowi

tail

grow

lanf

the

regr

curv

posthatch (hatching is considered 0 days posthatch - DPH) after which a plastic colored leg band was used. A Fish and Wildlife Band was placed on a leg after the nestling reached 15 DPH.

I recorded several measurements on each nestling. I obtained a body mass for each individual using a 50 gram Pesola accurate to ± 0.1 g. I also recorded the length of several body parts using a dial caliper accurate to ± 0.01 mm. These measures were:

(a) the length of the right tarsometatarsus (hereafter as tarsus), from its proximal protrusion at the joint with the tibiotarsus to its distal end at the joint with the halix;

(b) the length of right ulna;

(c) the length of the right wing chord, from the outer bend of the ulna to the tip of the ninth primary;

and, (d) the length of ninth primary on the right wing.

The growth of the tarsus, ulna and body weight increase were subjected to growth curve analysis following Ricklefs (1967). Briefly, this procedure entails transforming growth data using one of three growth curve equations: logistic, Gompertz or vonBertalanffy. I used the logistic curve because it provided the best fit based upon examining the average linear regression coefficients of the transformed data. Growth curve transformation produces two statistics: a growth cur

for

infl

(her

ana

who

fer

the

pri

wei

sub

bec

(B

a

ra

ou

sl

us

ag

wh

th

re

op

curve constant, which is the slope of the curve transformed to a line; and the age that the growth curve inflects, which is the age of most rapid growth (hereafter as the inflection point). For subsequent analyses, I used only those nestlings that fledged and whose growth rate constant and inflection point differed from 0.0 at a 95% confidence or greater. I used the heaviest weight, which occurs three to five days prior to fledging, for each nestling as the asymptotic weight value for curve fitting. This value had to be subsequently deleted from the curve fitting routine because of its high leverage on curve fitting estimates (Beaver, unpubl.).

Growth of the wing chord was analyzed by fitting a straight line by log transformation. Thus, only the rate of wing chord growth was analyzed. Growth of the outer ninth primary was analyzed by calculating the slope of its linear growth using linear regression. I used the x-intercept from the calculated line as the age of primary eruption.

During each growth measure visit, I also recorded whether the abdominal yolk sac was still present and if the eyes were opened. Because growth events were recorded every other day, the accuracy of these developmental events is ± 2 days.

Growth curve fitting requires an asymptotic value whi

cor

boo

of

ha

of

95

Th

a

cc

th

I

w

t

s

m

m

f

w

e

f

t

a

w

which is difficult to estimate. Because of this, I also compared the rate of growth for the linear phases of body weight increase between, and including, the ages of 3-10 DPH, for all nestlings. Those nestlings that had three of more growth measures and where the slope of the straight line differs from a slope of 0.0 with a 95% confidence were entered in subsequent analyzes. Those nestlings whose growth measures failed to produce a straight line differing from a slope of 0.0 were considered to grow abnormally and were not included in the growth analyses. For those nestlings that fledged, I also used the heaviest weight and the age that this weight was attained as independent measures of a nestling's health prior to fledging.

Feeding Behavior. From 1987 through 1989, I selected approximately half of the nests in the experimental design for food collection experiments to determine the pattern of food provisioning to nestlings. I followed the neck collaring technique of Hussell (1972) with some modifications. Rather than using pipe cleaners, I used flexible wire to constrict the passage of food moving down a nestling's esophagus. Care was taken to make sure that the constriction device was not affecting a nestling's behavior and that the trachea was not blocked. Food boluses were usually lodged str

(1

ne

bo

16

a

a

p

v

b

a

a

striction device. A small percentage of food boluses (11.3%) were, however, ejected into the nest by some nestlings. Nests were inspected for ejected food boluses during each visit.

Nestling feeding was monitored between 0900 and 1600 EST after the youngest nestling was at least 2 DPH and ceased once the oldest nestling reached 16 DPH. I allowed parents to feed their nestlings for 20 minute periods. At the conclusion of this 20 minute period, I visited the nest and examined each nestling for food boluses. I recorded which nestling received food and assigned a number to a food bolus which was collected and placed in a vial of 70% ethanol for later examination. To replace the collected food bolus, I gave the nestling an equal sized waxworm. Insects in the food boluses were keyed to the same size-taxa categories used for the insect traps. I monitored 3 nests at one time; all nests were at similar ages. In most cases, I was able to select one nest from each hatching treatment. I did not follow a set of nests for longer than two, one-hour periods per day.

Parental Care. In 1988 and 1989, I monitored parental investment by recording body mass changes over the nestling period. I weighed adults every other day

in
I
tr
ha
us
th
(i
to
ne
we
we
Be
of
th
re
ma

ar
ri
re
be
en
no

(W

in the evening (1900-2100 EST) when weather permitted. I used a passive trapping device of Magnusson (1984) to trap the adults. Within one day of the first egg hatching, I measured the body mass of the adults and used the maximum percentage of weight change between the first day of hatching and the last evening weight (in most cases, 12DPH or later in the nestling period) to calculate a percentage adult weight change for the nestling period. I also used the difference between the weight at hatching and the lightest adult evening weight as a measure of the maximum evening weight loss. Because I also collected body weights of parents during other times of the day, I took the difference between the evening weight at hatching and the lightest weight recorded during any part of the day to estimate the maximum percentage weight lost by parents.

Statistical Procedures. For all statistical analyzes, I used an alpha level of 0.05 as the criterion for determining the level of significance for rejecting null hypotheses. Results of tests falling between alpha levels of 0.10 and 0.05 are cautiously entertained as significant. When results of tests are non-significant, observed trends are discussed.

I used the statistical software package SYSTAT (Wilkinson 1990a) for all statistical analyses and

SYG

Bef

tes

an

of

Ba

of

a

r

a

c

c

r

I

I

s

SYGRAPH (Wilkinson 1990b) for graphical presentations. Before data were entered into any parametric tests, I tested for these assumptions of parametric tests (Sokal and Rohlf 1981): (1) normality, using the PPLOT routine of SYSTAT; and (2) homogeneity of variances using Bartlett's test. If data conformed to the assumptions of parametric tests, analysis of variances or covariances were conducted with the means and standard errors reported. Correlations were conducted to ascertain the amount of association of variables; all correlation coefficients reported are Pearson correlation coefficients unless specified otherwise. If data were not normal, data were first transformed and assumptions for parametric tests reexamined. Failing any attempts to normalize the data, data were subjected to nonparametric tests or are reported using descriptive statistics.

III. RESULTS

Natural Hatch Spreads. Figure 3 shows the normal hatching spread of clutches between 4 and 6 eggs. The hatching spread here represents the number of calendar days that hatching occurred. Only those clutches that: (1) had a 100% hatchability; (2) were incubated by ASY females; and (3) did not hatch during two critical cold spells (see below), are included here. Two and one

ha
no
ch
mo
ne
pe
ly
In
sp
da
n

e
w
a
I
b
f

half times as many clutches of 4 eggs hatched synchronously (all eggs hatched on the same day) than asynchronously. As clutch size increased to five eggs, the modal hatching spread increased to two days, although nearly half of the clutches hatched over a one day period. Clutch sizes of six hatched more asynchronously, with one nest hatching over a four day period. Interestingly, the amount of variation in hatching spreads increased with increasing clutch sizes. These data also show that hatching spreads were more synchronous than those reported by Zach (1982).

To determine the extent of weight hierarchies established at the site by tree swallows, I also weighed all nestlings in a brood on the first noon after an entire brood had hatched. From these weights, I calculated the coefficient of variation for each brood and compared the average coefficient of variation for clutch sizes 4 through 6. Figure 4 shows that variations in the weights of broods soon after hatching increase dramatically with increasing clutch size; the coefficient of variation is twice as great in 6 egg clutches as in 4 egg clutches.

Effects of experimental manipulation. I examined whether the original clutch size that females laid affected the outcome of the number of nestlings fledged

COUNT

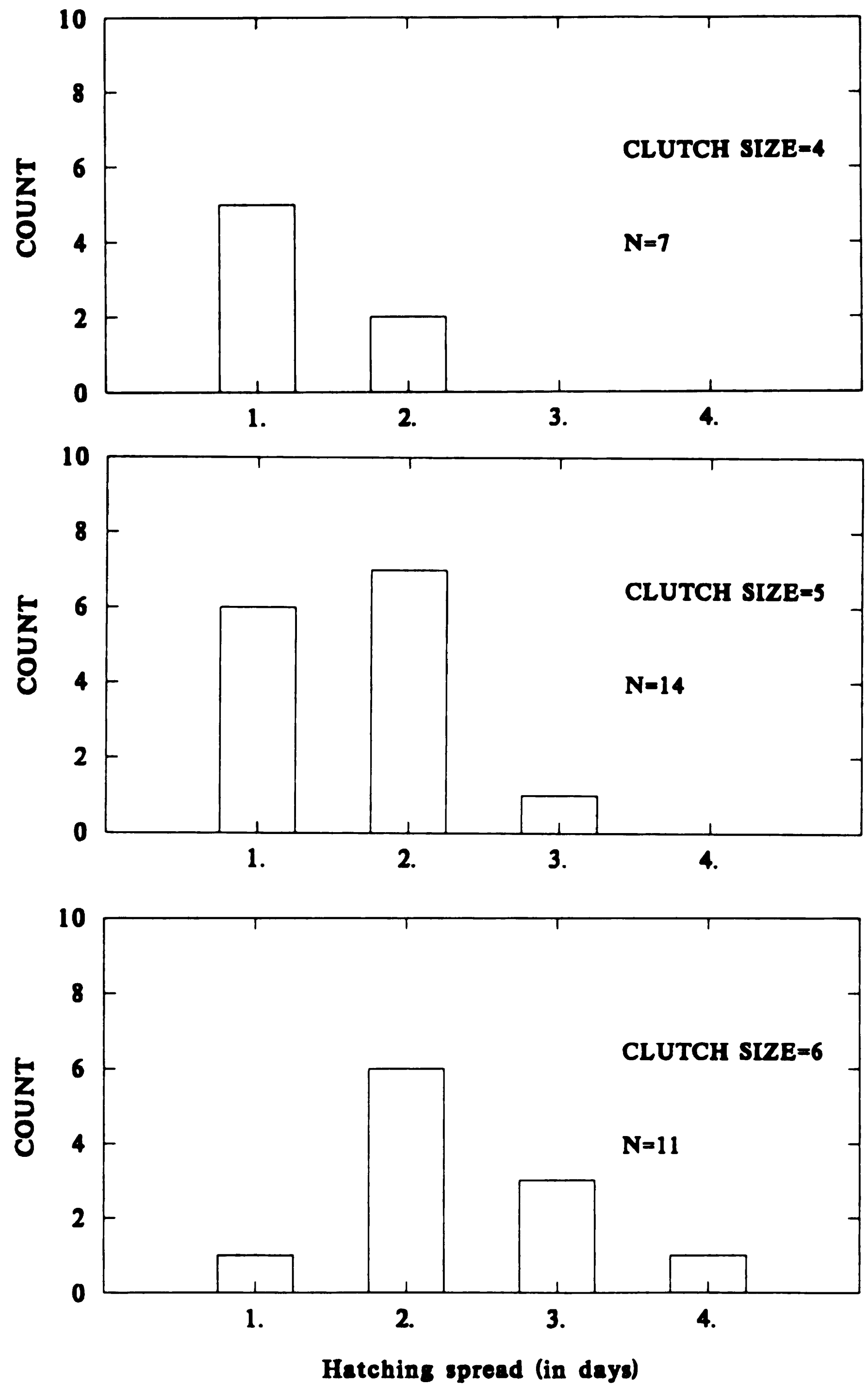


FIGURE 3.

Hatch spreads, by calendar days, for clutch sizes 4 through 6.

or

Gre

clu

the

fl

we

in

ar

a

i

s

i

P

t

or their growth rates. Perrins (1965) has found in the Great Tit (*Parus major*), that parents laying larger clutches are able to raise larger broods. I compared the clutch size against: (1) the number of nestlings fledged; and (2) the slope of the linear phase of body weight increase for nestlings. I found a small but insignificant correlation between original clutch size and the number of young fledged (Pearson r= 0.134, X^2 approx. = 0.891, P=0.345). I also found a small but insignificant correlation between the original clutch size and the slope of the linear phase of body weight increase (Pearson r= 0.042, X^2 approx. = 0.382, P=0.537).

I also compared the growth rates of those nestlings subjected to food bolus collections to those nestlings that were not subjected to food bolus collections. I was able to introduce hatching treatment and year of study as covariates in this particular analysis using both effects as coded variables. These results, given in Table 1, show that there was no difference in growth rates between nests that were subjected to the bolus experiment compared to those that were excluded from this experiment.

MEAN COEFF. OF VARIATION OF WEIGHTS

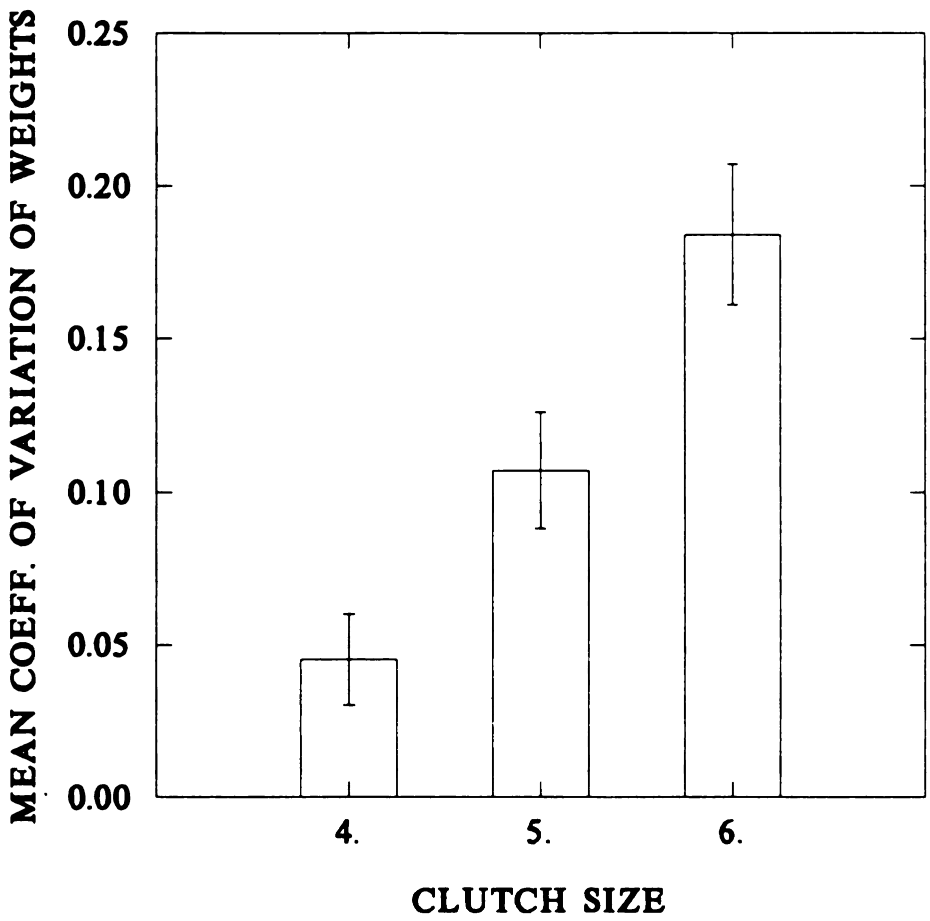


FIGURE 4.

The coefficient of variation of weights of broods on the first noon (12:00 EST) after natural hatching.

sta

fo

5

wi

li

eg

wh

nu

I

t

6

s

c

5

Egg weights. Figure 5 shows the mean and one standard error of egg weights by egg laying sequence for clutch sizes 4 through 6. Within clutches of 4 and 5 eggs, there was no linear relationship of egg weight with laying order. There was, however, a significant linear increase in egg weight with laying order in 6 egg clutches, described by the relationship:

$$y = 1.39 + 0.143x$$

where 'y' is the egg weight in grams and 'x' is the egg number in the laying order (R^2= 0.66, df=59, P=0.044). I also performed a Wilcoxon sign-ranks test to compare the weights of the first and last-laid eggs in 4,5 and 6 egg clutches. I all cases, the last egg laid was significantly heavier than the first-laid egg using a one-tailed probability test (4 egg clutches, P = 0.056; 5 egg clutches, P = 0.036; 6 egg clutches, P = 0.014).

Insect Abundances. Tow nets were operational for 27, 21, 28 and 30 days, for 1986 through 1989, respectively. Tow net data for 7 days in 1987 were not available. The average number of hours per day they were operational were 9.69, 10.52, 12.51 and 11.30 hours for these same years. A total of 1803 insects were collected in all of the tow nets.

Weather during the study was unusual. Two cold periods occurred during this study, one in 1986 and the

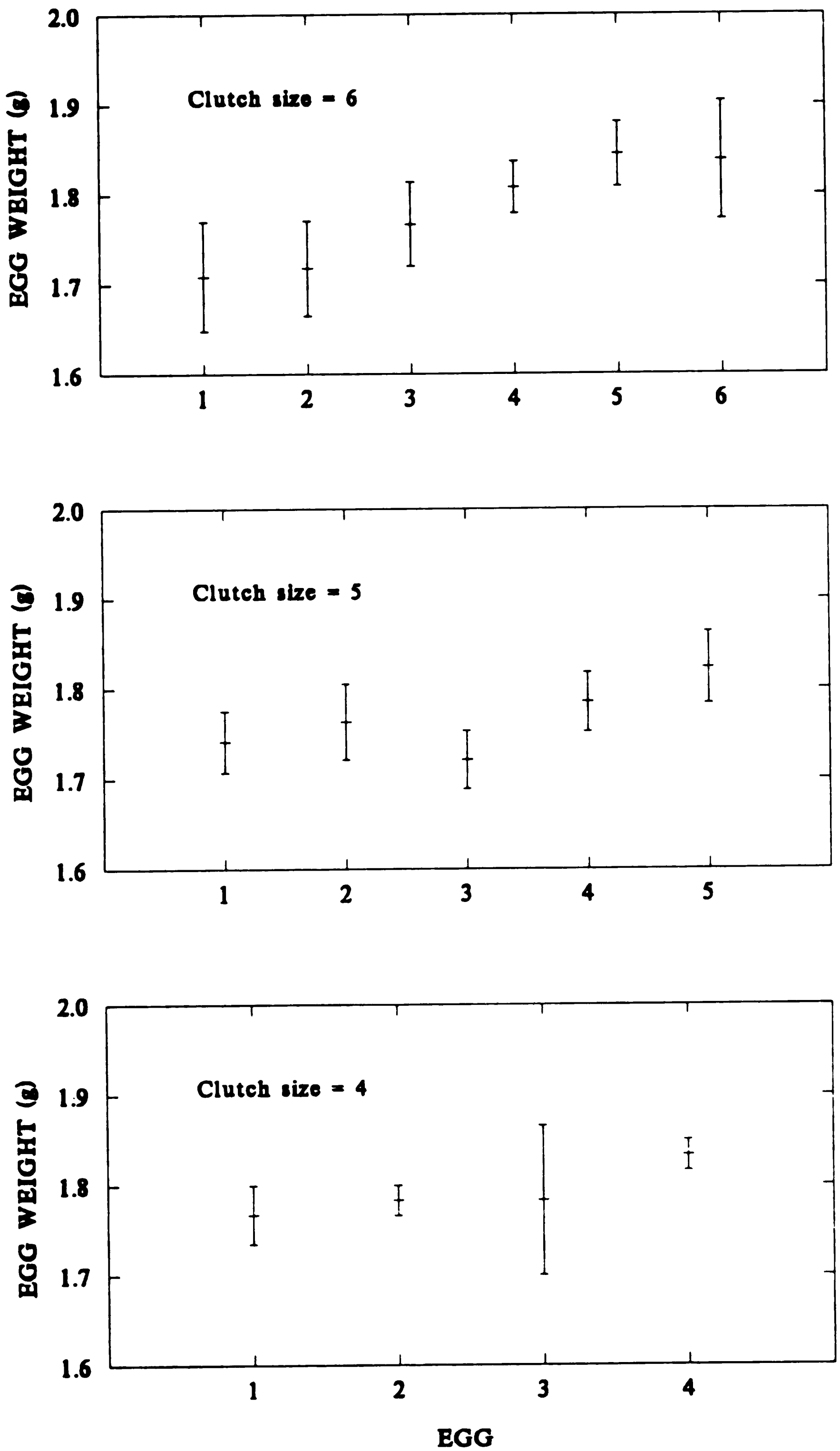


FIGURE 5.

Mean egg weights (± 1 S.E.) by laying sequence. Shown are egg weights for clutch sizes of 4 through 6.

Table 1. Analysis of covariance examining the effects of the bolus collection experiments on the linear nestling growth rate. I compared the linear growth rate between broods in the bolus experiment (exper.) with those that were excluded from this experiment (control). Hatching treatment (tmt) and year were used as a covariate to control for these effects.

SOURCE	SS	DF	MS	F-RATIO	P
Exp. v. cont.	0.011	1	0.011	0.069	0.794
Tmts	0.757	1	0.757	4.754	0.031
Tmt*exper.	0.384	1	0.384	2.407	0.123
Year	1.771	1	1.771	11.116	0.001
Year*exper.	0.007	1	0.007	0.046	0.831
Error	24.853	156	0.159		

other in 1989. In 1986, the cold period lasted between June 13th and June 15th; the cold period of 1989 lasted from June 7th to June 13th. In addition, a severe drought occurred during the entire 1988 season.

Figure 6 shows the pattern of daily IBI measures for each of the four years. The range of these IBI measures are from 0.0 mg/100km wind per day to 23 mg/100 km wind per day attained in 1987. The average IBI measures, for each year, are given in Figure 7. These data show that 1986 and 1987 had 5 times the insect abundances than in 1988 and 1989. The week long severe weather that occurred in 1989 at the study probably contributed toward lower average insect abundances. Good weather following the cold spell of 1986 and the small ponds at Floodwood probably resulted

FIGURE 6.

Daily IBI measures (mg of insect/100km of wind) for each year of the study. Days that information is not available is designated with an asterisk ('*').

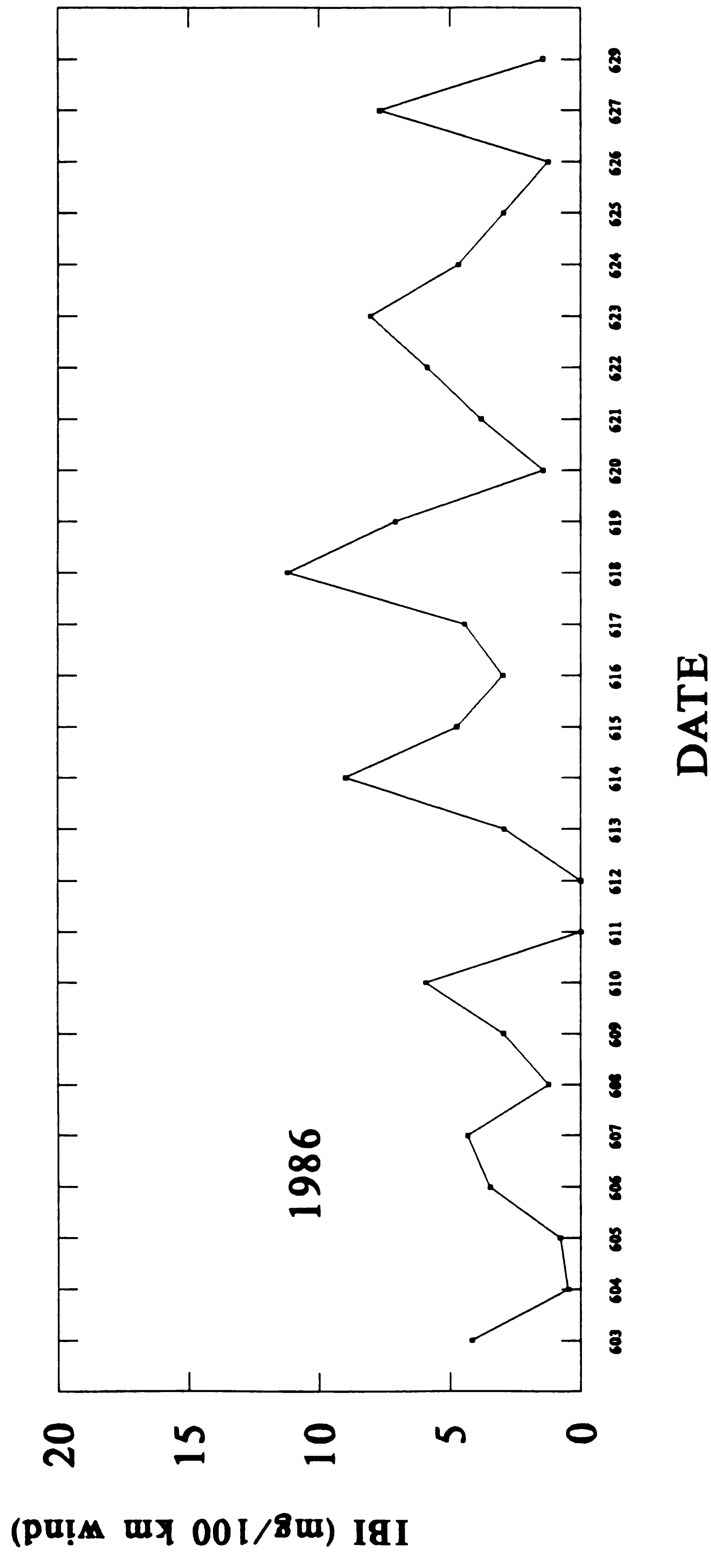

1986
IBI (mg/100 km wind)
0
5
10
15
20
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
629
DATE

FIGURE 6

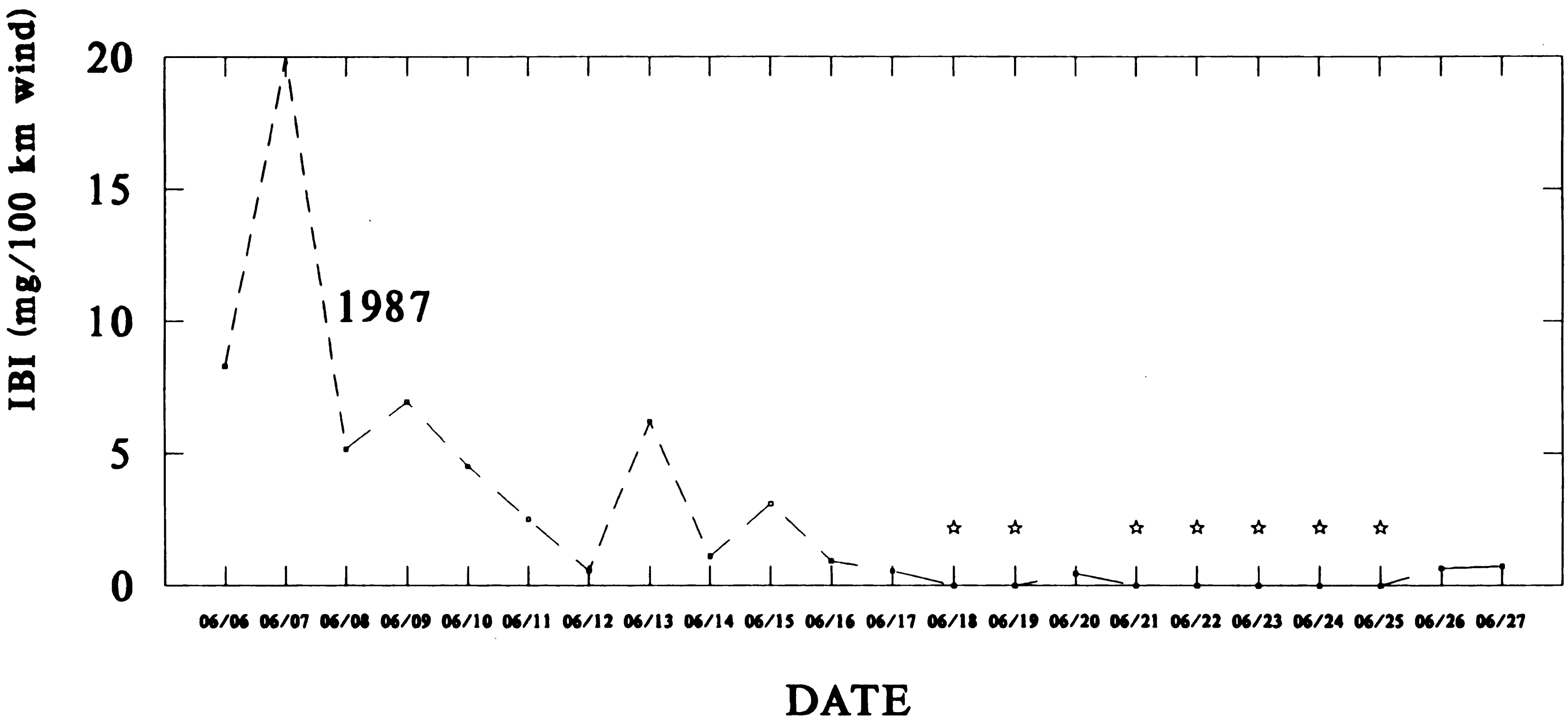

IBI (mg/100 km wind)
20
15
10
5
0
1987
06/06 06/07 06/08 06/09 06/10 06/11 06/12 06/13 06/14 06/15 06/16 06/17 06/18 06/19 06/20 06/21 06/22 06/23 06/24 06/25 06/26 06/27
DATE

FIGURE 6

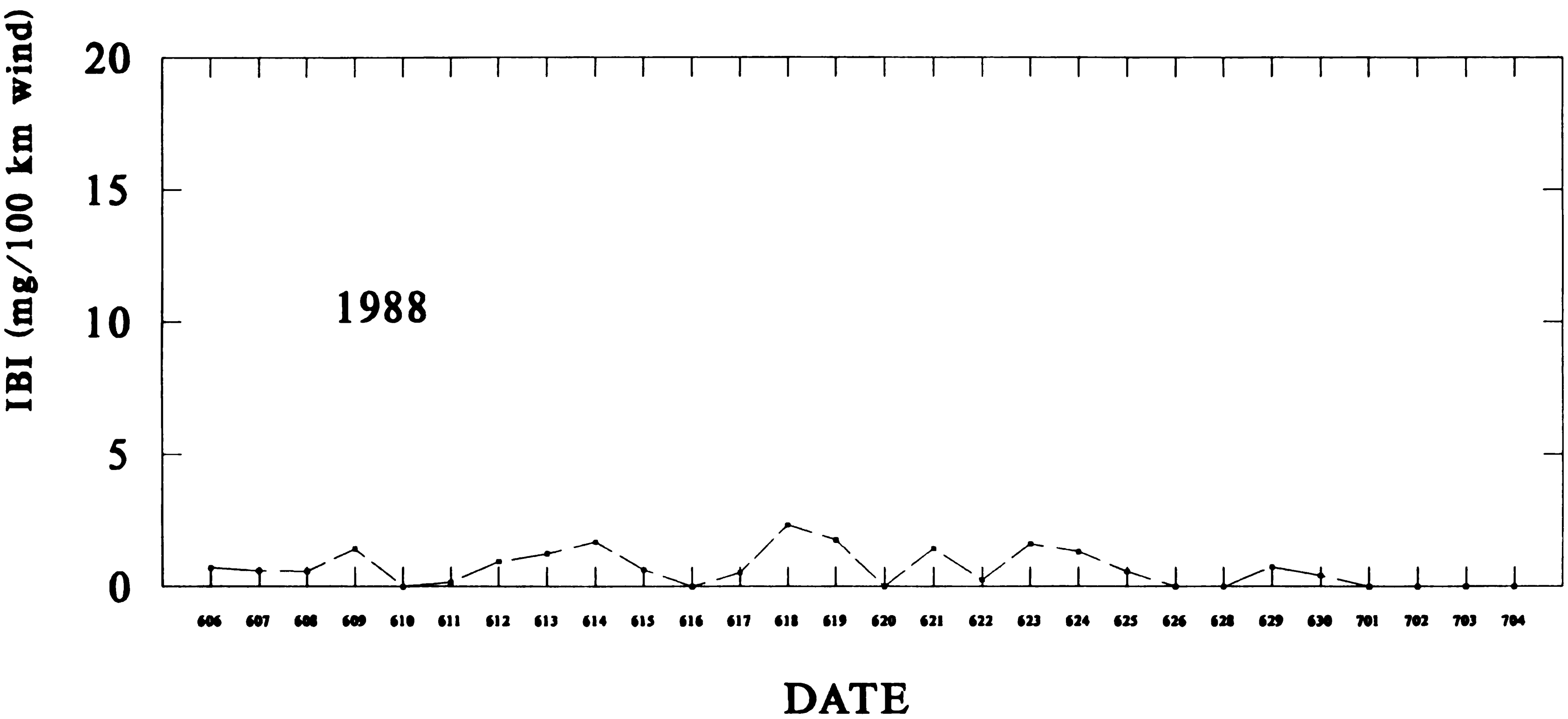

IBI (mg/100 km wind)
20
15
10
5
0
1988
606 607 608 609 610 611 612 613 614 615 616 617 618 619 620 621 622 623 624 625 626 628 629 630 701 702 703 704
DATE

FIGURE 6

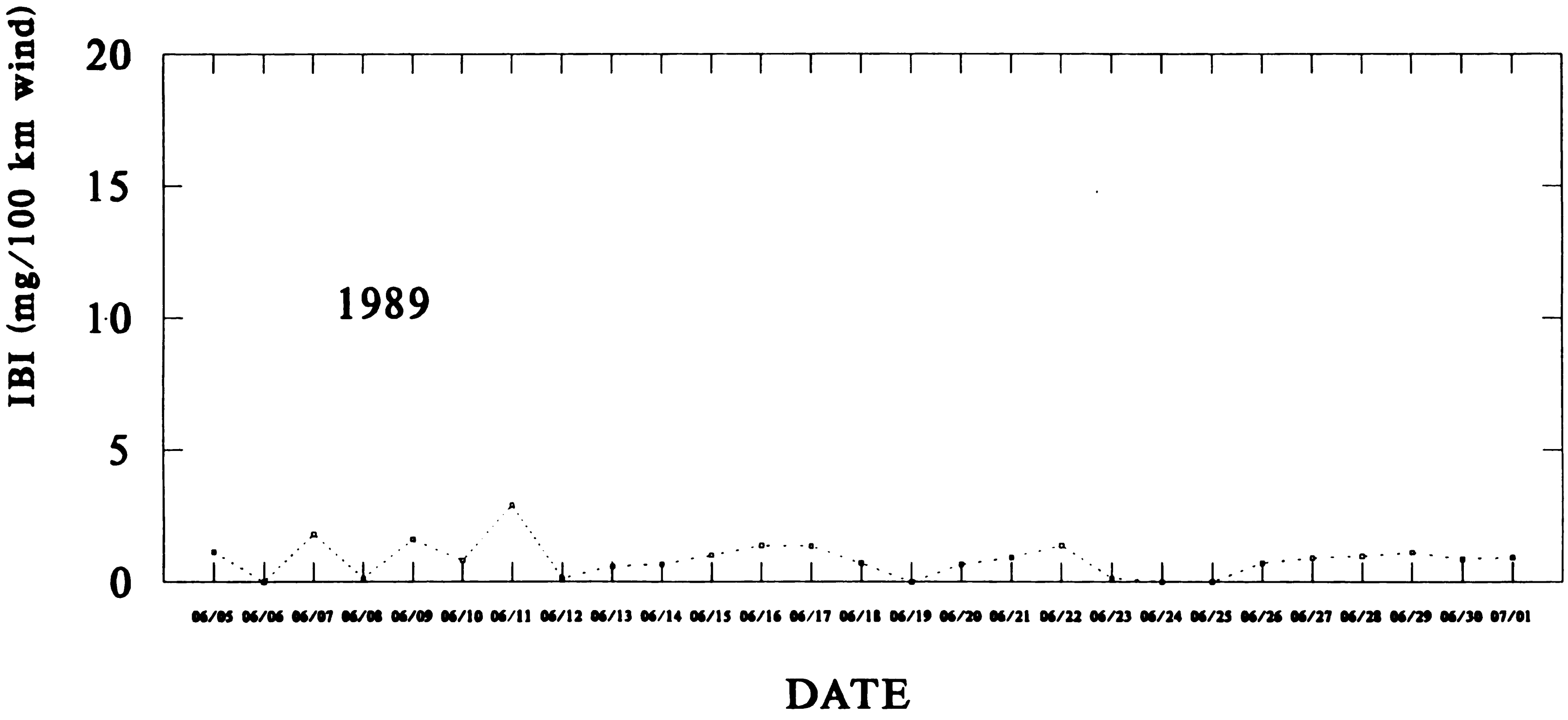

IBI (mg/100 km wind)
20
15
10
5
0
1989
06/05 06/06 06/07 06/08 06/09 06/10 06/11 06/12 06/13 06/14 06/15 06/16 06/17 06/18 06/19 06/20 06/21 06/22 06/23 06/24 06/25 06/26 06/27 06/28 06/29 06/30 07/01
DATE

FIGURE 6

in

als

ave

acc

the

mor

and

Bac

bec

the

tw

si

pa

as

(l

ed

pe

ne

an

er

we

in

le

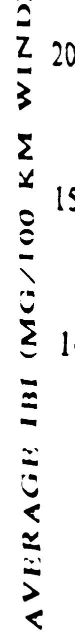
in

in IBIs similar to those occurring in 1987. Figure 7 also shows the mean IBI for each year and seven year averages at Hussell's three study sites. Taking into account Hussell and Quinney's more efficient tow nets, their Sewage Lagoon Site (SL) had IBI measures that were more than twice my average 1986 and 1987 IBI measures and 5 times the IBI values for 1988 and 1989. Their Backus Field Site (BF) contained far fewer insects because of the lack of any nearby ponds and had about the same daily IBI measures as occurred during the first two years of my study. Whenever large enough sample sizes exist, I compare the reproductive performance of parents raising broods in the first two years (hereafter as the MORE FOOD years) compared to the last two years (likewise, as the LESS FOOD years).

Figure 8 shows the percentage of insects collected in all of my tow nets by size and taxa. Forty-seven percent of these were dipterans, half of which were nematocerans and the other categorized as other dipterans. Also abundant in the tow net catches were homopterans (25%) and hymenopterans (9%). In low numbers were tabanids, hemipterans and ephemeropterans. Most insects in the other insect categories included coleopterans and arachnids. The most common size of insects caught in the tow nets were of the smallest

FIGURE 7.

Mean IBI measures (mg dry weight of insects/100 km of wind) for each year (± 1 S.E.). Also given are the seven year averages for three of Hussell and Quinney's Sites. Their sites are Sewage Lagoon (SG), Backus Field (BF) and Long Point (LP).


AVERAGE IBI (MG/100 KM WIND)
20
15

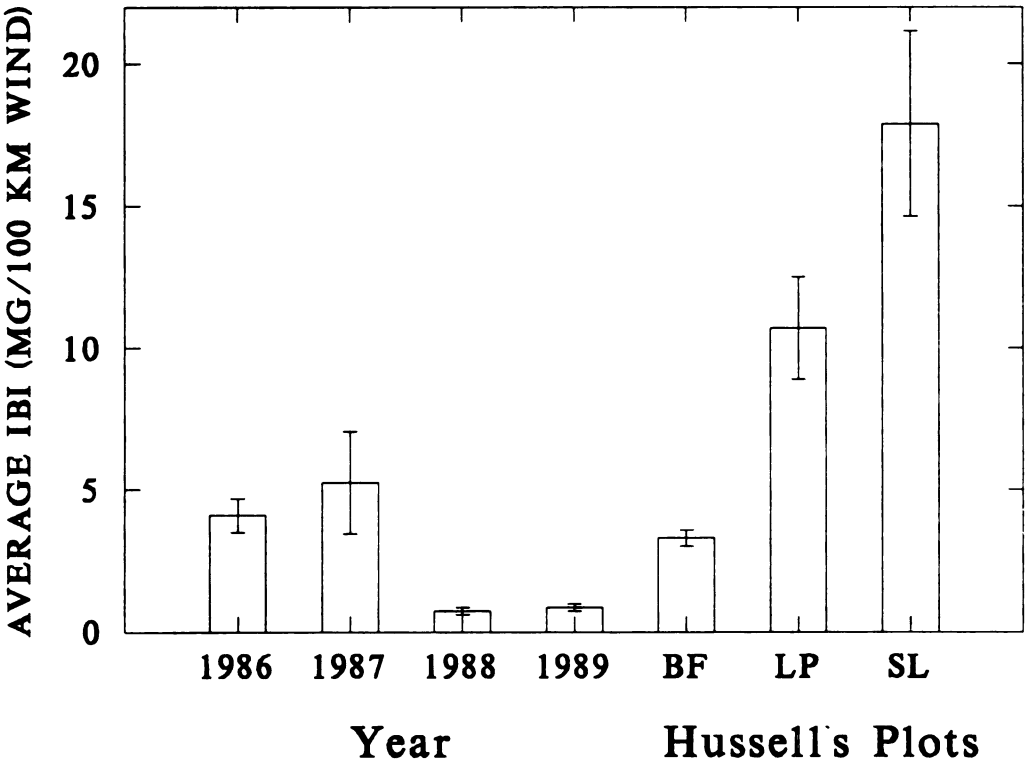

AVERAGE IBI (MG/100 KM WIND)
20
15
10
5
0
1986
1987
1988
1989
BF
LP
SL
Year
Hussell's Plots

FIGURE 7

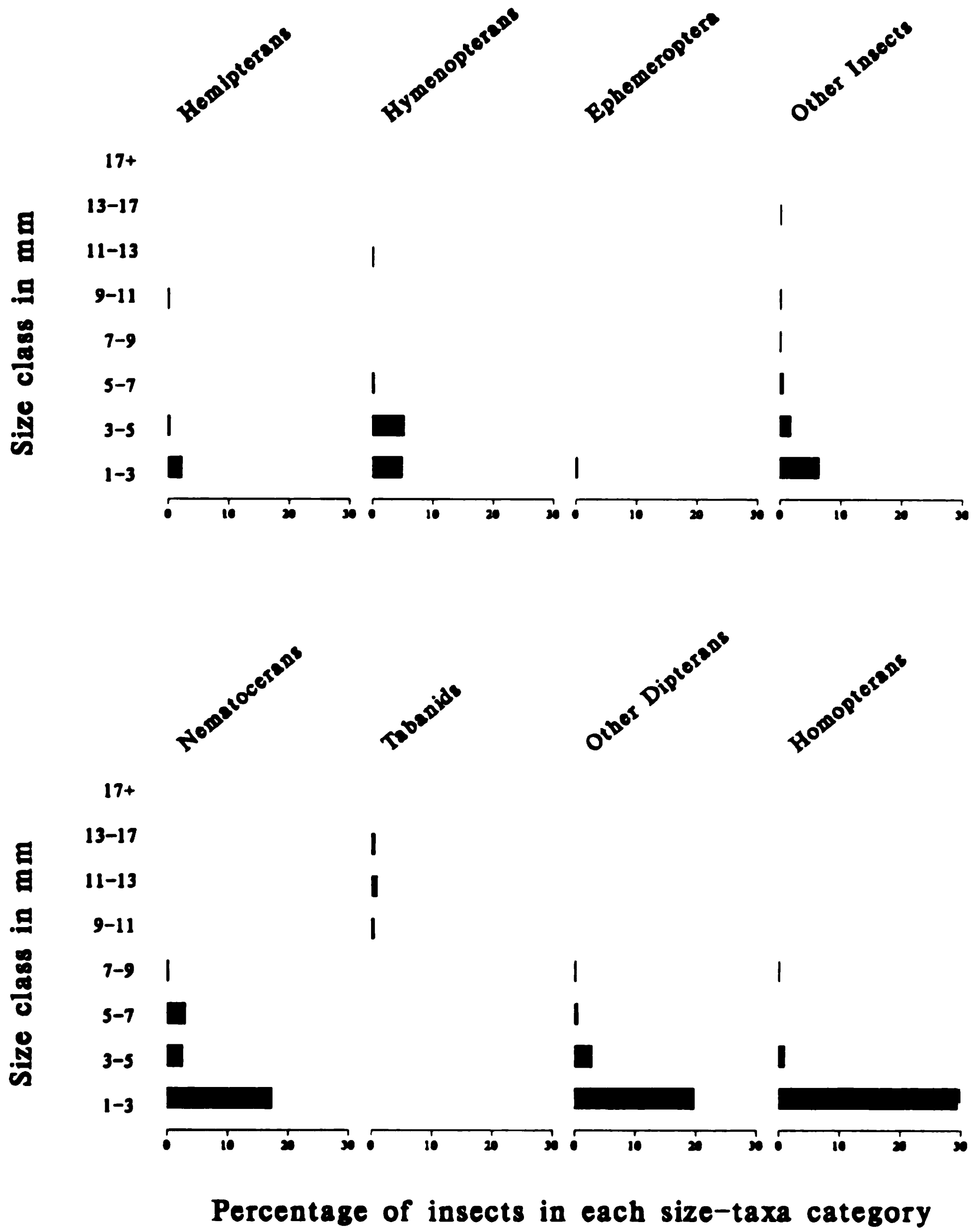


FIGURE 8.

Size-taxa distribution of insects (in percent of the total) captured by my tow nets for the entire four-year study.

size category, 1-3 mm (65%). Insects smaller than 1 mm were excluded from the above counts because they do not show up in food boluses of the tree swallow (Quinney 1983a, Hussell and Quinney 1987, this study).

The size-taxa distribution of insects trapped in Hussell's two nets are shown in Figure 9. Hussell and Quinney's nets captured slightly more nematocerans that mine. A correlation of the numbers of insects in each taxa between tow nets of differing construction did exist (Spearman rho = 0.922), suggesting that both tow net constructions performed similarly in sampling the insect fauna.

The Manitoba traps, operational for 24 days in 1988 and 25 days in 1989, trapped 2308 insects. Sixty-seven percent were tabanids and 31% were classified as other dipterans (Figure 10). The Manitoba traps were not operational for 4 days and 3 days, for 1988 and 1989 respectively, due to extremely strong winds. Daily Manitoba trap collections are given in Figures 11 and 12. The daily dry weights for 1988 (median= 1.12 grams) was significantly greater than for 1989 (median=0.074 grams, Mann Whitney U test, X^2=7.053, df=1, $P < 0.01$) but the numbers of insects caught in these traps was not significantly different between years (Mann-Whitney U test, $X^2 = 0.595$, df=1, $P = 0.441$). The low daily dry weights for the first two

Size class in mm

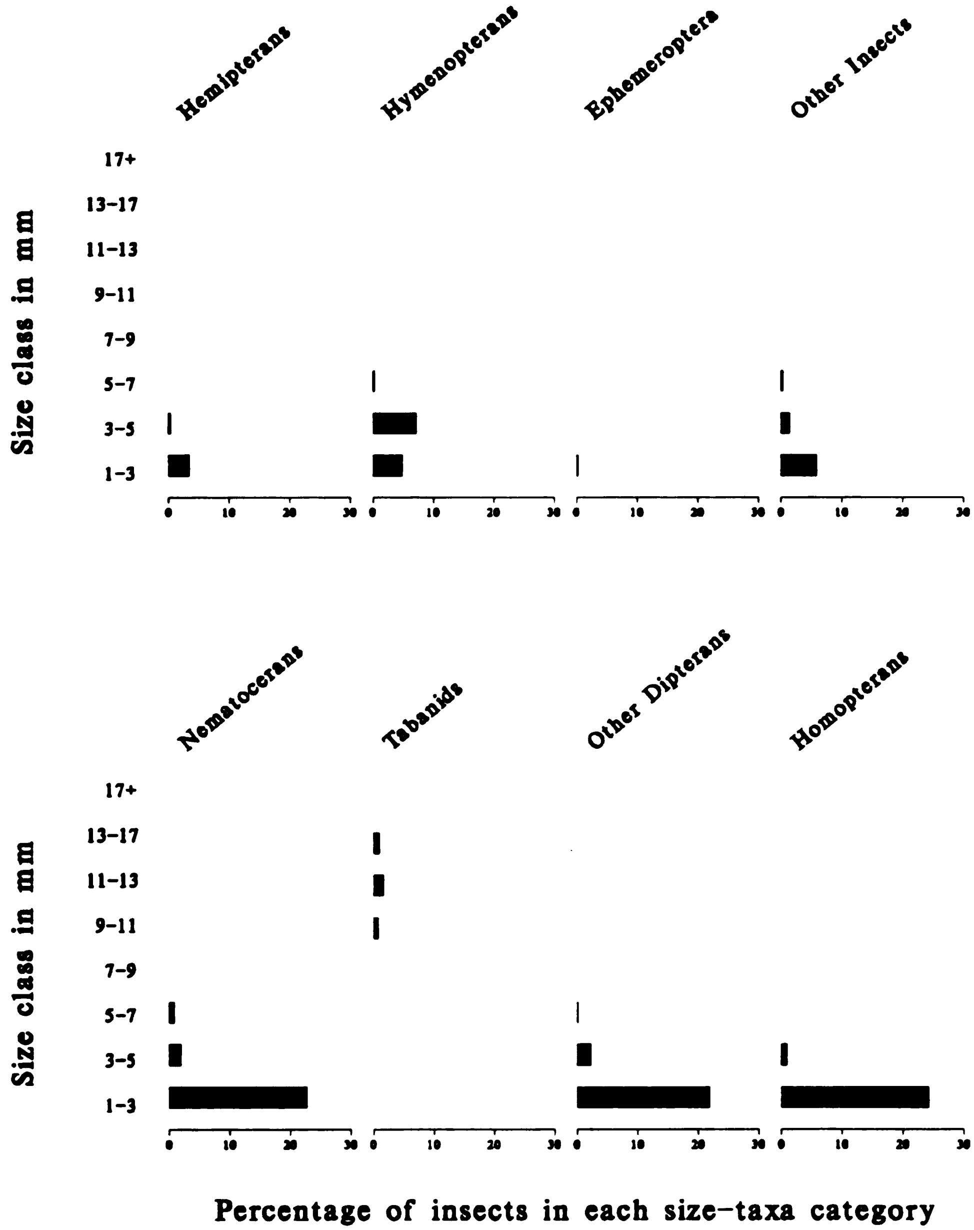


FIGURE 9.

Size-taxa distribution of insects (in percent of total) captured in Hussell and Quinney's version of the tow nets for the 1988 and 1989 seasons.

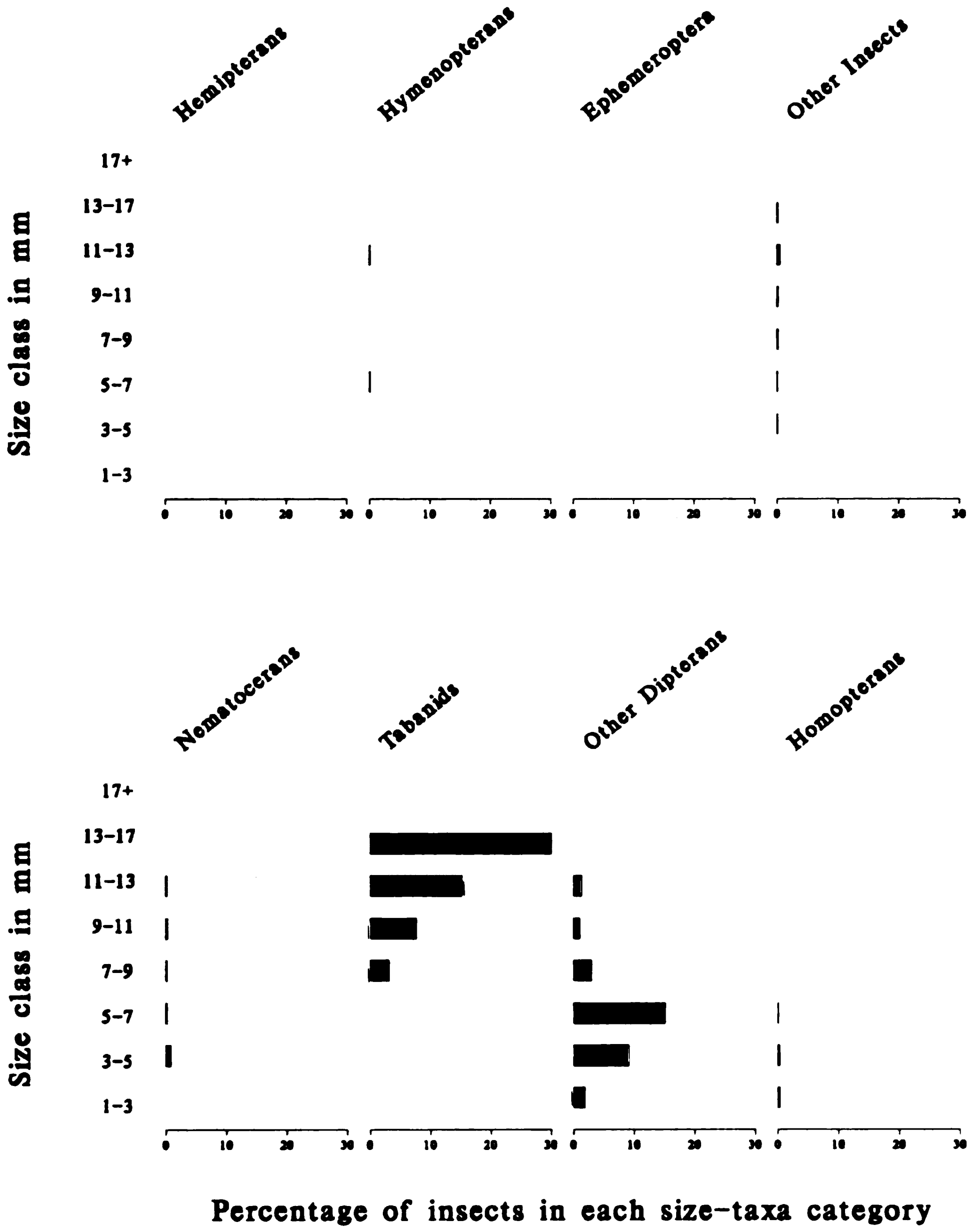
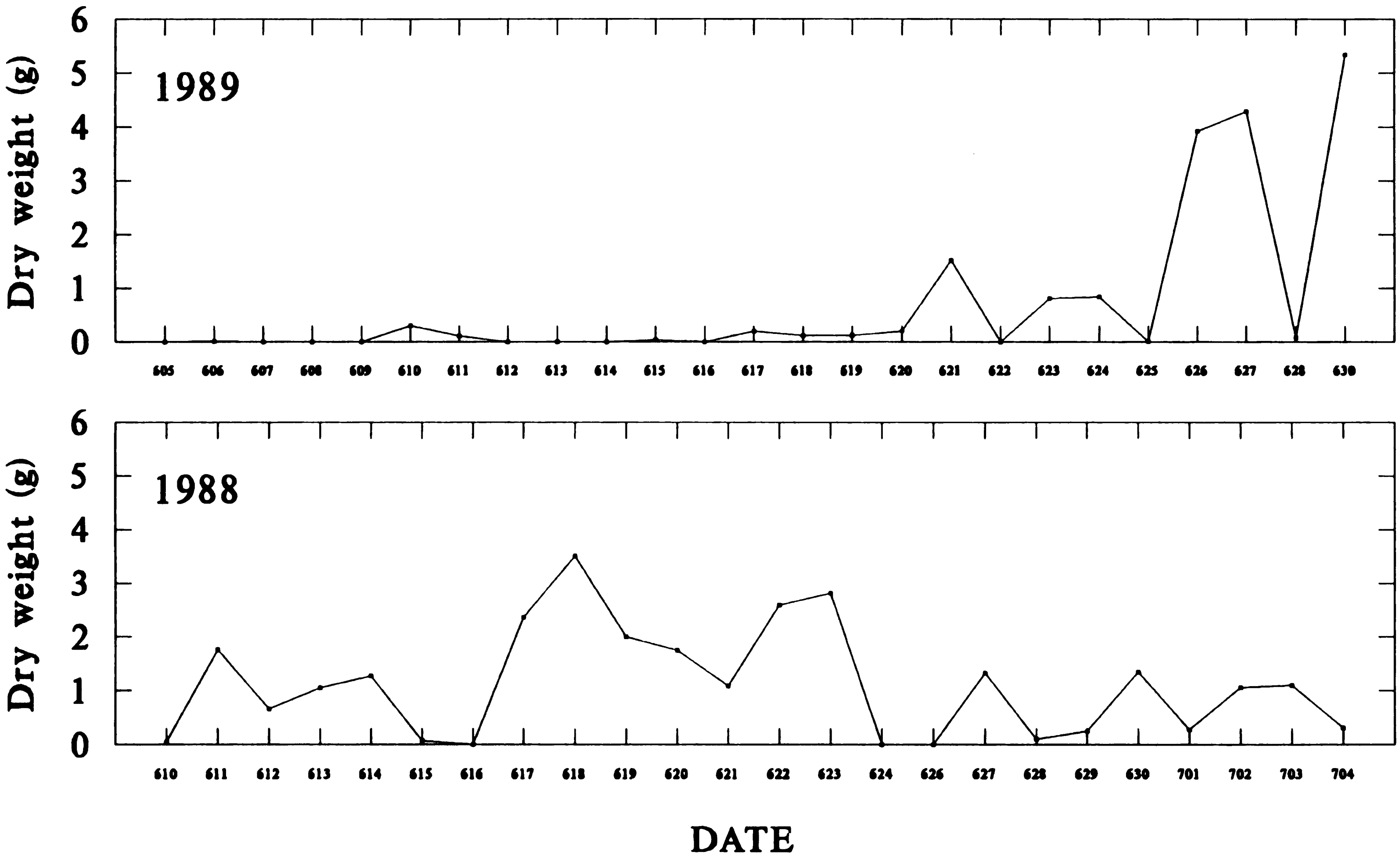


FIGURE 10.

Size-taxa distribution of insects (in percent of total) captured my the Manitoba traps for the 1988 and 1989 season.

FIGURE 11.

Daily dry weights of insects captured in the Manitoba traps for 1988 and 1989.



6
5
4
3
2
1
0
Dry weight (g)
1989
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
630
1988
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
626
627
628
629
630
701
702
703
704
DATE

FIGURE 11

FIGURE 12.

The daily numbers of insects captured in the Manitoba traps for 1988 and 1989.

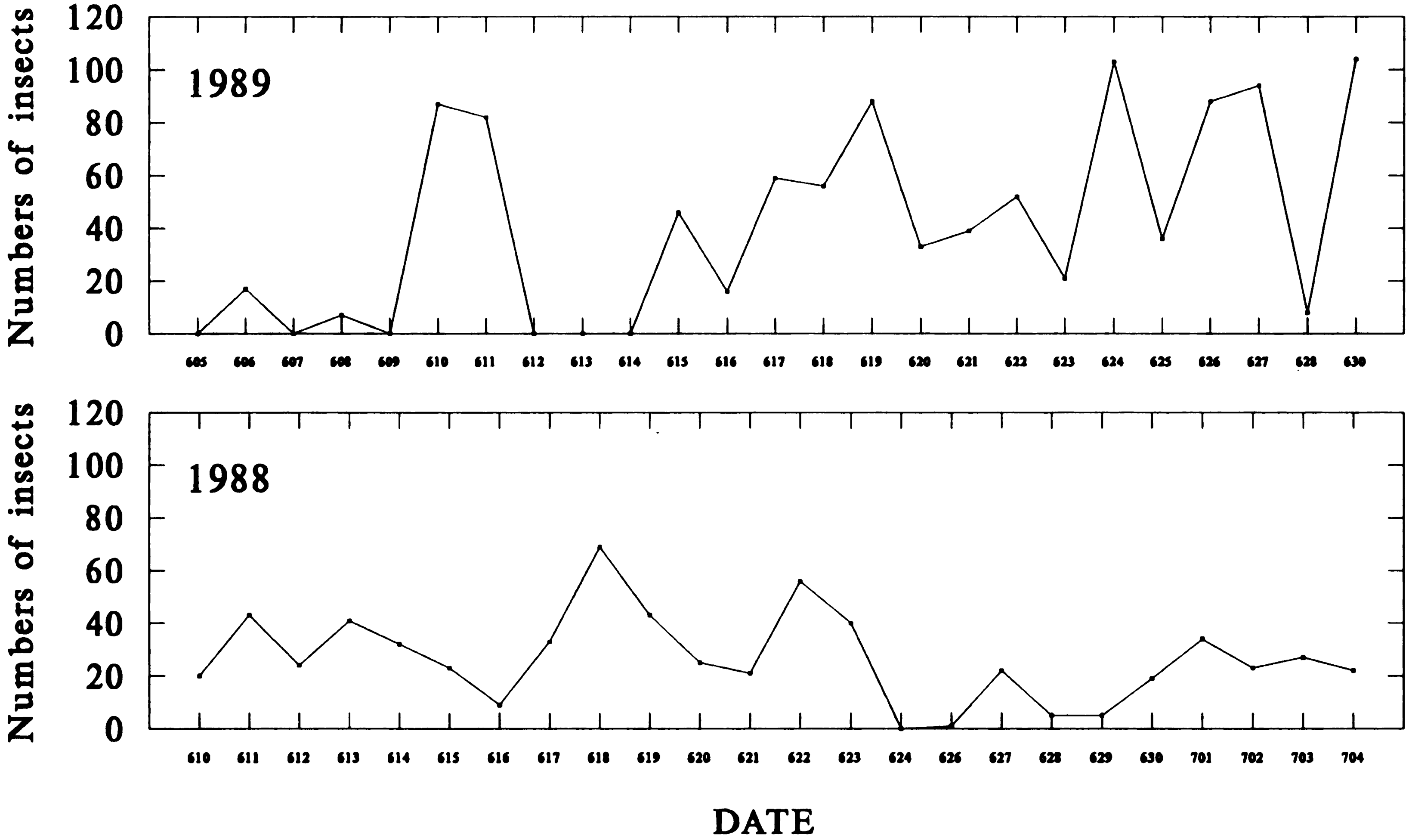

1989
1988
Numbers of insects
120
100
80
60
40
20
0
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
630
629
701
702
703
704
DATE

FIGURE 12

weeks of 1989 reflect the poor weather conditions during this period. The peaks and valleys of daily dry weights mirrors that of daily numbers of insects except during the poor weather period of 1989.

Insects caught in the Manitoba traps were much larger than those caught in the tow nets (Figure 10). Nearly one-third of all of the insects belonged to the 13-17mm, tabanidae category. In addition, the insects categorized as other dipterans caught in these traps were also larger than those in the other dipteran category trapped in the tow nets. Very few of the 1-3mm size class insects were found in the Manitoba traps.

I also found a significant positive correlation (Pearson $r=0.472$, $df=96$, $P < 0.001$) between the daily dry weight of insects trapped in the Manitoba traps and the daily dry weight of the insects collected in the tow nets. Thus, active insects were abundant during the same days that the wind-blown insects (e.g. nematocerans) were abundant. The dry weights and numbers of insects in the Manitoba traps were not correlated with daily wind speeds ($P > 0.50$ in both cases).

Fledging success and nestling death. Fledging success by year was 85% (51/60), 77% (46/60), 70% (60/85) and 57% (34/60) for 1986, 1987, 1988 and 1989, re

=

p

t

N

O

f

t

t

f

r

s

=

t

respectively. This difference was highly significant ($G = 12.71$, $df=3$, $P < 0.01$). During this four-year study, parents of SYNCHRONOUS broods fledged a greater proportion of their nestlings, followed by DOUBLE ASYNCHRONOUS and then SINGLE ASYNCHRONOUS broods (Figure 13). One SYNCHRONOUS brood was predated and was not used for fledging success calculations. Combining hatching treatments, nestlings hatching first (i.e. 'A' nestlings) fledged with a greater than 80% success rate, followed by 'B' chicks fledging at a lower than 50% rate and then 'C' chicks at a 25% rate. Fledging success was more pronounced between hatch positions ($G = 34.54$, $df=2$, $P \ll 0.001$) than across pooled hatching treatments ($G=5.3$, $df=2$, $P < 0.05$). In both asynchronous brood types, fledging success decreased with decreasing hatch position. The greatest fledging success was by 'A' chicks in DOUBLE ASYNCHRONOUS broods.

Fledging success was significantly greater in the first two years of the study (81%) compared to the latter two years of the study (65%) ($G = 10.08$, $df=1$, $P < 0.005$). During the two years of MORE FOOD abundance (Figure 14), fledging success increased, although not significantly, with more synchrony ($G= 1.30$, $df=2$, $P < 0.10$). During the LESS FOOD years, fledging success increased with greater hatching asynchrony ($G=0.72$, $df=2$, $P < 0.10$). All incidences of entire brood

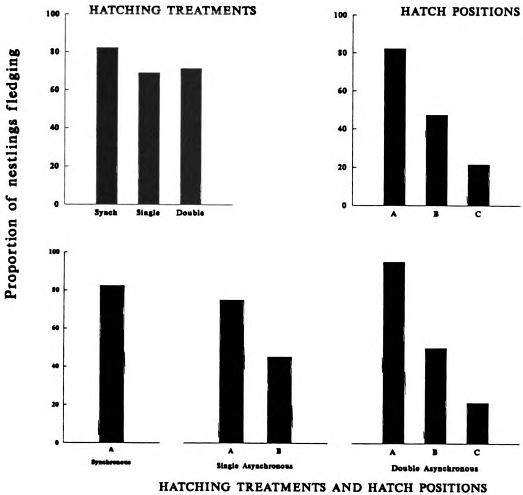


FIGURE 13.

Fledging success of nestlings for the four-year study by hatching treatment and hatch position.

starvation occurred during the LESS FOOD years. Entire brood starvation rate increased with increasing synchrony. Of SYNCHRONOUS broods, two nests (2/10 = 20%) experienced entire nest starvation during LESS FOOD years, and of SINGLE ASYNCHRONOUS broods, only one of these nests, (1/9 = 11%), experienced entire nest starvation. No DOUBLE ASYNCHRONOUS broods experienced entire brood starvation during the four year study. Additionally, the incidence of partial brood loss, which I defined as any broods fledging between 1 and 4 young, increased with greater asynchrony when food was more limited; partial brood loss occurred in 40%, 64% and 71% of the SYNCHRONOUS, SINGLE and DOUBLE ASYNCHRONOUS nests, respectively. However, partial brood loss was low in SYNCHRONOUS broods when there was more food, occurring in 25% of these nests, and was high in asynchronous broods, occurring in 77% and 57% of the SINGLE and DOUBLE ASYNCHRONOUS broods, respectively.

I also determined the incidence of brood reduction by calculating the survival of late-hatching nestlings relative to the 'A' chicks (survival 'B' or 'C' chick/survival 'A' chick). For MORE FOOD years, 'B' chicks in SINGLE ASYNCHRONOUS nests fledged at a 57% rate compared to 'A' chicks. In DOUBLE ASYNCHRONOUS broods, relative survival of 'B' and 'C' chicks was 77% and 63%, respectively. In

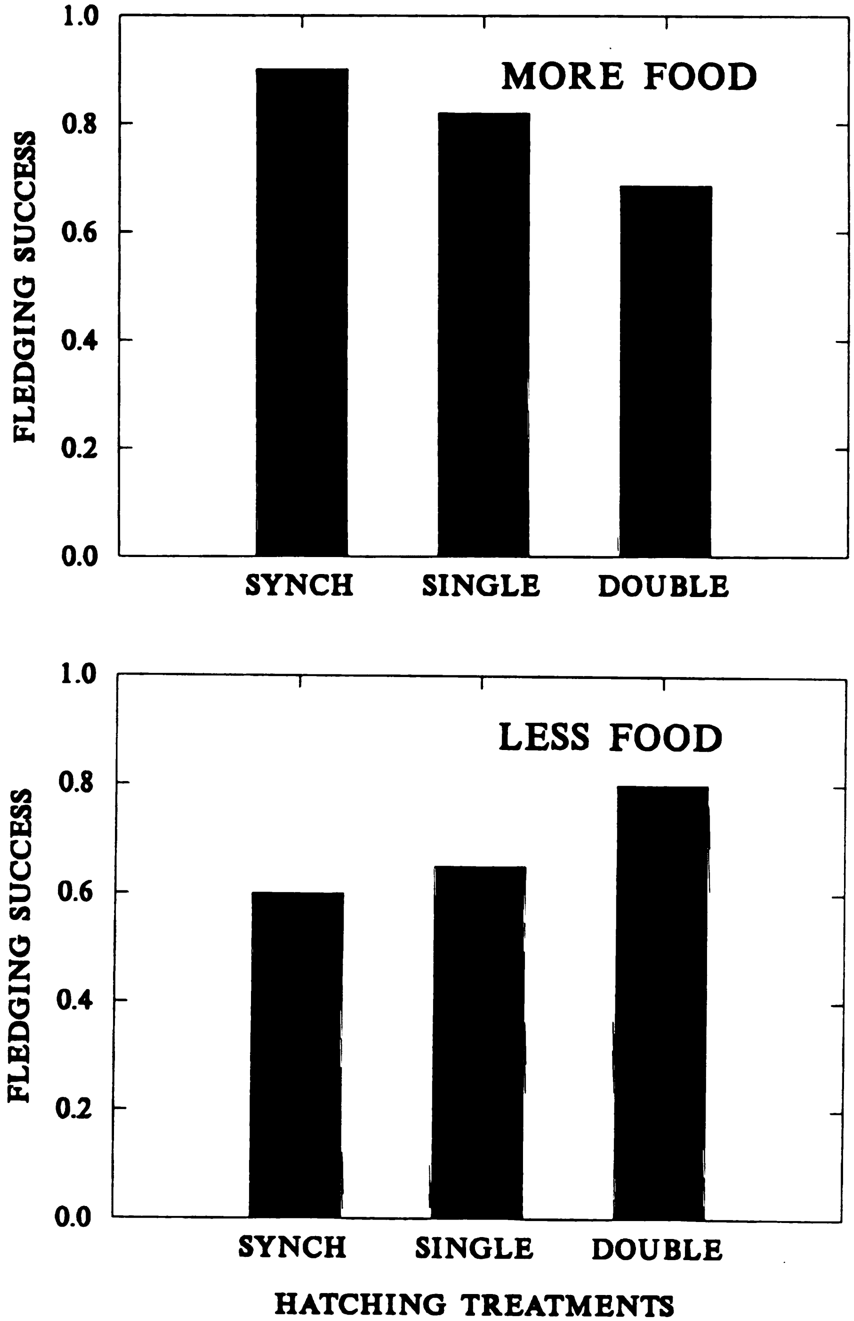


FIGURE 14.

Nestling fledging success by food year type, hatching treatment and hatch position. Food year types are MORE FOOD and LESS FOOD.

LESS FOOD years, the relative survival of 'B' chicks was 63% in SINGLE ASYNCHRONOUS broods, and 71% and 42%, for 'B' and 'C' chicks, survival of 'B' and 'C' chicks was 77% and 63%, respectively. In the LESS FOOD years, relative survival of 'B' chicks was 63% in SINGLE ASYN-CHRONOUS broods, and 71% and 42%, for 'B' and 'C' chicks, respectively, in DOUBLE ASYNCHRONOUS nests. Brood reduction, by the death of the 'C' chick, was most prominent in DOUBLE ASYNCHRONOUS broods when food was less abundant. Therefore, brood reduction in DOUBLE ASYNCHRONOUS broods increased the fledging success of these broods when food was less abundant compared to the other two hatching treatments.

The age that nestlings died, by hatch position and hatching treatment, is given in Figure 15. There is no significant difference between the age of nes-tling deaths in any of the hatching treatments (Krus-kal-Wallis, H=1.871, df=2, P=0.392). However, in DOUBLE ASYNCHRONOUS nests, the age of nestling death was significantly different between hatch positions (Kruskal-Wallis, H=8.88, df=2, P = 0.012); with 'C' chicks dying at a significantly younger age than 'B' chicks, which in turn, died earlier than the 'A' chicks.

Nestling deaths occurred significantly earlier

FIGURE 15.

Age of nestling deaths by hatching treatment and hatch position. Hatch position legend is located on the lower left corner of each plot.

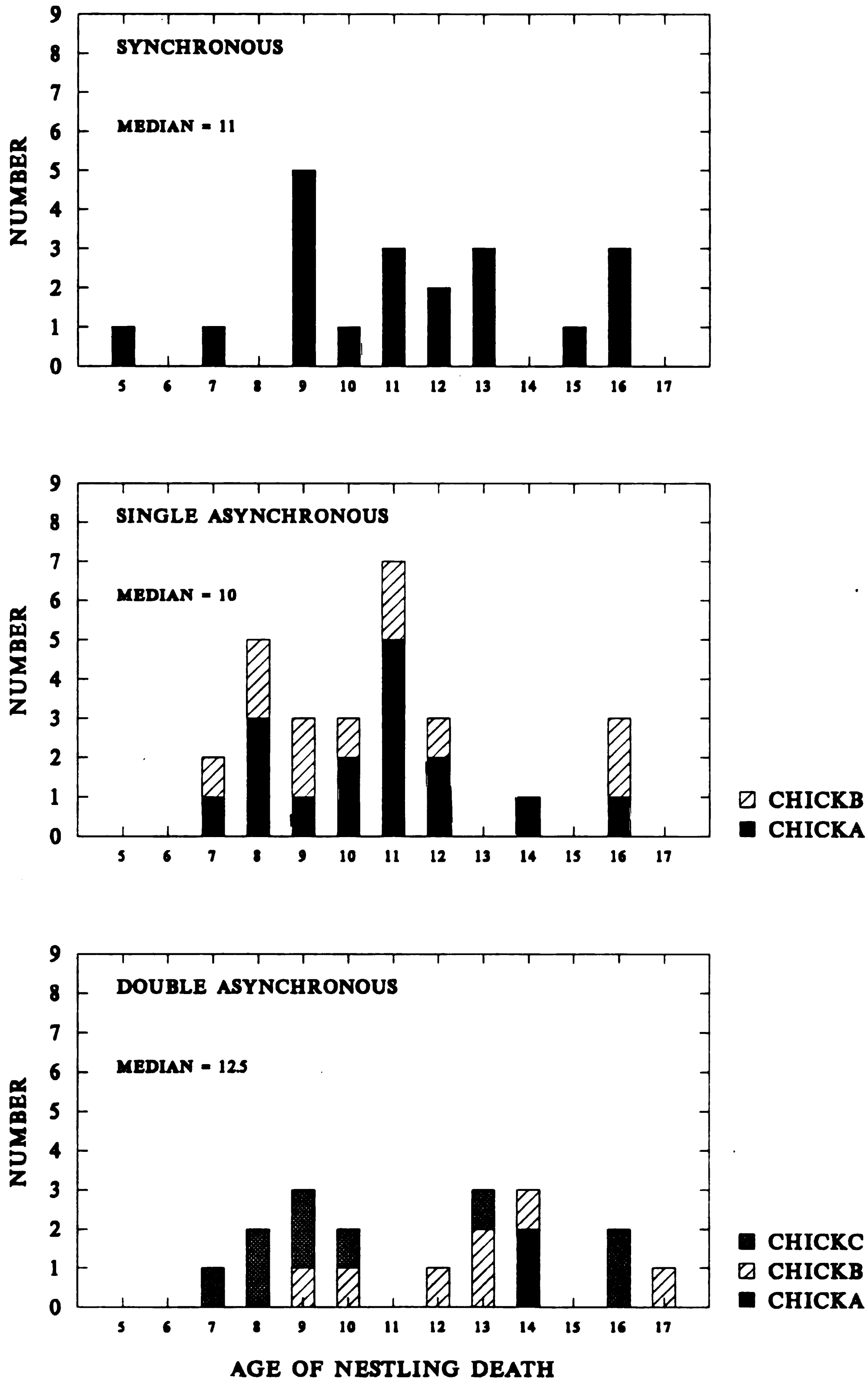

SYNCHRONOUS
MEDIAN = 11
SINGLE ASYNCHRONOUS
MEDIAN = 10
CHICKB
CHICKA
DOUBLE ASYNCHRONOUS
MEDIAN = 12.5
CHICKC
CHICKB
CHICKA
NUMBER
AGE OF NESTLING DEATH

FIGURE 15

in LESS FOOD years than in MORE FOOD years (Mann-Whitney, U=810.5, df=1, $P < 0.001$). There was no difference between hatching treatments in the age of nestling deaths during the MORE FOOD years (Kruskal-Wallis, H=2.653, df=2, P=0.265) or during the LESS FOOD years (Kruskal-Wallis, H=2.349, df=2, P=0.309). However, nestling deaths occurred at a significantly earlier age in LESS FOOD years compared to MORE FOOD years with increasing hatching asynchrony; at a slightly significant earlier age in SYNCHRONOUS broods (Mann-Whitney, U=55.0, df=1, P=0.056), to a significantly earlier age in SINGLE ASYNCHRONOUS broods (Mann-Whitney, U=121.5, df=1, P=0.031) to a very significantly earlier age in DOUBLE ASYNCHRONOUS broods (Mann-Whitney, U=550.0, df=1, P=0.008).

Nestling Growth and Development. Nestling growth curves for body weight increase, tarsus, ulna, wing chord and ninth primary growth, are given in Figures 16-20. The growth curve for body weight increase illustrates the four phases of tree swallow weight growth. The early phase of growth is a rapid, exponential trajectory which levels off to the second phase of growth which is linear. The third phase is characterized by growth rate cessation, where a peak in body mass is reached several days before fledging. Common of cavity nesting birds is the fourth phase of growth, weight recession, which occurs just prior fledging. Ricklefs (1968) has attributed this weight recession in hirundines to water loss due to feather growth and maturation. Growth of tarsus and ulna follow a similar logistic growth curve, growth of the wing chord models an exponential trajectory and the growth of the ninth primary approximates a linear relationship. Analysis of linear body weight growth, age of yolk depletion and eye opening are performed on all nestlings surviving long enough to obtain measures. All of these variables had heteroscadastic variances which could not be removed using transformation and one-way nonparametric analyses were performed. The analysis of body weight growth, tarsus, ulna, wing cord, primary and maximum weight are performed on those nestlings that fledged. These data adhered to the assumptions for the analysis of variance. I present growth data under four different subheadings: (1) growth of all nestlings; (2) growth of nestlings that fledged; (3) dynamics of nestling weights; and (4) affects of food abundance on nestling growth.

1. Growth of all nestlings. Nestling linear of growth rates for weight were significantly greater in MORE FOOD years than in LESS FOOD years (Mann-Whitney, $U = 3083.0$, $df=1$, $P = 0.022$). Nestlings in LESS FOOD years grew 10% slower than nestlings of MORE

FIGURE 16.

Mean body weight measures ($\pm$ 1 S.E.) of all nestlings by age (days post-hatch, DPH) and hatching treatment.

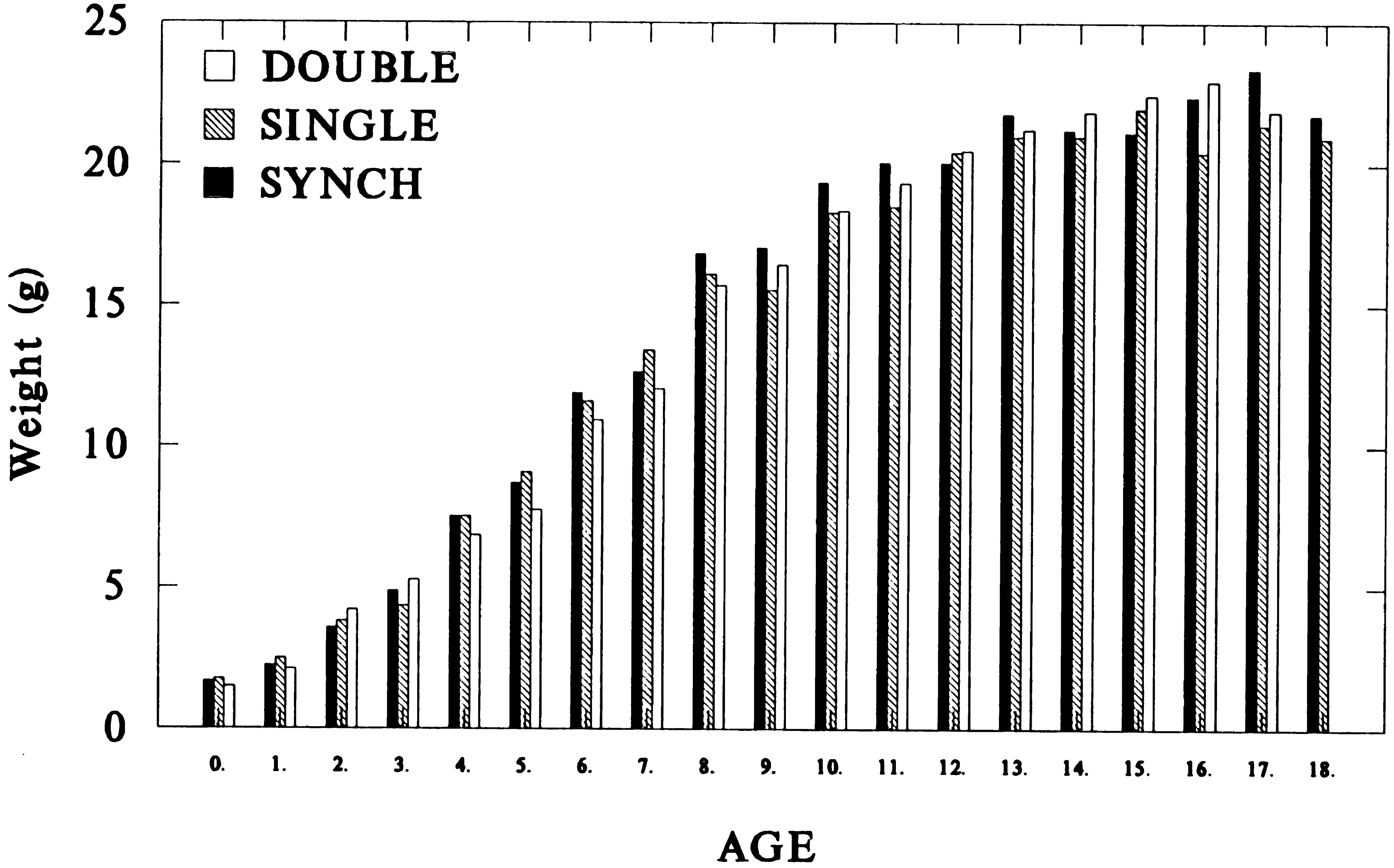
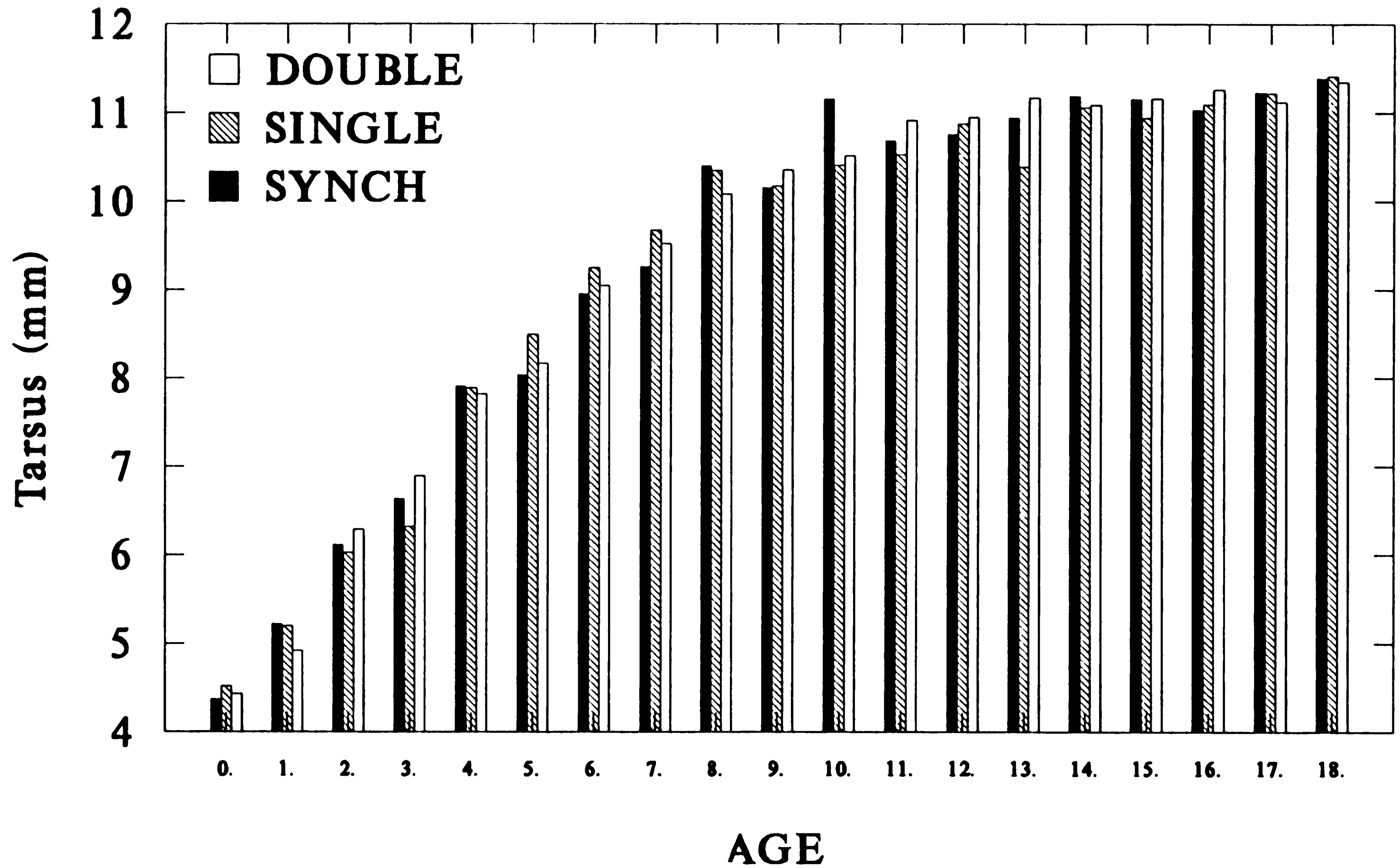

DOUBLE
SINGLE
SYNCH
Weight (g)
25
20
15
10
5
0
0.
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
AGE

FIGURE 16

FIGURE 17.

Mean tarsus measures ($\pm$ 1 S.E.) of all nestlings by age (days post-hatch, DPH) and hatching treatment.



DOUBLE
SINGLE
SYNCH
Tarsus (mm)
12
11
10
9
8
7
6
5
4
0.
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
AGE

FIGURE 17

FIGURE 18.

Mean ulna length measures ($\pm$ 1 S.E.) of all nestlings by age (days post-hatch, DPH) and hatching treatment.

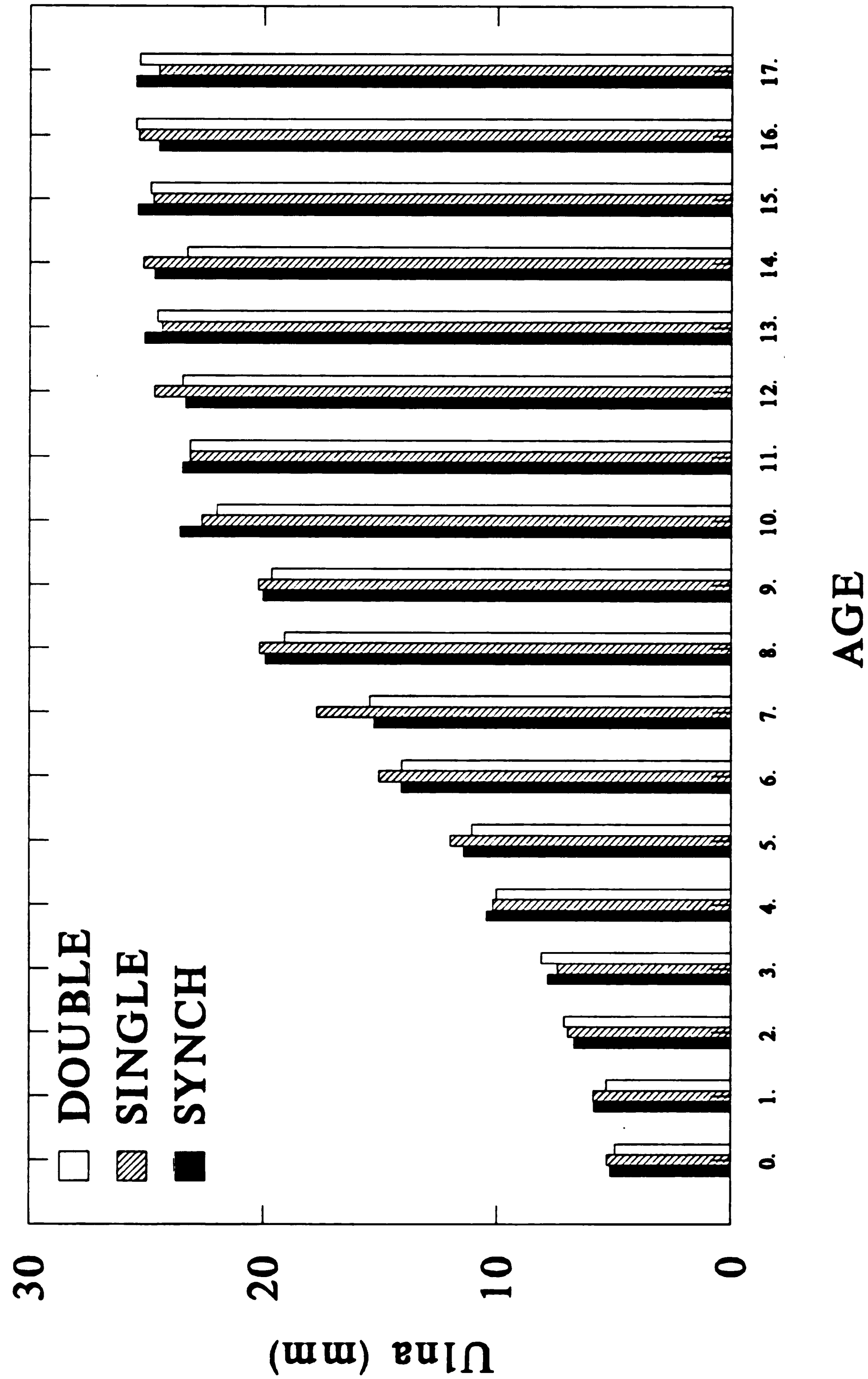

DOUBLE
SINGLE
SYNCH
Ulna (mm)
0
10
20
30
0.
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
AGE

FIGURE 18

FIGURE 19.

Mean wing chord measures (± 1 S.E.) of all nestlings by age (days post-hatch, DPH) and hatching treatment.

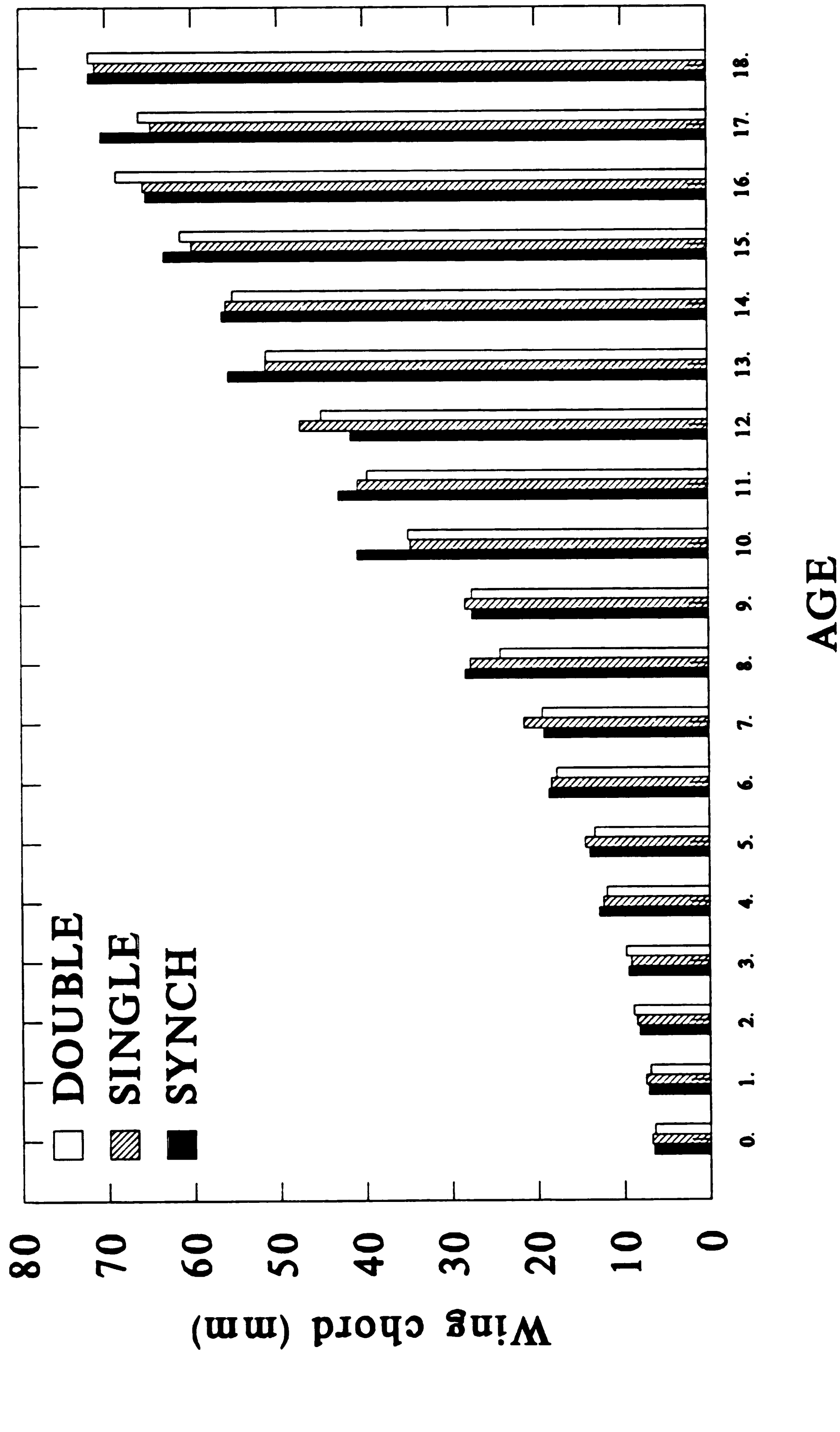

DOUBLE
SINGLE
SYNCH
Wing chord (mm)
0
10
20
30
40
50
60
70
80
AGE
0.
1.
2.
3.
4.
5.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.

FIGURE 19

FIGURE 20.

Mean length of ninth primary ($\pm$ 1 S.E.) for all nestlings by age (days post-hatch, DPH) and hatching treatment.

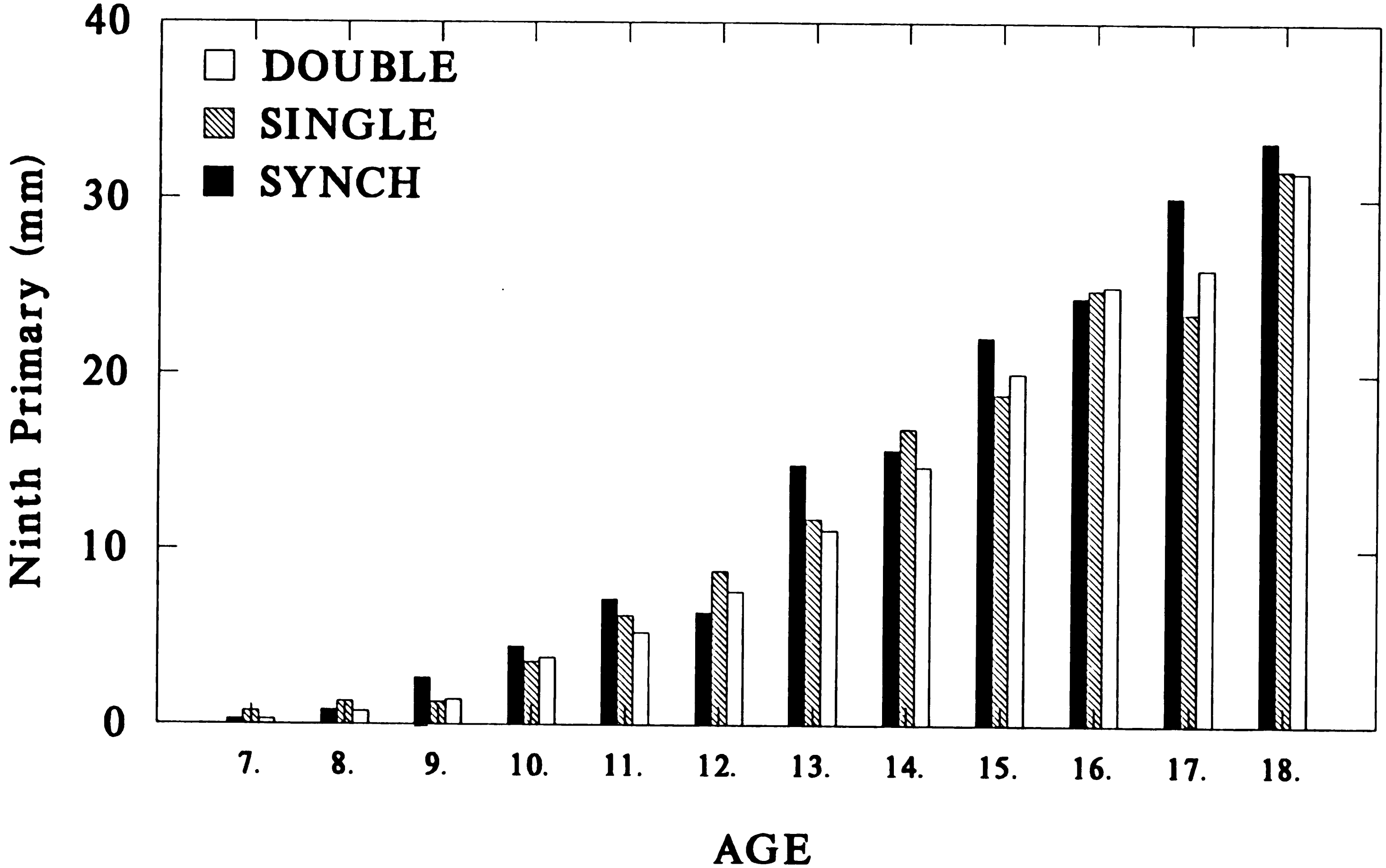

DOUBLE
SINGLE
SYNCH
Ninth Primary (mm)
0
10
20
30
40
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
AGE

FIGURE 20

FOC

SYN

two

bro

bet

Wal

FOO

were

P=0

incr

LESS

P=0.

almo

diff

tion

fitt

hatc

as u

tlin

CHRO

nous

diff

earl

trea

FOOD years. During MORE FOOD (Figure 21), nestlings in SYNCHRONOUS broods grew faster than nestlings in the two asynchronous broods; nestlings in asynchronous broods had similar growth rates. However, differences between hatching treatments were significant (Kruskal-Wallis, $H=15.47$, $df=2$, $P < 0.001$). During the LESS FOOD years, growth rates between hatching treatments were not significant (Kruskal-Wallis, $H=1.645$, $df=2$, $P=0.439$). The linear weight growth rates increased with increasing hatch position (Figure 22) in both MORE and LESS food years (Kruskal-Wallis, $H=7.422$, $df=2$, $P=0.024$). In the years of LESS FOOD, 'C' chicks grew almost half as fast as all of the 'A' chicks; this difference was not as great for these same hatch positions during the MORE FOOD years.

I also compared the number of nestlings not fitting the linear model by hatching treatment and hatch position. I considered nonlinear nestling growth as unhealthy growth. More than a quarter of the nestlings grew nonlinearly in the SINGLE and DOUBLE ASYNCHRONOUS nests. Only 13% of the nestlings in synchronous broods grew nonlinearly during this period. The differences in proportions of nestlings growing nonlinearly was significantly different between hatching treatments ($G=14.37$, $df=2$, $P < 0.01$) but not between

FIGURE 21.

Density plots of the linear phase of body weight growth for all nestlings by food year type and hatching treatment.

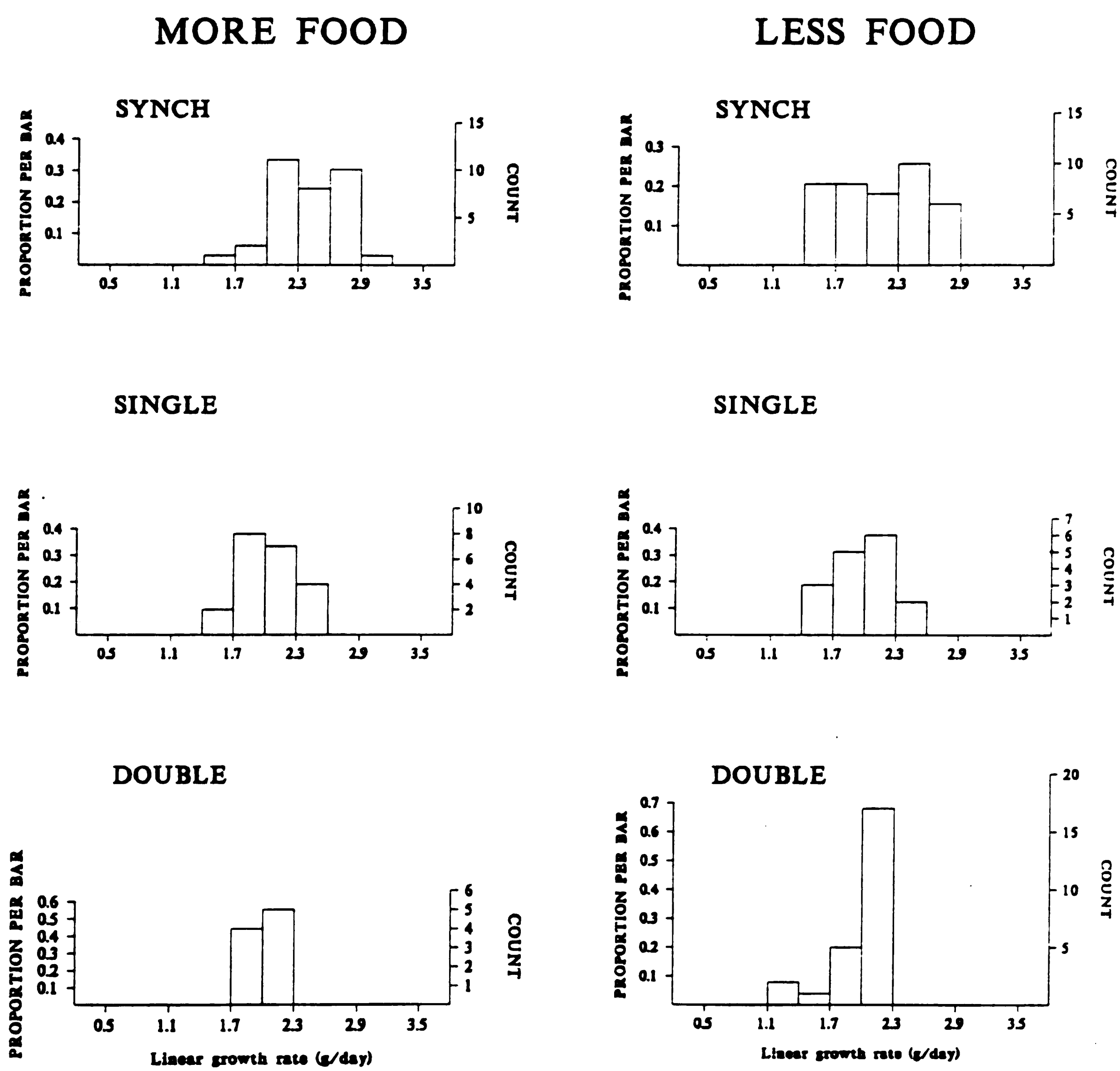
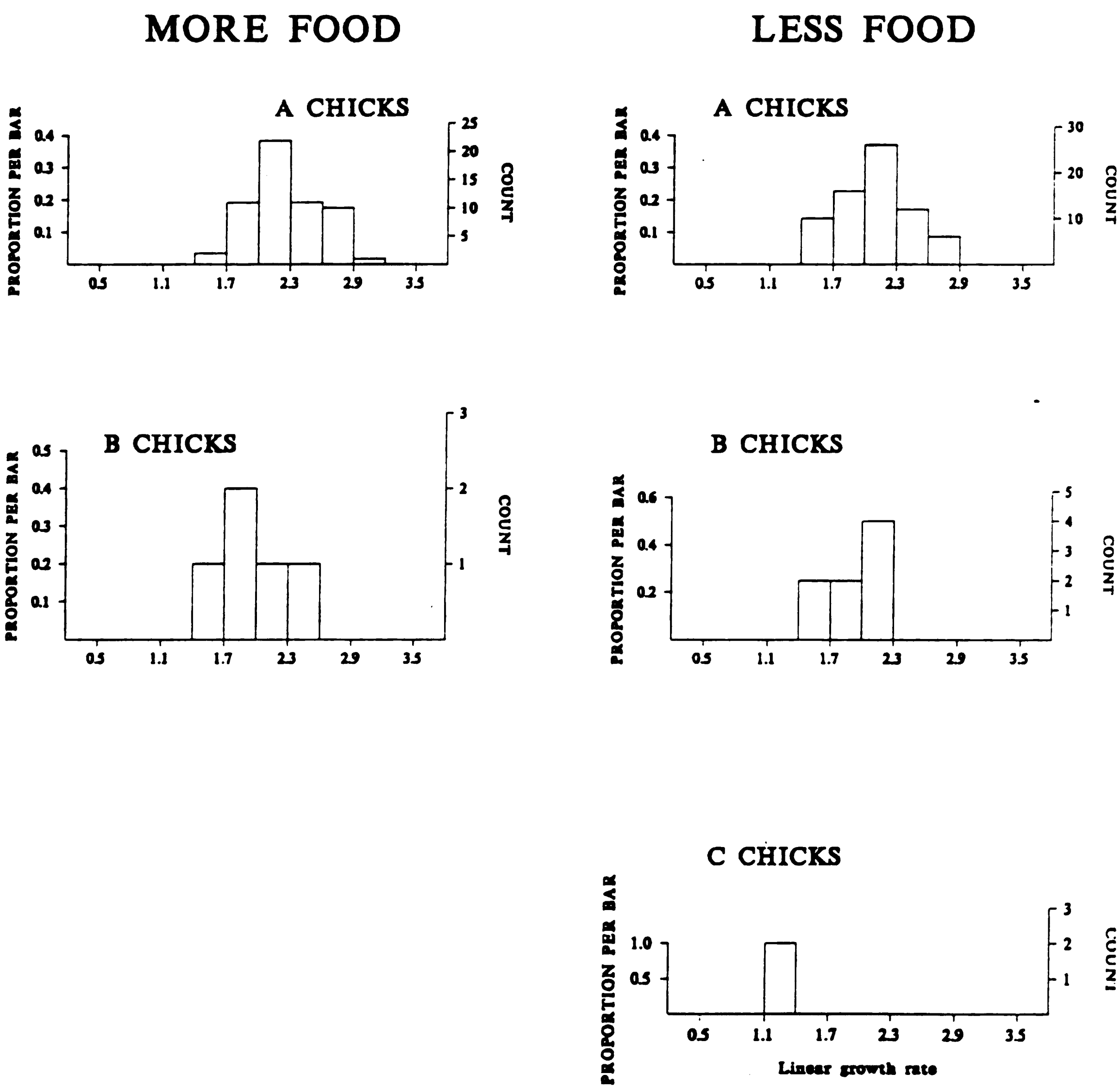

MORE FOOD
LESS FOOD
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
0.5
1.1
1.7
2.3
2.9
3.5
Linear growth rate (g/day)

FIGURE 21

FIGURE 22.

Density plots of the linear phase of body weight growth for all nestlings by food year type and hatch position.



MORE FOOD
LESS FOOD
A CHICKS
B CHICKS
C CHICKS
PROPORTION PER BAR
COUNT
0.5
1.1
1.7
2.3
2.9
3.5
Linear growth rate

FIGURE 22

hatch positions ($G=0.550$, $df=2$, $P > 0.30$). Interestingly, those nestlings growing nonlinearly where not more likely to die than fledge ($G=0.56$ $df=1$, $P > 0.30$).

The pattern of the age of yolk depletion between hatching treatments and food year types is interesting (Figures 23 and 24). Yolk depletion occurred significantly later during MORE FOOD years compared to LESS FOOD years (Mann-Whitney, $U=1149.0$, $df=1$, $P < 0.001$). In the MORE FOOD years, the age of yolk depletion increases with increasing asynchrony with differences between hatching treatments significantly different (Kruskal-Wallis, $H=25.69$, $df=2$, $P < 0.001$). In the LESS FOOD years, the opposite trend is observed with differences between hatching treatments also significant (Kruskal-Wallis, $H=6.592$, $df=2$, $P =0.032$). Yolk depletion occurred earlier with decreasing hatch position in the LESS FOOD years (Kruskal-Wallis, $H=3.639$, $df=2$, $P=0.162$). There were no differences in age of yolk depletion by hatch position in MORE FOOD years.

The eyes opened significantly later during the LESS FOOD years (Figure 25) compared to the MORE FOOD years (Mann-Whitney, $U=1852$, $df=1$, $P < 0.001$). Eye opening occurred later in DOUBLE ASYNCHRONOUS broods compared to other hatching treatments in the MORE FOOD years. The difference in the age of eye opening be-

FIGURE 23.

Density plots of the age of yolk depletion for all nestlings by food year type and hatching treatment.

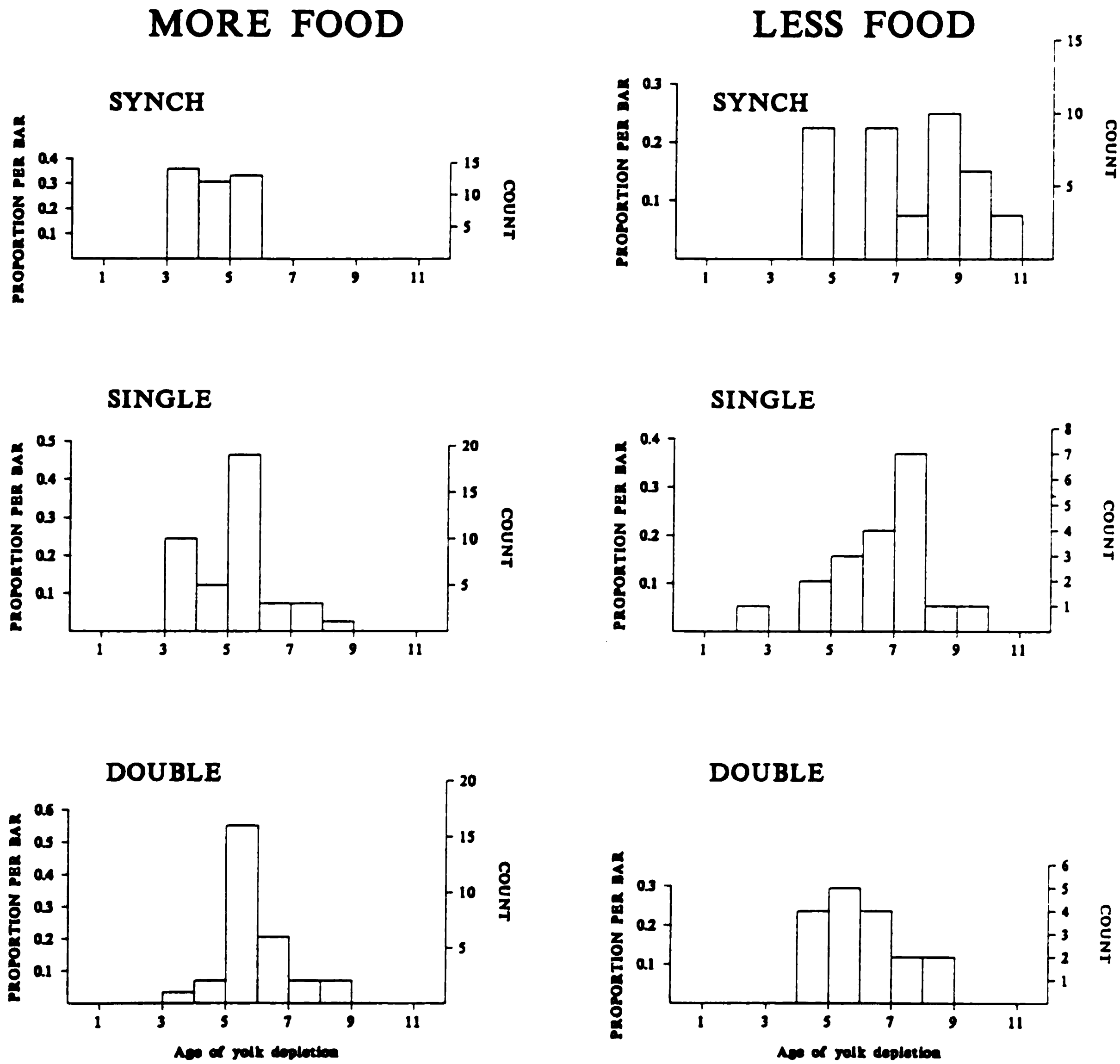

MORE FOOD
LESS FOOD
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
Age of yolk depletion

FIGURE 23

FIGURE 24.

Density plots of the age of yolk depletion for all nestlings by food year type and hatch position.

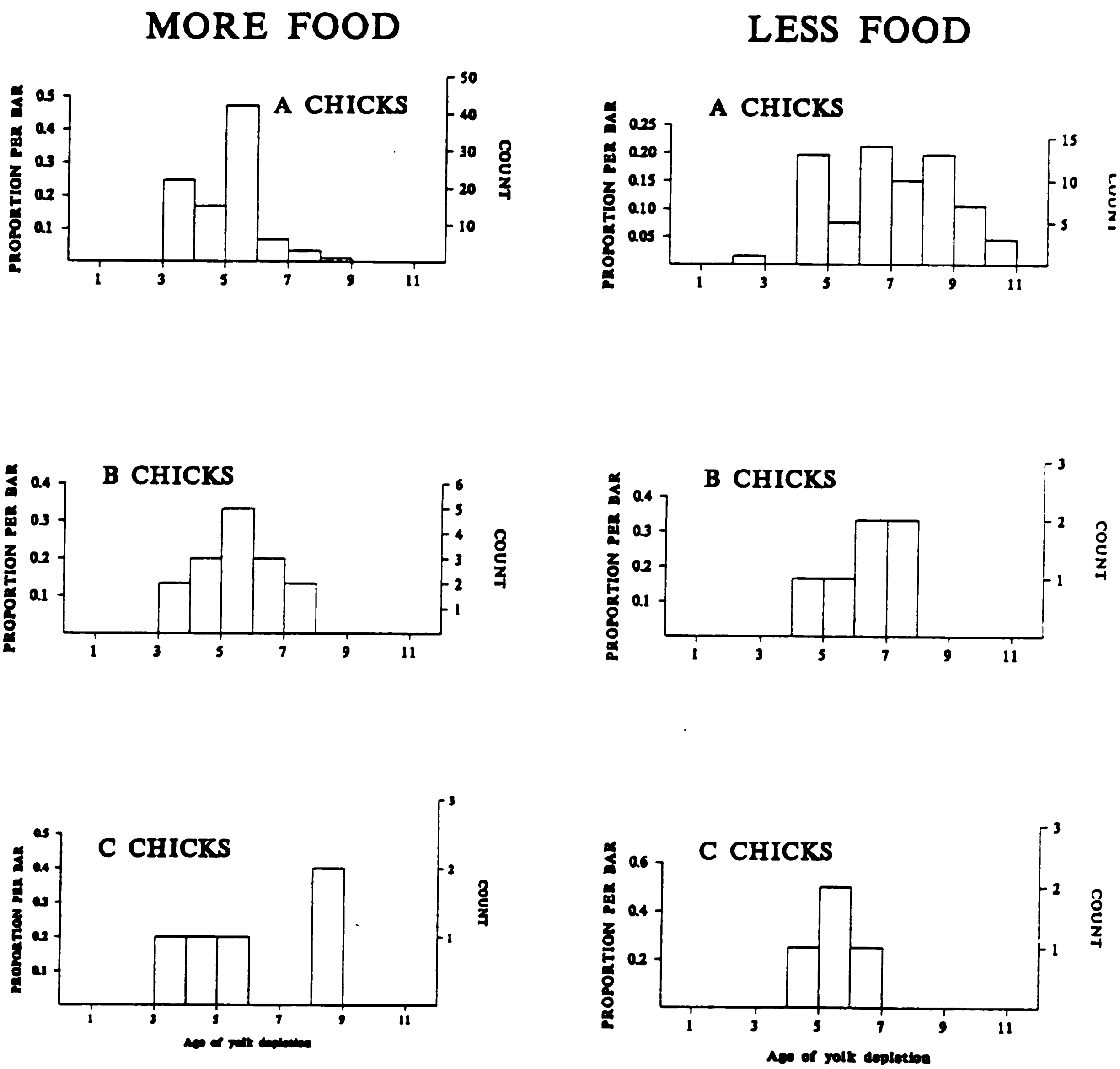

MORE FOOD
LESS FOOD
A CHICKS
B CHICKS
C CHICKS
PROPORTION PER BAR
COUNT
Age of yolk depletion

FIGURE 24

tween hatching treatments in these years is highly significant (Kruskal-Wallis, $H=23.957$, $df=2$, $P < 0.001$). In LESS FOOD years, eye opening occurred the earliest in the SINGLE ASYNCHRONOUS broods with the differences between hatching treatments also significant (Kruskal-Wallis, $H=6.375$, $df=2$, $P < 0.041$). By hatch position (Figure 26), eyes of the 'C' chick opened later than nestlings in the 'A' or 'B' hatch positions, although differences were not significant in either food year type.

2. <u>Growth of nestlings that fledged.</u> To reduce the number of growth variables to perform an analysis on those nestlings that fledged, I used all growth rates and age of developmental events as variables in a principal components analysis. I used the FACTOR module of SYSTAT to create two components for each analysis. The first two components of the principal components model explained nearly 60% of the variation for growth rates (Table 2A) and over 90% of the variation for the age of developmental events (Table 2B).

For the growth rate principal components analysis, I interpreted the first factor to be body growth because of high loadings of all growth rates except primary growth. I interpreted the second factor to be feather growth. Because of high loadings of all variables on the first component for the age of

FIGURE 25.

Density plots of the age of eye opening for all nestlings by food year type and hatching treatment.

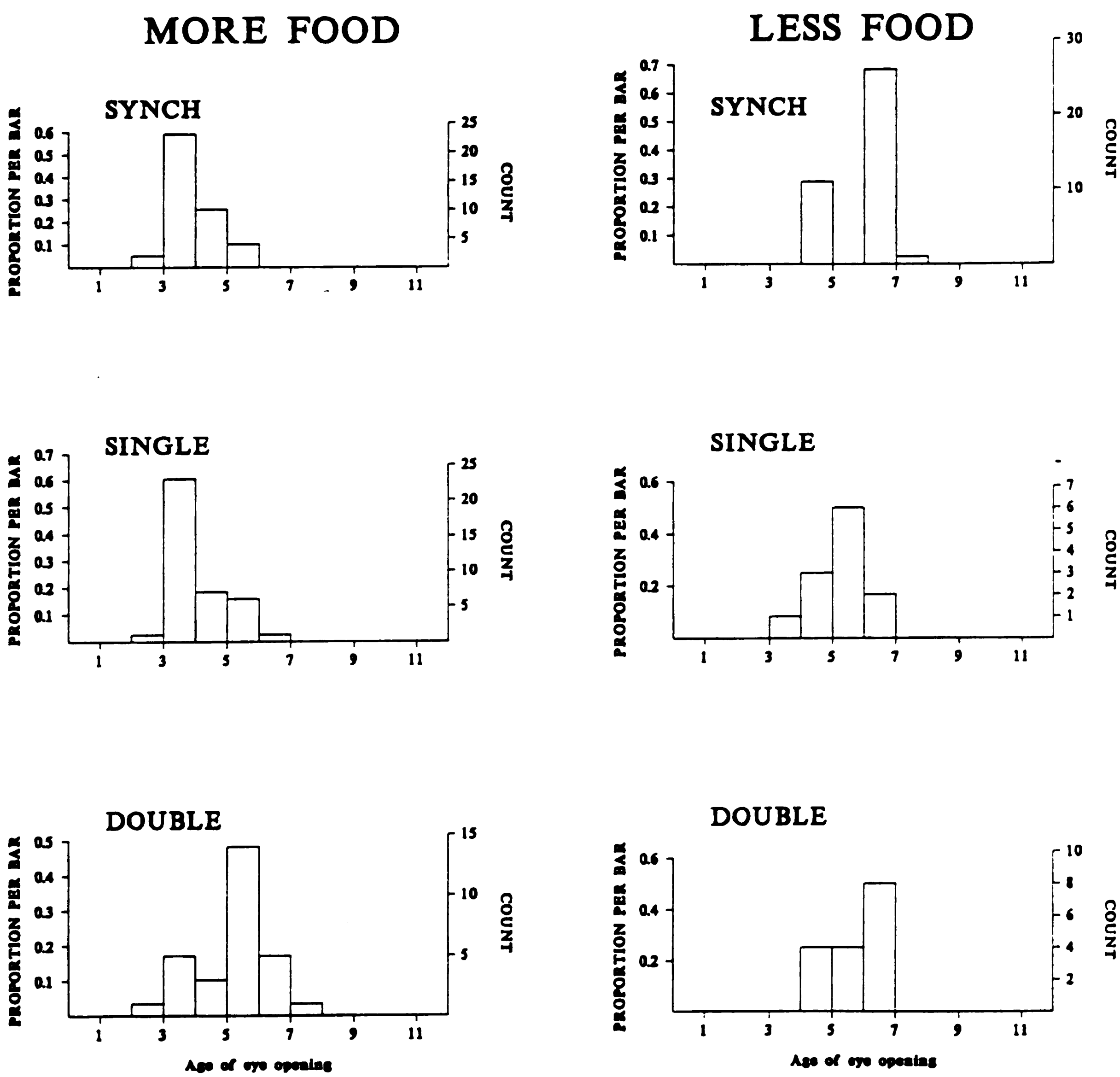

MORE FOOD
LESS FOOD
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
Age of eye opening

FIGURE 25

FIGURE 26.

Density plots of the age of eye opening for all nestlings by food year type and hatch position.

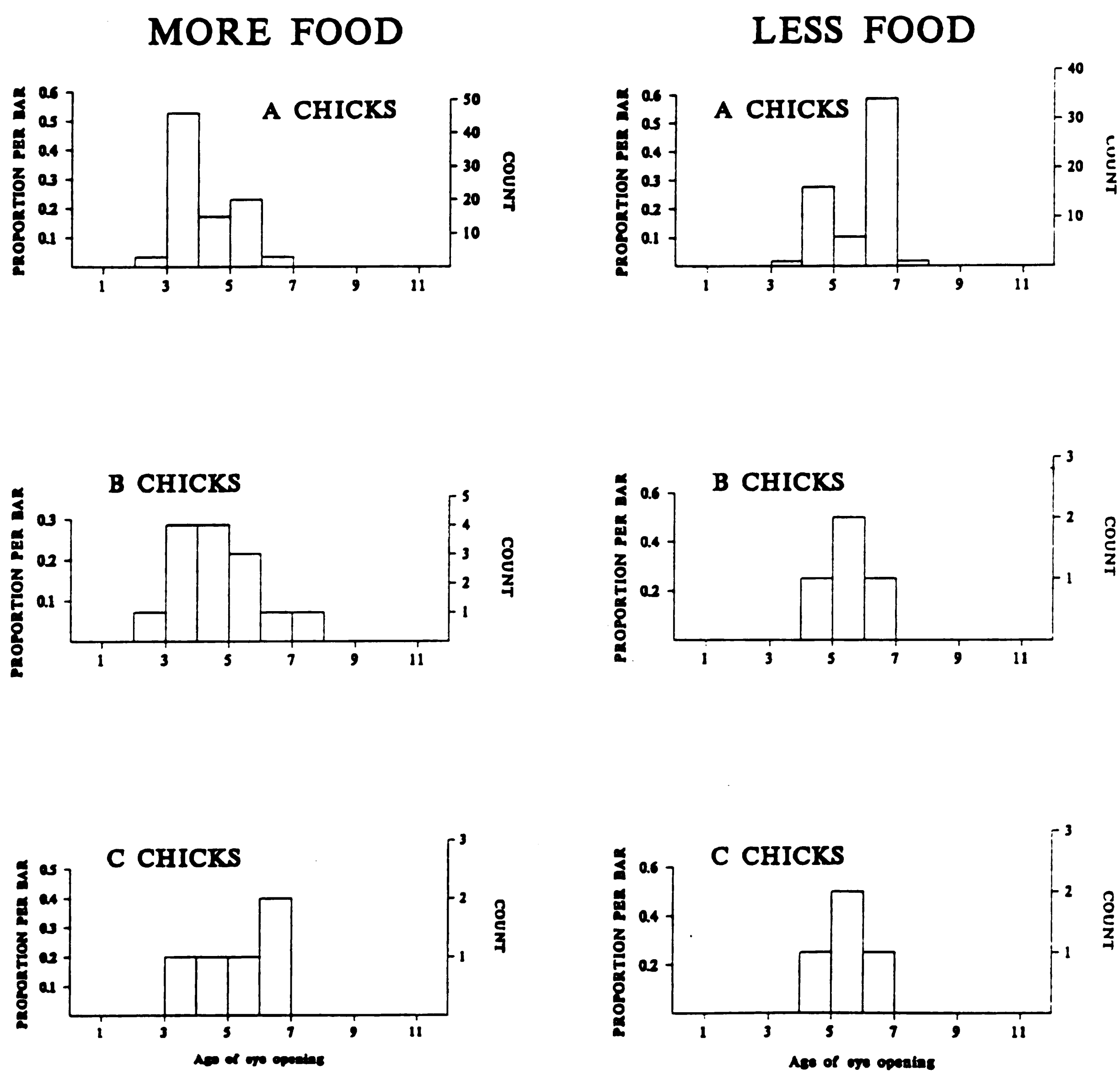

MORE FOOD
LESS FOOD
A CHICKS
B CHICKS
C CHICKS
PROPORTION PER BAR
COUNT
Age of eye opening

FIGURE 26

Table 2A. Component loadings of nestling growth rates on the first and second principal axes. Only those nestlings that fledged were used for this analysis. Growth rates included are the logistic growth rate constant for body weight, tarsus and ulna growth, the slope for the rate of body weight increase during the linear phase of growth, the exponential growth rate of the wing chord and the linear growth rate of ninth primary. Also given are the percentages of the total variance explained by each factor.

Growth Measure	PC(1)	PC(2)
Weight	0.718	0.260
Slope	0.693	0.310
Tarsus	0.765	-0.306
Ulna	0.471	-0.070
Wing	0.772	-0.241
Primary	0.056	0.918
Variance explained(%)	40.055	19.382

Table 2B. Component loadings for the age of nestling developmental events on the first and second principal axes. Only those nestlings that fledged were used for this analysis. The developmental events include the inflection point for logistic growth of body weight, tarsus, and ulna, the age of eye opening and yolk depletion and age of primary eruption.

Growth Measure	PC(1)	PC(2)
Weight	0.945	0.193
Tarsus	0.924	-0.145
Ulna	0.971	0.082
Primary	0.923	0.279
Yolk	0.903	-0.068
Eyes	0.892	-0.363
Variance explained(%)	85.871	4.648

developmental events, the first component is presumed to simply be the age of all developmental events with the second component the age of feather growth initiation.

Tables 3A and 3B give mean values for selected growth measures and the means for factor scores. The factor scores are adjusted to a normal probability distribution for the population with a mean of 0.0 and a standard deviation of 1.0. Table 3A shows that for PC(1), values greater than 0.0 are from nestlings that have body growth rates faster than the 4-year average. Growth rates (PC1) of nestlings raised in MORE FOOD years are significantly greater than nestlings raised in LESS FOOD years (Mann-Whitney, U= 2352, df=1, P = 0.001). Feather growth (PC2) of nestlings was faster when raised during MORE FOOD years compared to LESS FOOD years, although this difference was not significant (U=1871, df=1, P=0.403). Developmental events (PC1) occurred significantly earlier when nestlings were raised during MORE FOOD years (Table 3B) compared to LESS FOOD years (Mann-Whitney, U=216, df=1, P < 0.001). Lastly, feather development (PC2) started earlier by nestlings raised in MORE FOOD years compared to those raised in LESS FOOD years (U=812, df=1, P=0.024).

To determine the effects of food year

Table 3A. Means of growth rate principal components and selected growth measures, by food year type. Those growth measures provided were selected to help interpret the values for the factor scores.

Growth Measure	Means MORE FOOD	LESS FOOD
Factor(1)	0.253	-0.393
Slope	2.199	1.957
Weight (k)	0.494	0.439
Factor(2)	0.059	-0.092
Primary Rate	3.594	3.396

Table 3B. Means of age for developmental events principal components and selected growth measures, by food year type. Those growth measures provided were selected to help interpret the values for the factor scores.

Growth Measure	Means MORE FOOD	LESS FOOD
Factor(1)	-0.480	0.755
Weight Infl.	5.309	6.196
Factor(2)	0.237	-0.373
Primary Erupt	8.625	10.322

FIGURE 27.

Density distributions of PC(1) scores for rate of body growth by food year type and hatching treatment. Overlaid are normal probability plots to describe central tendency and dispersion.

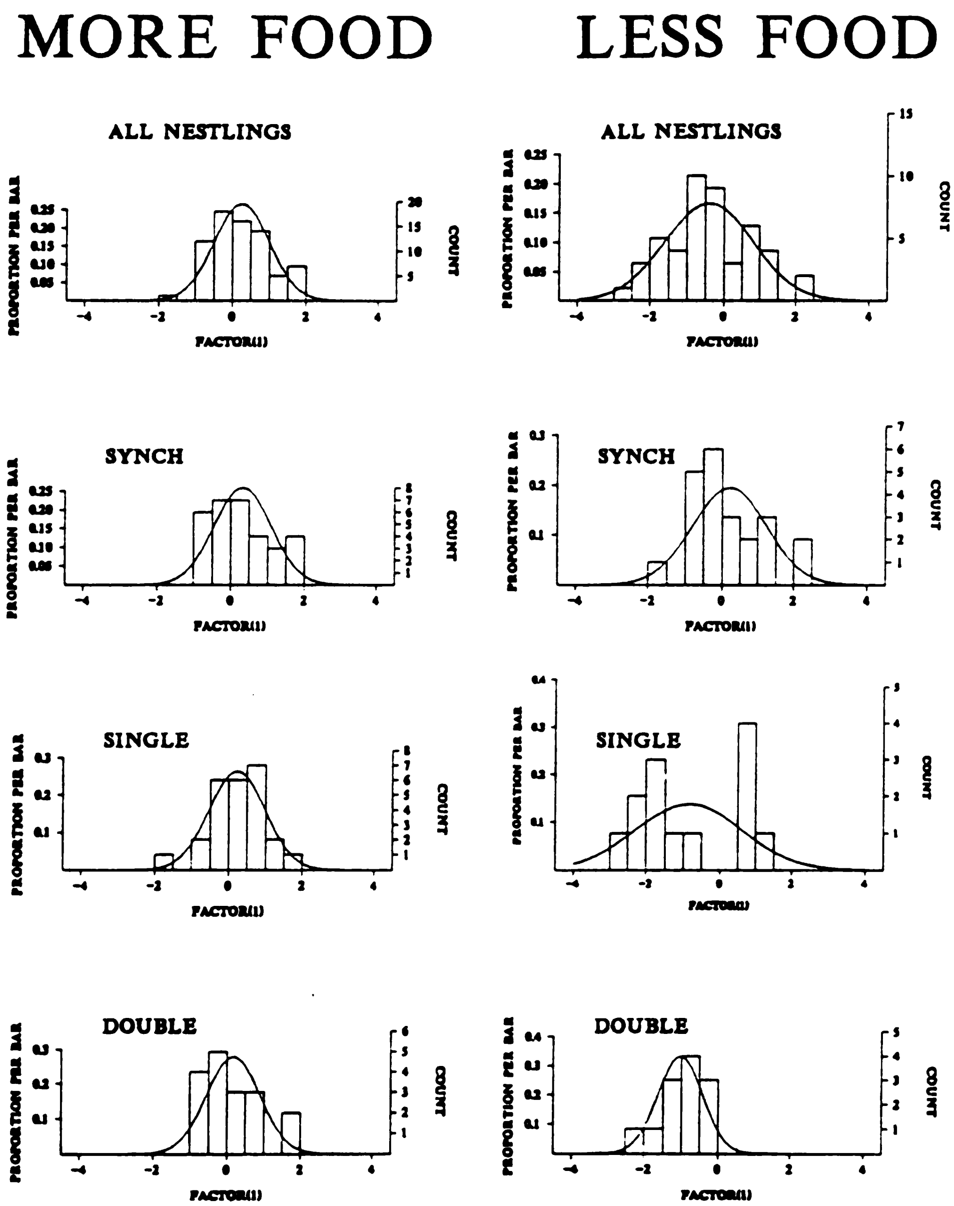

MORE FOOD
LESS FOOD
ALL NESTLINGS
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
FACTOR(1)

FIGURE 27

type and hatching treatment on each principal component, I plotted the frequency of factor score categories by food year type and hatching treatment. I overlaid a normal probability function on the histogram frequency distribution to aid in visualizing central tendency and variance. Body growth rates for nestlings that fledged (Figure 27) did not differ significantly between hatching treatments when food was more abundant (Kruskal-Wallis, H=0.634, df=2, P=0.728). However, body growth rates of nestlings did differ significantly between hatching treatments when food was less plentiful with median growth rates of nestlings increasing with increasing hatching synchrony. There was no significant difference between hatching treatments in the growth rates of feathers (Figure 28) within the MORE FOOD years (Kruskal-Wallis, H=0.774, df=2, P=0.646) or within the LESS FOOD years (Kruskal-Wallis, H=1.238, df=2, P=0.539).

Developmental events occurred earlier with increasing hatching synchrony in MORE FOOD years (Kruskal-Wallis 5.692, df=2, P=0.058) and with little variation within hatching treatment. In LESS FOOD years (Figure 29), the difference in the developmental events between hatching treatments was not significant (Kruskal-Wallis, H=2.104, df=2, P=0.349). During the MORE FOOD years, feather development started earlier in DOUBLE and SINGLE ASYNCHRONOUS broods than in SYNCHRONOUS broods; these differences were significant (Kruskal-Wallis, H= 7.716, df=2, P=0.021). During LESS FOOD years, the age of feather eruption did not different between hatching treatments (Kruskal-Wallis, H=4.321, df=2, P=0.115).

I subjected the maximum weights attained by nestlings that fledged to an analysis of variance. Transformation of data using logarithm was necessary to remove heteroscadastic variances between the groups. Table 4 shows that the maximum weight attained by nestlings that fledged was not statistically different by food year type or hatch position. However, there was a slightly significant

FIGURE 28.

Density distributions of PC(2) scores for rate of feather growth by food year type and hatching treatment. Overlaid are normal probability plots to describe central tendency and dispersion.

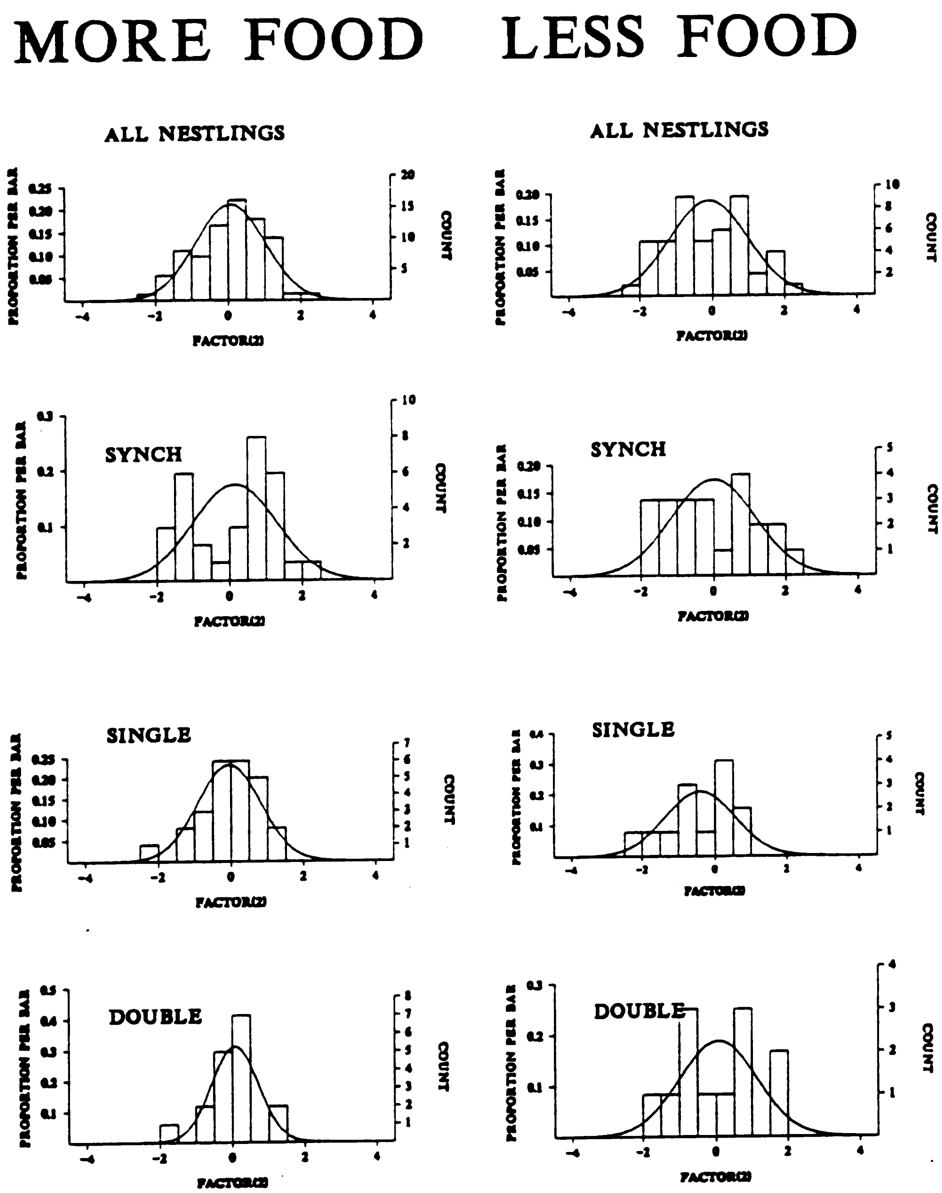

MORE FOOD
LESS FOOD
ALL NESTLINGS
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
FACTOR(2)

FIGURE 28

FIGURE 29.

Density distributions of PC(1) scores of the age that developmental events occurred by food year type and hatching treatment. Overlaid are normal probability plots to describe central tendency and dispersion.

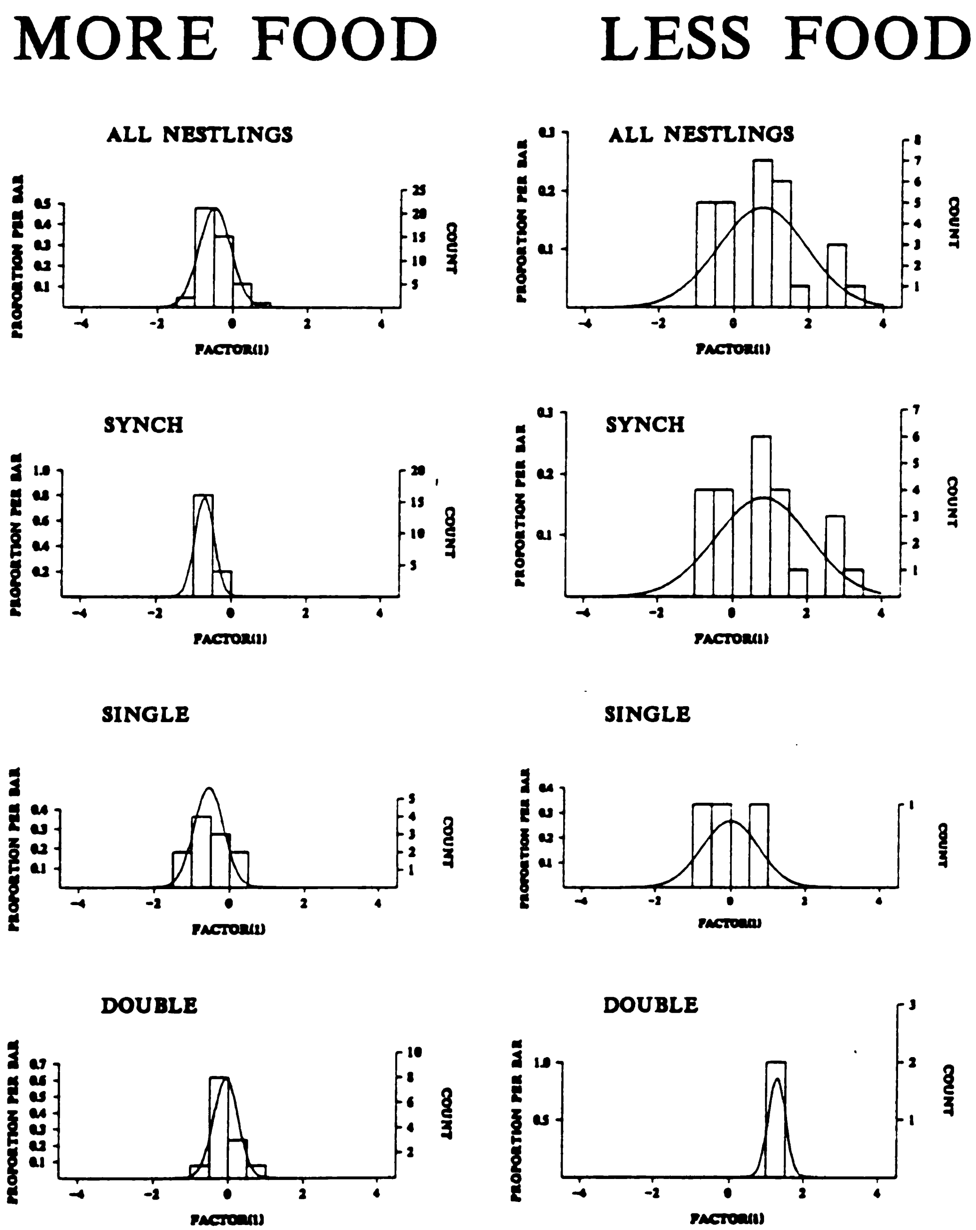

MORE FOOD
LESS FOOD
ALL NESTLINGS
ALL NESTLINGS
SYNCH
SYNCH
SINGLE
SINGLE
DOUBLE
DOUBLE
PROPORTION PER BAR
COUNT
FACTOR(1)

FIGURE 29

FIGURE 30.

Density distributions of PC(2) scores age of feather growth initiation by food year type and hatching treatment. Overlaid are normal probability plots to describe central tendency and dispersion.

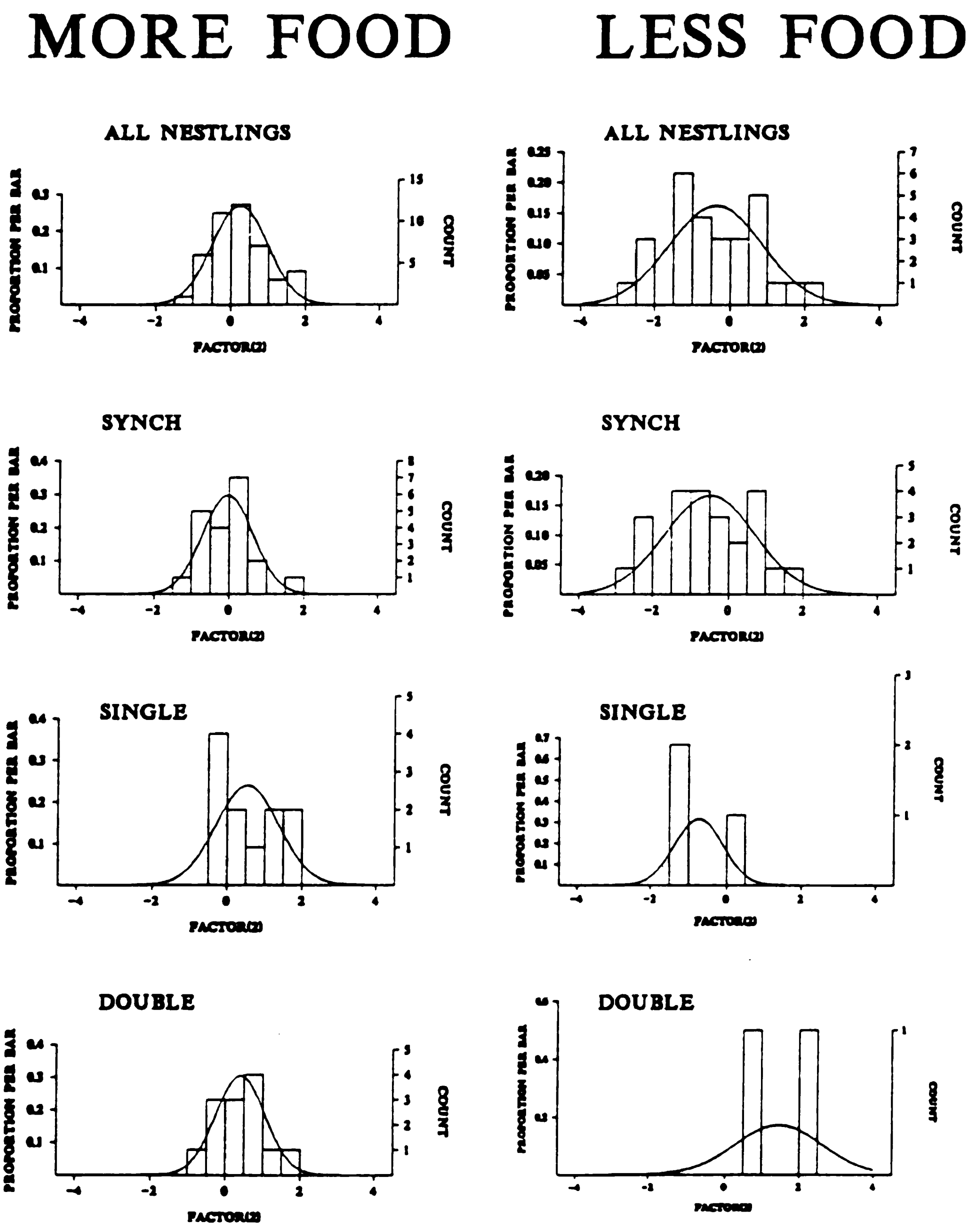

MORE FOOD
LESS FOOD
ALL NESTLINGS
SYNCH
SINGLE
DOUBLE
PROPORTION PER BAR
COUNT
FACTOR(2)

FIGURE 30

Table 4. Analysis of variance on the log transformed maximum nestling weights. Levels tested are food year type (food yr), hatching treatment (tmt) and hatch position (hatch).

SOURCE	SS	DF	MS	F-RATIO	P
Food Yr.	0.002	1	0.002	0.269	0.605
Tmt	0.039	2	0.019	2.670	0.072
Hatch	0.015	2	0.007	1.021	0.362
Error	1.385	191	0.007		

Table 5. Table of significant means from the analysis of variance for Table 4. Means are in their untransformed scale.

Grouping	Mean	SE
SYNCHRONOUS	22.226	0.208
SINGLE ASYNCHRONOUS	21.531	0.235
DOUBLE ASYNCHRONOUS	22.190	0.215

effect due to hatching treatment. Of the three treatments (Table 5), nestlings in SINGLE ASYNCHRONOUS broods reached the lowest maximum weight, followed by nestlings in DOUBLE ASYNCHRONOUS broods. Nestlings in SYNCHRONOUS broods reached the heaviest weights.

The age that the maximum weight was attained was influenced by the food year type and the hatching treatment (Table 6). Nestlings reached their maximum weights sooner when food was more plentiful (Table 7) compared to the LESS FOOD years. Nestlings raised during MORE FOOD years reached their maximum weights nearly two days earlier than those nestlings reared during LESS FOOD conditions. The age that maximum weight attainment occurred was later as hatching asynchrony increased (Table 7), with nestlings in DOUBLE ASYNCHRONOUS broods reaching maximum weights one full day after those nestlings in SYNCHRONOUS broods.

3. Dynamics of nestling weights. The number of times a weight ranking changed during the nestling period is given in Figure 31. For SYNCHRONOUS broods, rank 1 changed least often, followed by rank 5. For SINGLE ASYNCHRONOUS broods, rank 5 changed least often followed by rank 1. In DOUBLE ASYNCHRONOUS broods, rank 5 changed least often followed by rank 4 and then rank 1. Clearly, the heaviest and lightest nestlings stayed in their rankings throughout the nestling period

Table 6. Analysis of variance on the log transformed age of maximum nestling weight. Sources of variation are food year type (food yr.), hatching treatment (tmt) and hatch position (hatch).

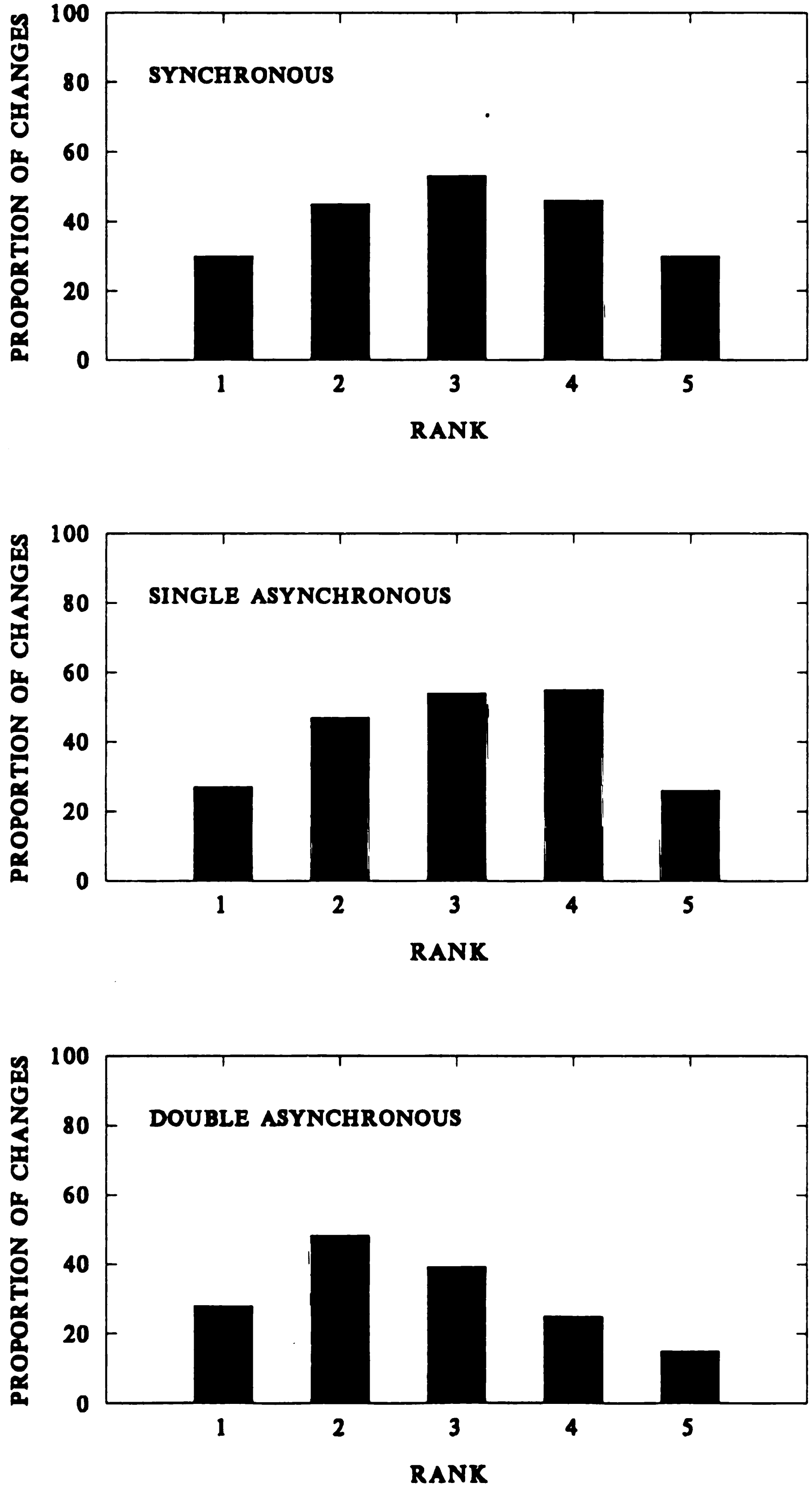
SOURCE	SS	DF	MS	F-RATIO	P
Food Yr.	0.780	1	0.780	32.802	0.000
Tmt	0.219	2	0.110	4.610	0.011
Hatch	0.026	2	0.013	0.554	0.576
Error	4.539	191	0.024		

Table 7. Table of significant means from the analysis of variance for Table 7. Means are in their untransformed scale.

Grouping	Mean	SE
MORE FOOD	12.960	0.178
LESS FOOD	14.745	0.245
SYNCHRONOUS	13.316	0.266
SINGLE ASYNCHRONOUS	14.029	0.256
DOUBLE ASYNCHRONOUS	14.385	0.327

FIGURE 31.

The proportion of changes within each weight ranking by hatching treatment. The heaviest nestling was assigned a rank of '1' and the lightest nestling was assigned a rank of '5'.



PROPORTION OF CHANGES
100
80
60
40
20
0
SYNCHRONOUS
1
2
3
4
5
RANK
PROPORTION OF CHANGES
100
80
60
40
20
0
SINGLE ASYNCHRONOUS
1
2
3
4
5
RANK
PROPORTION OF CHANGES
100
80
60
40
20
0
DOUBLE ASYNCHRONOUS
1
2
3
4
5
RANK

FIGURE 31

with rank changes occurring most often by the nestlings with the intermediate weights. Surprisingly, the 'B' chick in SINGLE ASYNCHRONOUS broods was the lightest nestling 71% of the time during MORE FOOD years and 59% during LESS FOOD years; the difference between year types was not significant ($G=0.30$, $df=1$, $P > 0.50$). In DOUBLE ASYNCHRONOUS broods, the 'B' chicks were the fourth heaviest nestling 47% and 53% of the time during the MORE and LESS FOOD years, respectively; the difference between food year types was also not significant ($G=0.37$, $df=1$, $P>0.50$). The 'C' chicks were also the lightest chicks 82% and 67% of the time, in MORE and LESS FOOD years, these differences were not significant between food year types ($G=0.37$, $df=1$, $P > 0.50$).

To determine if SYNCHRONOUS broods developed weight hierarchies as great as those in asynchronous broods, I calculated the coefficient of variation of body weights for all nestlings in a nest during each growth measure visit. The average coefficient of variation, by hatching treatment, is given in Figure 32. The variation of body weights in a brood increases with increasing hatching asynchrony. The mean coefficient of variation for body weights was on average twice as great in DOUBLE ASYNCHRONOUS as in SYNCHRONOUS broods.

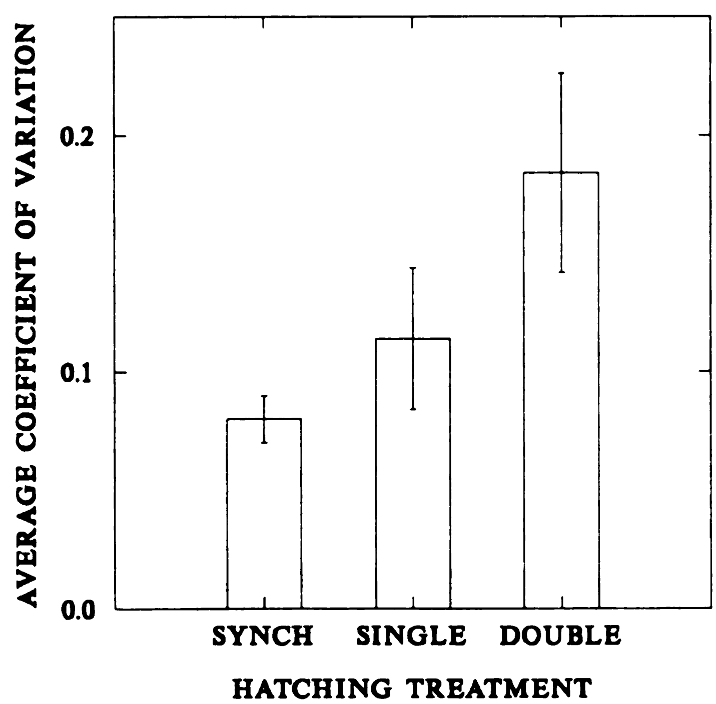


FIGURE 32.

The average coefficient of variation of nestling weights by hatching treatment (± 1 S.E.).

FIGURE 33.

The mean percent of nestling body weight (± 1 S.E.) deviating from the "normal" body weight with respect to the day of brood reduction. Weights are for nestlings that fledged and only those broods fledging 4 young are included. Periods represent 2-days.

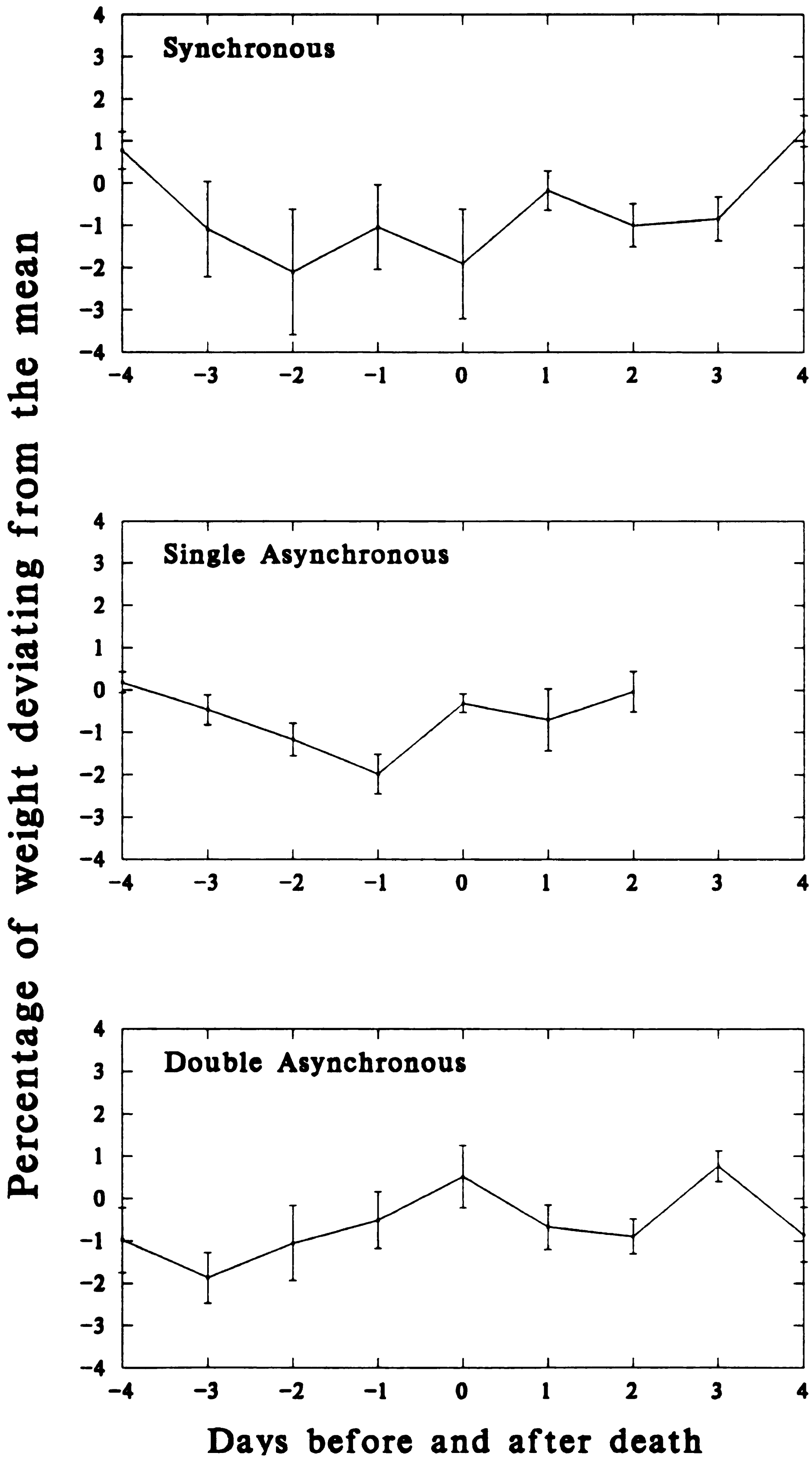

Synchronous
Single Asynchronous
Double Asynchronous
Percentage of weight deviating from the mean
Days before and after death
4
3
2
1
0
-1
-2
-3
-4

FIGURE 33

The nestling body mass deviations from "normal" on days preceding and following each brood reduction event are given in Figure 33. To construct this figure, I calculated the average nestling body mass for each age for nestlings in broods that fledged 5 young and considered this a nestling's "normal" mass. Then for all broods that fledged 4 nestlings, I took the difference between this "normal" mass and the body mass of the nestlings in the broods and divided this value by the "normal" mass for that nestling. This produced a value expressing the percentage of weight deviating from the "normal" weight for its age for each nestling. I then plotted the averages of these mass deviations from "normal" for the four nestlings in each brood that fledged using two day intervals preceding and following the loss of the 5th nestling. For SYNCHRONOUS broods, nestling weight dipped below the "normal" weight of that nestling for its age by 1% in the three day-interval previous to brood reduction (day of brood reduction = 0). Weights of the surviving nestlings remained below the "normal" weight for as many as 6 days after brood reduction. In SINGLE ASYNCHRONOUS broods, weights of surviving nestlings decreased between the 3rd day-interval to the 1st day-interval before brood reduction. Their weights returned to the "normal" for that age on the day of the nestling death and remained close to "normal" for as long as this comparison could be done. Interestingly, for DOUBLE ASYNCHRONOUS broods, nestling weights reached a low value on the 3rd interval previous to brood reduction and rebounded quickly back to the "normal" weight on the day that brood reduction occurred. Also of interest is that the average nestling weight reduction for all nests does not surpass 2% in any of the treatments, a possible critical growth reduction limit. Perhaps a tradeoff might exist between jeopardizing the potential survivor's health, and hence their chances of fledging at a substantial body weight, and the survival of the nestling singled out for eventual starvation.

Figure 34 shows the same comparison for nestling weight changes, with respect to the first brood reduction, but for broods that fledge three nestlings. Unfortunately, no SYNCHRONOUS broods fledged three young. Figure 34 shows that weights remained below "normal" for surviving nestlings throughout the entire phase of periods examined except for 4 days post-brood reduction in DOUBLE ASYNCHRONOUS broods. Weights below the average did occur in both hatching treatments prior to brood reduction. Nestling weights also dipped below the 2% weight loss value three times, once for SINGLE ASYNCHRONOUS broods just prior to brood reduction and

FIGURE 34.

The mean percent of nestling body weight (± 1 S.E.) deviating from the "normal" body weight with respect to the day of brood reduction. Weights are for nestlings that fledged and those broods fledging 3 young are included. Periods represent 2-days.

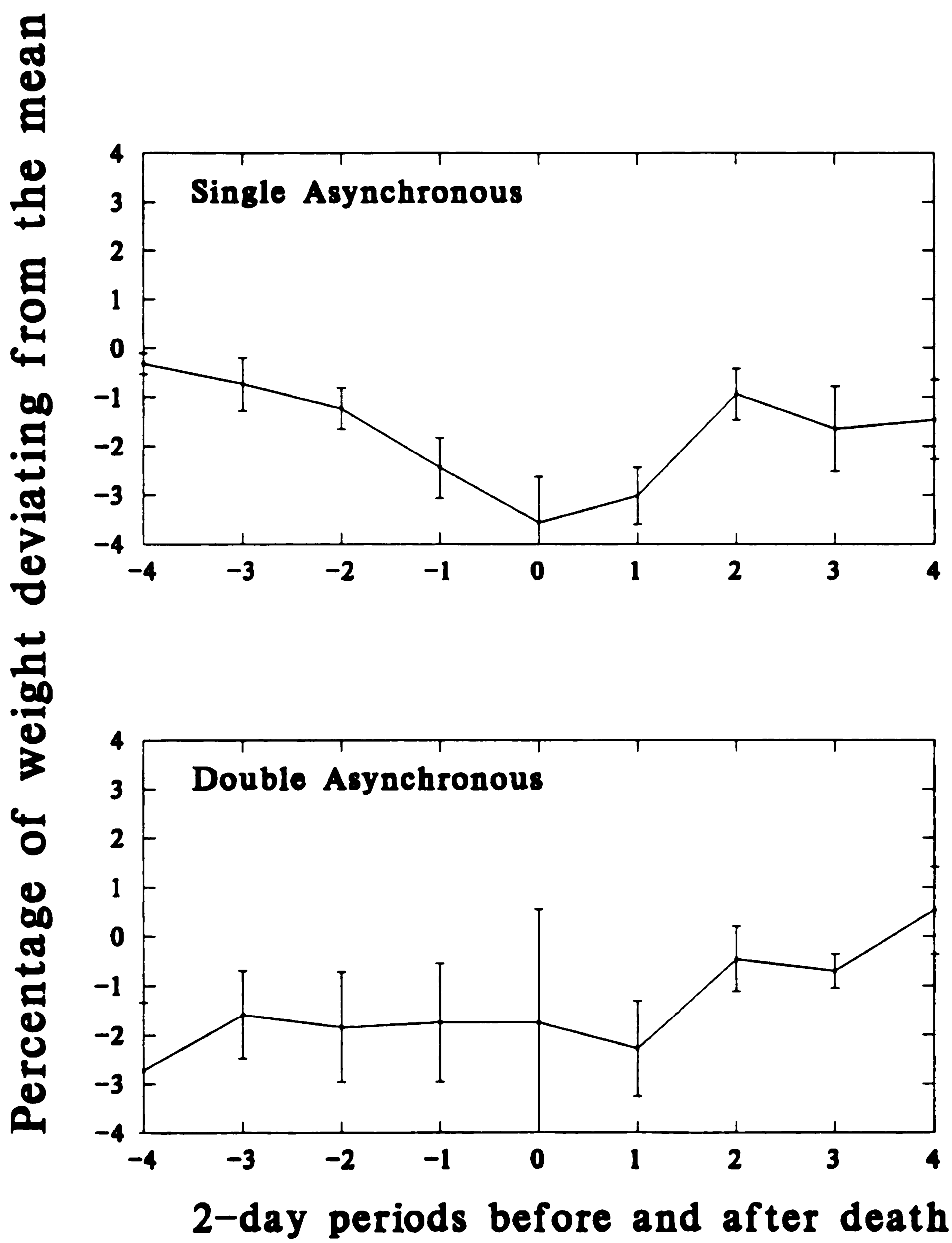

Percentage of weight deviating from the mean
Single Asynchronous
Double Asynchronous
4
3
2
1
0
-1
-2
-3
-4
-4
-3
-2
-1
0
1
2
3
4
2-day periods before and after death

FIGURE 34

twice in DOUBLE ASYNCHRONOUS broods; once before and once after brood reduction.

4. Nestling growth and daily food abundance. I also tried to determine whether daily IBI measures affected the rate of weight growth during the linear phase of body weight and the maximum nestling weight attained. I calculated the average daily IBI value during the linear phase of growth for each nestling. The correlation between daily IBI measures and the rate of linear body weight increase was not significant ($P=0.318$). However, I detected a significant correlation ($r=0.333$, $df= 195$, $P < 0.001$) between the maximum nestling weight and the daily average IBI that occurred from hatching of the nestling to the day that maximum weight occurred. There was also a significant positive correlation between the linear nestling growth rate and the average daily insect dry weights in the Manitoba traps ($r=0.215$, $df=195$, $P < 0.01$). The age of maximum weight attained by nestlings that fledged did not correlate strongly ($r=0.007$, $df=195$, $P > 0.10$) with daily IBI measures.

Feeding Behavior. I monitored 474, 20-minute feeding bouts to the nests from 1987 to 1989. During this period, a total of 736 food boluses were delivered containing a total of 14,859 insects. The size-taxa distribution for these boluses are given in Figure 35. Note that the scale for nematocerans differs from the other Orders. Eighty-six percent (12,749) of the insects were composed of dipterans. Of the dipterans, 67% (9990) were nematocerans. Other important diet items, in percent of the total number of insects, included homopterans (8%), hemipterans (1%), and ephemeropterans (2.5%). The most common size category preyed upon by tree swallows is 3-5mm (74%) followed by the 5-7mm category (12%). Thus tree swallows select insects of sizes less than those of insects trapped in Manitoba traps but larger than those most frequently found in the tow nets.

Tabanids accounted for only 1.5% of the total number of insects delivered to the nest. However, they accounted for 5% of the total dry weight of the insects delivered to the nest. Generally, one tabanid sufficed to make one bolus. Tabanids made up 1.3%, 2.6% and 0.3% of the food items delivered during the 1987, 1988 and 1989 breeding seasons, respectively. These proportions by year were significantly different ($G=124.9$, $df=2$, $P < 0.001$). The higher percentage of tabanids in food boluses during 1988 is probably due to the very dry and hot conditions during that season.

During MORE FOOD years, the amount of food parents delivered to the nest, per 20 minute feeding

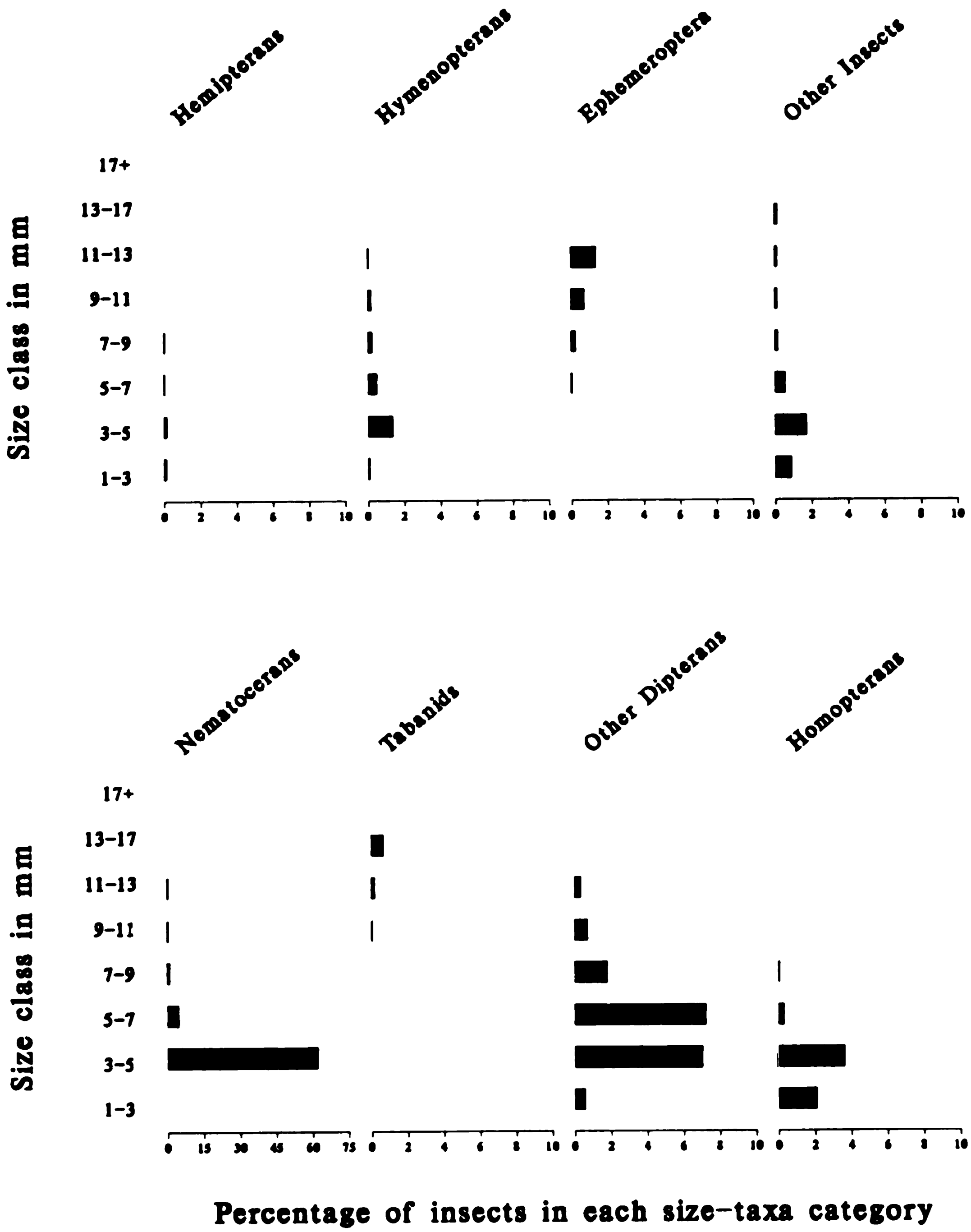


FIGURE 35.

Size-taxa distribution of insects (in percent of total) in food boluses for the 1987, 1988 and 1989 seasons.

session, when five nestlings were alive, increased with increasing hatching synchrony, with SYNCHRONOUS, SINGLE and DOUBLE ASYNCHRONOUS parents delivering 29.0 mg, 25.0 mg and 11.0 mg of food per 20 minutes, respectively. However, during the LESS FOOD years, the amount of food brought to the nest when five nestlings were alive increased with increasing hatching asynchrony, with SYNCHRONOUS, SINGLE ASYNCHRONOUS and DOUBLE ASYNCHRONOUS parents delivering 31.0 mg, 42.0 mg and 46.0 mg of food per 20 minutes, respectively. Surprisingly, the amount of food per feeding session was double during LESS FOOD years compared to MORE FOOD years. During MORE FOOD, the number of feeds to each nest during a feeding bout, when five nestlings were alive, did not differ significantly between hatching treatments ($G= 2.96$, $df=2$, $P > 0.10$), with DOUBLE ASYNCHRONOUS, SINGLE ASYNCHRONOUS and SYNCHRONOUS nests receiving 1.05, 1.92 and 1.72 feeds per 20 minutes, respectively. When food was less plentiful, parents of SINGLE ASYNCHRONOUS delivered fewer food boluses (1.73 boluses/20 minutes), followed by parents of DOUBLE ASYNCHRONOUS (1.96 boluses/ 20 minutes) and then parents of SYNCHRONOUS broods (2.17 boluses/20 minutes). These differences were also not significant ($G=1.37$, $df=2$, $P > 0.50$). The number of food boluses brought to the nest was almost significantly greater during the LESS FOOD years compared to the MORE FOOD years ($G=3.17$, $df=1$, $P < 0.10$). Thus, when food was more limited, parents brought more food to the nest, both in the amount of food and the number of food boluses.

The proportion of food delivered to each nestling by the nestling's hatch position, and for each year type, is given in Figure 36. To construct Figure 36, I used information on bolus samples from nests where all five nestlings were still alive in the nest (some feedings were monitored after nestlings died, these are excluded). In MORE FOOD years, the 'B' chick received more than 40% of the food delivered to the nest; each 'A' chick received about 15% of the food brought to the nest (note that 4x15 + 40 = 100%). In DOUBLE ASYNCHRONOUS broods, each 'A' chick received less than 10% of the food brought to the nest, the 'B' chick received slightly greater than 30% and the 'C' received about 40% of the food brought to the nest (also note that 3x10 + 30 + 40 =100%). Thus, the youngest nestlings during the MORE FOOD years received the most food brought to the nest.

A strikingly opposite trend in food apportionment is observed during the LESS FOOD years. The 'B' chicks received slightly more food than each 'A' nestling in a SINGLE ASYNCHRONOUS brood, but the 'C' chick in the

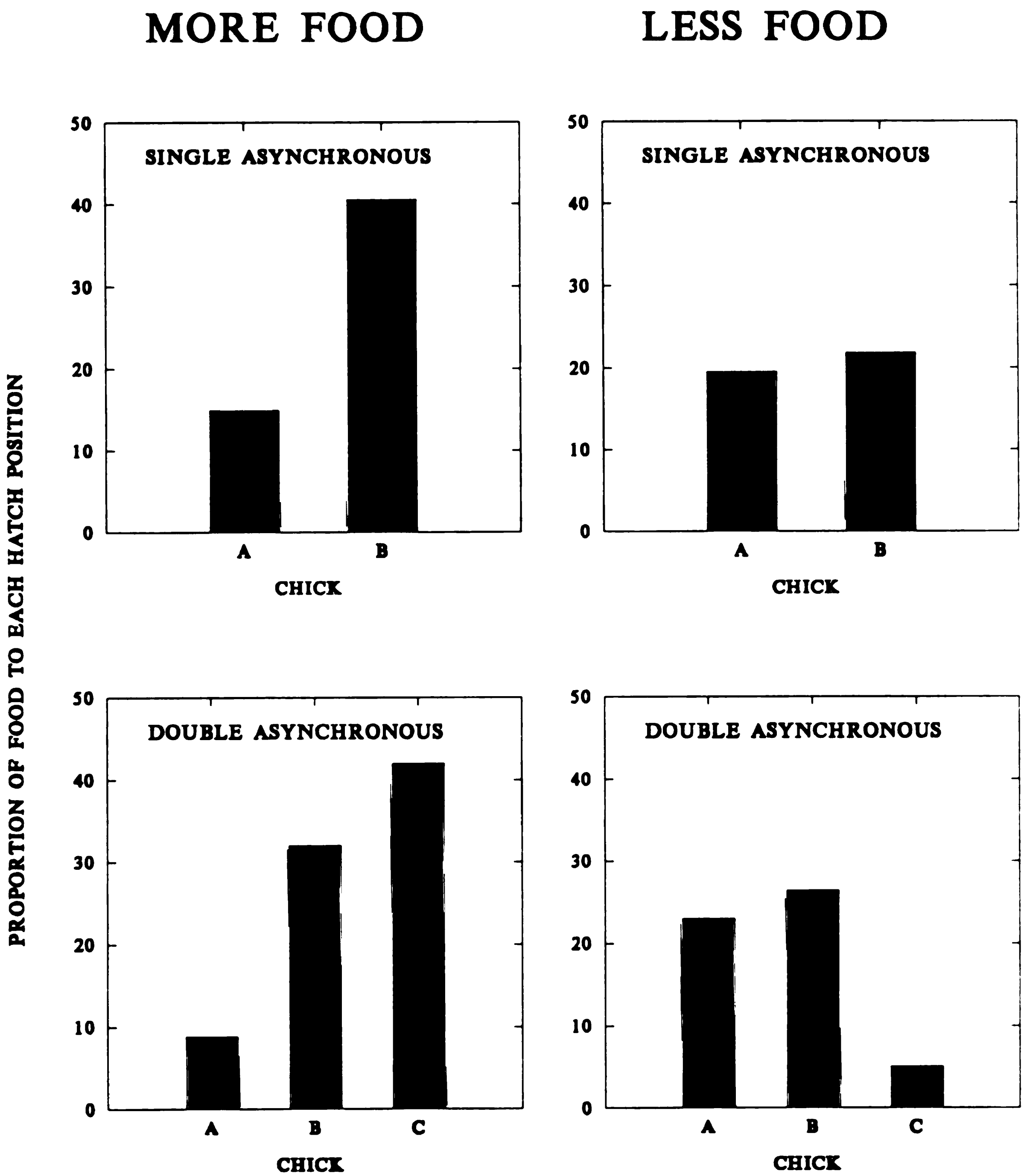


FIGURE 36.

The proportion of food delivered to each nestling according to hatch position and by food year type for SINGLE and DOUBLE ASYNCHRONOUS broods.

FIGURE 37.

The proportion of food and proportion of feeds delivered to each nestling according to its weight ranking by food year type for SYNCHRONOUS broods.

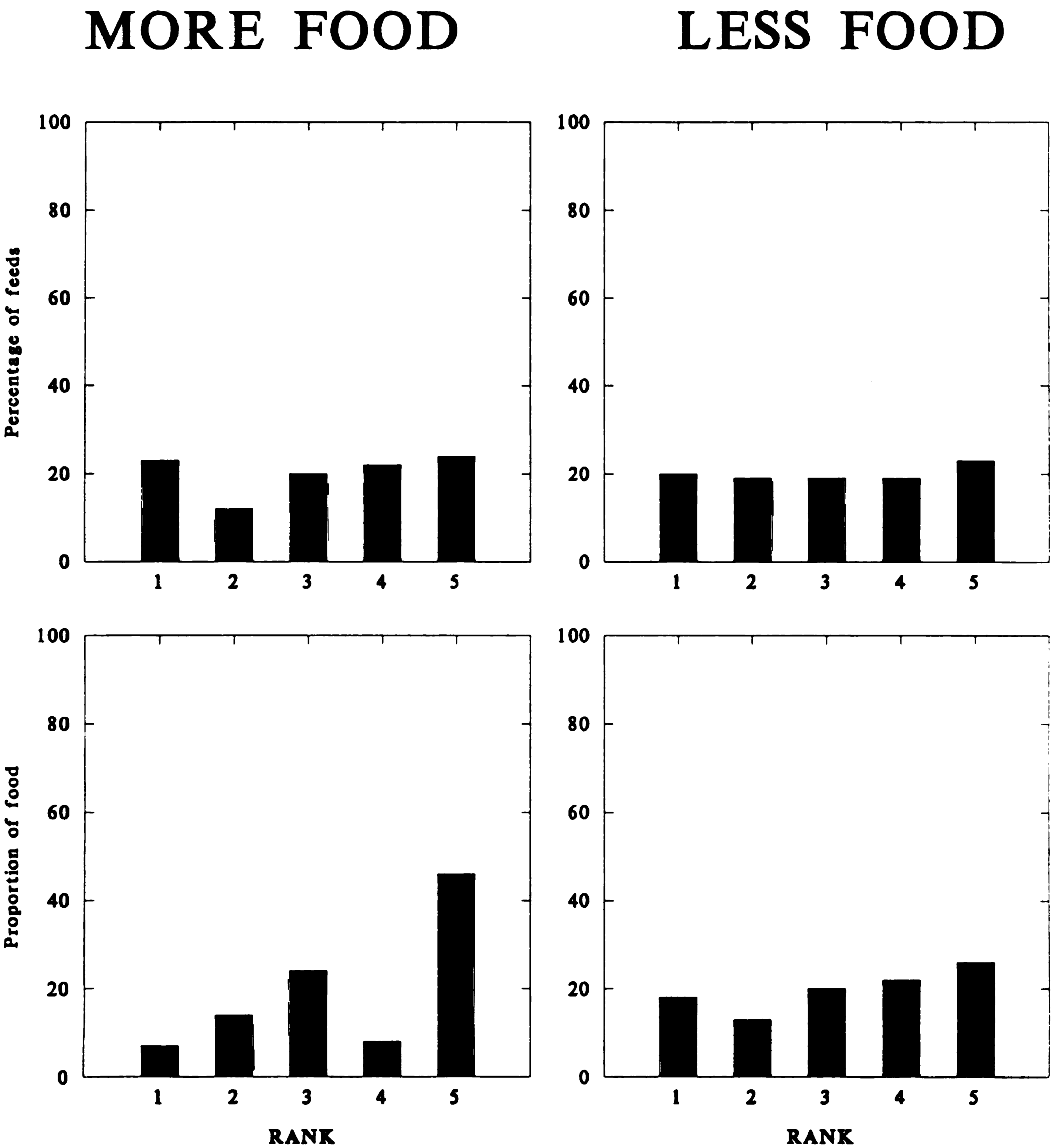

MORE FOOD
LESS FOOD
Percentage of feeds
Proportion of food
100
80
60
40
20
0
1
2
3
4
5
RANK

FIGURE 37

DOUBLE ASYNCHRONOUS broods received less than 5% of the food brought to the nest; the 'B' chick received the most at 26% and the 'A' chick received 23%. Clearly then, the 'C' chicks in DOUBLE ASYNCHRONOUS died from a lack of food during the LESS FOOD years.

Within SYNCHRONOUS broods, I examined the number of feeds and the amount of food given to each nestling according to its weight ranking (Figure 38). During MORE FOOD, the proportion of feeds to each nestling by its weight rank did not differ from a random feeding of nestlings by ranking ($G=2.99$, $df=4$, $P > 0.50$). The amount of food given to each nestling by its weight ranking did, however, differ significantly from a random apportionment of food ($G=235$, $df=4$, $P < 0.001$) with the lightest nestling receiving the largest food boluses brought to the nest. This same pattern is observed when food was less abundant, with the number of feeds to each nestling by its weight ranking not differing significantly from a random feeding of nestlings ($G=1.03$, $df=4$, $P > 0.90$). The amount of food given to nestlings appears to increase with decreasing weight ranking when food is less abundant ($G=68.0$, $df=4$, $P < 0.001$). Thus, the largest nestlings received the largest food boluses.

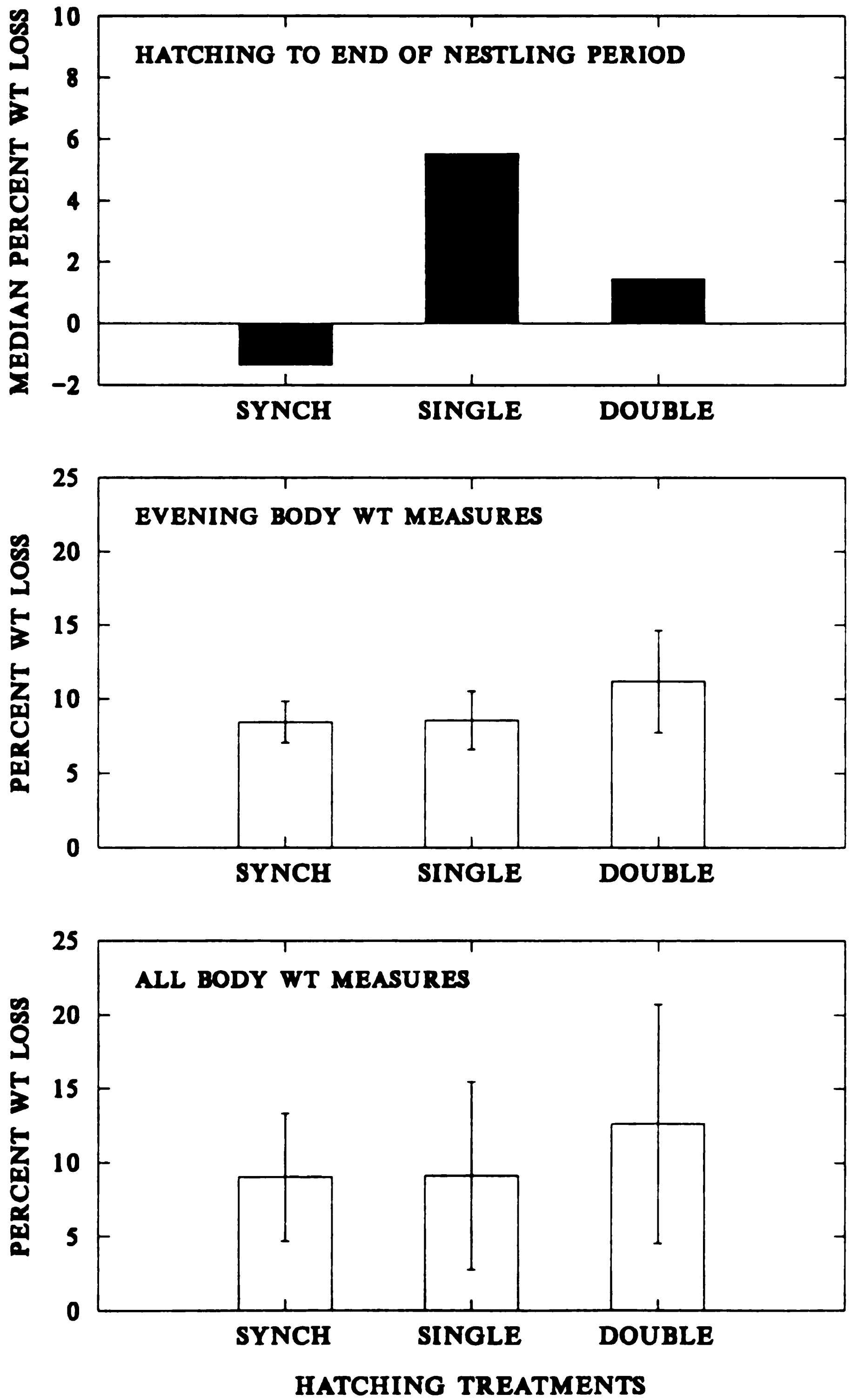
Parental Care. I weighed females on the evening within one day of her clutch hatching and followed their weight change by attempting to capture females every other evening until the oldest nestlings reached 18 DPH. I conducted this intensive weighing procedure only during the 1988 and 1989 season, thus, I am not able to compare weight changes of females during the more plentiful food seasons.

The percent difference between the weight of females at hatching to an evening during the later portion of the nestling period, is negative for those females raising SYNCHRONOUS broods. Females raising asynchronous broods gained weight during this period; the most gained by parents raising SINGLE ASYNCHRONOUS broods (Figure 38). I also calculated the maximum weight lost from the evening of hatching to any other time period (morning through evening) that I was able to obtain a body weight. These patterns show that DOUBLE ASYNCHRONOUS broods experienced the most weight loss during the nestling period, more so than the other two hatching treatments.

I also tried to determine the effect of daily IBI measures on the daily body weights of females. I found a slightly significant correlation ($r=0.111$, $df=250$, $0.10 < P < 0.05$) between the absolute weight of all females and daily IBI measures. One of the most drastic

FIGURE 38.

The (a) median percentage weight loss (from hatching to late in the nestling period) of females raising broods, by hatching treatment; (b) the average of the most percentage weight lost by females for ($\pm$ 1 S.E.)evening weighings from hatching date; and (c) the average of the maximum weight lost by females ($\pm$ 1 S.E.) from hatching date.



10
8
6
4
2
0
-2
MEDIAN PERCENT WT LOSS
HATCHING TO END OF NESTLING PERIOD
SYNCH
SINGLE
DOUBLE
25
20
15
10
5
0
PERCENT WT LOSS
EVENING BODY WT MEASURES
SYNCH
SINGLE
DOUBLE
25
20
15
10
5
0
PERCENT WT LOSS
ALL BODY WT MEASURES
SYNCH
SINGLE
DOUBLE
HATCHING TREATMENTS

FIGURE 38

changes in weight occurred during the cold spell of 1989. Prior to this cold spell, the evening median weight of females was 21.1 grams. The median of female evening weights dipped to 19.5 grams during the cold spell and then rose to 20.9 grams one week following the cold spell. The differences in the weights between the three periods was highly significant (Kruskal-Wallis, $P < 0.001$). One female, whose body weights were monitored (her nest was excluded from the study because she laid three eggs), was weighed at 23.2 grams on the day her clutch hatched (10 June). On the morning of the 15th of June, she weighed 16.8 grams, slightly more than 3/4ths her weight five days previous. By the 17th of June, she was captured again and weighed at 19.9 grams.

I also calculated the percentage weight change of a female from her weight when her clutch hatched to all evening measures and averaged these percentage weight changes for 2 day intervals previous to, and following, the first death in the nest. Because of small sample sizes, I had to combine data from all three hatching treatments. Figure 39 shows that the percentage weight change since hatching date is lowest 9-10 days prior to brood reduction. The weights increase, then fall again reaching a new minimum on the day of brood reduction. Adults appear to gain weight and reach their previous

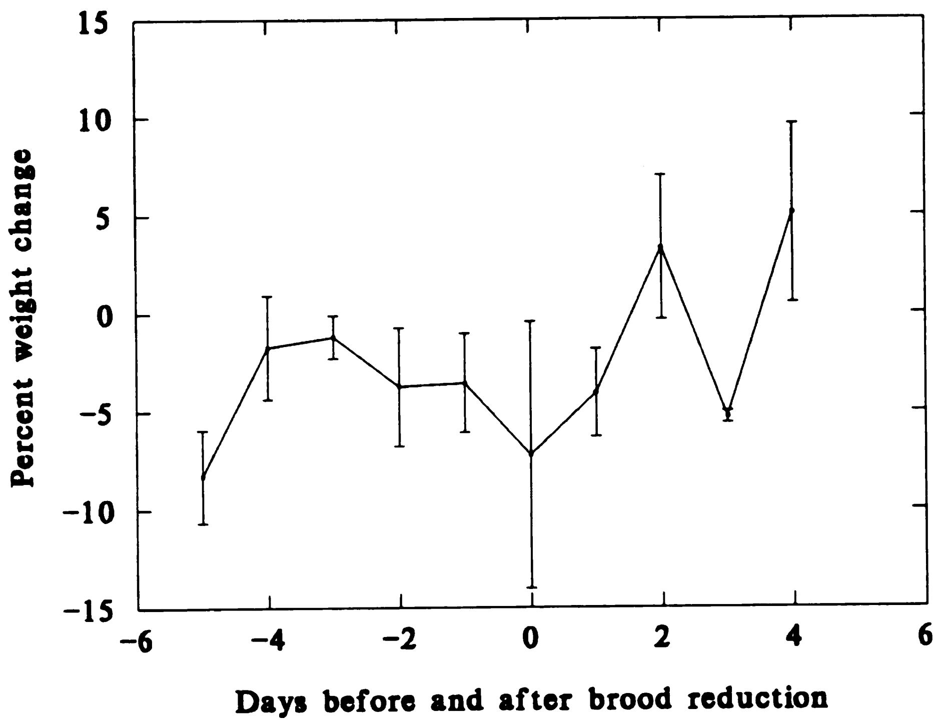


FIGURE 39.

The percent weight change of females from their weights at hatching averaged with respect to the day of brood reduction. All hatching treatments and only those broods that fledged 4 young are included.

weight at hatching 3-4 days after brood reduction. The lowest weights recorded did not occur during the cold snap of 1989.

IV. DISCUSSION

A. GENERAL RESULTS OF STUDY RELEVANT TO THE BROOD REDUCTION HYPOTHESIS

1. Natural Degree of Hatching Asynchrony

Several studies have reported that tree swallows hatch clutches asynchronously (Hussell and Quinney 1987, Quinney 1983b, Zach 1982, Paynter 1954). Zach reported a low number of nests hatching broods all on the same day (13.8%). I have found that hatching asynchrony is the most common form of hatching for large clutch sizes; hatching asynchrony increased with increasing clutch size. This study confirms that tree swallows hatch their clutches asynchronously. However, clutches appeared to hatch more synchronously than reported by Zach (1982). Nearly one-half of all 5 egg clutches hatched on the same day. Synchronous hatching also appeared to be the most common hatching pattern for 4 egg clutches.

I also found that a considerable amount of variation in hatching spreads occurred within a clutch size, and that the amount of variation in hatching spreads increased with increasing clutch size. Within 4 egg clutches, hatching occurred within a one to two day range. For 6 egg clutches, one nest out of twelve hatched on the same day and one nest hatched over a four-day period with most hatching over a two or three day period. Bryant (1978) reported variation in hatching spreads in the House Martin (Delichon urbica), increased with increasing clutch size. He also found that the modal hatching spread increased with increasing clutch size.

Despite the reduced degree of hatching asynchrony observed during my study compared to other studies, the natural degree of hatching asynchrony did, however, produce distinct weight hierarchies in the nest. These weight hierarchies, as reflected in the coefficient of variation of weights soon after hatching (Figure 4), increased with increasing degree of hatching asynchrony. Zach (1982) reported that weight hierarchies were established by hatching asynchrony with the heaviest nestling weighing twice that of the youngest nestling after all young had hatched. He found that weight hierarchies are continued well into the nestling period with pronounced asynchronous fledging (Zach 1982). I also found that weight hierarchies persisted in nests with the coefficient of variation of nestling weights throughout the nestling period increasing with increasing degree of hatching asynchrony.

I also found that egg weights increased with laying order (Figure 5), with the last laid egg weighing more than the first laid egg in 4, 5 and 6 egg clutches. Tree swallows hatch eggs in the order than they are laid (Zach 1982). Thus, egg size variation in a clutch does not contribute toward nestling weight hierarchies in asynchronous nests but rather egg weight variation tends to reduce them. Furthermore, in natural synchronous nests, subtle weight differences caused by the timing of egg hatching may be quickly offset by differences in egg weights making egg weight variation an unlikely contributing factor to weight hierarchies for SYNCHRONOUS broods.

2. Food Supplies

Food supplies during this study were more limited than at the two non-pond sites of Hussell and Quinney (1987). Food supplies during my 1986 and 1987 seasons (Figure 6-7) were near the seven-year average of food levels they reported for one study site (Backus Field) that lacked habitat favorable for high insect abundances. Thus, conditions during my entire four-year study were probably less than ideal for parents to raise five nestlings. Because the 1986 and 1987 insect abundances were similarly high and the insect abundances for 1988 and 1989 were similar but low, I assumed that the first two years provided parents with more food than the latter two years.

A comparison of insect fauna in tow net catches and insects in the food boluses suggest that tree swallow appear to feed on the most abundant type of insect available -- small dipterans. However, tree swallows are selective in their feeding, selecting dipterans larger than those most commonly found in the tow nets. This result is almost identical with the findings of Quinney and Ankney (1985) who found that tree swallows were selective in the size of the most abundant insect group at their site -- also small dipterans. Two explanations may exist to explain this. First, prey items smaller than 3mm may be difficult for tree swallows to efficiently locate. Second, the tow nets may not be sampling the insects that are available to tree swallows. Perhaps the insects of 3-7mm are the most abundant at heights above the tow nets. Holroyd's (1972) observations that 53% of the time parents foraged above heights of 5 meters seems to support this hypothesis.

3. Effects of Experimental Manipulations

I am able to conclude that the clutch size adjustment I performed had no apparent affects on the number of fledglings produced or the growth rates of nestlings. Additionally, linear nestling growth rates were not affected by the food collection procedures (Table 1). The establishment of synchronous hatching and two degrees of hatching asynchrony was not out of the range observed to occur naturally in 5 egg clutches. The natural weight hierarchies established in 4, 5 and 6 egg clutches (Figure 4) were very similar to the weight hierarchies maintained in SYNCHRONOUS, SINGLE ASYNCHRONOUS and DOUBLE ASYNCHRONOUS broods, respectively (Figure 32). For DOUBLE ASYNCHRONOUS broods, the average coefficient of variation of nestling weights maintained during the nestling period was 18%, the same value for the weights of nestlings soon after hatching in natural 6 egg clutches. Likewise, the coefficients of variation in nestlings weight during the nestling period in SINGLE ASYNCHRONOUS broods was 10%, very close to the 12% coefficient of variation of nestlings weights found soon after 5 egg clutches hatched. The coefficient of variation of nestling weights during the nestling period in SYNCHRONOUS broods was slightly higher, 7.5%, than the coefficient of variation (4.9%) found soon after 4 egg clutches hatched. Thus, the experiment of increasing hatching asynchrony (i.e. DOUBLE ASYNCHRONOUS) mimicked the effects that would have been found in naturally asynchronous 6 egg clutches, and SYNCHRONOUS broods mimicked the degree of synchronous hatching of 4 egg clutches. Moreover, the manipulation of hatching patterns had the added advantage of excluding the effects of initial clutch size.

One effect that I did not directly test for is whether parents raise genetic offspring better than foster offspring. Burtt (1977), Burtt and Tuttle (1988), Hussell (1988) and Beaver (unpub.), in nestling switching studies using tree swallows, found that parents raise foster offspring as well as genetic offspring. These results are consistent with other studies on other species which have shown that growth rates and fledging success is dependent upon the quality of the parent rather than on the genotype of the nestling (Ricklefs and Peters 1981). Although it has been shown that tree swallow parents imprint on nestlings using plumage characteristics prior to fledging, the switching experiment at hatching avoided parent's identifying their offspring and thus affecting the production of broods by hatching treatment. Moreover, if tree swallow parents are able to recognize their own offspring by plumage characteristics and if they stopped feeding foster offspring at this time, then deaths from not being fed would occur at a consistent age throughout the hatching treatments and occur late in the nestling period when nestlings have feathers. Nestling deaths were concentrated within the first 15 days of the nestling period, thus ruling out the effect of parent recognizing offspring effect on the results of this study.

B. EXAMINING THE BROOD REDUCTION HYPOTHESIS

1. Objectives of Study

According to the brood reduction hypothesis, hatching asynchrony could be adaptive if it produced a weight and age hierarchy in the nest that aided parents in reducing the brood in the event food becomes limiting. On the other hand, the lack of feeding hierarchies in synchronous broods during food shortages should cause the entire brood to starve. The purpose of this study was to determine if, in tree swallows : (a) conditions necessary for brood reduction occur; (b) the mechanisms of brood reduction are in place; (c) brood reduction, if it occurs, has any adaptive value; and (d) if other reproductive tactics exist to compliment a brood reduction strategy.

2. Prerequisites for Brood Reduction

Lack predicted that brood reduction would be beneficial if (i) food is unpredictable; (ii) the nestling period is long; and (iii) food levels affect parental performance. I discuss each of these in turn.

Brood reduction and hatching asynchrony should be beneficial to parents if parents cannot predict, at the completion of ovulation, future food levels for the upcoming nestling period (Lack 1948, 1954). If parents could predict future food levels, then the most adaptive behavior would be for parents to lay eggs that will hatch the maximum number of nestlings they could raise given the pending food levels. Brood reduction, therefore, should not be necessary. O'Connor (1978) suggested that unpredictability of food levels would be reflected in food levels that change randomly from day to day.

Hussell and Quinney (1987) have measured daily insect abundances from the time of nest initiation to the end of the fledging period at their study sites for seven years. They found no correlation between the food levels occurring during egg laying and levels occurring during the nestling period; thus, prey of the tree swallow appears unpredictable at the time of egg laying. Moreover, in three out of the four years during my study, the variance of daily IBI measures occurred at randomly. This random insect abundance levels were probably tied to random daily weather events. Severe weather events affecting IBI were relatively common during this study. Two lengthy cold spells occurred, one in 1986 and the other in 1989, where temperatures dropped below 45 F^{o}. Aerial insects during these periods were non-existent. Severe weather events causing high mortality rates in nestlings and adults have been reported several times (see review in Zach 1982). Thus, the unpredictability of daily food supply of the tree swallow tied to the unpredictability of daily weather events.

Lack also suggested that birds with longer nestling periods should be at a greater risk of facing food limitations sometime during the nestling period. The average nestling period for tree swallows has been reported to be 18 days to 22 days (Low 1936, Bent 1942, Kuerzi 1941, Quinney et al. 1986). I did not follow nests closely enough to determine the length of each nestling's stay in the nest because disturbing nestlings after 18 DPH causes pre-mature fledging (Quinney 1983b). The average nestling period for most ground nesting birds is 13.2 days (Lack 1948). For cavity nesting birds, the average nestling period is 30-50% longer. Ground nesting birds probably have shorter nestling periods because of heavy predation (Lack 1948, Nice 1954). However, the long nestling period of tree swallows may be necessary because they are aerial insectivores and they will require good flight feathers and functional flight capabilities when they leave the nest.

The prerequisite of long nestling periods for brood reduction to be favorable has not received much attention in the literature. It is quite possible, though, that this is not a necessary prerequisite. Birds that have short nestling periods could be even more apt to require brood reduction. For example, a one day food crash might not effect a slow growing species such as the tree swallow but may necessitate brood reduction in a faster growing species. Thus, the condition requiring brood reduction might be the length of food limitation relative to the length of the nestling period.

Another, but yet neglected condition of the brood reduction hypothesis is that the reproductive performance of parents must depend upon food levels. Quinney (1983b) and Quinney et al. (1986) have shown that clutch sizes of the tree swallow correlate with the insect abundances occurring during the egg laying period. Growth rates and the age of primary eruption of nestlings has also been found to correlate with the average insect abundances during the nestling period (Quinney 1983b, Quinney et al. 1986). I have also found a correlation between daily insect abundance and the maximum weight that nestlings attained and the age of yolk depletion. Body growth rates and primary growth rates were also faster in years of more food. In addition, age of developmental events occurred earlier and primaries erupted earlier when food was more abundant. Furthermore, I found a slightly significant correlation between the daily body mass of adults and the daily insect abundance. There was also a significant correlation between the dry weights of the insects caught in the Manitoba trap and linear nestling growth rate.

The amount of food brought and the number of food boluses brought to the nest, per feeding session, was however, inconsistent with food abundances affecting parental performance. Parents brought more food and in more food boluses when food was less abundant compared to when food was more abundant. However, there are two lines of evidence to suggest that parental performance was curtailed at my study site because of low insect abundances. First, Wiggins (1990), in a study on the tree swallow in British Columbia, found that parents made between 4-5 trips to the nest per 20 minutes. Quinney (1986) also found that tree swallows at an insect rich site made 4-5 trips/20 minutes to the nest. Both figures are well above the 1-2 trips/20 minutes that I recorded during my study. Second, Quinney (1986) reported that broods received about an average of 760 mg of wet weight of insects in a twenty minute period. If insects are 90% water, then parents

delivered 3-4 times as much food as parents during my study. Thus, in comparison to other studies, the amount of food brought to the nest appears to be food dependent.

Lack also stated that another condition for brood reduction is that parents should only occasionally be able to raise their entire brood. Brood reduction should be necessary a majority of the time. I found that tree swallow parents rarely raised all five nestlings. Nestling mortality during this study was variable; the highest was 43% in 1989 and lowest was 15% in 1986. These figures are within the ranges reported by researchers who conducted studies at other localities. Kuerzi (1941) reported a mortality rate of 18.5% and 27.5% in two different years of his study, the later of which he considered high. Quinney (1983) reported fledging success rates of 88% and Low (1933) reported variable fledging success rates, with mortality varying between 19-53% of nestlings. However, parents should also be able to raise their entire brood in some years. If parents cannot, then natural selection should favor laying smaller clutch sizes. The results of De Steven (1980), though, do suggest that there are some years where conditions are favorable for rearing large broods. She reported fledging success that was nearly 100% in five and six nestling broods.

Fledging success was even in excess of 90% in broods enlarged to 9 nestlings. Thus it appears that tree swallow parents require brood reduction because they rarely raise all nestlings in their broods, however, natural selection will not favor smaller clutch sizes because they may be able to raise a large sized brood during some years.

In summary, the first condition for brood reduction to occur, namely, unpredictable food resources, applies to the prey items of the tree swallow. The second condition of long nestling periods also applies but its necessity is questionable. Third, it has been shown elsewhere, and here, that food levels affect the reproductive performance of tree swallows. Only the amount of food brought to the nest was inconsistent with this third prerequisite for brood reduction, although, compared to other studies conducted under more favorable food conditions, parents appeared to be restricted in bringing more food to the nest because of the reduced food levels during my study. Lastly, I have argued that parents most often cannot raise their entire brood and most broods need to be reduced. Additionally, there is some evidence to suggest that parents can raise their entire broods during some years, thus selection will not favor smaller brood sizes over laying large broods and using brood reduction.

3. Mechanisms of Brood Reduction

The brood reduction hypothesis states that brood reduction should occur when food is limited. The weight hierarchy within the brood should allow the largest nestling to acquire food until it is satiated; the next largest should win the next series of feeding bouts until it is satiated; and then so on, down the weight hierarchy (Ricklefs 1965). When food is in short supply, parents will need additional time between foraging trips to collect enough food to bring back to the nest. If this time is sufficiently long, then time will pass where the largest nestlings will become hungry before the last-hatched nestling gets fed. Thus, the last-hatched nestling eventual starves during a food limited period. A necessary condition for this mechanism is that hatching asynchrony should establish substantial competitive feeding hierarchies so that the last-hatched nestling gets fed only if its nestmates are satiated. Also according to the brood reduction hypothesis, natural selection should select against synchronous hatching because these broods lack weight and age hierarchies. Thus, partial brood loss is not an option and instead, the entire brood may starve when food is limited.

I have found that, when food is limited, the incidence of partial brood loss increases with increasing hatching asynchrony (Figure 14). Relative survival decreased with decreasing hatch position with the youngest nestlings' relative survival always less than 100%. Those nestlings that died in these nests were the youngest nestlings. Thus, when food was scarce, part of the brood died and those dying were the youngest chicks in the brood. Because the last-hatched nestling in DOUBLE ASYNCHRONOUS broods died, the first-hatched nestlings had a high fledging rate. This caused the DOUBLE ASYNCHRONOUS broods to have the highest fledging success of all hatching treatments when food was limited.

The feeding bout observations revealed that when food is limited, the last-hatched nestlings are not fed (Figure 36). The 'C' chick in DOUBLE ASYNCHRONOUS broods received less than 8% of the food brought to the nest during the LESS FOOD years. Thus, its death is due to starvation. This starvation was also quick, as reflected in the early deaths of later-hatched nestlings. Earlier ages of yolk depletion by 'C' chicks in DOUBLE ASYNCHRONOUS broods when food was scarce also suggests that these nestlings needed to draw upon food reserves more often than their older nestmates.

Also consistent with the brood reduction hypothesis is my finding that entire brood loss increases with increasing hatching synchrony. Entire brood starvation occurred only during the LESS FOOD years. Weight hierarchies did appear to result in SYNCHRONOUS broods but not to the degree that weight hierarchies existed in either of the asynchronous hatching treatments. Furthermore, the weight hierarchies did not create feeding hierarchies. Nestlings were fed at random, with respect to their weight ranking, when food was less abundant. Nestlings in DOUBLE ASYNCHRONOUS broods were also fed at random with 'B' chicks receiving as much food as the 'A' chicks. Thus it appears that entire brood starvation occurred in SYNCHRONOUS and SINGLE ASYNCHRONOUS broods because parents did not single out a nestling to starve. Possibly, the feeding hierarchy was not as well established in SINGLE ASYNCHRONOUS broods as they were in DOUBLE ASYNCHRONOUS broods to produce a quick starvation of one nestling.

It is probable that the last-hatched nestling did not get fed because of its small size. Hatching asynchrony contributed toward the last-hatched nestling always being the smallest because it was found in this weight ranking the most often. In addition to the disparity of weight among nestlings, the older nestlings may have the added advantage of a day or two advance in development of eyes to help locate parents and to increase their food intake. Moreover, this disparity in eyesight development was increased because the eyes of younger nestlings opened at a significantly later age.

One of the more interesting findings of this study is that, when food was more plentiful, the last-hatched nestling received a majority of the food (Figure 36). It is possible that when food is abundant, parents might preferentially feed the younger nestling in an attempt to counteract the weight hierarchy established by hatching asynchrony. It is difficult to explain why these nestlings that were fed the most food eventually died. One possible explanation is that I monitored feedings for only one of the MORE FOOD years, 1987. The first two weeks of this year produced the highest food levels observed during the entire study. Food levels then decreased during the last few weeks of the season. Thus, I may have measured the parent's attempts to offset the weight hierarchies by preferentially feeding the last-hatched nestling, but food levels soon afterward may have become so scarce that brood reduction may have been re quired. This food year for some parents may have been a low food year for those raising nestlings toward the end of the nestling period.

There have been several studies that have shown that nestling begging interactions differ according to food levels. Proctor (1975) and Evans and McMahon (1987) have shown that the intensity of sibling competition increases with decreasing food levels. Mock *et al.* (1987) have suggested that nestlings, by monitoring their own nourishment level, can "detect" low insect abundances. When food is in short supply, then inter-sibling competition is fierce which would lead to brood reduction. On the other hand, when food is adequate, then all nestlings are fed. This mechanism allows nestlings to be adequately fed when food is more plentiful to counteract the weight hierarchy established by hatching asynchrony, but when food is scarce, sibling competition for food can elicit brood reduction.

Two of my results, however, appear to be inconsistent with the brood reduction hypothesis. First, during the LESS FOOD years, partial brood loss did occur in SYNCHRONOUS broods when food was scarce. The slight weight hierarchies that developed in SYNCHRONOUS broods did not contribute toward a differential feeding of the broods when food was scarce. Thus the risk of raising a SYNCHRONOUS brood, entire brood loss, may at times be avoided, but how the partial brood loss occurred is uncertain. Second, during the MORE FOOD years, brood reduction did appear to occur in the

asynchronous broods almost to the same degree as it did in the LESS FOOD years. Partial brood loss occurred because 'B' and 'C' chicks died. Amundsen and Stokland (1988) suggest that the youngest nestlings in an asynchronous nest could die when food is plentiful if it gets buried by its larger siblings. This appears an unlikely cause of death in my study since these nestlings were fed more food than their older siblings. More research is needed to try to understand why these nestlings die when food does not appear to be limiting.

In the tree swallow, therefore, most data suggests that hatching asynchrony facilitates brood reduction when food is limited. The last-hatched nestlings of DOUBLE ASYNCHRONOUS broods receive less food when food is less abundant. In addition, SYNCHRONOUS broods experienced the most entire brood starvation, as predicted by the brood reduction hypothesis. Entire brood starvation seemed to occur because parents fed nestlings at random. Starvation also occurred in SINGLE ASYNCHRONOUS broods because 'A' and 'B' chicks were fed with an equal frequency and equal amounts of food. However, partial brood loss rather than entire brood loss occurred in some SYNCHRONOUS broods. Thus the risks of SYNCHRONOUS hatching may be different from Lack's original hypothesis. Additionally, brood reduction did appear to occur when food was more plentiful.

The reasons for these deaths is still unclear because these nestlings received the most food. More studies are needed on the begging behaviors of nestlings under different food conditions.

4. Reproductive Tactics Consistent with Brood Reduction

I also examined whether other reproductive tactics of the tree swallow are consistent with brood reduction. Specifically, I determined if egg weights correlated with their laying sequence and whether survival-promoting tactics are employed previous to brood reduction. Survival-promoting tactics would be highly beneficial to parents if short-term food level fluctuations occur.

I have found that the last-laid egg of a clutch is consistently heavier than the first-laid egg. As clutch sizes increase, the differences between the first and last egg also increase. My findings of egg weight variation in a clutch are, however, different from the findings of Zach (1982). He measured the width and length of eggs and calculated egg volumes and found that egg size decreased with laying order. It is quite possible, that both egg size and egg weights do change with laying order in the tree swallow; this would have the effect of changing egg density with laying order. If this is true, then tree swallow eggs might be provisioned differently. Bryant (1978) has shown that the eggs in House Martin (Delichon urbica) clutch are provisioned differently with last-laid eggs containing more water.

Clark and Wilson (1981) have argued that increasing egg size with laying order is inconsistent with the brood reduction hypothesis because the least amount of investment should be placed in the offspring with the least chance of fledging. Slagsvold et al. (1984) took this one step further and examined egg size patterns with laying order and found that many birds either increase or decrease egg size with laying order. He postulated that birds laying larger last eggs adopt a brood survival strategy; those laying a small final egg adopt a brood reductionist strategy.

However, laying larger last-laid eggs may not be inconsistent with the brood reduction hypothesis (Magrath 1990). A larger last-laid egg may increase the fledging success of the last-hatched nestlings when food is plentiful and thus may compliment the brood reduction strategy (Howe 1978, Magrath 1990). Howe (1978) and DeSteven (1978) have also argued that weight variation at hatching due to egg size variation is oftentimes removed by unequal feeding of nestlings soon after hatching.

It is also quite possible that egg size variation with laying sequence may be selectively neutral with respect to a brood reduction strategy. Egg size may increase with laying order due to physiological tendencies during ovulation. Egg size variation may also be influenced by daily food abundances, and thus might occur because of an increase in daily food abundances during egg laying.

Survival-promoting reproductive tactics do seem to occur prior to brood reduction. I estimated the condition of nestlings prior to and after brood reduction in broods where 4 and 3 nestlings fledged. I compared the three different hatching treatments. Body weights of surviving nestlings were 1-2% below the normal weights prior to brood reduction. In SYNCHRONOUS broods, body weights of nestlings did not return to normal for several days after brood reduction. In SINGLE ASYNCHRONOUS broods, nestling weights returned to the normal weight on the day of brood reduction; in DOUBLE ASYNCHRONOUS broods, nestling weights returned to normal prior to brood reduction. Thus it appears that the surviving nestlings benefit most by a brood reduction sooner as hatching asynchrony increases.

Weights of parents change prior to and after brood reduction. Parents seem to loose the most weight just prior to brood reduction. If weight loss reflects parental investment (sensu Drent and Daan 1980), then parents tend to increase their expenditure to make up for low food levels. Brood reduction does, therefore, appear to be a last result.

In summary, egg weights do increase with laying order. However, I argue that this does not necessarily conflict with the brood reduction hypothesis as suggested by some researchers. Survival promoting reproductive tactics do appear to occur in the tree swallow. I found that nestling weights are maintained below their average prior to brood reduction and parents also increase their investment.

5. The Adaptive Value of Brood Reduction

The crux of the brood reduction hypothesis is that hatching asynchrony and brood reduction should be adaptive for parents. Williams (1966a) states that an adaptive trait should increase a parent's lifetime reproductive success compared to an alternative trait. Unfortunately, it is difficult to monitor the reproductive productivity of vertebrate parents over their entire lifespan. Alternatively, ecologists have sought to examine an adaptation at its proximate level and attempt to measure the effects of the adaptation in any one of several short-term effects (in sensu Williams 1966b). I propose that hatching asynchrony and brood reduction is adaptive for tree swallows because it increases lifetime production of offspring by either increasing annual productivity or increasing annual survival of parents. Below, I present four possible adaptive scenarios.

a. Hatching asynchrony and brood reduction are favored over synchronous hatching when bad food years are most frequent. During the LESS FOOD years, fledging success increased with increasing hatching asynchrony. This increased fledging success appears to result from brood reduction. The last-hatched nestling is starved allowing the first hatched nestling to fledge. Moreover, a high percentage of SYNCHRONOUS nests experienced entire brood loss. These two mortality patterns allowed parents raising DOUBLE ASYNCHRONOUS broods to fledge the most young when food was in short supply. Thus, it appears that DOUBLE ASYNCHRONOUS broods are the most productive during years of scarce food.

On the other hand, asynchronous hatching seems to be maladaptive when food is more plentiful. During the MORE FOOD years, fledging success decreased with increasing hatching asynchrony. Deaths in asynchronous broods appeared to be due to the weight or age hierarchy established by hatching asynchrony. Greater productivity of synchronous broods during more favorable food and greater productivity of asynchronous broods when food is scarce is consistent with the findings of other studies that have manipulated broods to establish different hatching treatments under different food conditions. Magrath's (1989) study on the Fieldfare (Turdus pularis) found that hatching asynchrony produced more nestlings that lived two weeks past fledging when food was limited. On plots where food was supplemented, broods adjusted for synchronous hatching produced more offspring surviving to two weeks postfledging. Skagen (1988), in a study on the Zebra Finch (Poephila guttata), found that nestlings from asynchronous broods fledged at lower weights than fledglings from broods adjusted for synchronous hatching. Amundsen and Stokland (1988) have argued that brood reduction during food plentiful conditions is maladaptive.

Magrath (1989) has suggested that, if hatching asynchrony carries a cost when food is plentiful, then natural selection will favor hatching asynchrony and brood reduction over hatching synchrony when poor food years are most common. Lack (1954) suggested that for hatching asynchrony and brood reduction to be adaptive, parents must be subjected to more years of scarce food than plentiful food. I present a quantitative model of how the frequency of good and bad food years selects for hatching patterns in Chapter 4.

This frequent bad year adaptive scenario would also explain why there is a lot of variation in hatching spreads within a clutch size. If good years occurred most frequently for a short time period, this would favor hatching synchrony and a hatching synchrony gene would be maintained in the population. Alternatively, a series of bad food years would help maintain an asynchronous hatching gene. Thus, this adaptive scenario could explain how a polymorphic population could exist and be a result of fluctuating natural selection.

b. Hatching asynchrony increases geometric mean fitness. There have been several suggestions that natural selection may select for reduced variance in offspring number per year as well as the average in offspring production (Gillespie 1974, 1977). Clearly, SYNCHRONOUS broods are at a greater risk of having higher variances in offspring number than asynchronous broods. It has been suggested (e.g. Lacey *et al.* 1980, Cooper and Kaplan 1982) that rather than comparing the arithmetic means of reproductive success of various traits, a researcher should instead compare the geometric means of reproductive success. I calculated geometric means for the productivity of broods for all four years for each hatching treatment; these are shown in Figure 40. This comparison shows that, for all four years, the geometric mean of fledging success for the DOUBLE ASYNCHRONOUS broods is 10% greater than the geometric means of fledging success for the other two hatching treatments.

The importance of variation in reproductive success of different hatching patterns may be overlooked. Several studies have reported that broods adjusted for synchronous hatching are more productive than the normal asynchronously hatched clutch (see Amundsen and Stokland 1988 for review) but did not compare variances in their hatching treatments. Two studies presented data to allow variances to be compared. Bryant and Tatner (1990) found that, in the white-bellied swiftlet (Collocalia esculenta), fledging success in synchronous broods was 1.19 nestlings per two nestling broods while fledging success in asynchronous broods was 0.86 nestlings/2 nestling broods. However, fledging success for synchronous broods was more variable than for asynchronous broods. Using data from their Table 4, I found that using a geometric mean reduced these fledging success differences by more than 10%. However, even with variances incorporated, synchronous broods were still more productive than asynchronous broods. Haydock and Ligon (1986) reported

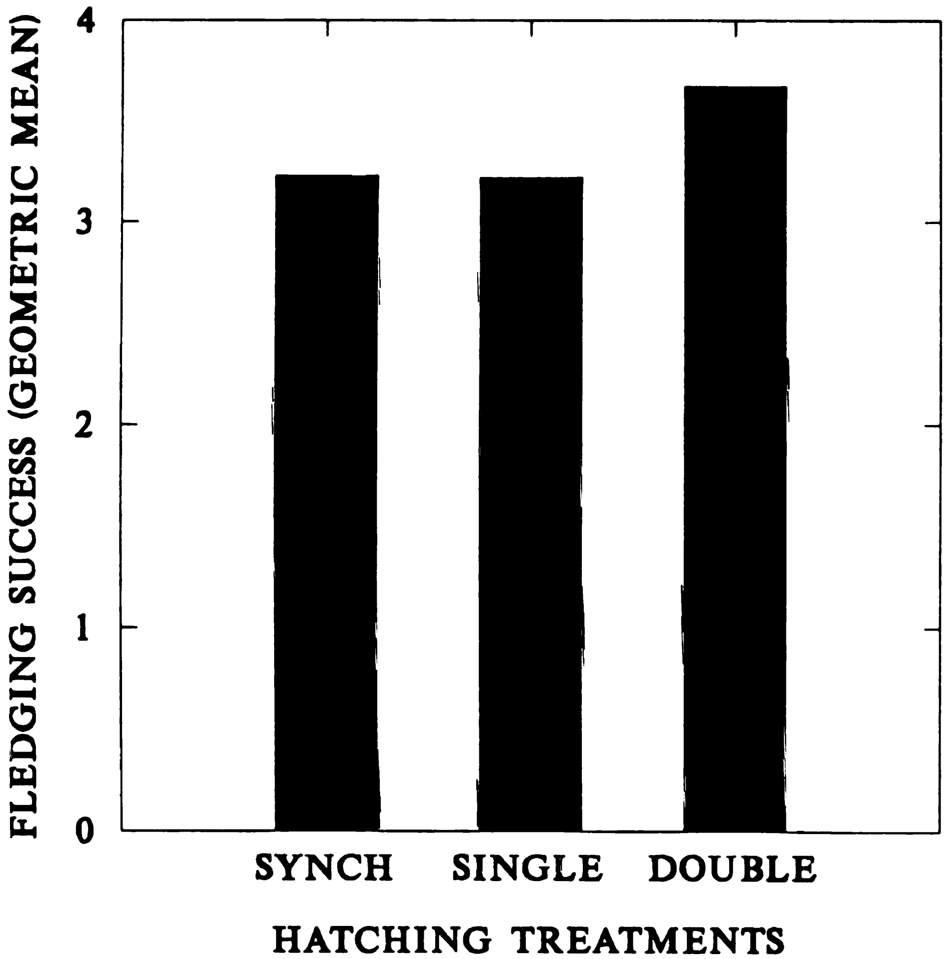


FIGURE 40.

Geometric means of fledging success for all four years, by hatching treatment.

that broods of the Chihuahuan Raven (*Corvus cryptoleucus*) adjusted for synchronous hatching also fledged more nestlings than asynchronous broods. Their data also show that the range of fledging success values for synchronous broods was more than double compared to fledging success values for asynchronous broods. Thus, in both studies, synchronous broods experienced a higher variance in reproductive success.

A geometric mean fitness model has been used to explain why many birds lay fewer eggs than the most productive clutch in the population (Boyce and Perrins 1987). Boyce and Perrins (1987) have suggested that natural selection favors smaller clutch sizes than the most productive clutch size because parents laying large clutches experience high variance from year to year when good, moderate and bad food years occur. Their geometric mean fitness model adequately predicted the mean clutch size in the population when annual variance in reproductive success was introduced.

In conclusion, the high variation in fledging success by broods hatched synchronously may lower a parent's fitness. More researchers should calculate a geometric mean for reproductive measures that influence fitness.

c. *Hatching asynchrony allow parents to temporally track the environment.* Temme and Charnov (1987) have suggested that hatching asynchrony and brood reduction can allow parents to temporally track a constantly changing environment and to reduce their brood when it becomes "evident" to parents that the current brood size cannot be successfully raised. Parents of synchronous broods do not have the option of quickly reducing the brood because no feeding hierarchy exists in the brood.

I have found that prior to brood reduction, nestling weights are decreased below an average weight for their age. It appears that a maximum of a 2% nestling weight loss from the average occurs, after which brood reduction is then carried out. Hatching asynchrony may be adaptive because it may allow parents to reduce the brood quickly once a certain limit is reached after survival-promoting tactics, such as maintaining nestling weights below the average, are used. If, however, food levels return to ample levels, then parents might find enough food to raise the entire brood. The switch between survival-promoting and brood reduction tactics would benefit parents that prey on food levels that change on a daily basis. This is certainly applicable for tree swallows.

If survival-promoting tactics prior to brood reduction are favored by natural selection, then mechanisms that allows parents to monitor how close nestlings are to a critical weight loss from the average. Hussell (1988) has suggested that parents adaptively monitor the hunger level of the brood using the brood's overall begging intensity. I propose that parents might be able to use hunger levels to determine how close the brood is to a critical lower weight reduction. Once the brood reaches this hunger level, brood reduction is initiated.

In summary, it appear that asynchronous hatching might allow tree swallow parents to track an environment that is changing daily and allows them to initiate brood reduction once a certain brood hunger level is reached. I suggest that parents might be able to monitor the how close nestlings are to a critical weight reduction by monitoring the average hunger level of the brood.

d. Hatching asynchrony reduces parental investment when food is limited. Parents that invest the least amount of energy into their offspring can expect to live longer lives and hence produce more offspring in their lifetime (Williams 1966a, Drent and Daan 1980). I have found some evidence to suggest that parents raising asynchronous broods during food scarce years invest less in the offspring that they raise.

Over the course of the nestlings period, DOUBLE

ASYNCHRONOUS parents invested slightly less energy into nestlings that eventually died. Their chicks, especially their 'C' chicks, died sooner than nestlings in either of the two nests. Furthermore, parents of asynchronous broods gained weight during the nestling period while parents raising SYNCHRONOUS broods lost weight. Having a heavy weight at the end of the nestling period may be more important for tree swallows than for other passerines because tree swallows begin their southward migration one to two weeks after the nestlings have fledged (Butler 1988). Asynchronous parents during LESS FOOD years also were able to bring more food to the nest.

There have been few studies that have investigated parental investment with respect to hatching asynchrony. Gibbons (1987) found that Jackdaw (Corvus moneula) parents of asynchronous broods invested less in reproduction compared to broods adjusted for synchronous hatching because nestlings in asynchronous broods died earlier. Fujioka (1985b) found that, in the Cattle Egret (Bubulcus ibis), parents raising asynchronous broods made fewer trips to the nest than parents raising even-aged broods. This reduced parental investment in asynchronous nests was attributed to reduced nestling demands. Broods adjusted for synchronous hatching exhibited more frequent sibling aggression. Thus, hatching asynchrony reduces sibling aggression that is spurred by a lack of a feeding hierarchy established by hatching asynchrony.

I did, however, obtain one result that is inconsistent with the scenario that brood reduction reduces parental investment. I found that parents of DOUBLE ASYNCHRONOUS broods experienced the greatest reduction in their body weights compared to parents raising either of the two hatching treatments. Coming closer to a maximum weight loss suggests that these parents may have placed themselves at a greater risk of dying than the other two groups of parents (in sensu Drent and Daan 1980).

In summary, I argue that hatching asynchrony and brood reduction can reduce parental investment. This would have the benefit of increasing a parent's chances of surviving to reproduce again. This in turn would increase the number of offspring a parent could produce in a lifetime. I explore the ramifications of introducing effects of hatching asynchrony on parental survival in chapter 4.

IV. Conclusions

I manipulated broods of the tree swallow to establish three different hatching patterns, hatching synchrony and two degrees of hatching asynchrony, to determine if the brood reduction hypothesis is an adequate explanation for hatching asynchrony in tree swallows. I measured the reproductive performable of parents raising these three broods during MORE and LESS food years. I found that brood reduction mechanisms do exist during years of less food. Nestlings in inferior hatch positions are not fed and they eventually starve. I also found that survival-promoting tactics occur prior to brood reduction in effect complimenting brood reduction. These same mechanic may be responsible for its adaptive value because parents might be able to track a temporally varying environment. Three other adaptive scenarios are also presented. I propose that hatching asynchrony and brood reduction are adaptive for parents if bad food years occur more frequently than good food years, that hatching asynchrony and brood reduction increase parental fitness because they reduce variation in reproductive success and finally that hatching asynchrony may reduce parental investment because nestlings die earlier in asynchronous broods.

CHAPTER 3

A REVISION OF LACK'S BROOD REDUCTION HYPOTHESIS USING A GAME THEORY MODEL

I. INTRODUCTION

In many altricial birds, incubation commences prior to the laying of the last egg of the clutch (Clark and Wilson 1981). This behavior produces 'hatching asynchrony', which results in broods where some nestlings hatch a day or more later than others, so that nestlings differ in ages and weights. The most cited adaptive explanation for the occurrence of hatching asynchrony is the one proposed by David Lack (1947, 1948 and 1954) called the brood reduction hypothesis. According to Lack, hatching asynchrony could be adaptive if it produced a competitive feeding hierarchy within a brood. If food becomes scarce, the youngest nestlings starve because the oldest and strongest nestlings receive the food brought to the nest by their parents. Hatching asynchrony increases a parent's lifetime productivity because large clutch sizes can be quickly reduced when food is scarce. When food is plentiful, the entire large-sized brood is raised. On the other hand, Lack assumed that if the same large-sized brood is hatched synchronously when food is scarce, every nestling will be effected by food shortages and all nestlings might starve. Lack thought that hatching asynchrony would be beneficial for parents which cannot predict, at the time of egg laying, food levels for the upcoming nestling period.

Most support for the brood reduction hypothesis is indirect. It has been reported that the last-hatched nestling grows more slowly and dies more frequently than its siblings (e.g. Mishaga 1974, Bryant 1978, Zach 1982, Bechard 1983, and Greig-Smith 1985 and others); that the last-hatched nestling receives smaller amounts of food than its siblings (e.g Groves 1984, Horsfall 1984, Fujioka 1985b, and Forbes and Ankney 1987); that larger clutches experience more partial brood starvation (e.g. Howe 1976, Skagen 1988) and that hatching asynchrony tends to increase in degree among those birds nesting late in the season (e.g. Murphy and Fleischer 1986, Slagsvold 1986). In the latter case, the degree of hatching asynchrony is increased because it is thought that food becomes more unpredictable as the season progresses.

There have been, however, several major criticisms of the brood reduction hypothesis. Several researchers (e.g. Clark and Wilson 1981, Slagsvold et al. 1984) have argued that the common occurrence of increasing egg size with laying order among species hatching broods asynchronously is inconsistent with the brood reduction hypothesis. They argue that the least investment in egg size, not the most, should be placed in the nestling having the least chance of survival.

The brood reduction hypothesis has also been criticized on the grounds that hatching asynchrony may not be required to facilitate brood reduction (Clark and Wilson 1981). Clark and Wilson's (1981) literature review showed that, at least for several species of birds, the number of young starving was often greater than the number of nestlings set at a competitive disadvantage with hatching asynchrony. In addition, partial brood starvation can occur as frequently in synchronously hatched broods as it does among asynchronously hatched broods (e.g. Howe 1978). Thus, factors other than hatching asynchrony may facilitate nestling starvation when food is scarce.

Amundsen and Stokland (1988) have argued that hatching asynchrony can result in brood reduction even when food is plentiful. They reviewed several experimental studies and showed that when food is plentiful, naturally hatched asynchronous nests are, on average, less productive than nests that are adjusted to simulate synchronous hatching. They concluded that the brood reduction hypothesis cannot adequately explanation the adaptive significance of hatching asynchrony if last-hatched nestlings die when food is plentiful.

Another criticism of the brood reduction hypothesis has been that, because it has been presented only verbally, the hypothesis is difficult to apply to field data. The hypothesis could be made more testable if it was quantitative rather than qualitative (Magrath, 1990). A quantitative hypothesis would also clarify the assumptions.

Finally, the brood reduction hypothesis has not been widely accepted because alternative hypotheses have not been ruled out as plausible explanations. The most notable of these hypotheses are the "peak-demand reduction hypothesis" (Hussell 1972), the "predation hypothesis" (Hussell 1972), the "nest-failure hypothesis" (Clark and Wilson 1981), the "sibling rivalry reduction hypothesis" (Hahn 1981), the "nest-crowding hypothesis" (Slagsvold 1982) and the insurance hypotheses (see Magrath, in press, for a review). Unfortunately, very few studies have attempted to rigorously test any of these hypotheses.

The aim of this chapter is to present a quantitative model of Lack's original brood reduction hypothesis using the game theory techniques of Lewontin

(1961). I show that, even if hatching asynchrony causes occasional brood reduction when food is plentiful, hatching asynchrony can be adaptive because the lifetime productivity of parents will be increased compared to hatching synchrony. I conclude with a presentation of the assumptions and predictions of this brood reduction model.

II. THE MODEL

Lewontin (1961) was the first to suggest that the game theory technique of the social sciences could be a useful tool for evolutionary biologists. Lewontin developed several different types of models. Here, I shall follow the theoretic he labeled as 'states of nature' games. These games allow evolutionary biologists to compare two or more different phenotypes that exist in environments that are characterized by the alternation of some qualitative trait, such as wet and dry or good and bad seasons.

Suppose years exist either as 'good' or 'bad' depending upon the level of food. Each type of year represents a different 'state of nature'. A good food year is one in which, if any nestling mortality occurs, it is not caused by a lack of available food in the environment. A bad food year, on the other hand, is one in which poor food levels in the environment cause nestling mortality.

Let there be two or more alternative strategies that 'play' against these states of nature. Allow one strategy to consist of synchronous hatching. The parents' payoff is the recruitment of the entire brood of size 'B' into the next generation during good years because no nestling is set at a competitive disadvantage. In keeping with the brood reduction hypothesis, in a bad year, let all nestlings be equally affected by reduced food levels. As a result, each nestling will have a reduced chance of surviving until its reproductive age (hereafter, simply as 'nestling survival') compared to its chances in a good year. Let the expected nestling survival of synchronous hatching be denoted as 's', a value that should always be less than 1.0. The payoff for hatching young synchronously in a bad food year then becomes 's*B'.

Consider the alternative strategy to be represented by parents hatching one nestling a day after all of the rest. During a good year, these parents expect to recruit all of their first-hatched nestlings, which number 'B-1', into the next generation. However, suppose that the last-hatched nestling has a reduced probability of surviving until its reproductive age because of the competitive feeding hierarchy established by hatching asynchrony. Let the probability of the last-hatched nestling surviving until its reproductive age be 'q'. The payoff for these parents in good years becomes 'B-1+q'. In a bad year, asynchronously hatched broods are reduced by starving the last-hatched nestling; the remaining nestlings, however, survive to reproductive age. Figure 41 shows the payoff matrix of these two hatching strategies in good and bad food years.

Now, let us suppose that good food years occur randomly, and with a certain frequency, 'j'. From the payoff matrix in Figure 41, the expected number of nestlings from synchronously hatched broods surviving until their reproductive age, per year, is:

$$E(P_s) = j*B + (1-j) * (s*B) \qquad (1)$$

and for parents that are raising a brood in which one nestling hatches a day later than its siblings:

$$E(P_a) = j* (B-1 + q) + (1-j) * (B-1). \qquad (2)$$

Hereafter, equation (2) will be simplified by allowing R = 'B - 1 + q'.

Lack predicted that brood reduction and hatching asynchrony should increase lifetime productivity because parents can lay large clutches. Ricklefs (1977) has shown that nestling survival rates decrease exponentially as the brood size increases. Following

FIGURE 41.

Payoff matrix for two alternative hatching strategies generated by the game theory model.

	GOOD YEAR	BAD YEAR
SYNCH	B	$s * B$
ASYNCH	$B - 1 + q$	$B - 1$

FIGURE 41

Ricklefs (1977), let nestling survival, 'p', as a function of brood size, approximate:

$$p(B) = \exp(-a*B)$$

where 'a' is a constant relating nestling survival to brood size, 'B', (effects of predation and mortality events between breeding seasons are excluded). The constant 'a', hereafter referred to as the 'brood size dependent mortality constant', will take on values between 0.1 and 1.0. [Ricklefs (1977) uses a more complex form of $\exp(-a*B^{x})$, where 'x' represents a curve fitting parameter. When this equation is fit to data, values of 'a' range from 0.01 to 1.0×10^{-14}. Excluding 'x' from the equation and recalculating 'a' changes the range for 'a' to 0.1 to 1.0.] A smaller value of 'a' reflects increased nestling survival as brood size increases (Figure 42a). Multiplying exp(-a*B) times the brood size, B, generates the classic brood size dependent "productivity" curve (Charnov and Krebs 1974), such as the one shown in Figure 42b.

Incorporating the effects of brood size on the reproductive success of parents yields the following expected number of recruits into the next generation for synchronously hatched broods:

$$E(P_s) = (j * B * e^{-aB}) + [(1-j)*(s*B) * e^{-aB}] \quad (3)$$

and for parents raising an asynchronously hatched brood:

$$E(P_a) = (j * R * e^{-aB}) + [(1-j)*(B-1) * e^{-a(B-1)}]. \quad (4)$$

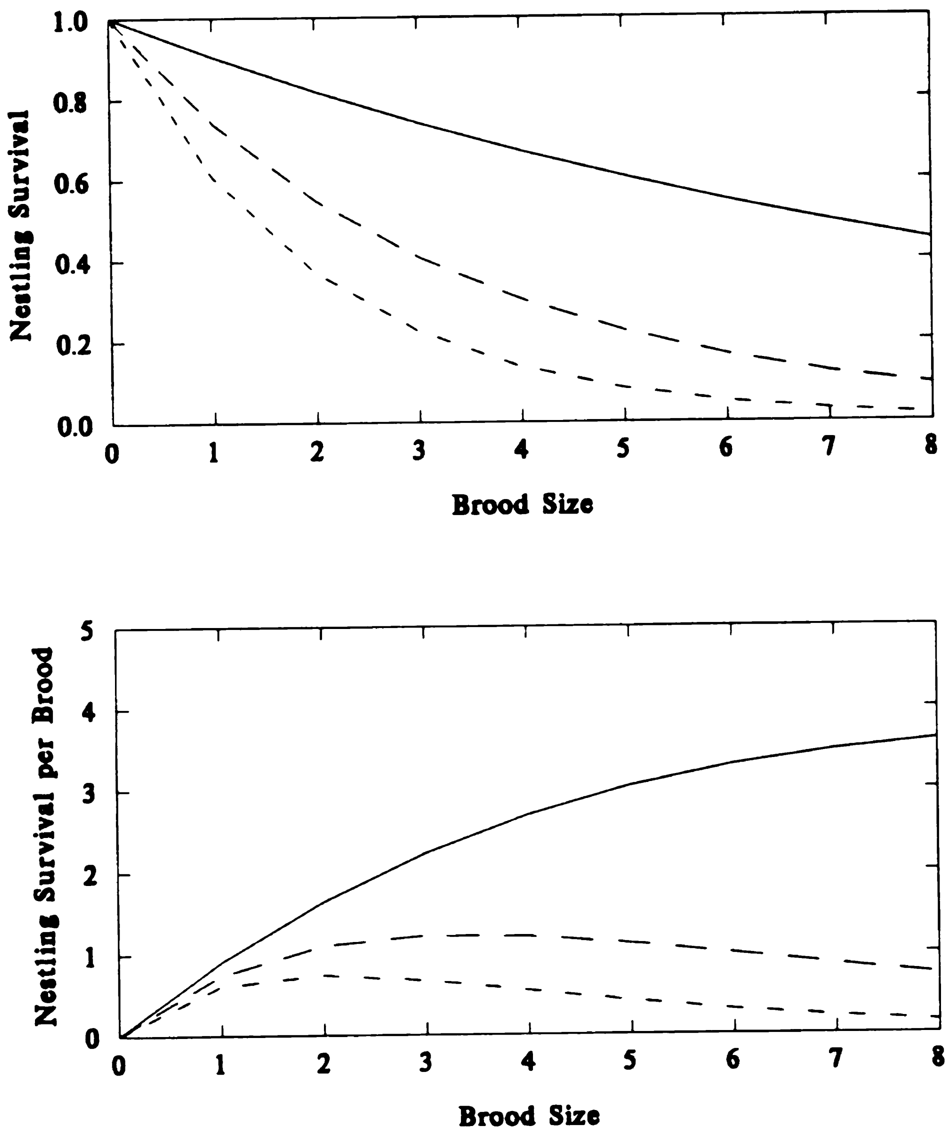


FIGURE 42

The (A) probability of each nestling surviving to reproductive age and (B) the total number of nestlings per brood surviving to their reproductive age, both as a function of brood size.

Finally, let us consider that a certain sized brood will be more difficult for parents to raise during bad years compared to the same sized brood in good years. This is because parents will need additional time and energy to collect the necessary amounts of food for the brood relative to the time and energy expended for the same sized brood in good years. Incorporating this effect into the model can be accomplished by introducing a bad years effect variable, 'c', into the second term of each expression above. The expected productivity of synchronous hatching becomes:

$$E(P_s) = (j * B * e^{-aB}) + [(1-j)*(s*B) * e^{-acB}] \quad (5)$$

for parents raising an asynchronously hatched brood:

$$E(P_a) = (j * R * e^{-aB}) + [(1-j)*(B-1) * e^{-ac(B-1)}]. \quad (6)$$

When 'c' exceeds 1.0, nestling survival will be reduced when raised in a bad year compared to being raised in a good year.

I will assume that natural selection favors the hatching pattern that produces, on average, the greatest number of nestlings that survive until their reproductive age. I shall use the ratio of $E(P_a)$ to $E(P_s)$, hereafter referred to as HPR (hatching productivity ratio), to reflect the intensity of selection for hatching asynchrony over hatching synchrony. If the HPR is greater than 1.0, then hatching asynchrony will be favored over hatching synchrony.

To determine whether the environment in which the parents breed favors hatching asynchrony over hatching synchrony, I shall use the frequency of good years, 'j', for which HPR = 1.0 (i.e. neither hatching pattern is favored over the other) and compare this value against the frequency of good years that occurs in the breeding environment. This threshold value of 'j', denoted as 'T_j', can be calculated by setting equation (5) equal to equation (6) and solving for 'j' to yield:

$$T_j = \frac{[(B-1)*e^{-ac(B-1)}] - [B*s*e^{-acB}]}{B*e^{-aB} - B*s*e^{-acB} - R*e^{-aB} + (B-1)*e^{-ac(B-1)}} \quad (7)$$

Hatching asynchrony will be favored over synchronous hatching when the 'j' in the environment is less than 'T_j'. .pa

III. RESULTS

I ran computer simulations to explore the relationship between, and the effects of, the variables in this brood reduction model. From these simulations, several predictions are generated regarding the conditions favoring hatching asynchrony and brood reduction over synchronous hatching. I used values for variables that best illustrated predictions and that were within ranges I would expect to occur in nature.

The relationship between HPR and the frequency of good years, 'j', for a brood size of five, is given in Figure 43. When good years are not frequent (i.e. when 'j' is low), hatching asynchrony is favored over hatching synchrony, because the HPR is greater than 1.0. As the frequency of good years increases, hatching asynchrony becomes less favorable. As good years become very frequent, hatching synchrony is favored over hatching asynchrony. Note that the threshold value of the frequency of good years, 'T_j', is determined graphically from Figure 43 as the point where the hatching productivity ratio curve intercepts the HPR value of 1.0. Here, 'T_j' is equal to 0.825. Also note that, since 'T_j' is fairly high here, hatching asynchrony is favored over synchronous hatching over a large range of environments; those with a high frequency of good years to those with a high frequency of bad years.

The average number of offspring, per brood, that survive until their reproductive age (i.e. productivities) for hatching asynchrony and hatching synchrony, versus brood size, are given in Figure 44. The maximum productive brood size for an asynchronously hatched brood is larger than for a synchronously hatched brood. Furthermore, the greatest possible productivity for either hatching strategies is for a large, asynchronously hatched brood; here, for a brood size of six.

FIGURE 43

The HPR (hatching productivity ratio) as it varies with the frequency of good years. The threshold frequency of good years, T_j, is also given and indicated by the dotted line. Parameter values are 'B'=5, 'a'=0.2, 's'=0.7, 'q'=0.7 and 'c'= 1.0.

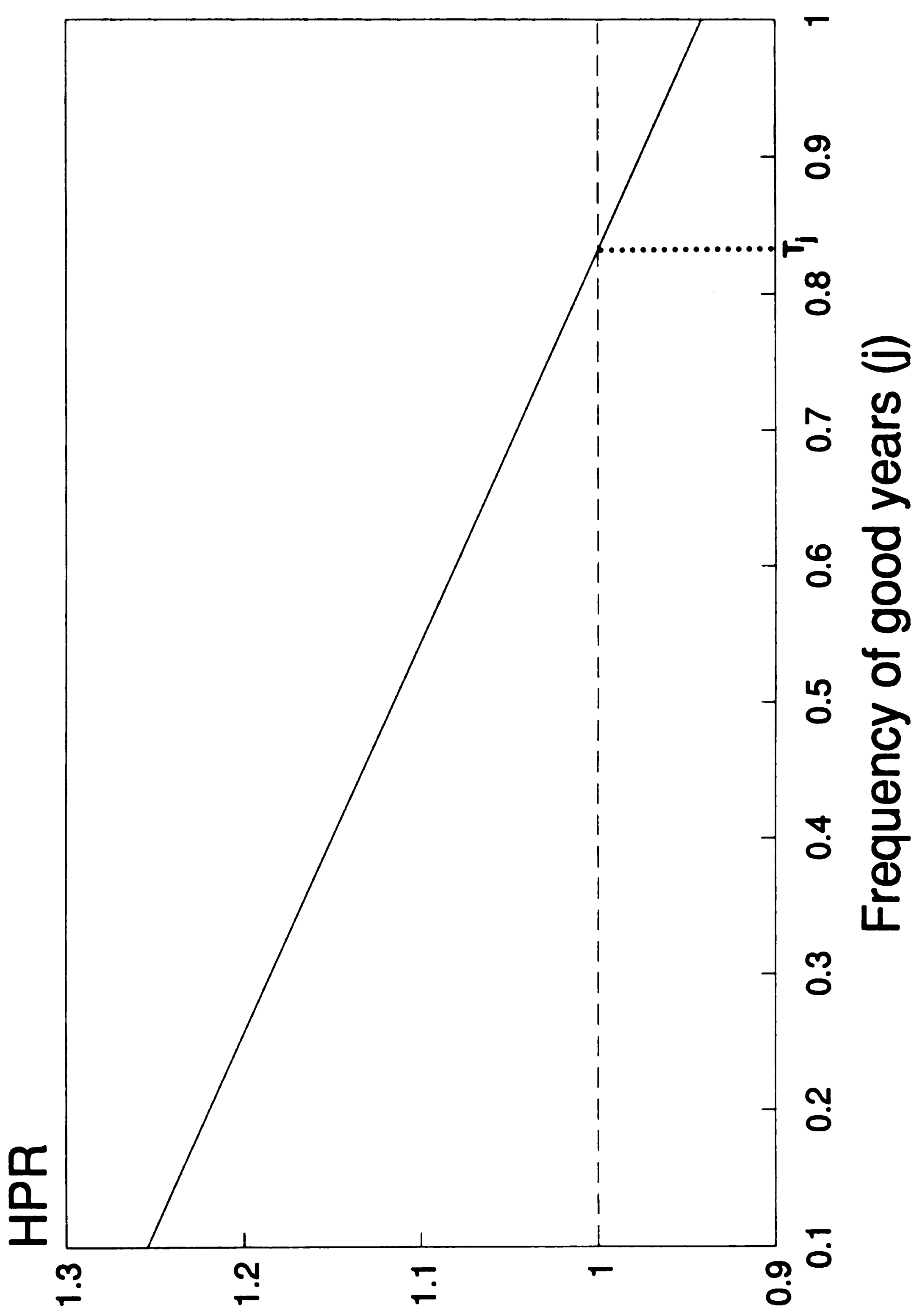

HPR
1.3
1.2
1.1
1
0.9
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
T_j
Frequency of good years (j)

FIGURE 43

FIGURE 44

Productivity of hatching asynchrony and hatching synchrony versus brood size. Parameter values are 'B'=5, 'a'=0.2, 's'=0.7, 'q'=0.7 and 'c'=1.0.

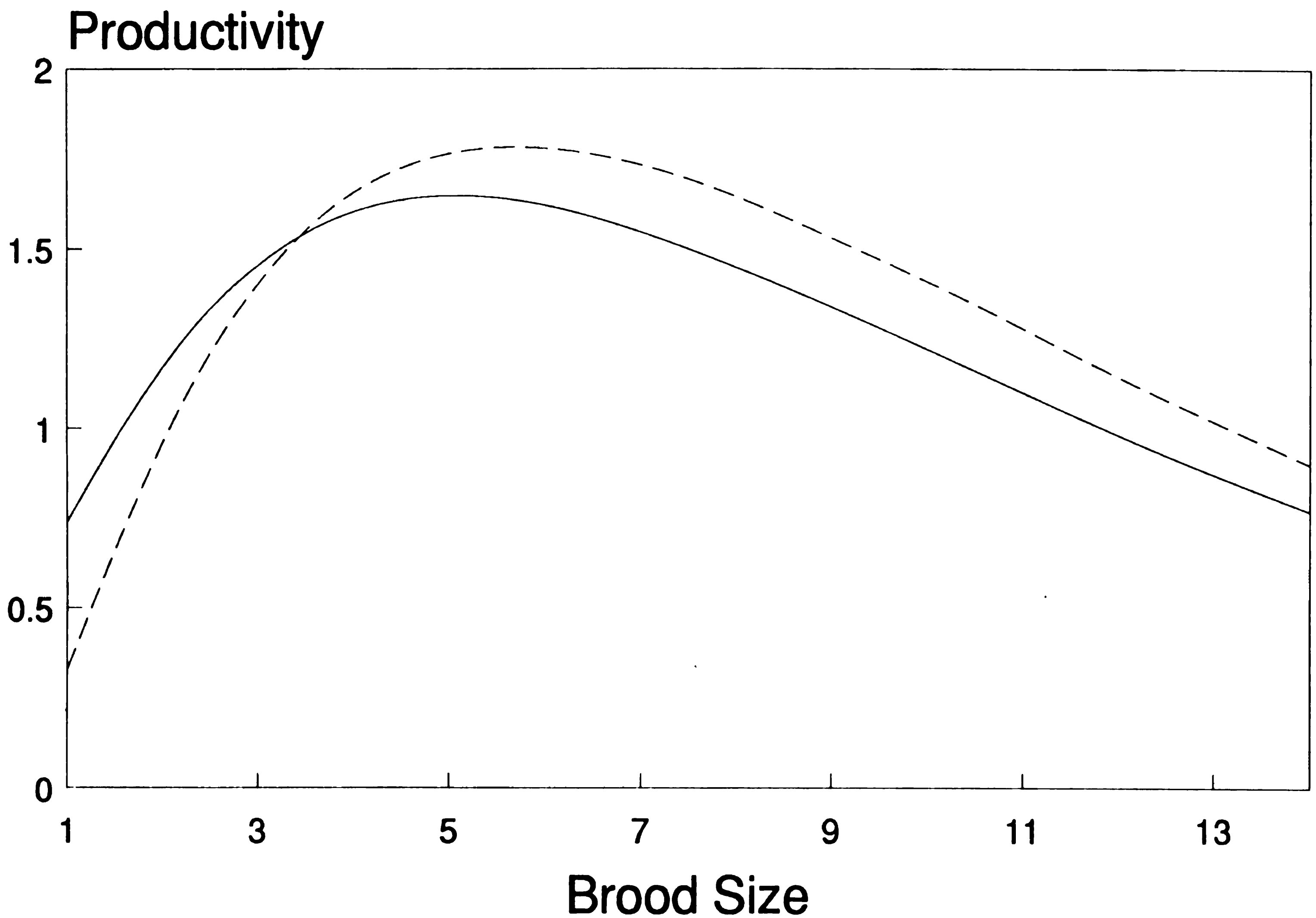


FIGURE 44

The HPR values for different 's' and 'q' values, when all other variables are held constant, are shown in Figure 45a. The model is consistent with the intuitive notion that hatching asynchrony is favored over hatching synchrony when 'q' is high, and when 's' is low. Also note that 's' has a greater effect than 'q' on HPR values because 's' affects an entire brood while 'q' affects only one nestling.

However, as 'q' approaches zero, then parents of asynchronously hatched broods will essentially be producing 'B-1' offspring in good and bad food years. Figure 45b shows that in some instances, a synchronously hatched brood of size 'B-1' may be a better strategy to employ than either a synchronously hatched brood of size 'B' or an asynchronously hatched brood of size 'B'. I used the productivity ratio of synchronously hatched broods of size 'B-1' to asynchronously hatched broods of size 'B' to represent the reduced brood size advantage (RBA). When 'q' is very low, it is more favorable for parents to begin with a small ('B-1'), synchronously hatched brood. When 'q' is near 1.0, however, a large ('B'), asynchronously hatched brood is more productive than a synchronously hatched brood of either 'B-1' or 'B', as represented by HPR values greater than 1.0 and RBA values less than 1.0. When 'q' values are

FIGURE 45

HPR values (A) as a function of 'q' and 's' with parameter values of 'B'=5, 'a'=0.2 and 'c'=1.0 (for 's' iterations, 'q'=0.7 and for 'q' iterations, 's'=0.7); and (B) as a function of 'q' for brood sizes of 'B' and 'B-1', where RBA denotes the reduced brood size advantage, see text for details; (C) as a function of 'a' and 'c'.

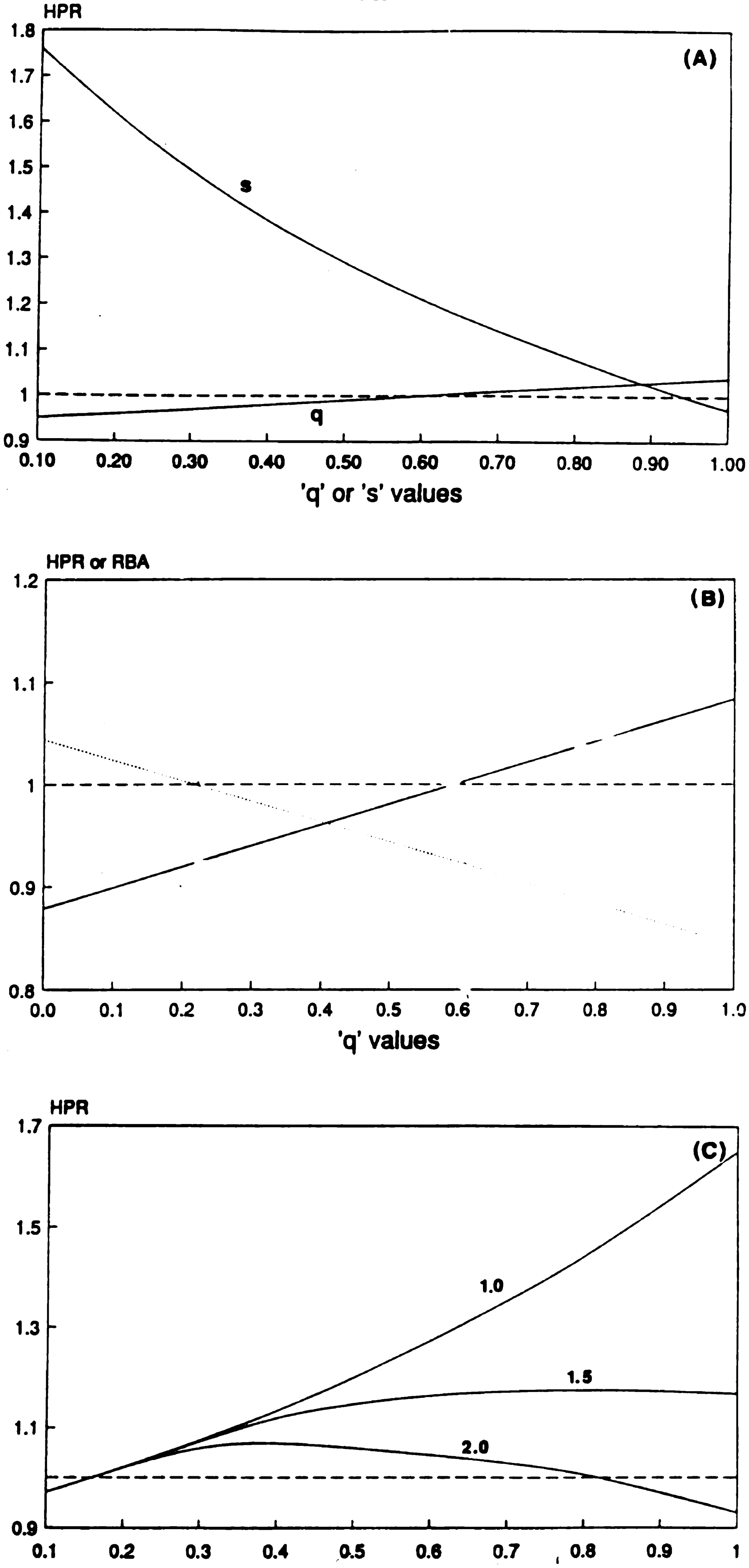

HPR
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
(A)
s
q
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
'q' or 's' values
HPR or RBA
1.2
1.1
1
0.9
0.8
(B)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
'q' values
HPR
1.7
1.5
1.3
1.1
0.9
(C)
1.0
1.5
2.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

FIGURE 45

intermediate, the better strategy is for parents to lay large broods, hatched synchronously.

Figure 45c shows the effect of the brood size dependent mortality constant, 'a', and the bad years effect constant, 'c', on HPR values. When the effects of 'c' are excluded (i.e. 'c'=1.0), and 'a' is increased (i.e. as a larger brood becomes more difficult to raise), HPR values increase as well. This is because, when 'a' is large, there is a large difference in the ability to raise an asynchronously hatched brood of size 'B' compared to raising the reduced brood of size 'B-1'; as a result, brood reduction is beneficial. Interestingly, when bad years are severe (i.e. when 'c' > 1.0), hatching synchrony is favored over hatching asynchrony. This is because, as 'c' increases, nestlings raised in good years eventually make up a greater proportion of lifetime productivity; this proportion also increases with increasing values of 'c' (Table 8). Hatching synchrony is favored over hatching asynchrony because hatching synchrony is more productive during good food years.

The values of 'T_j', as a function of 'q' and 's', are provided in Figure 46a. When 'q' is high and 's' is low, the frequency of good years may be very high and still favor hatching asynchrony over hatching synchrony.

Table 8. The expected yearly reproductive success of parents hatching nestlings synchronously and asynchronous in good and bad food years. The ratio presented represents the proportion of lifetime reproductive success that is gained during good food years calculated as (good food years)/(good + bad food years).*

	SYNCHRONOUS BROODS			ASYNCHRONOUS BROODS		
'c'	good	bad	ratio	good	bad	ratio
1.0	1.839	1.472	0.5556	1.766	1.797	0.4956
1.2	1.839	1.205	0.6042	1.766	1.532	0.5355
1.4	1.839	0.986	0.6509	1.766	1.305	0.5750
1.6	1.839	0.808	0.6949	1.766	1.112	0.6136
1.8	1.839	0.661	0.7356	1.766	0.948	0.6507

* The parameter values are 'B'=5, 'a'=0.1, 'q'=0.8 and 's'=0.8'.

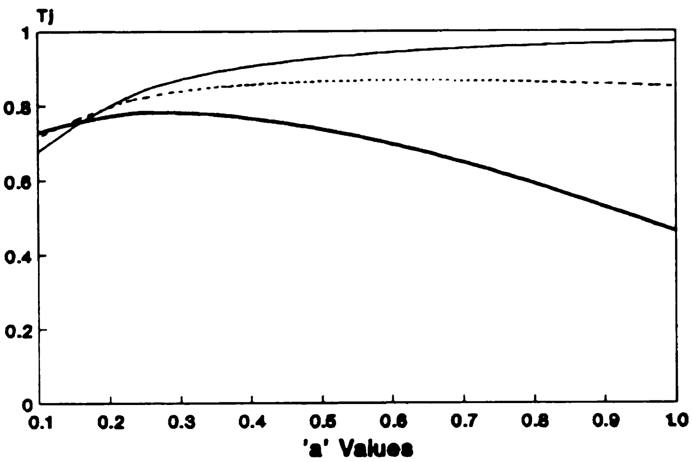
For example, when 's' is 0.8 and 'q' is 0.8, then T_j is 0.815 (when all other variables are held constant). All environments that have good years with a frequency of 0.815 or less will favor hatching asynchrony over hatching synchrony.

This graph also shows that T_j values immediately become zero after a large 's' value. In the model, when 's' becomes greater than '(B-1)/B', then hatching synchrony becomes more productive than hatching asynchrony during bad food years as well as during good food years. For Figure 46a, synchronous hatching becomes more productive than asynchronous hatching when the 's' value is more than 4/5 or 0.80. In such cases then, brood reduction via hatching asynchrony will not be favored over hatching synchrony, according to the brood reduction hypothesis.

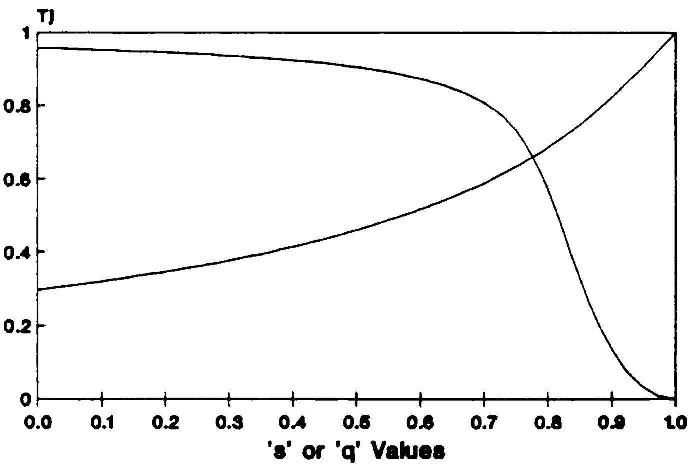
The value of T_j, as a function of the brood size dependent mortality, 'a', and the bad years effect constant, 'c', is shown in Figure 46b. As 'a' increases, when the effects of 'c' are excluded, hatching asynchrony is increasingly favored in environments with frequent good food years. This is because the cost to asynchronously hatched broods during a good food year is comparably less than costs to synchronously hatched broods during a bad food year, and hence, good years can be frequent. However, when 'c' increases, the range of environment types favoring hatching asynchrony over hatching synchrony is reduced. The benefits of a brood reduction strategy during a bad food year becomes reduced because larger values of 'c' reflect lower proportions of nestlings produced during

FIGURE 46

T_j values (A) as a function of 'a' and 'c' (upper solid line, c=1.0; dotted line, c=1.5; bold line, c=2.0. (B) as a function of 'q' (increasing with increasing abscissa values) and 's' (descreasing with increasing abscissa values) with parameter values of 'B'=5, 'a'=0.2 and 'c'=1.0 (for 's' iterations, 'q'=0.7 and for 'q' iterations, 's'=0.7).



Tj
1
0.8
0.6
0.4
0.2
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
'a' Values



Tj
1
0.8
0.6
0.4
0.2
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
's' or 'q' Values

FIGURE 46

FIGURE 47

Expected productivities of hatching synchrony (A) and asynchrony (B). Given are good food year (...), bad food year (___), and the mean (- - -) productivities between both year types.

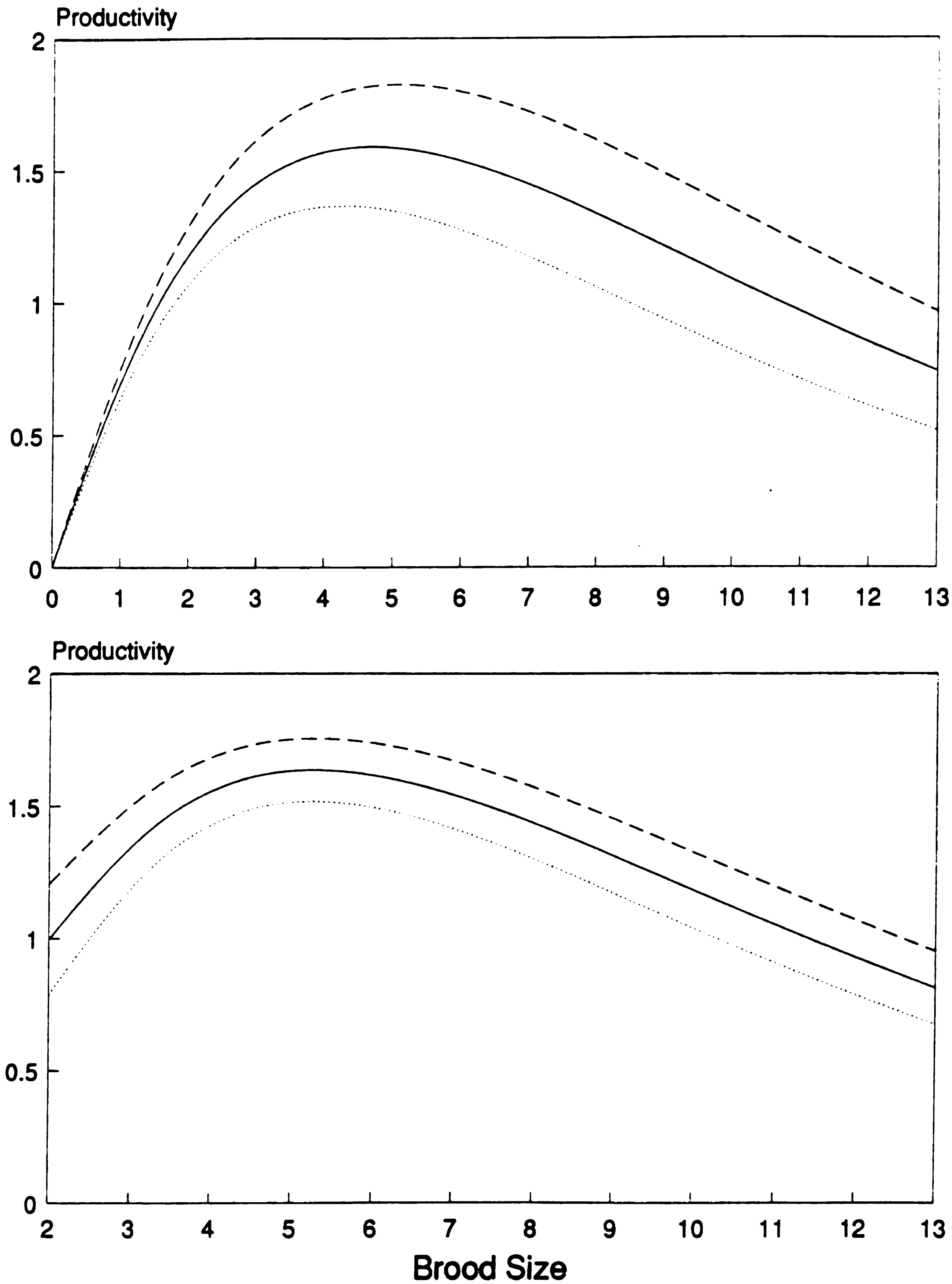

Productivity
2
1.5
1
0.5
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13
Productivity
2
1.5
1
0.5
0
2 3 4 5 6 7 8 9 10 11 12 13
Brood Size

FIGURE 47

bad food years compared to good food years.

The expected productivities of hatching synchrony and asynchrony, in good years and bad years, as a function of brood size, are shown in Figures 47a and 47b, respectively. A comparison of these two figures shows that the number of young fledged is more variable between good and bad years for broods hatched synchronously compared to those hatched asynchronously. In other words, hatching asynchrony tends to yield a more stable number of young surviving until their reproductive age when two types of years occur.

IV. DISCUSSION

A. Introduction

Amundsen and Stokland's (1988) review of several experimental studies on various species showed that, during good food years, survival rates of last-hatched nestlings of asynchronously hatched broods were lower than their siblings and nestlings in nests simulated for synchronous hatching. These researchers argued that if brood reduction occurs as a result of hatching asynchrony when food is plentiful, then the brood reduction hypothesis cannot be viewed as an adaptive explanation. I constructed this model to examine whether introducing a risk of the last-hatched nestling dying as a result of asynchronous hatching, even when food is plentiful, is less favorable than hatching synchrony. I have shown that brood reduction and hatching asynchrony can be adaptive because hatching asynchrony can increase a parent's lifetime productivity over hatching synchrony.

Allowing the last-hatched nestling to have lower survival rates compared to siblings and nestlings of synchronously hatched broods during plentiful food years, may at first seem counter-intuitive. However, there are several factors that may contribute toward the death of the last-hatched nestling when food levels are good. First, Amundsen and Stokland (1988) suggested that the last-hatched nestling, because of the feeding hierarchy established by hatching asynchrony, may become malnourished and starve. This is feasible if parents regulate their feeding rate to the begging intensity of the entire brood (von Haartman 1953, Hussell 1988). When only one or two nestlings of large broods beg, parents tend to devote time instead rather than feeding the begging nestlings. If the last-hatched nestling is consistently fed last, then its lone begging may not be effective to elicit a feed. Starvation ensues, therefore, because the food brought to the nest is limited rather than by food limitations in the environment.

Second, the last-hatched nestling may die during a good food year as a result of intense sibling rivalry established by hatching asynchrony. Mock (1984, 1987) and Fujioka (1985a), have shown that last-hatched nestling ardeids commonly die from physical attacks by their older and larger siblings. There is some evidence that last-hatched nestlings may die from physical attacks made by older siblings in other birds as well (Bryant and Tatner 1990).

Third, parents raising asynchronously hatched broods may also experience difficulties feeding nestlings differing in development states. For example, if the youngest nestling must be forced fed, as are most altricial hatchlings (Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, 1983), and the older nestlings are fed based on their begging activity, then parents may preferentially feed the older nestlings. Thus, during transitional developmental periods, older nestlings may grow faster at the expense of the younger nestling resulting in their starvation. Feeding asynchronously hatched broods may be less efficient then, than synchronously hatched broods when nestlings are at different ages (although, see Hahn 1981).

Fourth, the last-hatched nestling may die more frequently than its siblings if parents preferentially provide care for fledged nestlings after fledging (Clark and Wilson 1981). The last-hatched nestling may not receive enough care if it fledges a day later than its siblings or fledges at a premature age.

Lastly, Slagsvold (1982, 1985, 1986) provided evidence showing that, in some species, the last-laid egg in less likely to hatch than first-laid eggs. He speculated that a lower hatchability is caused by inadequate incubation temperatures during hatching due to females being off the nest to forage for their first-hatched nestlings. Thus, costs of asynchronous hatching could even occur prior to the nestling period.

Occasional brood reduction during good food years is a result of hatching asynchrony that needs further confirmation by field researchers. In particular, more studies are needed to understand the causes of death in last-hatched nestling. If asynchronously hatched nests are, however, more productive than synchronously hatched nests when food is good, then my present game theory model and its predictions do not apply. The frequency of good years would be selectively neutral to hatching asynchrony because hatching asynchrony would be favored over synchronous hatching in good and bad food years.

B. Model Specifications

1. Assumptions

Many of the model's assumptions were made implicitly or explicitly by Lack or by researchers who have tested the hypothesis. Despite the large number of studies that have tested the brood reduction hypothesis (see review by Magrath, 1990), very few have attempted to examine whether Lack's assumptions hold. Here, I present arguments supporting the assumptions made in my model, show how some of the assumptions differ from those made by Lack, show where alternative assumptions can be made, and present ways that these assumptions may be tested. I also point out which assumptions need further confirmation by field researchers.

A1. Annual food levels are either good or bad. I have assumed that yearly food levels can be classified into types. Recognizing only two types of years keeps the model simple, instructive and also follows from Lack's original hypothesis. Unfortunately, very few studies investigating the reproductive performance of birds have measured natural food levels over extended periods (e.g. Bryant 1978, Hussell and Quinney 1987), making it difficult to determine whether this assumption is realistic.

The simplest way to categorize whether a year is good or bad is to compute the sum of daily food levels and compare this annual total across years. However, short-term spurts or shortages of food, which may be hidden in a total annual food measure, may be more important in characterizing the nestling period as good or bad rather than a sum of daily food abundances. This may be important in species utilizing resources which are highly variable on a daily or even hourly basis (e.g. Bryant 1978 or Hussell and Quinney 1987) or in cases where there are critical periods affecting nestling survival (Hussell 1972). In addition, food levels can be difficult to measure, and, even when food is measurable, the data may be difficult to interpret because parents do not always feed on all items, or in proportion to the items in traps (Bryant 1975).

One solution to the problem of classifying or measuring food levels is for researchers to examine mortality patterns, over several years, from asynchronously hatched nests and nests simulated for synchronous hatching. To be consistent with the present model, annual mortality patterns within each brood size should match the patterns predicted in Figure 41. Controlling food levels either by supplementing natural food (e.g. see Magrath 1989) or conducting experiments in the laboratory (e.g. see Skagen 1988) may also solve the difficulties of measuring natural food levels.

A2. Only two, heritable hatching strategies exist. Other degrees of hatching asynchrony are not possible alternative strategies within the present model. Clark and Wilson's (1981) review of the hatching asynchrony literature showed that over 75% of altricial species hatch their clutches either synchronously or asynchronously with one nestling hatching a day later than the rest. If this review is representative of all altricial birds, then this model will apply to most altricial species.

Implicit in the present model, as in all adaptive explanations, is the assumption that the adaptive trait has a heritability of 1.0 (Fisher 1930, Williams 1966b, Endler 1986). No studies have examined the heritability of hatching patterns. However, making the assumption that $h^2 = 1.0$ keeps the model simple and the predictions more congruent.

A3. Natural selection favors those parents employing hatching strategies that produce more offspring surviving to reproductive age than alternative hatching strategies. Lack assumed that natural selection favors reproductive tactics "corresponding with the greatest number of young for which the parents can, on the average, find enough food". (Lack 1967, p. 22). To test this condition of the model, researchers should measure nestling survival to reproductive age. Unfortunately, most studies that have examined the brood reduction hypothesis have not followed nestlings past fledging (Magrath, 1990). The failure to record nestling mortality has been largely due to the difficulty in following nestlings that disperse from their natal grounds. Researchers have, instead, collected data on indirect measures of a nestling's chance of surviving to reproductive age, the most common being fledging mass (Magrath, 1990). Heavier nestlings at fledging have a greater chance of surviving until their reproductive age (Perrins 1965). However, this may not be a reliable measure for all species. If used, researchers should attempt to confirm its value for the study species by correlating fledgling return rates with fledging mass.

The most convenient method to compare the reproductive value of alternative strategies is to manipulate nesting conditions and to establish alternative hatching pattern(s). This has been a popular method to test the brood reduction hypothesis (see Amundsen and Stokland 1988 for review). However, researchers should heed Magrath's (1990) advice and establish adequate controls for these experiments.

I also assumed that hatching asynchrony has no

effect on parental survival. Williams (1966b) states that natural selection will favor traits that maximizes the lifetime production of offspring surviving until their reproductive age. I consider parental survival in the model presented in Chapter 4.

A4. In bad years, nestling mortality rates are greater in synchronously hatched broods than in asynchronously hatched broods. Lack's version of the brood reduction hypothesis assumes that, when food is scarce, the last-hatched nestling of an asynchronously hatched brood is starved, whereas for a synchronous brood, each nestling risks starvation which would result in an entire brood starving. Lack essentially assumed that feeding hierarchies, which would facilitate brood reduction, cannot be established in a synchronous brood.

Clark and Wilson (1981) argued that Lack's assumptions for synchronously hatched broods rarely hold. They reported that in several synchronously hatched species, partial broods starved before entire broods starved. The game theory model that I have presented, though, can accommodate partial brood starvation in synchronous nests in bad years and still follow the spirit of the original brood reduction hypothesis. The variable 's', the survival rate for synchronously hatched broods, could represent the proportion of an entire synchronous brood surviving until reproductive age rather than the equal probability that each nestling survives to reproductive age. Synchronous broods can thus be subjected to one of two forms of risk in this game theory model, entire brood starvation or partial brood starvation. For brood reduction to be favorable, risks associated with synchronous hatching in bad food years should be greater than losing the youngest nestling(s) to selective starvation in asynchronously hatched nests.

Clark and Wilson (1981) also argued that, because weight hierarchies can result in broods that were initially adjusted for hatching synchrony, the mechanism set up for brood reduction, size hierarchies, can be established without hatching asynchrony. Several studies (see Magrath, 1990, for review) have since shown, however, that establishing weight hierarchies in broods adjusted for synchronous hatching is an inefficient way to facilitate brood reduction. In synchronously hatched broods where weight hierarchies have resulted, nestlings starved late in the nestling period; in asynchronously hatched broods, nestlings died soon after hatching. If parents of synchronously hatched broods invest energy and time into offspring that will eventually be starved, then they may unnecessarily reduce their own chances of surviving to breed again; a condition that natural selection does not favor (in sensu, Williams 1966b).

A5. Parents cannot predict future food supplies. This model also assumes, as did Lack, that adults cannot forecast, at egg laying, food levels for the upcoming nestling period. If parents could make this assessment during egg laying, then they would adjust their clutch sizes to correspond to the maximum number of offspring they could raise during upcoming conditions. They would hatch their clutches synchronously because brood reduction would not be required.

Many studies have not determined whether parents are able to predict future food levels (Magrath, in press). Qualitatively, however, the degree of predictability of food resources and the preponderance of asynchronous hatching seems to correlate well with latitude. Clark and Wilson (1981) showed that tropical species, which rely on scarce but predictable food (Ashmole 1965, Ricklefs 1980), hatch their clutches synchronously. On the other hand, food resources in temperate regions are much less predictable and birds hatch their clutches predominantly asynchronously (Clark and Wilson 1981).

A6. Food levels are the sole ultimate factor affecting hatching patterns. I have assumed that no factors other than food levels affect hatching patterns. Among these other factors are the dynamics of nestling growth (Hussell 1972) and the patterns of nest predation (Clark and Wilson 1981); factors suggested as important by alternative hypotheses. I have made this assumption to keep the model simple and testable; however, I believe that alternative hypotheses may also adequately explain the adaptive value of hatching asynchrony in altricial birds.

2. Predictions

Many of the predictions generated from this game theory model are similar to those made by Lack. Here, I present the predictions of this model, indicate how researchers may test these predictions, and show how to estimate values for the variables contained in this game theory model.

P1. Hatching asynchrony and brood reduction are favored over synchronous hatching when 'q' is high, and 's' is low. I have shown that hatching asynchrony and brood reduction are favored when the survival of the last-hatched nestling to reproductive age, 'q', is high, and nestling survival in synchronously hatched broods, 's', is low. These two conditions will also produce a high T_j value.

To determine if hatching asynchrony will be favored over hatching synchrony based upon the values of 's' and 'q', two methods can be employed if researchers only have fledging success data. First, a researcher may estimate values for 'q', or 's', and rely on these estimates to decide if hatching asynchrony is favored over synchronous hatching. This procedure may be necessary if a researcher has nestling mortality data for only one food condition. The value of 'q' and 's' can be estimated as follows. The fledging success of the last-hatched nestling in asynchronously hatched broods, N_{lhn}, will be a product of the survival rate due to hatching asynchrony and of brood size:

$$N_{lhn} = q * e^{-aB}. \qquad (8)$$

The survival rate of each first-hatched nestling will be a function only of brood size:

$$N_{fhn} = e^{-aB}. \qquad (9)$$

where N_{lhn} is the fledging success of the last-hatched nestlings of asynchronously hatched broods during good food years and N_{fhn} is the fledging success of first-hatched nestlings of asynchronously hatched broods during good food years. Substituting (8) into (9) and rearranging gives:

$$q = N_{lhn}/N_{fhn}. \qquad (10)$$

An estimate of 's' can be obtained likewise. The survival rate of each nestling in synchronously hatched broods during a bad food year, N_{sb}, will be a product of the risk associated with raising a synchronously hatched brood and the survival rate due to brood size:

$$N_{sb} = s * e^{-aB} \tag{11}$$

and the survival rate of each first hatched nestling in asynchronously hatched broods during a bad food year, N_{ab}, is a function only of brood size:

$$N_{ab} = e^{-a(B-1)}. \tag{12}$$

Substituting the left side of (11) into the brood size survival rate expression of (12) gives a conservative estimate of 's' after rearranging:

$$s = N_{sb}/N_{ab}. \tag{13}$$

where N_{sb} is the fledging success of each nestling from broods simulated for synchronous hatching and N_{ab} is the fledging success of each first-hatched nestling of asynchronously hatched broods.

A second possible way to determine if hatching asynchrony is favored over synchronous hatching is to use fledging success of broods from good and bad food years to estimate T_j. Equations (5) and (6) may be rewritten as:

$$P_s = (j * F_{sg}) + (1-j) * F_{sb} \tag{14}$$

and

$$P_a = (j * F_{ag}) + (1-j) * F_{ab} \tag{15}$$

where F_{ag} is the fledging success of asynchronously hatched broods in good food years, and F_{sg} and F_{sb} are the fledging success of synchronously hatched broods in good and bad food years, respectively. T_j is calculated, as before, by setting (14) equal to (15), and solving for 'j':

$$T_j = \frac{F_{ab} - F_{sb}}{F_{ab} + F_{sg} - F_{ag} - F_{sb}}. \qquad (16)$$

For these to be adequate estimates, mortality patterns must follow the payoff matrix of Figure 41, initial brood sizes for all treatments must be the same, and the food year type must be determined.

The latter of the two above approaches might yield more insightful results. Values of T_j, calculated from either (7) or (16), can be compared between closely related species hatching nestlings differently. Species having high T_j values, for example, should hatch nestlings asynchronously in more types of environments than closely related species having a low T_j value.

Unfortunately, such a comparison of the hatching literature cannot be accomplished at this time. Only a handful of published studies can be analyzed using either of these two procedures because most studies that have tested the original brood reduction hypothesis have failed to report conditions or food levels during the study. I have analyzed the data from my earlier data analysis chapter and two experimental studies to show how each method may be used to determine if hatching asynchrony is favored over synchronous hatching.

From my earlier Chapter 2, I found that the fledging success from asynchronous broods in the less food years was 3.3 nestlings and 4.1 nestlings in the more food years (from Figure 14). Fledging success in synchronous broods in the less food years was 3.0 nestlings and was 4.5 nestlings for the more food year. This gives a T_j value of 0.43. Thus, good years must not occur any more frequently than 0.43 for asynchronous hatching to produce more nestlings per brood than synchronously hatched broods.

Amundsen and Stokland (1988), in a study conducted on the Shag (Phalacrocorax aristotelis) during a relatively good food year, found that the last-hatched nestling suffered a higher mortality rate than its siblings or than nestlings in synchronously hatched broods. They reported that 91% of first-hatched nestlings in asynchronously hatched broods fledged; the same fledging rate for nestlings in broods adjusted for hatching synchrony. Last-hatched nestlings in asynchronously hatched broods fledged 88% of the time. If fledging rate is correlated to the chance of the nestling surviving until its first reproductive year, as it might be since fledging mass was similar for all fledglings, then the value of 'q' is estimated to be 0.97 (0.88/0.91), an extremely high value. Thus, hatching asynchrony and brood reduction may be favored over synchronous hatching, contrary to their claims.

Magrath (1989) conducted an experimental study on the blackbird (Turdus merula). He manipulated food supplies and recorded the number of fledglings alive four weeks after fledging from simulated synchronous and natural asynchronously hatched broods. All parents began raising four nestlings. Using data from his Table 1, I estimated the following values: for asynchronous nests, F_{ag} = 2.23 and F_{ab} = 2.08; and for synchronous nests, F_{sg} = 2.88 and F_{sb} = 1.38 Using (11) above, T_j is 0.52. This is a vlue that, according to Magrath (pers. comm.), is a reasonalble T_j value as these birds breed in environments that are often "poor". For hatching asynchrony and brood reduction to be favored over hatching synchrony, the frequency of good years in the breeding environment must be less than T_j.

P2. If the frequency of good years, 'j', is high, then selection should favor a large value of 'q' in asynchronously hatched broods. Selection may favor strategies that increase the survival rate of the last-hatched nestling, 'q', when good years are frequent. There are several possible factors that may increase 'q'.

First, Howe (1978) has suggested that laying a large final egg may increase the last-hatched nestling's chance of fledging when food is plentiful because this may reduce the weight hierarchy established by hatching asynchrony. There is some evidence to suggest that larger eggs give rise to larger hatchlings which grow more rapidly because they contain more nutrient reserves (Parsons 1970, Nisbet 1973, Schifferli 1973, and Williams 1980). Laying a large final egg to increase the survival rate of the last-hatched nestling counters Clark and Wilson's (1981) argument that the brood reduction hypothesis and a larger last-laid egg lead to conflicting effects. This game theory model predicts that brood reduction and hatching asynchrony may be favored over synchronous hatching if the last-laid egg is the largest of the clutch.

Second, the last-hatched nestling can use special begging behaviors to counteract the feeding hierarchy established by hatching asynchrony to acquire its food during a good food year. For example, Bengtsson and Ryden (1981, 1983) have shown that the last-hatched nestling can increase its chances of being fed by gaining access to nest positions where parents prefer to feed or by displaying a high rate of spontaneous begging. Parents engaged in feeding the brood notice this nestling first. The last-hatched nestling's chances of receiving food increases which in turn increases its chances of surviving. Alternatively, parents could preferentially feed the last-hatched nestling more often so that it catches up in its development to that of its siblings (Hussell 1972, Bryant 1978).

Lastly, the last-hatched nestling can develop motor and sensory skills at an accelerated rate so it may compete more effectively against siblings. Khayutin et al. (1988), in a study of the Pied Flycatcher (Ficedula hypoleuca), found that last-hatched nestlings can develop neurologically at an accelerated rate because they compete against older nestlings having more advanced sensory and motor skills. This accelerated development is possible, they speculate, because rates are not under tight genetic control.

P3. If the frequency of good years, 'j', is low, then selection might favor a low 'q' value because intense feeding hierarchies will often be required in asynchronously hatched broods. The value of 'q' may have some effects on the ease of reducing an asynchronously hatched brood during a bad food year. These effects are not considered mathematically in the present model. For example, the value of 'q' might reflect the feeding hierarchy intensity among nestlings in the brood. Intense feeding hierarchies, in asynchronously hatched broods, will lead to efficient brood reduction which should benefit parents during a bad food year; the last-hatched nestling will be easily outcompeted for food and it will die quickly. However, when this intense feeding hierarchy is present in asynchronously hatched broods during good food years, it might result in a low 'q' value. Thus, when good years are rare (i.e. 'j' is low), a low 'q' value might be selected for because efficient brood reduction will often be necessary.

If bad food years favor low 'q' values, and good years favor high 'q' values (see P2), then the value of 'q' probably represents to parents raising asynchronously hatched broods a balance between efficient brood reduction during bad food years and the risk of losing this nestling during good food years. Selection might favor an optimum 'q' value depending on the value of 'j' and how 'q' is related to efficient brood reduction. Factors that might influence 'q' values are summarized in Table 2.

Interestingly, there have been some reports that the intensity of sibling rivalry within a nest increases with decreasing levels of food (Drummond and Garcia, 1989). This may represent a beneficial strategy for these parents so that 'q' is high when a good food year occurs and efficient brood reduction can be carried out through intense feeding hierarchies during a bad food year. More studies are needed to determine whether this pattern is common and what types of parent-offspring interactions are involved.

P4. Hatching asynchrony and brood reduction are favored over synchronous hatching when initiating large clutch sizes. This model predicts, as does Lack's original hypothesis, that large broods will benefit from hatching asynchrony. This is because large broods can be raised in good food years and reduced to a size that can be raised when food is scarce.

This prediction holds, however, only if two conditions are met. First, the brood size dependent mortality constant, 'a', cannot be a small value. Small 'a' values reflect no differences between being able to successfully raise an initially large-sized brood, 'B', and a brood of size, 'B-1'. Thus parents cannot benefit from a reduced brood size when the value of 'a' is small.

Second, a large brood is favored over a smaller brood only when 'q' is sufficiently large. If 'q' is very small, then parents will produce nearly 'B-1'

Table 9. Factors that might increase or decrease the value of 'q'*. .rm80

INCREASE 'q'	DECREASE 'q'
large last-laid egg	small last-laid egg
LHN increases neural development	low hatchability of last-laid egg
LHN adopts special begging behaviors	premature fledging of LHN infrequent
infrequent sib rivalry	frequent sib rivalry
selective feeding of LHN	feed largest nestlings first

* LHN = last-hatched nestling.

number of young in both good and bad food years. In such cases then , parents should then invest in a smaller brood of a size 'B-1'. This is especially important if larger brood sizes reduce parental survival.

To test this prediction of the model, researchers need to conduct hatching pattern manipulations for different clutch sizes. This will allow searchers to calculate a value for 'a' using the linear regression techniques of Ricklefs (1977) and to determine whether large clutch sizes are more productive for asynchronous hatching than for synchronous hatching.

P5. When bad food years are severe, hatching synchrony is favored over asynchronous hatching. When the severity of bad years is increased, (i.e. when 'c' is increased), nestlings produced during good food years comprise a greater proportion of a parent's lifetime productivity. As a result, synchronous hatching becomes more productive over a lifetime than asynchronous hatching.

The value of 'c' is most easily estimated from nestling mortality data from synchronously hatched broods during a bad food year. Recall that, during a bad food year, the probability of each nestling surviving to reproductive age as a function of brood size, is:

$$p(B) = \exp(-a*c*B). \tag{17}$$

The natural logarithm of this expression gives:

$$-a*c*B = \ln[p(B)]. \tag{18}$$

Solving for 'c' produces this equation:

$$c = \ln[p(B)]/-a*B. \tag{19}$$

All that is needed to solve this equation is the value of 'a', which must be calculated during a good food year.

An interesting implication of the prediction made here is that more variable food resources should favor hatching synchrony over hatching asynchrony. However, this prediction is inconsistent with trends for birds differing in their food habits. Insects, abundances which are tied to short-term weather patterns (Bryant

1975, Hussell and Quinney 1987), are thought to be more variable from year to year than seed and nectar supplies. Insectivorous birds are typically more asynchronous hatchers than nectar and seed eaters (Clark and Wilson 1981).

P6. Hatching asynchrony and brood reduction may reduce annual variation in reproductive success further increasing lifetime productivity. The present model shows that hatching asynchrony and brood reduction allow parents to recruit a stable number of nestlings into the next generation each year compared to synchronous hatching. Several researchers (e.g. Gillespie 1974, 1977; Cooper and Kaplan 1982; Lacey *et al.* 1983) have suggested that natural selection will favor a reduced variance in expected productivity even at the expense of a lower mean annual productivity. This is possible when there is a negative second derivative with respect to an independent factor related to fitness (in this case, brood size, 'B'). Fig. 4 shows that the change in the slope of the productivity curve declines with brood size, giving a negative second derivative. Thus, hatching asynchrony may be further favored over hatching synchrony because it reduces the variance in yearly reproductive success.

There is some evidence to suggest that hatching asynchrony does produce less variation in reproductive success between good and bad food years than synchronously hatched broods. Magrath (1989) reported that synchronously hatched broods experienced significant differences in fledging success between supplemented and food stressed treatments. On the other hand, fledging success was not significantly different between these same two food level treatments for broods hatched asynchronously. Haydock and Ligon (1986), in a study on the Chihuahuan Raven (*Corvus cryptoleucus*), found that asynchronously hatched broods had a much lower variability in fledging success and fledging masses between good and bad food years than broods simulated for hatching synchrony. Similarly, Shaw's (1985) study of the Blue-eyed Shag (*Phalacrocorax atriceps*) revealed that total brood loss was much higher in simulated synchronously hatched broods than in asynchronously hatched broods.

V. SUMMARY

A recent literature review by Amundsen and Stokland (1988) showed that, when food was plentiful, the last-hatched nestling of asynchronously hatched broods died more frequently than its nestmates or nestlings in synchronously hatched broods. They argued that if the last-hatched nestling died as a consequence of hatching asynchrony, then the brood reduction hypothesis does not adequately explain the adaptive significance of hatching asynchrony in altricial birds. Using a game theory approach, I allowed the last-hatched nestling to have a lower survival rate compared to its siblings and nestlings in synchronously hatched broods during good food years. I showed that hatching asynchrony and brood reduction can increase a parent's lifetime productivity if two general conditions are met. First, the risks of raising synchronously hatched broods must be greater than losing one nestling to selective starvation in an asynchronously hatched brood during a bad food year. Second, the risks of raising an asynchronously hatched brood during a good food year must be offset by the benefits of raising the same brood during a bad food year.

Several predictions were generated using computer simulations. I showed that hatching asynchrony is favored over synchronous hatching when good food years are not very frequent, when the survival of last-hatched nestlings in asynchronously hatched broods during good food years is high, when the survival rate of nestlings raised in synchronously hatched broods during bad food years is low, or when bad food years are not characterized as severe.

I also addressed other criticisms of the original brood reduction hypothesis. I have argued that increasing egg size with laying order compliments, rather than contradicts, the brood reduction hypothesis, because it may increase the survival of the last-hatched nestlings during good food years. Also, when food is scarce, the occurrence of partial brood loss in synchronously hatched broods does not conflict with the brood reduction hypothesis because it has been shown that hatching asynchrony facilitates efficient brood reduction which may benefit parents.

CHAPTER 4

A MATHEMATICAL MODEL FOR HATCHING ASYNCHRONY AND BROOD REDUCTION

I. INTRODUCTION

In birds, the parent that incubates the eggs can control the hatch interval of a clutch (Lack 1947, Clark and Wilson 1981). When the hatch interval is less than one day, hatching is referred to as synchronous. On the other hand, if the clutch of eggs hatches over a period of more than one day, then hatching is said to be asynchronous. Hatching asynchrony is possible because the female lays her eggs in intervals, often one egg per day, so that when incubation is commenced in the middle of the egg laying period, eggs present at the start of incubation hatch at the same time. Eggs laid after incubation has been started hatch after the first eggs on successive days. The most evident result of hatching asynchrony is that nestlings in a brood differ in ages and weights.

Hatching asynchrony was first recognized as a reproductive strategy employed by only a few birds, such as the raptors (Lack 1947). After more careful observation of hatching patterns, this list grew to include birds in many groups, mostly nonpasserines (Lack 1954, 1968). More recently, Clark and Wilson (1981), in a extensive review of hatching asynchrony in birds, found that hatching asynchrony is more common than hatching synchrony. More than 80% of the birds including nearly all orders of altricial birds examined by Clark and Wilson, hatch clutches over more than 24 hour period. They found that most altricial birds hatch clutches over a two or three day period.

There have been many attempts to explain the adaptive significance of hatching asynchrony. The most widely cited explanation is that of David Lack (1947, 1948, 1954, 1968), called the 'brood reduction hypothesis'. He suggested that hatching asynchrony establishes a competitive feeding hierarchy within the brood. When food becomes limited, the larger, older nestlings easily compete better than the last-hatched nestlings for food and the last-hatched nestling is starved. The reduced brood is more adequately nourished during food shortages and nestlings have a greater chance of fledging. Hatching asynchrony produces more nestlings than a same-sized brood hatched synchronously because it is assumed that no nestling can be efficiently singled-out for starvation and all nestlings in a brood are affected by the reduced food supply.

Consequently, the entire synchronous brood risks starvation when food is scarce. Lack predicted that brood reduction facilitated by hatching asynchrony would benefit parents lacking the ability to predict, at the start of incubation, the food levels during the upcoming nestling period.

Some researchers (see Amundsen and Stokland 1988) have argued that competitive feeding hierarchies established by hatching asynchrony for the purposes of brood reduction is maladaptive. This criticism has arisen because it has been observed that the last-hatched nestling in asynchronously hatched nests sometimes starves when food is plentiful (cf. Amundsen and Stokland 1988). Amundsen and Stokland (1988) have claimed that if the last-hatched nestling dies when food is plentiful, then brood reduction should be viewed as a consequence of hatching asynchrony. They claim that other hypotheses, especially nonadaptive hypotheses, should be given more merit as explanations for the significance of hatching asynchrony.

I addressed this criticism of the brood reduction hypothesis with an earlier model that allowed the last-hatched nestling to have a reduced survival to reproductive age because of its inferior position in the feeding hierarchy established by hatching asynchrony. I showed that hatching asynchrony and brood reduction can increase the expected number of nestlings per clutch for parents when they initiate large clutches, when limited food years occur often, and when the cost to synchronous hatching is high during a limited food year. .rm64

My earlier model does not, however, address the adaptive significance of clutches hatched over more than a two day period. Thus, the significance of the hatching pattern of many birds can not be directly addressed by this model. Second, my earlier model also assumed that only two different types of food conditions could occur in nature: plentiful and limited food. Parents are most likely subjected to wide range of food years to occur during the nestling period with moderate food years being the most frequent food year type. Third, my earlier model was not in a form to rigorously examine tradeoffs between brood size and degree of hatching asynchrony that will yield the most offspring per brood. Lastly, in my earlier model, I assumed that there were no effects of hatching asynchrony on parental survival. The effect of hatching asynchrony has been largely ignored (although see Proctor 1975, Gibbons 1987 and Magrath 1988).

Here, I present an extension of my earlier model. I examine the effects of a continuous distribution of food year s, where moderate food years are the most frequent, on the degree of hatching asynchrony and brood size that produces the most offspring per year. In particular, I examine whether a continuous distribution of food years selects most for brood size or degree of hatching asynchrony. I also describe the conditions where parental survival can most affect the most productive form of hatching and brood size. I present the results of computer simulations of the model and discuss the predictions of the model.

II. EXTENDED MATHEMATICAL MODEL FOR BROOD REDUCTION AND HATCHING ASYNCHRONY

A. Introduction

The following model presentation has three parts. First, I present the portion of the model that expresses food years as a continuum where moderate food years are the most frequent. I then consider how nestling survival to reproductive age (hereafter as nestling survival) is influenced by hatch position over the food year continuum for various hatching forms (i.e. any degree of asynchronous hatching or synchronous hatching) and for different brood sizes. I then present the third portion of the model that shows how annual adult mortality influences the number of offspring parents can produce in their lifetime. A list of the model's variables is contained in Table 10.

B. Food Year Type Continuum

Consider an environment where many different food years occur and each food year can be classified by yearly food levels with each food year designated as 'x'. Let the best food year have a value of x=0.0 and the worst food year x=1.0. The best food year should be one in which enough food exists so that parents may easily raise their entire brood. The worst food year, on the other hand, should be one in which food scarcity makes rearing all nestlings impossible and nestling deaths occur. Allow moderate food years to be represented by values between these two extremes. If moderate food years are most frequent, then the frequency of each food year could be expressed using a normalized probability distribution:

$$\mathrm{freq}\ (x) = \frac{1}{sd*\mathrm{sqrt}(2*pi)}\ e^{-0.5[(x-u)/sd]^2} \qquad (1)$$

where 'x' is the food year value, 'u' is the mean of all food year s, and 'sd' is the standard deviation for these food years. The objectives of this model are to understand the effects of 'u' and 'sd' on what form of hatching and brood size that yields the most productive brood.

Table 10. List of variables contained in model.

Symbol	Description
	Food Year Type Variables
x	- food year type (represents the average amount of food per year)
u	- the mean of the food year distribution
sd	- the standard deviation of the food year distribution
	Hatch Position and Brood Size Variables
N	- hatching form (N=0 hatching synchrony, N > 0 is asynchronous hatching)
B	- brood size
N^*	- optimal hatching form
B^*	- optimal brood size
i	- hatch position for latter-hatched nestlings (e.g. i=1 for nestlings hatching a day later than first-hatched nestlings)
	Nestling Survival Variables
Q	- the combined survival of all latter-hatched nestlings
k	- survival difference between nestlings by hatch position
S	- survival rate of each first-hatched nestling
beta	- survival of nestlings along food year continuum due to the number of first-hatched nestlings
z	- survival of nestlings along food year continuum (referred to as the 'slope function')
a	- brood size dependent mortality constant
	Adult Mortality Variables
m(B)	- annual adult mortality due to brood size
m(N)	- annual adult mortality due to hatching form
L(B)	- lifespan of adult for m(B)
L(N)	- lifespan of adult for m(N)
	Variables for Number of Offspring Surviving
P	- expected productivity (i.e. number of offspring produced to reproductive age) of parents if food years conform to a normal probability distribution
R	- number of offspring surviving to reproductive age as a function of hatching form
E	- number of offspring surviving to reproductive age as a function of brood size
F	- number of offspring produced in a lifetime that survive until their reproductive age.

C. Nestling Survival by Hatch Position

Let us now consider nestling survival. Nestling survival should be affected by: (1) a nestling's hatch position; (2) the number of nestlings in a brood; and (3) the amount of food that exists during the breeding season. Let the degree of hatching asynchrony be denoted using integer values of 'N': where synchronous hatching is N=0; one nestling hatching a day after its siblings is N=1; and so on, to complete hatching asynchrony. Those nestlings hatching after the first-hatched nestlings shall be referred to collectively as 'latter-hatched nestlings' and will number 'N'. The first-hatched nestlings will be referred to as the '0' chicks, those hatching a day later as the '1' chicks, those hatching two days after the '0' chicks as the '2' chicks, and so on.

The survival of all '0' nestlings in nests of all hatching forms should be 1.0 during the best food years because parents can easily feed these nestlings. Let the survival of '0' nestlings decrease so that their minimum survival will occur during a worst food year. Consider also that all '0' nestlings in a nest will represent a synchronously hatched brood of size 'B-N'. The brood reduction hypothesis predicts that, when food is scarce, entire brood starvation will increase linearly with an increasing number of first-hatched nestlings (O'Connor 1978). Thus, the survival of '0' nestlings will decrease along the food year continuum as a function of the number of the '0' nestlings, which will always number 'B-N' for all hatching forms. It therefore follows that the survival of each first-hatched nestling in each nest will be:

$$S(B,N) = (1 - beta * x). \tag{2}$$

The variable 'x' represents the food year. The variable '   ' is expressed as a function of the number of '0' nestlings and a nestling slope function:

$$beta = (B-N) * z. \tag{3}$$

The nestling slope function 'z' takes on values less than 1.0 and quantifies the degree to which nestling survival decreases with food years. Larger 'z' values mean that nestling survival decreases rapidly across the food year continuum compared to small 'z' values.

The survival of latter-hatched nestlings along the food year continuum can be quantified using a similar linear expression. The survival of latter-hatched nestlings should be less than 1.0 during the best food year because of their inferior hatch position (see discussion of my previous model to see why this occurs). A '1' nestling in an N=1 asynchronous hatching nest should have a lower survival value than any '0' nestling in a same-sized, synchronously hatched brood. Let the survival difference in their nestling survival values from '0' chicks and between each successive of the latter-hatched nestlings be 'k' ('k' should be between 0.0 and 1.0). The survival of latter-hatched nestlings should also decrease with increasing number of '0' chicks that they must compete against. In addition, the survival of latter-hatched nestlings should also decrease with decreasing food levels. Denoting the hatching position of latter-hatched nestlings with 'i' (e.g. i=1 is a '1' chick), the survival of <u>all</u> latter-hatched nestlings becomes:

$$Q(B,N) = \sum_{i=1}^{N} [(1.0 - (B-N+i) * z * x) - (i * k)] \quad (4)$$

The expression (i*k) quantifies the amount the i^{th} nestling's survival is decreased relative to a '0' nestling in a synchronously hatched brood.

The number of nestlings produced each year surviving until reproductive age, as a function of hatch position, will be equal to the number of first-hatched nestlings present in the nest (i.e. 'B-N' number of nestlings), times the probability that each nestling survives to reproductive age, plus the number of latter-hatched nestlings surviving to reproductive age:

$$R(B,N) = S*(B-N) + Q. \quad (6)$$

Following my earlier model, and Ricklefs (1977), allow each nestling's survival in a nest to decrease exponentially with increasing brood size as such:

$$E(B) = e^{(-a*B)}. \qquad (7)$$

The variable 'a' is the same as 'a' in my earlier model. It relates brood size and nestling survival. Large 'a' values reflect that the most productive brood size is small. Ricklefs (1977) has shown that 'a' takes on values less than 1.0 and, for the most part, is a species specific value (see Ricklefs 1977 for the use of this equation and Temme and Charnov 1987, for a similar modeling application).

The expected proportion of a parent's annual productivity for a food year, P_x, can be calculated as the product of all nestling survival values due to hatch position, [equation (6)], and nestling survival due to brood size, [equation (7)], times the frequency of the food year in question [equation (1)]:

$$P_x = freq(x) * R * E \qquad (8)$$

The total annual expected productivity will be equal to the sum of all proportions of annual expected productivities for all food years. This can be written as the following integral:

$$P(B,N) = integral \{freq(x) * R * E\} dx. \qquad (9)$$

The maximum annual productivity parents can expect, as described in (8), can be determined by calculating the partial derivatives of 'P' with respect to 'B' and 'N', and finding this maximum, or when:

$$\frac{dP}{dB} = \frac{dP}{dN} = 0.0 \qquad (10)$$

The brood size and degree of hatching asynchrony that produces the maximum annual productivity values will be designated as B^* and N^*, respectively.

D. Annual Parental Mortality

Natural selection should favor those parents that employ the hatching strategy that produces, in a lifetime, the greatest number of offspring that survive until reproductive age (Williams 1966a, Stearns 1976, Endler 1986). Parents can increase their lifetime fecundity in two major ways: increase annual productivity or decrease annual adult mortality. Any decrease in an adult's annual mortality will increase an individual's lifespan.

Charnov and Kreb's (1974) model of the effect of adult mortality and brood size on a parent's lifetime production of offspring assumed that adult mortality increased proportionately with brood size. Let us make the same assumption here and assume that annual adult mortality, 'm', increases proportionately with increasing brood size so that the lifespan of a parent becomes:

$$L(B) = 1/[m(B)*B]. \tag{11}$$

where L(B) is the lifespan of an individual as a function of brood size and 'B' is the original brood size. Now let us also consider adult mortality caused by a function of hatching form employed. Permit adult mortality to either increase or decrease proportionately with the degree of asynchronous hatching so that the parent's lifespan, as a function of brood size and degree of asynchronous hatching, can be represented by:

$$L(B,N) = 1/[(m(B)*B + m(N)*(N+1))] \tag{12}$$

where m(N) is mortality caused by the degree of hatching asynchrony and 'N' is the degree of hatching employed (note: (N+1) was used because m(N) could not be directly multiplied by 'N' , N=0 would always produce no annual adult mortality). Adult mortality due to hatching form, m(N), can be any value between -1.0 and +1.0 (a positive value would reflect adult mortality increasing with increasing hatching asynchrony and a negative value would reflect that adult mortality decreases with increasing hatching asynchrony). The sum of the adult mortalities due to brood size and hatching asynchrony should not be larger than 1.0 ['m(B)*B + m(N)*(N+1) = 1.0' would represent a semelparous species]. The number of offspring produced in a parent's lifetime, will be equal to the number of offspring produced per year (equation 9) times the number of years the adult lives and breeds:

$$F(B,N) = L(B,N) * P(B,N) \qquad (13)$$

where F(B,N) is the number of offspring produced in a parent's lifetime as a function of brood size and hatching form.

III. RESULTS

A. Introduction

I ran computer simulations on the present mathematical model and addressed these two questions:

(1) what is the effect of a continuous distribution of food years on the most productive hatching form and brood size when moderate years are most frequent?

(2) what conditions do annual adult mortality influence the hatching form and brood size that will produce the most offspring in a lifetime?

I used the annual productivity forms of the model, equation (8) through (10), to address the first question. In particular, I address whether the variables of this present model yielding the most productive brood favor a parent's adjustments in brood size or hatching form. The form of the model as equation (13) is used to address the second question qualitatively.

B. Food Year Type Distribution on Nestling Survival

Figure 48 shows the effect of food years on nestling survival, by hatch position ('i') and hatching form ('N'). I produced this figure using a standard deviation for year distribution, 'sd', of 0.25, a mean of the food year distribution, 'u', of 0.50, a nestling survival difference by hatch position, 'k', of 0.15, and a brood size dependent mortality constant, 'a', of 0.05. The survival slope function, 'z', was set at 0.25. All nestlings are from a brood size of five. Here we see that an increase in the number of '0' nestlings decreases nestling survival as annual food levels decrease. This was the original intention of introducing a nestling slope function that was a function of brood size (see equation (3)). Note also that the survival of the very last-hatched nestling in an asynchronous brood is always less than the survival of first-hatched nestlings in a synchronously hatched brood. In addition, this figure also shows that, with the current values for all variables, nestlings in synchronous nests never survive in food years of 0.8 or worse. When the nestling slope function is larger than the 0.25 used here, then the slope of all nestling survival values along the food continuum will become steeper; when it is smaller than 0.25, then the nestling survival values will become more horizontal across the food year continuum.

The expected proportion of annual productivities along the food year distribution (equation (8)) for

Figure 48.

Nestling survival values by hatch position for three different hatching forms along the food year continuum. Solid line is for nestlings in an N=0 nest, dashed lines for nestlings in a N=1 nest and dotted lines for nestlings in N=2 nest.

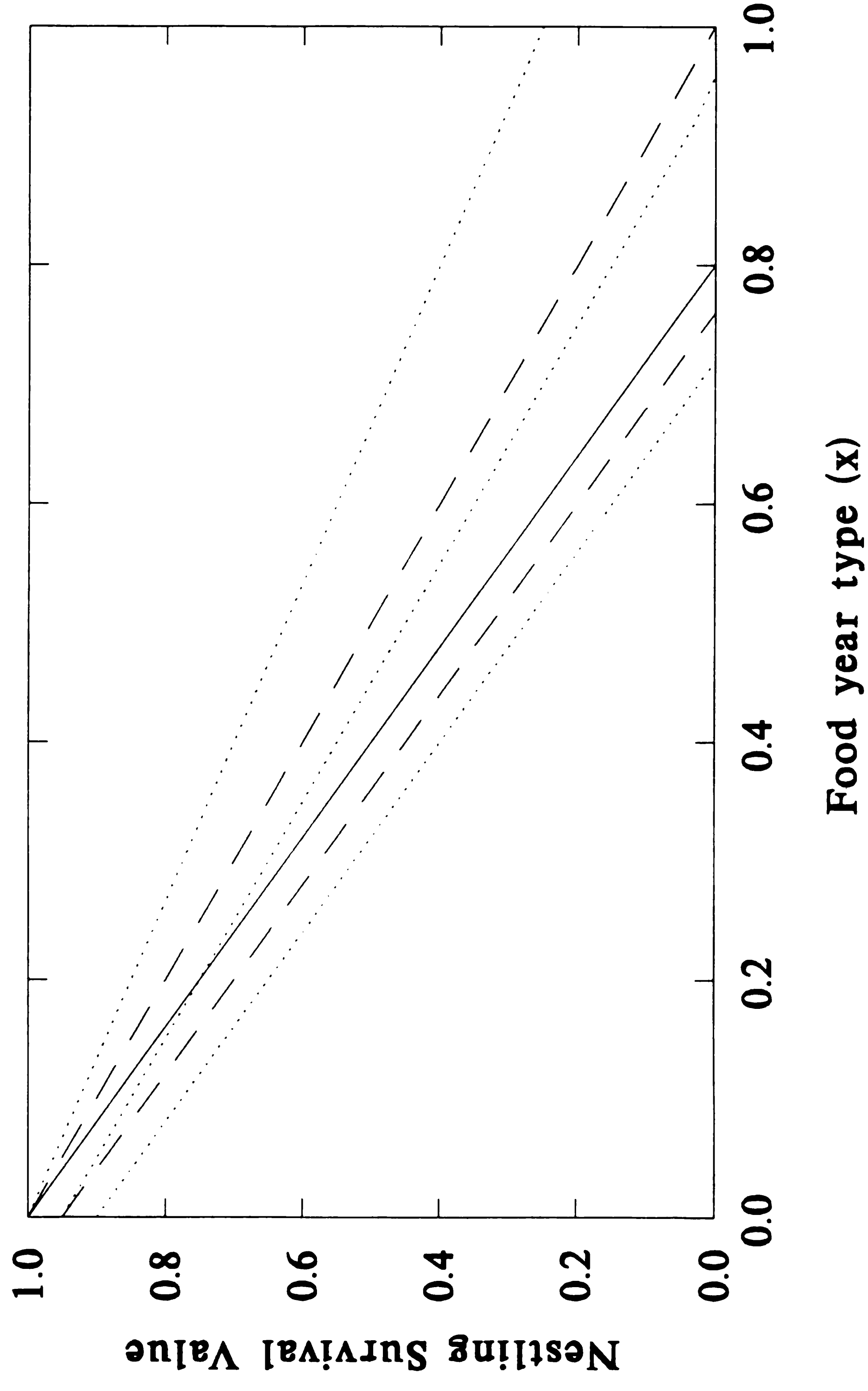


FIGURE 48

Figure 49.

The expected proportion of brood productivity for each food year for three different nestling slope function, 'z', values. a) for 'z'=0.05; b) for 'z'=0.15; and c) for 'z'=0.50.

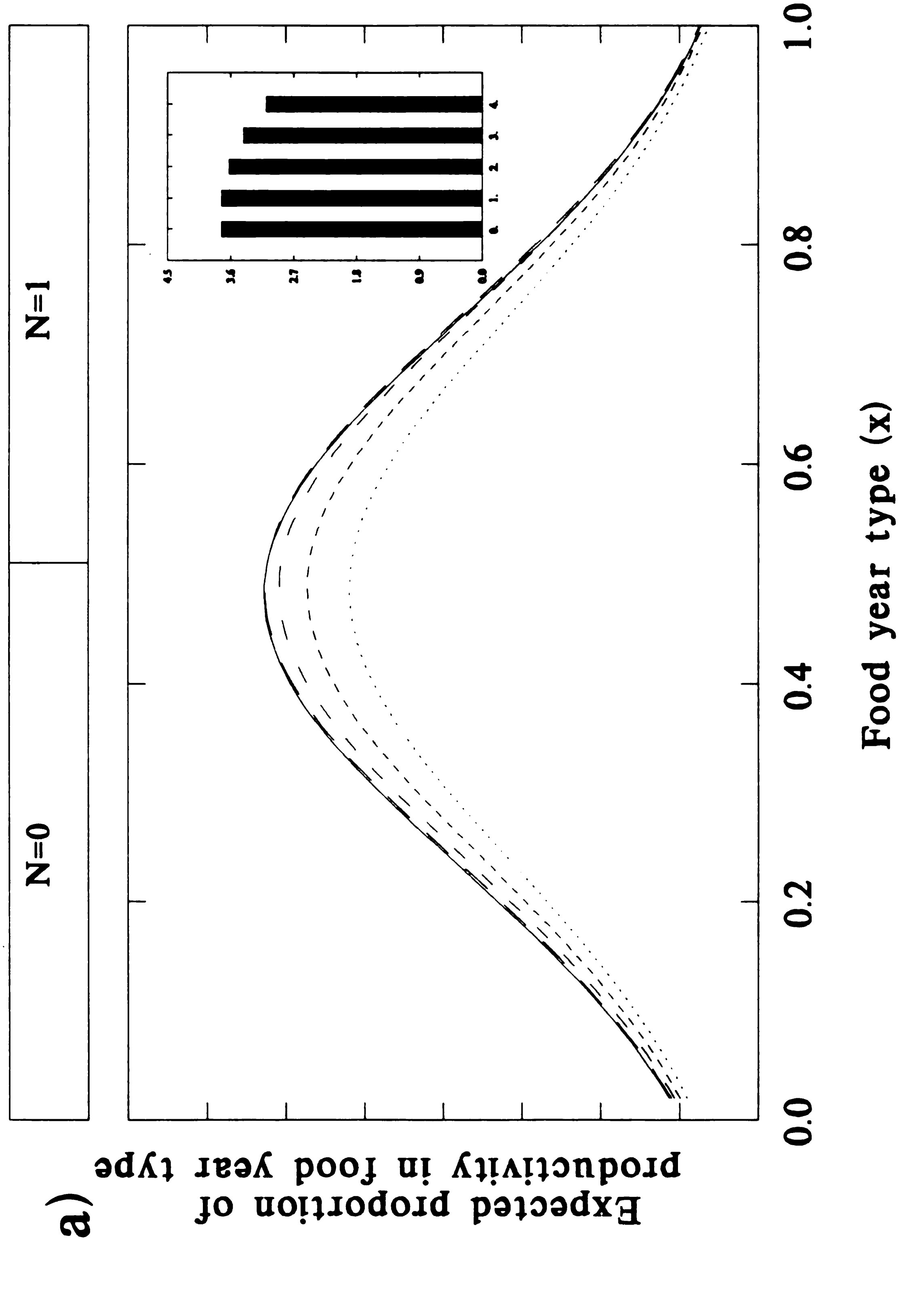

a)
N=0
N=1
Expected proportion of
productivity in food year type
Food year type (x)
0.0
0.2
0.4
0.6
0.8
1.0

FIGURE 49

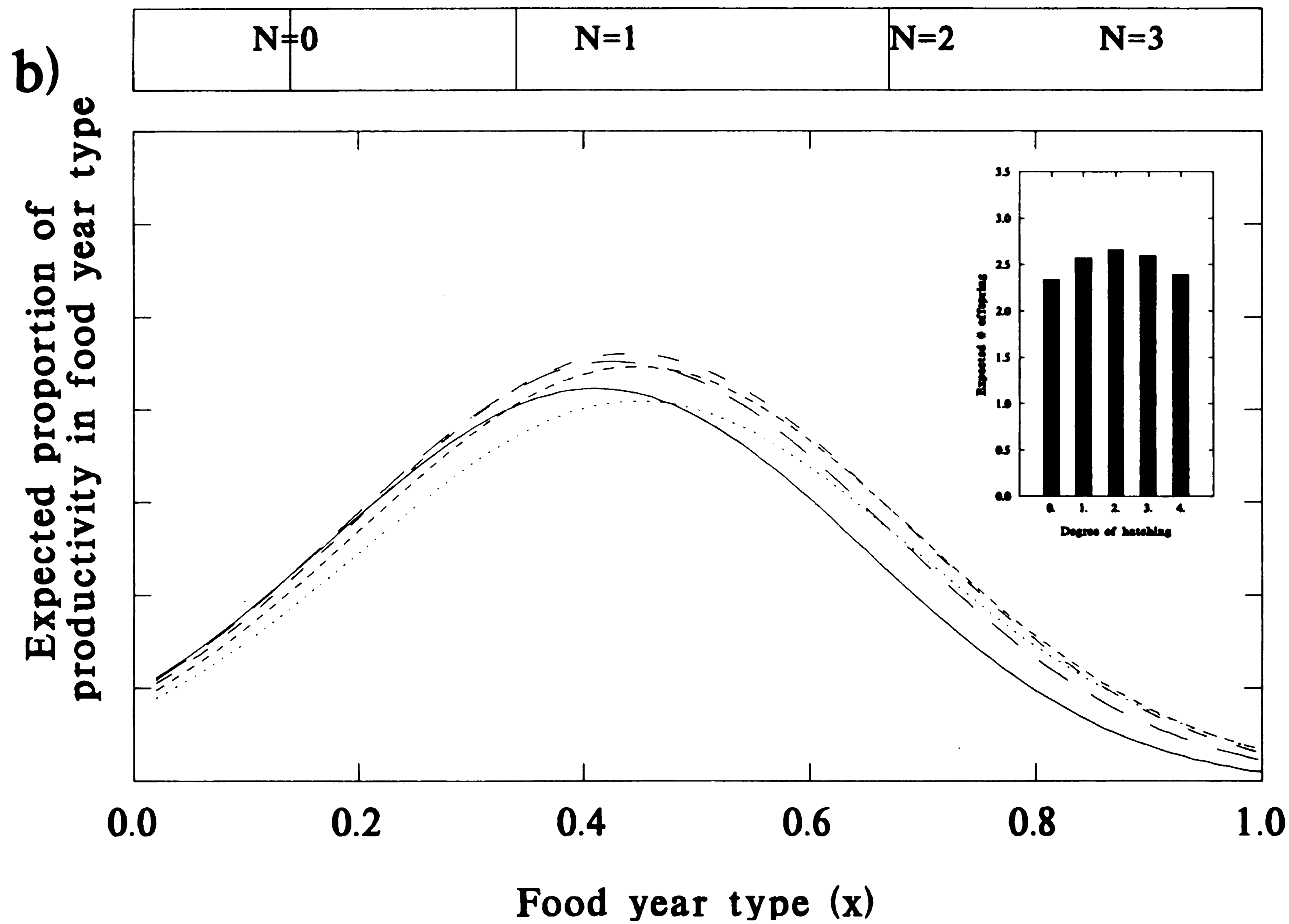

b)
N=0
N=1
N=2
N=3
Expected proportion of productivity in food year type
0.0
0.2
0.4
0.6
0.8
1.0
Food year type (x)
Expected # offspring
Degree of hatching

FIGURE 49

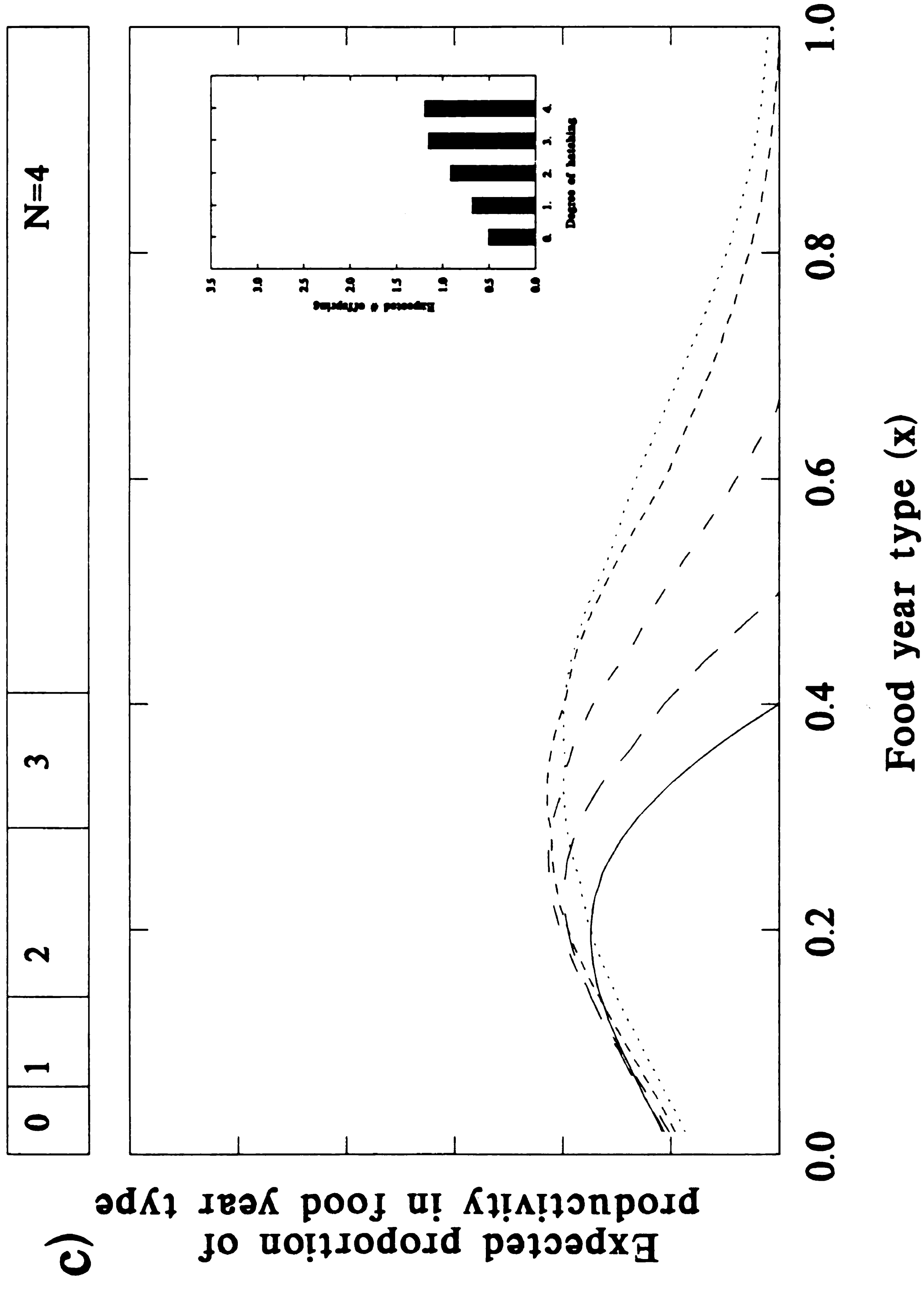

c)
Expected proportion of productivity in food year type
Food year type (x)
0.0
0.2
0.4
0.6
0.8
1.0
N=4
0
1
2
3
Degree of hatching

FIGURE 49

three different nestling slope function values, 'z': 0.05, 0.15 and 0.50, are given in Figures 49a-c, respectively. These figures show all five different hatching forms (N=0 through N=4) for a brood size of five. I used the same values for these variables as I did to construct Figure 48. The most productive forms of hatching for a range of food years (which I call N_{max}, and which should not be confused with N^*) are also given in these figures at the top. Inset in each figure is the value of the productivity integral for each hatching form (the value of equation (9) for each 'N'). Note that in just about every case, the greatest proportion of the expected annual productivity comes from moderate food years because these food years are the most frequent.

Figure 49a shows how a small nestling slope function, 'z' affects the expected proportion of annual productivity for a brood size of five. Note that when the nestling slope function, 'z', is small (0.05), synchronous hatching is the most productive form of hatching in most of the food years; N_{max}=0 for food years 0.0 through 0.81. For food years worse than 0.81, N_{max}=1. Any other degree of hatching asynchrony (i.e. for N > 1) will never be the most productive form of hatching in any food year. Since synchronous hatching is the most productive in most of the food years, then natural selection will select for it over any form of asynchronous hatching because parents can expect to raise the most offspring per year given the food year distribution. The expected annual productivity for all hatching forms (inset) shows that annual productivity decreases with increasing degree of hatching asynchrony.

When the nestling slope function, 'z', is increased (Figure 49b) for a brood size of five, synchronous hatching is still the most productive form of hatching when food years are toward the best food year (i.e. N_{max}=0). As the food year becomes one where less food exists in the environment, the most favored hatching form is a greater degree of hatching asynchrony. For the very worst food year, complete hatching asynchrony (i.e. N_{max}=4) is the most productive form of hatching. This figure shows that N^*=2 is the most productive form of hatching when moderate food levels exist during breeding (inset).

Very large nestling slope functions, 'z', selects heavily against synchronous hatching because a high proportion of broods starve in most food years (Figure 49c). Entire brood starvation decreases with increasing hatching asynchrony because there are fewer '0' nestlings in the brood. When 'z' is very large, then the expected annual brood productivity increases with

Table 11. The B^* and N^* values for iterations of model's 'k' (survival difference between latter-hatched nestlings), 'z' (nestling survival across food type continuum), 'a' (brood size dependent mortality constant) and 'u' (mean of food year type distribution) variables. Values used to construct this table are: a = 0.05, z= 0.25, k=0.10, u=0.50, and sd=0.25.

'z'	B^*	N^*	'u'	B^*	N^*	'sd'	B^*	N^*
0.02	9	0	0.25	7	2	0.0500	2	1
0.06	9	1	0.30	7	2	0.1000	3	2
0.10	9	2	0.35	6	2	0.1500	3	2
0.14	7	2	0.40	6	2	0.2000	5	3
0.18	6	2	0.45	5	2	0.2500	6	4
0.22	5	2	0.50	5	2	0.3000	6	4
0.26	5	2	0.55	5	2	0.3500	6	4
0.30	5	2	0.60	5	2	0.4000	6	4
0.34	4	2	0.65	4	2	0.4500	6	4
0.38	4	2	0.70	4	2	0.5000	6	4

Table 11, continued.

'k'	B^*	N^*	'a'	B^*	N^*
0.020	7	6	0.00500	7	4
0.040	6	4	0.01000	6	3
0.060	6	4	0.02000	6	3
0.080	5	3	0.03000	5	2
0.100	5	2	0.04000	5	2
0.120	5	2	0.05000	5	2
0.140	5	2	0.10000	4	1
0.160	5	2	0.20000	3	1
0.180	5	2	0.30000	2	0
0.200	4	1	0.40000	2	0

increasing hatching asynchrony (inset). Here, a high degree of asynchronous hatching, $N^*=3$, is the most productive form of hatching a brood of five nestlings.

Thus far, we have examined the model by keeping brood size constant. Equation (10) gives us the means to examine which brood size and hatching form that will yield the most productive brood. Table 14 shows the results of iterating 'z' over a large range of values and determining the most productive form of hatching, N^*, and brood size, B^*. I used the same values as I did to construct 49 to construct this table. When the nestling slope function ,'z', is small, large synchronous broods are the most productive brood size and hatching form. As 'z' increases, the most productive form of hatching is greater asynchronous hatching. Larger 'z' values also favor initializing smaller brood sizes. Notice that 'z' affects brood size adjustments more so than degree of hatching asynchrony to produce the most productive brood.

The mean in the food year distribution, 'u', affects B^* values but not N^* values. When the mean of the food year distribution is shifted to the left, large broods are favored (Table 11). This is because a large brood can be raised in good food years and hatching synchrony is the most productive form of hatching in these food years. Likewise, a shift in the food year distribution to the right favors a smaller brood sizes hatched completely asynchronously because poor food years selects against large broods. A shift in the mean of the food year distribution does not affect the degree of hatching asynchrony that yields the most productive brood because changes in 'u' do not affect the shape productivity curve along the food year type distribution (i.e. 'u' does not affect the shape of the curves that we saw in Figures 49a-c).

A change in the spread of the food year distribution, 'sd', affects the values of both B^* or N^* (Table 11). As 'sd' increases, parents can expect a higher frequency of more diverse year types to occur. This favors hatching asynchrony because parents can employ brood reduction if the food year is on the bad food year side. In addition, they can also raise a major portion of the brood if the food year is on the good food year side. A larger spread in the food year distribution (i.e. larger 'sd') also favors larger brood sizes because more good food years occur more frequently and good food years favor large brood sizes.

When the survival difference between nestlings in successive hatch positions is small (i.e. when 'k' is small), the most productive brood is from a hatching form that approaches complete hatching asynchrony (Table 11). This is logical because when 'k' is small, the costs of asynchronous hatching when food is plentiful is low. These costs outweigh the costs of initiating a synchronous brood because all nestlings in these broods die when food is scarce. Likewise, when 'k' is large, costs to asynchronous hatching is high so that synchronous hatching is the most productive form of hatching. Notice that 'k' influences mostly N^* rather than B^* values. For the range of 'k' iterated, N^* went from complete hatching asynchrony to N=1 hatching asynchrony. Over this same range of 'k' values, B^* changed by only 3 nestlings.

Table 11 also shows the brood sizes, B^*, and hatching form, N^*, that yields the most productive brood for different values of the variable 'a', the brood size dependent mortality constant. When 'a' is a small value, then the most productive brood is a large brood hatched asynchronously. As 'a' increases in value (i.e. as the same-sized, large brood is more difficult to raise), then the most productive brood is smaller. These results of productivity on brood size were intended (see equation (7)). However, an increase in 'a' also decreases the degree of hatching asynchrony that yields the most productive brood. This is because as 'a' decreases, broods are easier to raise in most food years but may require brood reduction if the food year turns out to be a bad food year. This is an identical result of my previous model.

C. Annual Parental Mortality

Figure 50a shows a productivity landscape produced from equation (9) for different brood sizes and hatching forms. Note that, with the conditions specified, the most productive form of hatching and brood size is $N^* = 2$ and $B^* = 8$. To aid in visualizing where the maximum productivity occurs along the brood size and hatching form axes, I also included a contour plot of the productivity landscape. This contour plot is located on the x-y facet of this figure.

Figure 50b shows an adult annual mortality plane where adult mortality decreases slightly with an increasing degree of hatching asynchrony ($m(N)=0.05$) and increases slightly more with increasing brood size ($m(N)=0.10$). Plotted on bottom of the page on the x-y facet (Figure 50c) is a contour of adult lifetime production of offspring, $F(B,N)$, as calculated from the quotient of the productivity landscape of Figure 50a and adult mortality of Figure 50b (I used equation (13) to produced Figure 50c).

Let us now examine, qualitatively, how the landscapes in Figure 50a and 50b can influence the position of the brood size and hatching form that yields the most productive brood when an individual's lifetime is considered. There will be two different

Figure 50.

A productivity landscape as a function of brood size and hatching form. Also included is adult mortality plane described as a function of brood size and hatching form (z-axis is component of fitness). See text for details.

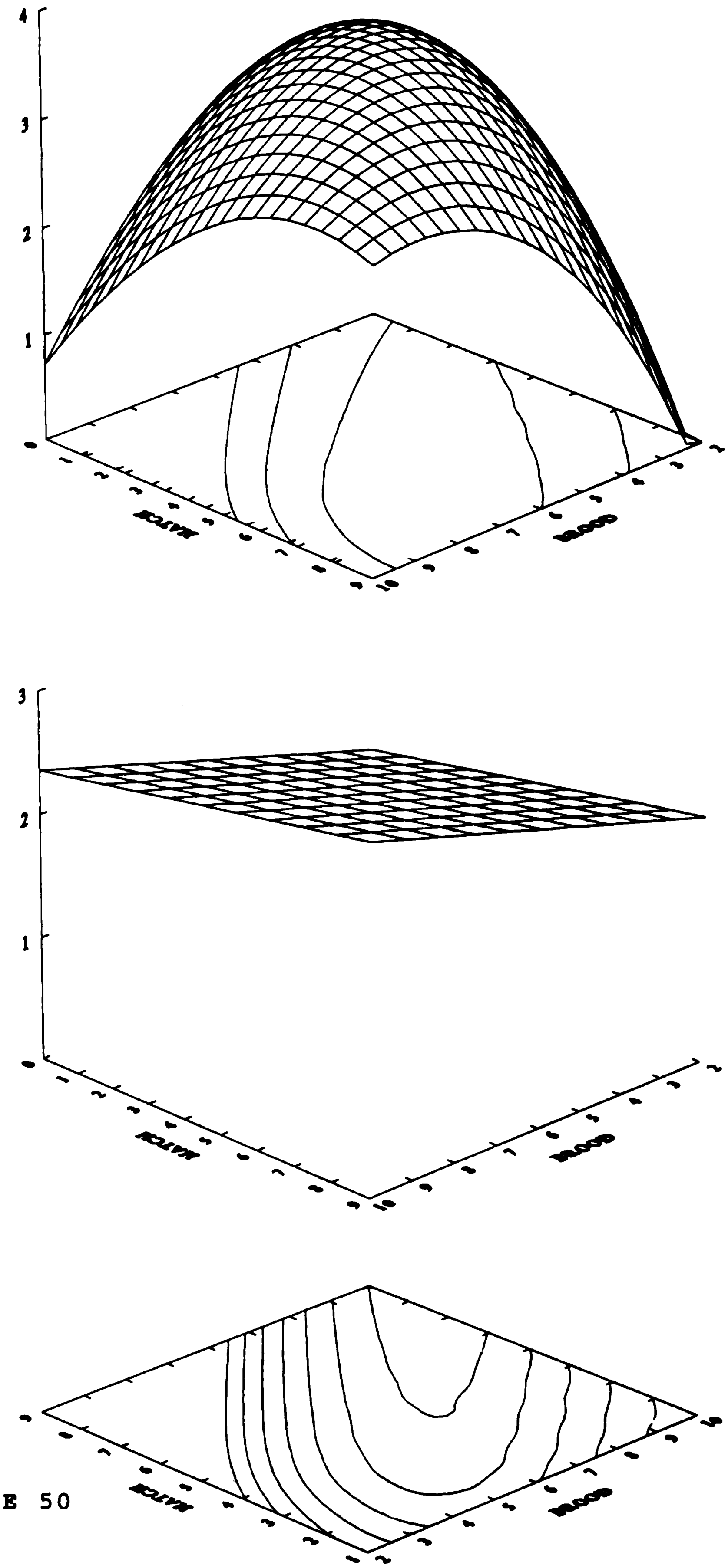


FIGURE 50

conditions that will most affect a parent's lifetime production of offspring. First, as we can see from Figures 50a and 50b, natural selection will change the most productive brood size and hatching form from those calculated from annual productivities (equation (10)) when the slope of the adult mortality plane differs from 0.0. For example, Figures 50a and 50b show that a slight increase in adult annual mortality as a function of the degree of hatching asynchrony increases the most productive form of hatching from $N^*=2$ (as we see in Figure 50a) to $N^* = 4$. The change in the most productive brood size when adult mortality increases with brood size is from $B^*=8$ to $B^*=5$. If adult mortality decreases with increasing hatching asynchrony, then the most productive hatching form will be smaller than the N^* calculated from the annual productivity form of the model (equation (9)).

The second condition that will effect the number of offspring a parent produces in a lifetime will be the shape of the productivity landscape. Lande and Arnold (1983) have shown that the intensity of selection depends upon the concavity of a fitness function along a character gradient. When the productivity landscape (Figure 50a) lacks a lot of curvature, small changes in annual adult mortality will cause a large shift in B^* and N^* values calculated from annual productivity (equation (9)). Thus, even when adult mortality as a function of brood size of hatching form is very small, it can still have a large effect if the annual productivity plane is relatively flat.

There are several variables in the annual productivity form of the model that effect the curvature of the productivity landscape. I plotted three different values for each variable in the productivity equation (equation (9)) on the brood size and hatching form facets of the productivity landscape (Figures 51 through 53). I chose values from Table 14 that produced hatching synchrony, an intermediate degree of hatching asynchrony and complete asynchronous hatching so that a full range of values for each variable would be represented. The largest value of the three is plotted as a dotted line, the intermediate value as the dashed line and the smallest value of the variable is plotted using a solid line. In particular, I ask what values of the model's variables will produce a flat productivity landscape.

Figure 51 contains those variables influencing the food year distribution portion of the model. We can see that the standard deviation of the food year distribution, 'sd', has the same degree of curvature along the hatching form facet, 'N', for all three

Figure 51.

The effect of different 'sd' and 'u' values on the curvature of the productivity landscape along the 'N' and 'B' facets.

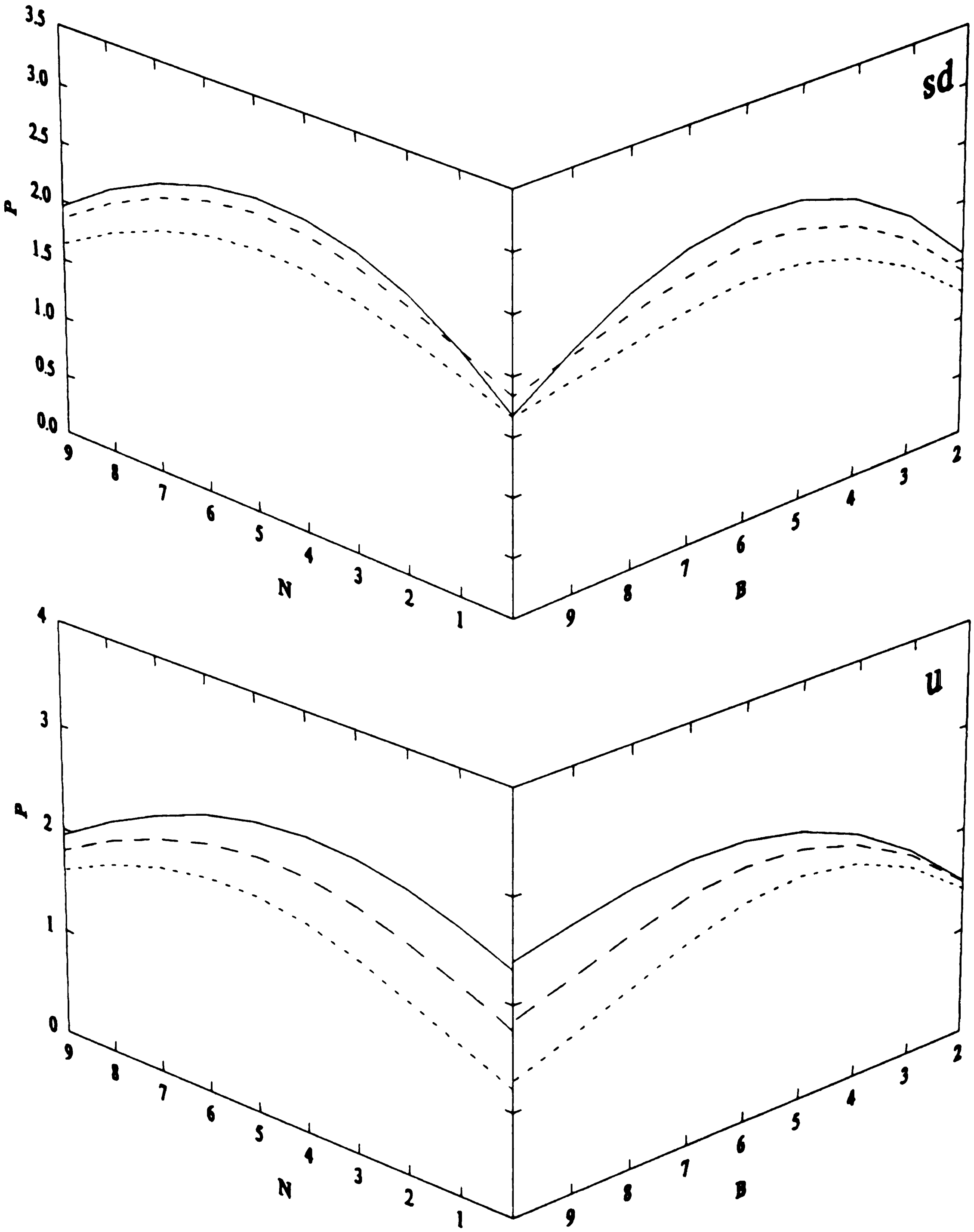

3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
P
sd
9
8
7
6
5
4
3
2
1
N
9
8
7
6
5
4
3
2
B
4
3
2
1
0
P
u
9
8
7
6
5
4
3
2
1
N
9
8
7
6
5
4
3
2
B

FIGURE 51

Figure 52.

The effect of different 'k' and 'z' values on the curvature of the productivity landscape along the 'N' and 'B' facets.

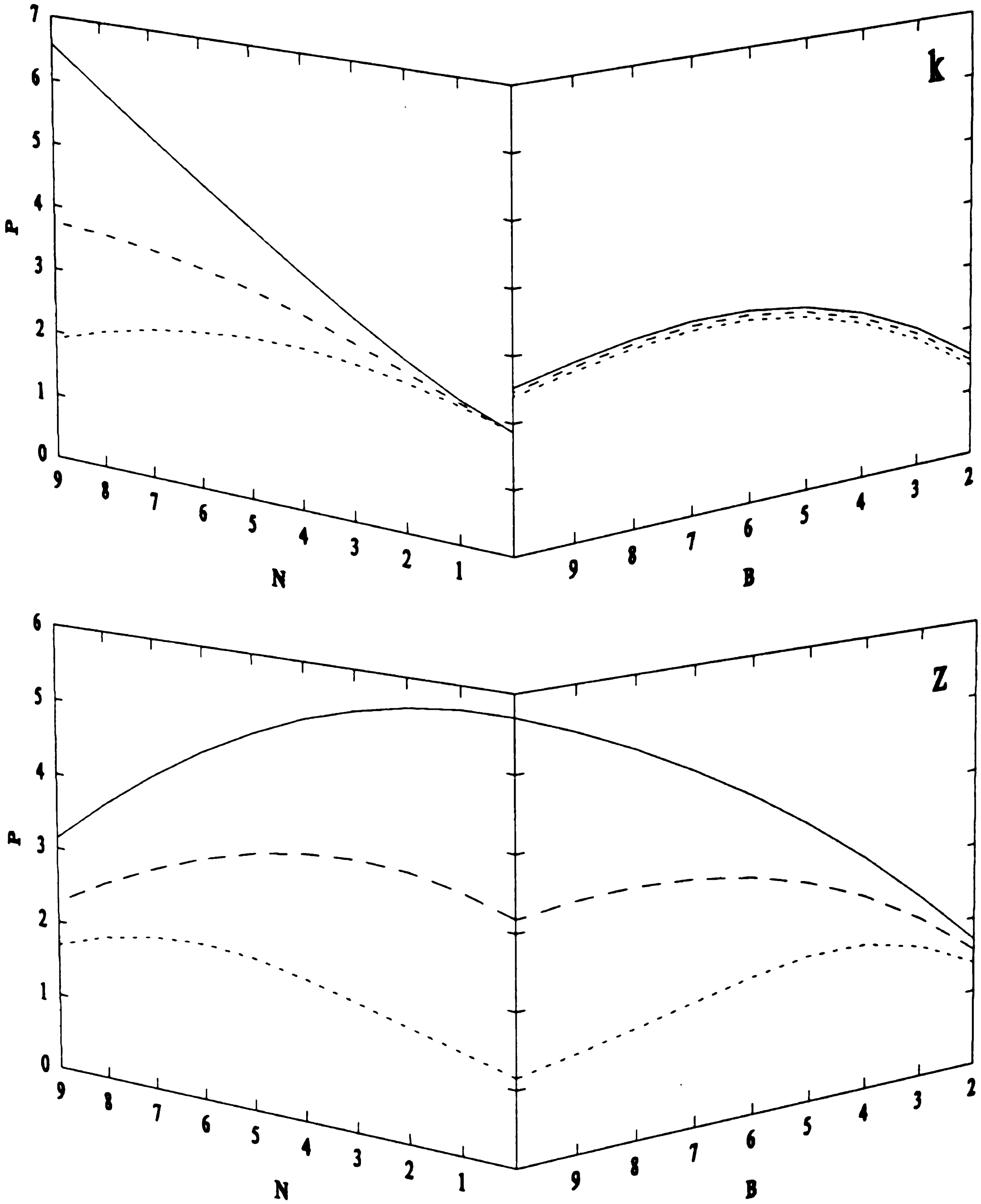

k
P
7
6
5
4
3
2
1
0
9
8
7
6
5
4
3
2
1
N
9
8
7
6
5
4
3
2
B
Z
P
6
5
4
3
2
1
0
9
8
7
6
5
4
3
2
1
N
9
8
7
6
5
4
3
2
B

FIGURE 52

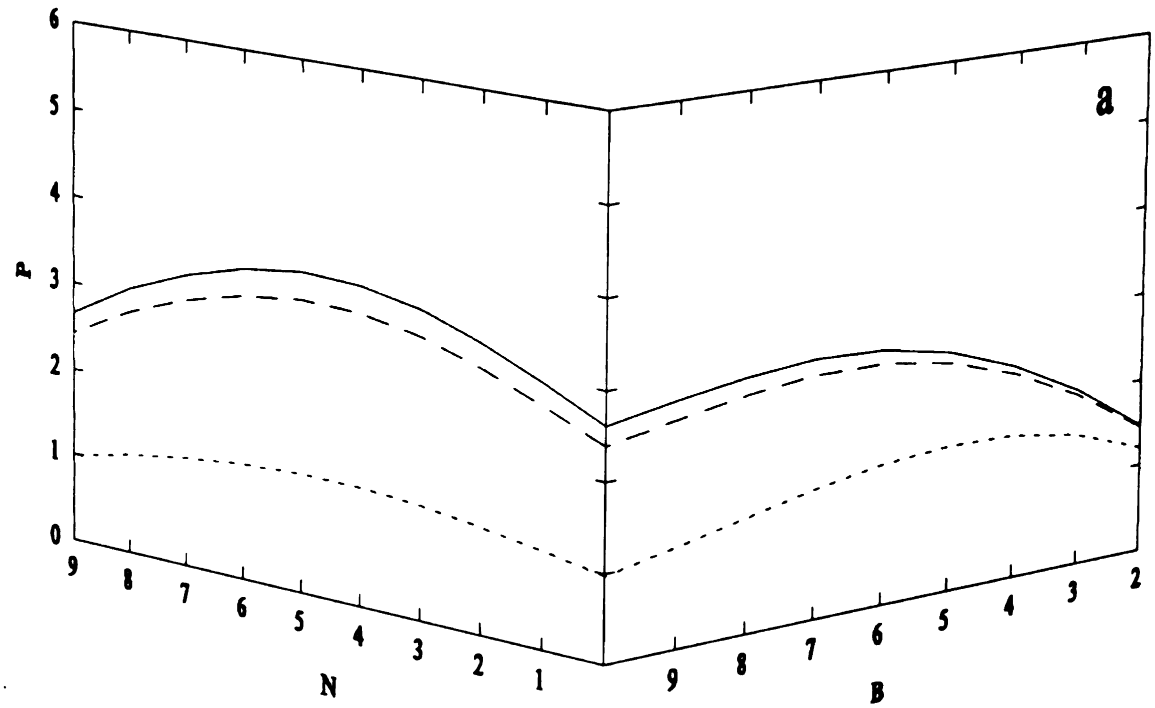


Figure 53.

The effect of different 'a' values on the curvature of the productivity landscape along the 'N' and 'B' facets.

variables (sd = 0.05, solid line; sd = 0.25, dashed line; sd= 0.50, dotted line). However, these three values differ in the degree of curvatures along the brood size facet, 'B'. Larger values of 'sd' produce a slightly flatter productivity landscape. Thus, when adult mortality, as a function of brood size, m(B), is changed slightly, natural selection will favor a larger change in the brood size that yields the most offspring per year, compared to when 'sd' is small. On the other hand, different values of the mean of the food distribution, 'u', produces similar degrees of curvature in the annual productivity landscape. Thus changes in adult annual mortality will have the same effect in the magnitude of the shifts in B^* and N^* from the annual productivity form of the model to the lifetime form of the model.

Figure 52 shows the effect of the slope function, 'z', and differential survival by hatch position, 'k', on the curvature of the annual productivity landscape. We can see that large values of 'z' produce a flatter productivity landscape, both along the brood size and hatching form facets, than do small values of 'z'. Thus, any small changes in annual adult mortality can change either N^* or B^* more so when 'z' is large. Three values for the survival difference between hatch positions, 'k', are also shown here in Figure 53. We can see that when 'k' is small, the 'N' facet of the productivity landscape lacks the most curvature. Different values of 'k' do not produce different degrees of curvatures along the 'B' facet of the annual productivity landscape.

Lastly, Figure 53 shows the effects of 'a', the brood size dependent mortality constant, on the curvature of the annual productivity landscape. We can see that a large value of 'a' produces a flatter annual productivity landscape than small 'a' values along the hatching form facet. On the other hand, the three values of 'a' depicted here do not influence the shape of the annual productivity landscape along the brood size facet.

IV. DISCUSSION

A. Introduction

My earlier model compared the expected annual productivities of parents raising synchronous broods and asynchronous broods where one nestling was one day younger than its siblings. I allowed upcoming food years to be unpredictably good or bad. I found that by allowing the last-hatched nestling in an asynchronously hatched nest to have a lower survival rate compared to first-hatched nestlings when food was good, natural selection could still favor asynchronous hatching over synchronous hatching. Asynchronous hatching was more productive than synchronous hatching when good food years were infrequent, when costs to synchronous hatching was high in bad food years and when parents initiated large clutches.

It is probably more realistic that birds are subjected to a wide variety of food years where some types are more frequent than others. Thus, my earlier model may be considering only the extreme in food years that could occur. In addition, my earlier model also did not consider degrees of hatching asynchrony other than broods where one nestling hatches a day later than the rest of the brood. Lastly, my previous model assumed that hatching asynchrony did not affect parental survival. The objectives of this present model were to modify this earlier model by considering all possible hatching forms within a brood size and also consider nestling survival along a continuous distribution of food years where moderate food years are the most frequent. I used this model to address two questions:

(1) what is the effect of a continuous distribution of food years on the most productive hatching form and brood size when moderate food years are most frequent?

(2) how does annual adult mortality influence the

hatching form and brood size that will produce the most offspring in a lifetime?

I will discuss the predictions of this model in relation to these two questions. I also address how this model may be combined with other hypotheses that present reasons for the adaptive significance of hatching asynchrony.

B. Food Year Distribution on the Most Productive Hatching Form and Brood Size

I have found that when nestling survival decreases rapidly across a continuum of food years that parents could potentially breed in, then adjustments in brood size are favored over adjustments in the degree of hatching asynchrony. A large decline in nestling survival across the food year continuum favors smaller brood sizes over larger ones.

I have also found that a shift in the mean of the food year distribution also favors an adjustment of brood size over adjustments in the degree of hatching asynchrony. When good food years are most frequent, large broods are easily raised when food is good and brood reduction is not required often. The costs of raising broods during good food years outweigh the benefits accrued by parents during infrequent bad food years. In addition, if there is a large spread in the food year distribution (i.e. when 'sd is large), some form of hatching asynchrony will yield the most productive brood.

I have also shown that changes in 'k', survival difference due to hatch position, favors adjustments in brood size and degree of hatching asynchrony. When 'k' is small, then large asynchronous broods yield the most productive brood. As 'k' increases, costs to asynchronous hatching increases making more synchronous broods the most productive brood.

In my previous model, I found that, as the brood size dependent mortality constant, 'a', is increased, hatching asynchrony was more productive than hatching synchrony. This present model generates a different prediction. When 'a' is increased, synchronous hatching is favored.

This present model emphasizes the need for researchers to carry out studies for more than one year and to measure food abundance. Studies conducted for one or two years which find that the model degree of hatching asynchrony is not the most productive form of hatching cannot claim that brood reduction is maladaptive. Studies must examine long term consequences of reproductive traits on fitness. Furthermore, this model also extends Lack's brood reduction hypothesis by treating a continuum of food year distributions. I have shown that even during moderate food year types, some form of hatching asynchrony and brood reduction can be more productive than synchronous hatching. Lack (1947, 1948, 1956, 1968) never addressed whether hatching asynchrony or hatching synchrony would be more productive for moderate food year types. Thus, this model treats all food year types and shows how hatching asynchrony and brood reduction can be adaptive.

C. Adult Mortality on the Most Productive Hatching Form and Brood Size

I have introduced into the present model the effects of adult annual mortality both as a function of brood size and hatching form employed. I assumed that annual adult mortality increased proportionately with increasing brood size and either increased or decreased proportionately with the degree of hatching asynchrony.

I have shown that if adult annual mortality decreases with increasing hatching asynchrony, then natural selection will favor more asynchronous hatching, compared to when adult mortality is not considered. On the other hand, an increase in adult mortality with increasing hatching asynchrony will favor more hatching synchrony. A larger change in adult mortality as a function of brood size or hatching form will select for larger changes in brood or hatching form that was predicted from when just annual productivity is considered.

This model also shows that small curvatures of the annual productivity landscape and small changes in adult annual mortality along a hatching form or brood size gradient can influence large shifts in the brood size and hatching form yielding the most offspring per year. This is interesting because some researchers have claimed that if parental survival is changed little by a character gradient, it must have very little influence on the selection of that character (e.g. DeSteven 1980, Bell 1984, Boyce and Perrins 1987). I have shown, however, that small changes in adult mortality with brood size or hatching form may change the brood size and hatching form that produces the most productive brood. I explored the model and examined conditions of the variables that produced the least concave productivity landscape. I found that the productivity landscape is relatively flat along the brood size gradient when the standard deviation in the food year continuum, 'sd', is large, and when the nestling slope function, 'z' is large. The productivity landscape is relatively flat along the hatching form gradient when: (1) the difference in nestling survival by hatch position, 'k', is small; (2)

the nestling slope function, 'z', is large; and when (3) the brood size dependent mortality constant, 'a', is large.

D. Implications of the Model to Field Research

The predictions of this present model have several implications toward results of field experiments that are common in the examination in the role of hatching asynchrony. Many researchers (see Amundsen and Stokland 1988 for a review) have manipulated broods to simulate hatching synchrony and a degree of hatching asynchrony greater than that employed naturally by a species. This present model shows that during some breeding seasons, hatching synchrony might yield the most productive brood, and that during other breeding seasons, an increased degree of hatching asynchrony might yield the most productive brood. Thus, researchers should use caution in declaring the degree of hatching asynchrony in a population as maladaptive if these broods are not the most productive in the experimental design. It is entirely possible for unnatural degrees of hatching asynchrony to be the most productive form of hatching. Additionally, this model also underscores the need to measure food abundances and to conduct studies over many years.

This model also considers new types of measures for researchers to report and examine carefully to determine the adaptive value of hatching asynchrony in their study species. First, researchers should carefully examine the difference in survival values between hatch positions. When large differences in nestling survival exist between hatch positions, then hatching asynchrony will not be the most productive brood in all food years. Second, this model also emphasizes the need to understand more about the effects of hatching asynchrony over a wide range of food conditions. In addition, it is also desirable to determine what food conditions might represent the most frequent food year available to parents. Third, researchers need to examine adult annual mortality and do so in relationship with the other variables presented in this model. This model is the first model to incorporate both annual reproductive success and adult mortality affects on the hatching form and brood size that will yield the most productive brood size. This model underscores the importance of examining all both fitness components and to analyze the shape of the fitness components with respect to hatching form and brood size. Finally, this model is in a form that can allow researchers to begin comparing different species to determine if brood reduction can explain the common occurrence of hatching asynchrony that is observed in altricial birds.

E. Relationship of the Present Brood Reduction Model to Alternative Hypotheses

Presently, a myriad of adaptive hypotheses exist that attempt to explain the adaptive significance of hatching asynchrony (see Magrath, 1990, for review). However, only two hypotheses have been introduced as a quantitative model; these are the peak load reduction hypothesis (Mock and Schwagmyer 1990) and the nest-failure hypothesis (Clark and Wilson, 1981).

There has been a general agreement among researchers (see Magrath 1990) that all adaptive hypotheses explaining the significance of hatching asynchrony are not mutually exclusive. In fact, it is highly probable that selection by more than one factor may play a role in favoring the specific degree of hatching asynchrony in any bird species. For example, the nest-failure hypothesis and the brood reduction hypothesis (in the present model's form) could both explain the significance of hatching asynchrony in any given species. The nest-failure hypothesis states that hatching asynchrony is favored in species where the per diem nest-failure rate due to predation (see Magrath, 1989 for another possible cause of nest-failure) is greater during the incubation period than during the nestling period (see also Hussell 1983, for another form of this model). Hatching asynchrony could be one mechanism that adjusts the amount of exposure an offspring experiences as either an egg or a nestling. The nest-failure reduction model examines this also as a function of brood size.

Combining both models mathematically could be accomplished relatively easily. The adaptive landscape produced by the present continuous brood reduction model (see Figure 4a for example), for example, could be constrained using Lagrange multipliers on the partial derivatives dP/dB and dP/dN. Thus, predation could produce a brood size and degree of hatching asynchrony that could be further selected upon to produce the most productive brood. Such an approach could prove fruitful since there is currently no unified approach to the problem of hatching asynchrony. Quantifying other verbal adaptive hypotheses could also help researchers understand the relationships between all of these adaptive hypothesis.

V. CONCLUSIONS

This present model was constructed to determine the effects of a continuum of food years where moderate food years are the most frequent would have on the hatching form and brood size that would produce the most productive brood. I also introduced effects of parental survival, as a function of brood size and hatching form, into this model. I found that hatching asynchrony is favored over more synchronous hatching when: (1) the costs to asynchronous hatching, reduced survival of latter-hatched nestlings in good food years, is low; (2) when the nesting slope function along the food year continuum is high; and (3) when the mean in the food year distribution is not toward the best food year side of the food year continuum. I also found that adult mortality can influence the brood size and hatching form that produces the most productive brood type in a parent's lifetime. Adult mortality has its greatest influence on the hatching form and brood size that yields the most productive brood when: (1) adult mortality along a brood size or hatching form continuum is large; and (2) when the annual productivity landscape is relatively flat. Furthermore, this model is in a form that can be used to combine other models that exist to explain the adaptive significance of hatching asynchrony.

LITERATURE CITED

Anderson, D. J. 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. American Naturalist 135:334-350.

Amundsen, T. and J. N. Stokland. 1988. Adaptive significance of asynchronous hatching in the shag: a test of the brood reduction hypothesis. Journal of Animal Ecology 57:329-344.

Ashmole, N. P. 1965. Adaptive variation in the breeding regime of a tropical sea bird. National Academy of Sciences U.S.S. 53:311-318.

Bechard, M. J. 1983. Food supply and the occurrence of brood reduction in swainson's hawk. Wilson Bulletin 95:233-242.

Bell, G. 1984. Measuring the cost of reproduction. I. The correlation structure of the life table of a plankton rotifer. Evolution 38: 300-313.

Bengtsson, H. and O. Ryden. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. Z. Tierpsychol. 56:255-272.

Bengtsson, H. and O. Ryden. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit Parus major. Behavioral Ecology and Sociobiology 12:243-251.

Bent, A. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publications, New York.

Boyce, M. and C. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142-153.

Bryant, D. M. 1975. Breeding biology of house martins Delichon urbica in relation to aerial insect abundance. Ibis 117:180-216.

Bryant, D. M. 1978. Establishment of weight hierarchies in the broods of house martins Delichon urbica.

Ibis 120:16-26.

Bryant, D. M. and P. Tatner. 1990. Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters. Animal Behavior 39:657-671.

Burtt, E. 1977. Some factors in the timing of parent-chick recognition in swallows. Animal Behavior. 25:231-239.

Burtt, E. H. and R. M. Tuttle. 1988. Effect of timing of banding on reproductive success of tree swallows. Journal of Field Ornithology 54:319-323.

Butler, R. 1988. Population dynamics and migration routes of tree swallows, Tachycineta bicolor, in North America. Journal of Field Ornithology 59:395-402.

Charnov, E. and J. R. Krebs. 1974. On clutch-size and fitness. Ibis 116:217-219.

Clark, A. B. and D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. Quarterly Review of Biology 56:253-277.

Cooper, W. S. and R. H. Kaplan. 1982. Adaptive "coin-flipping": a decision-theoretic examination of evolved characteristics. Journal of Theoretical Biology 92:401-415.

DeSteven, D. 1978. The influence of age on the breeding biology of the tree swallow (Iridoprocne bicolor). Ibis 120:516-523.

DeSteven, D. 1980. Clutch size, breeding success and parental survival in the tree swallow Iridoprocne bicolor. Evolution 34: 278-291.

Dorward, D. F. 1962. Comparative biology of the white booby and the brown booby Sula spp. at Ascension. Ibis 103b:174-200.

Drent, R. H. 1975. Incubation. Avian Biology, vol V., Eds. Farner, D.S., J. R. King and K. C. Parkes. Academic Press, New York.

Drent, R. H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea

68:225-252.

Drummond, H. and C. C. Garcia. 1989. Food shortage influences sibling aggression in the blue-footed booby. Animal Behavior 37:806-819.

Dunlop, 1913. On incubation. British Birds. 7: 105-114.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.

Evans, R. M. and B. F. McMahon. 1987. Within-brood variation in growth and condition in relation to brood reduction in the American pelican. Wilson Bulletin 99: 190-201.

Fisher, R. A. 1930. Genetical theory of natural selection. Clarendon Press, Oxford.

Forbes, M. R. L. and C. D. Ankney. 1987. Hatching asynchrony and food allocation within broods of pied-billed grebes Podilymbus podiceps. Canadian Journal of Zoology 65:2872-2877.

Fujioka, M. 1985a. Sibling competition and siblicide in asynchronously hatching broods of the cattle egret Bubulcus ibis. Animal Behavior 33: 1228-1242.

Fujioka, M. 1985b. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. Behavioral Ecology and Sociobiology 17:67-74.

Gibbons, D. W. 1987. Hatching asynchrony reduces parental investment in the jackdaw. Journal Animal Ecology 56:403-414.

Gillespie, J. H. 1974. Natural selection for within-generation variance in offspring number. Genetics 76:601-606.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist 111:1010-1014.

Gould and Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royal Society London B 205:581-598.

Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling stonechats Saxicola torquata. Journal of Zoology London. A. 205:453-465.

Groves, S. 1984. Chick growth, sibling rivalry and chick production in American black oystercatchers. Auk 101:525-531.

Haartman, L. von. 1953. Was reizt den Trauerfliegenschnapper (Muscicapa hypoleuca zu futtern? Vogelwarte 16: 157-164.

Hahn, D. C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. Animal Behavior 29:421-427.

Haydock, J. and J. D. Ligon. 1986. Brood reduction in the Chihuahuan raven: an experimental study. Ecology 67:1194-1205.

Holroyd, G.L. 1972. A comparison of resource use by four avian species of aerial insect feeders. M. Sc. Thesis, University of Toronto.

Horsfall, J. A. 1984. Brood reduction and brood division in coots. Animal Behavior 32:216-225.

Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the common grackle. Ecology 57:1195-207.

Howe, H. F. 1978. Initial investment, clutch size, and brood reduction in the common grackle (Quiscalus quiscula). Ecology 55:75-83.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecological Monographs 42:317-364.

Hussell, D. J. T. 1983a. Tree swallow pairs raise two broods in a season. 95:47-471.

Hussell, D. J. T. 1983b. Age and plumage color in female tree swallows. Journal of Field Ornithology.

Hussell, D. J. T. 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. American Naturalist 131:175-202.

Hussell, D. J. T. and T. Quinney. 1987. Food abundance and clutch size of tree swallows _Tachycineta bicolor_. Ibis 129:248-258.

Ingram, 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76: 218-226.

Khayutin, S. N., L. P. Dmitrieva and L. I. Alexandrov. 1988. Psychobiological aspects of the acceleration of postembryonic development in the asynchronous breeder, pied flycatcher (_Ficedula hypoleuca_). International Journal of Comparative Psychology 145-166.

Klomp, H 1970. The determination of clutch size in birds, a review. Ardea 58:1-124.

Kuerzi, R. G. 1941. Life history studies of tree swallows. Proceedings of the Linnean Society, N.Y. 52-53:1-52.

Johnson, C. G. 1965. The comparison of suction trap, sticky traps and tow net for the quantitative sampling of small airborne insects. Annual Applied Biology. 37:268-285.

Lacey, E. P., L. Real, J. Antonovics and D. G. Heckel. 1983. Variance models in the study of life histories. American Naturalist 122:114-131.

Lack, D. 1947. The significance of clutch size. Parts I and II. Ibis 89:302-352.

Lack, D. 1948. The significance of clutch size. Part III. Ibis 90:25-45.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London.

Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37: 1210-1226.

Lewontin, R. C. 1961. Evolution and the theory of games. Journal of Theoretical Biology 1:382-403.

Low, S. H. 1933. Further notes on the nesting of the tree swallows. Bird-banding 4:76-87.

Magrath, R. D. 1988. Hatching asynchrony in altricial birds: nest failure and adult survival. American Naturalist 131:893-900.

Magrath, R. D. 1989. Hatching asynchrony and reproductive success in the blackbird. Nature 339:536-538.

Magrath, R. D. 1990. Hatching asynchrony in altricial birds. Biological Reviews.

Mead, P.S. and M. Morton. 1985. Hatching asynchrony in the mountain white-crowned sparrow (Zonotrichia leucophrys oriantha): a selected or incidental trait? Auk 102: 781-792.

Mishaga, R. 1974. Notes on asynchronous hatching and nestling mortality in white-necked ravens. Wilson Bulletin 86:174-176.

Mock, D. W. 1984. Infanticide, siblicide and avian nesting mortality. Pages 3-30 in G. Hausfater and S. B. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine, New York, N.Y.

Mock, D. W. 1987. Siblicide, parent-offspring conflict, and unequal parental investment. Behavioral Ecology and Sociobiology 20:247-256.

Mock, D. T. Lamey. and B. Ploger 1987. Proximate and ultimate roles of food amount in regulating egret sibling aggression. Ecology 1987.

Mock, D. T. Lamey, C. Williams and A. Pelletier. 1987. Flexibility in the development of heron sibling aggression: an interspecific test of the prey-size hypothesis. Animal Behavior 35:1386-1393.

Mock, D. and G. Parker. 1986. Advantages and disadvantages of egret and heron brood reduction. Evolution 403:459-470.

Mock, D. and P. Schwagmeyer. 1990. The peak-load reduction hypothesis for avian hatching asynchrony. Evolutionary Ecology 4: 249-260.

Murphy, M. T. and R. Fleischer. 1986. Body size, nest predation and reproductive patterns in brown thrashers and other mimids. Condor 88:446-455.

Nice, M. M. 1954. Incubation periods throughout the ages. Centaurus 3:311-359.

Nisbet, I. C. T. 1973. Courtship feeding, egg size and breeding success in common terns. Nature 241:141-142.

Nisbet, I. C. T. and M. E. Cohen. 1975. Asynchronous hatching in common and roseate terns, Sterna hirundo and S. dougallii. Ibis 117: 374-379.

O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Animal Behavior 26:79-96.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the herring gull (Larus argentatus). Nature 228:1221-1222.

Paynter, R, 1954. Interrelations between clutch-size, brood-size, prefledging survival, and weight in Kent Island tree swallows. Bird-banding 25:136-148.

Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit, Parus major. J. Anim. Ecol. 34:601-647.

Proctor, D. 1975. The problem of chick loss in the South Polar Skua Catharacta maccormicki. Ibis 117: 452-459.

Quinney, T. 1983a. Tree swallows cross a polygyny threshold. Auk 100: 750-754.

Quinney, T. 1983b. The relation between food abundance and reproductive success of tree swallows. Ph. D. Thesis, University of Western Ontario.

Quinney, T. 1986. Male and female parental care in tree swallows. Wilson Bulletin 98:147-149.

Quinney, T. and C. D. Ankney. 1985. Prey size selection by tree swallows. Auk 102: 245-250.

Quinney, T., D. J. T. Hussell and C. D. Ankney. 1986. Sources of variation in growth of tree swallows. Auk 103:389-400.

Ricklefs, R. E. 1965. Brood reduction in the curve-billed thrasher. Condor 67:505-510.

Ricklefs, R. E. 1967. A graphical method for fitting equations to growth curves. Ecology 48:978-983.

Ricklefs, R. 1968. Patterns of growth in birds. Ibis 110:419-451.

Ricklefs, R. E. 1977. A note on the evolution of clutch size in altricial birds. Pages 193-214 in B. Stonehouse and C. Perrins, ed. Evolutionary ecology. University Park Press, Baltimore, Md.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38-49.

Ricklefs, R. E. and S. Peters. 1981. Parental components of variance in growth rate and body size in nestling European Starling (Sturnus vulgaris) in eastern Pennsylvania. Auk 98:39-48.

Ryden, O. and H. Bengtsson. 1980. Differential begging and locomotory behavior by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. Z. Tierpsychology 53:209-224.

Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling great tits Parus major. Ibis 115:549-558.

Shaw, P. 1985. Brood reduction in the blue-eyed shag Phalacrocorax atriceps. Ibis 127:476-494.

Skagen, S. K. 1988. Asynchronous hatching and food limitation: a test of Lack's hypothesis. Auk 105:78-88.

Slagsvold, T. 1982. Clutch size, nest size and hatching asynchrony in birds: experiments with the fieldfare. Ecology 63:1389-1399.

Slagsvold, T. 1985. Asynchronous hatching in passerine birds: influence of hatching failure and brood reduction. Ornis Scand. 16:81-87.

Slagsvold, T. 1986. Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. J. Anim. Ecol. 55:1115-1134.

Slagsvold, T., J. Sandvik, G. Rofstad, O. Lorentsen and M. Husby. 1984. On the adaptive value of intra-clutch egg-size variation in birds. Auk 101:685-697.

Sokal, R. and F. Rohfl. 1981. Biometry. W.H. Freeman and Co. New York.

Stearns, S. 1976. Life-history tactics: A review of the ideas. Quarterly Review of Biology 51: 3-47.

Steele, R. G. and J. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, Inc. New York.

Stinson, C. H. 1979. On the selective advantage of fratricide in raptors. Evolution 33: 1219-1225.

Temme, D. M. and E. Charnov. 1987. Brood size adjustment in birds: economical tracking in a temporally varying environment. Journal of Theoretical Biology 126: 137-148.

Thorsteinson, A. G. Braken and W. Hanec. 1965. The orientation behavior of horse flies and deer flies (Tabanidae, Diptera). III. The use of traps in the study of orientation of tabanids in the field. Entomolgy: Experimental and Applied :189-192.

Wiggins, 1990. Clutch size, offspring quality, and female survival in tree swallows - an experiment. Condor 92:534-537.

Williams, A. J. 1980. Variation in weight of eggs and its effect on the breeding biology of the great skua. Emu 80:198-202.

Williams, G. C. 1966a. Natural selection, the costs of reproduction and a refinement of Lack's principles. American Naturalist 100:687-690.

Williams, G. C. 1966b. Adaptation and natural selection: a critique of some evolutionary thought. Princeton University Press, Princeton.

Wilkinson, L. 1990a. Systat: The system for statistics. Evanston, IL, SYSTAT, Inc.

Wilkinson, L. 1990b. Sygraph: The system for graphics.

Evanston, IL, SYSTAT, Inc.

Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the crow (Corvus corone). Journal of Animal Ecology 43:479-498.

Zach, R. 1982. Hatching asynchrony, egg size, growth and fledging in tree swallows. Auk 99:695-700.