THE UNIVERSITY OF CALGARY

HATCHING ASYNCHRONY AND BROOD REDUCTION IN THE

SWAINSON'S HAWK

BY

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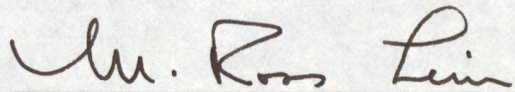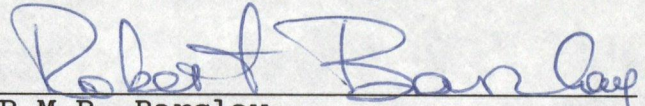
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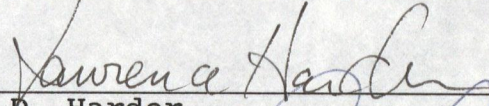
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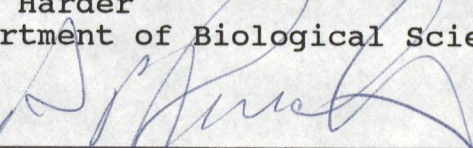
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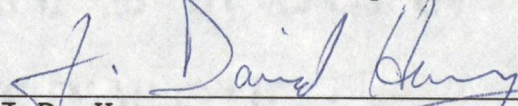Department of Biological Sciences

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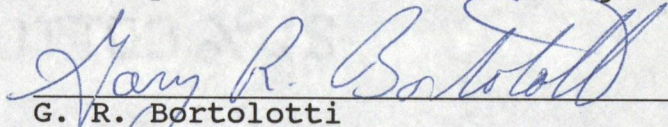Department of Biological Sciences

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ABSTRACT

Lack (1947, 1954, 1968) proposed that hatching asynchrony
is adaptive because it creates a size hierarchy within the
brood which facilitates adjustments in brood size during
food shortage. Although this hypothesis has been tested in
a variety of species, the results have been equivocal and
the hypothesis has yet to be tested in any species of
raptor. The purpose of this study was to determine the
extent of hatching asynchrony and its effects on brood
reduction in the Swainson's Hawk (Buteo swainsoni) and to
use manipulation experiments to test the brood reduction
hypothesis in this species.

All measures of reproductive success varied significantly
among 1987, 1988 and 1989. Nestling mortality and brood
reduction were most common in 1988, a year of drought and
relatively low food availability. In all years the
youngest, smallest chick was the usual first victim of brood
reduction. Starvation rather than direct sibling aggression
appeared to be the major cause of nestling mortality.

Experimental manipulation of the degree of hatching
asynchrony revealed that brood reduction tended to be more
efficient (i.e. occur earlier) in asynchronous broods. The
oldest chick in asynchronous broods fledged at a heavier
weight than did its siblings or than did the heaviest young
in experimentally manipulated synchronous broods.

In 1988, a year of drought, asynchronous and synchronous

broods did not differ significantly in the number of young
fledged. However, older chicks in asynchronous broods were
significantly heavier than the heaviest chicks in
synchronous broods at the time of fledging. If fledging
weight is correlated with post-fledging survival then
asynchronous broods may have been more productive under poor
conditions, as predicted by the Brood Reduction Hypothesis.

Results provide support for Lack's Brood Reduction
Hypothesis but are also consistent with the Sibling Rivalry
Hypothesis suggesting that hatching asynchrony in Swainson's
Hawks may be maintained by a combination of factors. This
study provides little evidence in support of other
hypotheses of hatching asynchrony. Year-to-year variation
in the effects of hatching asynchrony serve to demonstrate
the need to examine the question of the adaptive
significance of hatching asynchrony in a life history
context.

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CHAPTER 1

GENERAL INTRODUCTION

1.   Hatching Asynchrony

Most birds lay their eggs at intervals of one day.
This represents a physiological constraint acting on all
birds because it takes approximately 24 hours for an ovum to
pass down the oviduct and for the albumen, shell membranes,
and eggshell to be secreted around the fertilized egg
(Gilchrist 1968). If incubation begins when the last egg is
laid, the entire set of eggs (clutch) will hatch within a
few hours of each other (synchronous hatching). This
pattern of incubation and hatching is typical of precocial
species (Pettingill 1970), whose young hatch feathered,
open-eyed, and capable of locomotion, thus allowing them to
move away from the nest within a few hours of hatching.
However, the majority of birds begin incubation prior to the
laying of the last egg (Lessells and Avery 1989). As a
result, the embryos within a clutch begin development at
different times and the clutch hatches over a period of
several days (hatching asynchrony) creating an age, and
hence size, hierarchy within the brood. Hatching asynchrony
is typical of altricial species (Lessells and Avery 1989)

whose young hatch naked, blind, and incapable of locomotion (Pettingill 1970).

The major hypothesis concerning the adaptive significance of hatching asynchrony, as originally postulated by Lack (1947, 1954, 1968), is the Brood Reduction Hypothesis. It proposes that females of many species produce larger clutches and, subsequently, larger broods than average feeding conditions permit them to rear to fledging, and that initial brood sizes are subsequently adjusted (through the death of one or more nestlings) to meet prevailing food conditions. Thus in years of high food availability the entire brood may be raised, while in years of average or lower food availability, a portion of the brood is eliminated.

Lack argued that brood reduction is facilitated by hatching asynchrony because it generates a size hierarchy among nestlings within the brood. In times of food shortage, such a hierarchy allows for quick and efficient elimination of smaller, less-competitive (and typically younger) brood members at a minimum cost to parents and surviving siblings. This cost is comprised of energy wasted in feeding a chick, or in competing with a chick, that will die prior to fledging. If the clutch hatched synchronously, producing young all of the same size, and presumably of the same competitive ability, all would suffer equally and the parents might lose the entire brood through starvation.

More recently, the Brood Reduction Hypothesis has been modified from Lack's original formulation (Mock and Parker 1986; Lloyd 1987; Magrath 1989, 1990; Amundsen and Slagsvold 1991). This modified hypothesis argues that hatching asynchrony facilitates early brood reduction which in turn allows for a more efficient distribution of parental resources within the brood. This redistribution of parental resources might enhance the growth and survival of the remaining nestlings (Lloyd 1987; Amundsen and Slagsvold 1991), and/or parental survival and future reproduction (Gibbons 1987).

Although Lack's hypothesis has been the predominant explanation of hatching asynchrony for almost four decades numerous other hypotheses have also been proposed. Alternative, although not mutually-exclusive, explanations for the adaptive significance of hatching asynchrony include:

(1) Nest Failure Hypothesis (Clark and Wilson 1981, 1985). Asynchronous hatching reduces the interval between the laying of the first egg and the fledging of the first chick and therefore reduces the period during which the entire clutch or brood is susceptible to nest predation. Asynchronous hatching will be particularly favoured if eggs are more susceptible to predation than are nestlings.

(2) Hurry-up Hypothesis (Hussell 1972; Clark and Wilson 1981). Hatching asynchrony shortens the interval between

the laying of the first egg and the hatching of the first young. If food resources are at their peak, or if they are beginning to decline, parents benefit by hatching at least some of their young earlier because food will be more abundant at that time.

(3) Sexual Conflict Hypothesis (Slagsvold and Lifjeld 1989a, b). Asynchronous hatching extends the nestling period and represents an attempt on the part of the female to "manipulate" the male into providing care over a longer period, thus restricting his opportunity to attract an additional mate.

(4) Insurance Egg Hypothesis (Dorward 1962; Stinson 1979; Cash and Evans 1986; Anderson 1990). Asynchronous hatching leads to a quick and efficient elimination of the youngest sibling should the older chicks prove viable. The last-laid egg acts as insurance against infertility of an earlier-laid egg or early loss of an older chick. An insurance function for the last egg is thought to be most important in species with clutches of two (Anderson 1990), but insurance eggs may also play a role in the evolution of clutch size in general (Mock and Parker 1986).

(5) Brood Parasitism Hypothesis (Power et al. 1989). Hatching asynchrony and the resulting size hierarchy within the brood facilitates an adjustment in brood size in the event of intra- or inter-specific brood parasitism. Brood reduction may result in the loss of the hosts' own young but

hatching asynchrony may still be favoured if survival
declines rapidly with increasing brood size (Magrath 1990).

(6) Brood Sex Ratio Hypothesis (Slagsvold 1990). In
sexually-dimorphic species male and female nestlings may
differ significantly in size and food requirements. Thus
the total food requirements of the brood may be
unpredictable at the time of clutch formation. Hatching
asynchrony facilitates brood reduction in the face of
unpredictable food requirements of the brood.

(7) Sex-Ratio Manipulation Hypothesis (Howe 1976, 1979;
Burley 1986; Magrath 1990). Hatching asynchrony, along with
a bias towards males among last-hatched chicks, allows for
brood reduction and the manipulation of secondary sex ratios
within the brood.

(8) Peak-Load Reduction Hypothesis (Hussell 1972, 1985;
Bryant 1978). Hatching of the clutch over a period of
several days ensures that each chick reaches its peak energy
demand at a different point in the nestling period. Thus
the peak energy demand of the entire brood is lower than it
would have been had the clutch hatched synchronously and all
young reached their peak energy demand simultaneously.

(9) Dietary Diversity and Food Supply Hypothesis
(Magrath 1990). Hatching asynchrony serves to reduce the
number of nestlings that require a scarce or small food type
at any one time. In addition, the size of food items
delivered to the brood could affect the distribution of food

among the nestlings, particularly if older, larger young are capable of monopolizing access to delivered food. In this case hatching asynchrony ensures that certain brood members enjoy preferred access to food items delivered to the nest (Mock 1984b, 1985).

(10) Sibling Rivalry Hypothesis (Hahn 1981). The hierarchy of size and competitive ability generated by asynchronous hatching results in a clear dominance hierarchy that serves to reduce the number and intensity of aggressive encounters among siblings at an energetic saving to both offspring and parents.

(11) Nestling Identification Hypothesis (Gottlander 1987). Hatching asynchrony may facilitate parental identification of individual nestlings by creating size differences among siblings. Parents capable of identifying individuals within the brood could then distribute food among the nestlings so as to maximize brood productivity, manipulate the sex ratio of the brood, or allow one sex to spend more time foraging (Magrath 1990).

(12) Larder Hypothesis (Murton and Westwood 1977). Asynchronous hatching and the presence of an "extra" egg provides the older brood members with a sibling "larder" which may be consumed during periods of food shortage. This hypothesis is obviously restricted to those species that practice cannibalism.

In addition to the adaptive hypotheses outlined above

several nonadaptive explanations of hatching asynchrony have been put forward.

(1) <u>Constraints</u> <u>on</u> <u>Incubation</u> <u>Hypothesis</u> (Slagsvold 1986). This hypothesis argues that the need of females to forage during the egg-laying period acts as a constraint on the onset of full incubation and thus on the observed degree of hatching asynchrony. In times of food shortage the female must spend more time foraging and will delay the onset of full incubation for as long as possible (i.e. until near the end of the egg-laying period). Under these conditions the clutch will hatch more synchronously. When ambient temperature (and presumably food supply) is higher a female should enjoy higher foraging success and thus be capable of commencing full incubation earlier in the egg-laying period. Under these conditions the clutch will hatch asynchronously.

(2) <u>Constraints</u> <u>on</u> <u>Egg</u> <u>Laying</u> <u>Hypothesis</u> (Bryant 1978; O'Connor 1979). This hypothesis suggests that poor feeding conditions may increase the interval between the laying of successive eggs in the clutch and thus increase the observed hatching asynchrony if full incubation begins prior to the laying of the last egg. Under these conditions the degree of hatching asynchrony is constrained by feeding conditions present at the time of laying.

(3) <u>Phylogenetic</u> <u>Constraints</u> <u>Hypothesis</u> (Mead and Morton 1985). This hypothesis argues that hatching asynchrony is

merely an epiphenomenon generated by physiological
constraints related to hormonal changes involved in the
switch from egg-laying to incubation behaviour. Because
prolactin is responsible for both the termination of egg-
laying and the onset of incubation, females are expected to
begin full incubation at the laying of the penultimate egg
in the clutch (Mead and Morton 1985).

Although Lack's Brood Reduction Hypothesis is the most
widely-accepted explanation for the evolution and
maintenance of hatching asynchrony (Bryant and Tatner 1990;
Magrath 1990), it is important to emphasize that the above
hypotheses are not mutually exclusive. Thus, it is
difficult to establish with certainty the contribution of
each factor to the maintenance of hatching asynchrony as a
general phenomenon. A further complication arises because
hatching asynchrony may be maintained by different selective
factors in different species.

2. Hatching Asynchrony and Brood Reduction in Raptors

Ingram (1959, 1962) was the first to review hatching
asynchrony and brood reduction in birds of prey. Although
his work was restricted primarily to the Short-eared Owl
(Asio flammeus), he favoured the Brood Reduction and
Insurance Egg Hypotheses for all raptors (i.e. hawks,

falcons, eagles, owls, and vultures).

Subsequent research (Stinson 1979; Edwards and Collopy 1983; Simmons 1988) has revealed that the frequency and proximal causes of brood reduction vary from species to species. Species in which brood reduction occurs in more than 90% of broods are said to engage in obligate brood reduction (Mock 1984a; Simmons 1988). Conversely, species in which brood reduction occurs in fewer than 90% of broods are said to practice facultative brood reduction.

Obligate brood reduction is typical of many large, long-lived tropical raptors that have a clutch size of two but which rarely, if ever, produce two fledglings from a single brood (Mock 1984a; Bortolotti 1986; Simmons 1988). These species are also characterized by significantly longer inter-hatch intervals than similar species that do not practice obligate brood reduction (Edwards and Collopy 1983). These longer inter-hatch intervals lead to greater size discrepancies (and presumably, competitive and aggressive differences) between siblings, facilitating the formation of a dominance hierarchy and brood reduction (Edwards and Collopy 1983). The younger chick is the usual victim of brood reduction and perishes either from injuries resulting directly from sibling aggression, or as a consequence of being "intimidated" by its older sibling into remaining on the periphery of the nest where it dies of exposure or starvation. Mortality of this type is termed

siblicide or cainism (O'Connor 1978; Mock 1984a). In species with obligate brood reduction, siblicide usually takes place early in the nestling period and in the absence of any food shortage (Simmons 1988).

In contrast, facultative brood reduction is typical of smaller, non-tropical raptors with clutches larger than two and with smaller inter-hatch intervals (Edwards and Collopy 1983; Simmons 1988). Included in this group is the Swainson's Hawk (Buteo swainsoni). As with obligate brood reduction, the youngest and/or smallest chick tends to be the first victim of brood reduction. Mortality may result from siblicide, from starvation (as a result of the inability of the competitively-weaker chick to obtain a sufficient share of food brought to the nest), or from the combination of these factors.

Although sibling aggression has been described in detail for several species of raptors with obligate brood reduction (Meyburg 1974, 1978a, b; Gargett 1977, 1978), the adaptive significance of brood reduction in these species remains unclear. Brown et al. (1977) compared the number of fledglings produced by species of African eagles with clutch sizes of one and two and found that species that laid two eggs produced no more young than did species with a clutch of one. These authors thus claimed that sibling aggression leading to brood reduction among nestling African eagles was essentially maladaptive. However, as pointed out by Stinson

(1979), because of interspecific differences in body size, life-span, and general ecology, the comparisons on which this claim was based were inappropriate. Stinson (1979) and Mock (1984a), on the other hand, favoured the Insurance Egg Hypothesis as an explanation for asynchronous hatching in these species but admitted that this hypothesis has yet to be tested adequately.

Simmons (1988) examined hatching asynchrony and sibling aggression in raptors with obligate brood reduction and a clutch of two. He proposed that sibling aggression and brood reduction would be favoured by natural selection if the presence of a second chick honed the competitive abilities of the older sibling and increased the probability that it would survive the post-fledging period and eventually achieve breeding status. This hypothesis assumes that the population is always at or very near carrying capacity and that new breeding opportunities are extremely rare. Simmons' hypothesis may act in concert with an insurance egg function in maintaining observed clutch size and hatching asynchrony but, like the Insurance Egg Hypothesis, it has yet to be tested in raptors (Anderson 1990). Simmons' hypothesis is restricted to species with obligate brood reduction and is not intended as a general explanation of hatching asynchrony. For this reason it will not be considered further.

As is the case among species showing obligate brood

reduction, the evolutionary significance of hatching asynchrony and brood reduction among raptor species with facultative brood reduction remains unclear (Mock 1984a). The majority of studies dealing with facultative brood reduction in raptors have been primarily descriptive, severely limited by small sample sizes and have lacked the manipulative experiments required to test the hypotheses adequately (Stinson 1980). The purpose of this study is to investigate the adaptive significance of hatching asynchrony and facultative brood reduction in the Swainson's Hawk.

3. Biology of the Swainson's Hawk

The Swainson's Hawk breeds in prairie or plains habitat from Alaska to California and as far east as Missouri (Bent 1937). In Canada it breeds locally in British Columbia and quite commonly in southern Alberta, southern Saskatchewan and southwestern Manitoba (Godfrey 1966). Although the Swainson's Hawk has been placed on the "Blue List" of threatened or endangered species (Tate 1986), it continues to breed in large numbers in southern Alberta. Indeed, breeding densities of Swainson's Hawks in this area rank among the highest on record (Rothfels and Lein 1983).

In the spring, Swainson's Hawks migrate from their wintering range in Argentina and arrive in southern Alberta between mid-April and early May (Torrance 1984). They nest

in open farmland or grassland and build their own stick nests or make use of old nests, including those of the American Crow (Corvus brachyrhynchos), which they enlarge (Torrance 1984). Studies of banded adults (Fitzner 1978) indicate a strong tendency for breeding pairs to return to the same territory year after year.

In southern Alberta egg laying commences in mid- to late May and is followed by approximately five weeks of incubation. The clutch, consisting of 1-5 eggs laid at intervals of 1-2 days, hatches asynchronously with an inter-hatch interval of approximately 2 days (Olendorff 1971; Bechard 1983). Fledging occurs when the young are approximately five to seven weeks old, in late July to mid-August (Torrance 1984).

Almost all incubation is performed by the female, who leaves the nest only for brief periods to consume prey provided by the male (Fitzner 1978). Following hatching the male continues to supply the female with food for herself and the nestlings until the young are about three weeks old. At this point the female begins to assist with foraging duties. During the early nestling period the female may spend as much as 80% of the daylight hours brooding the young. In addition to provisioning the female and chicks, the male is also primarily responsible for nest defense, which commonly involves encounters with corvids, conspecifics and other raptors (Fitzner 1978).

In southern Alberta, Swainson's Hawks feed primarily on small mammals (which comprise over 90% of prey biomass delivered to nests), particularly the Richardson's ground squirrel (Spermophilus richardsoni), which comprises over 85% of prey biomass found in active nests on the study area (Torrance 1984). Swainson's Hawks also feed on young snowshoe hares (Lepus americanus), white-tailed jackrabbits (Lepus townsendii), and birds, including waterfowl, shorebirds, Gray Partridge (Perdix perdix) and passerines (Schmutz et al. 1980; Torrance 1984).

In a study of Swainson's Hawks in southeastern Washington, Bechard (1983) found that when brood reduction occurred, it usually took place 3-4 weeks after hatching and that the smallest chick was the usual first victim of brood reduction. Siblicide and cannibalism have also been documented in Swainson's Hawks (Pilz 1976; Pilz and Seibert 1978; Bechard 1983). However, it is not clear to what extent sibling aggression is responsible for nestling mortality nor what conditions are likely to trigger such aggression.

4. General Objectives

As mentioned above, the evolutionary significance of hatching asynchrony and facultative brood reduction in

raptors remains unclear (Stinson 1979; Mock 1984a). Indeed, recent attempts to test hypotheses about the adaptive significance of hatching asynchrony in a variety of species have produced equivocal and often contradictory results (see Chapter 4). Swainson's Hawks were selected as the subject for this investigation because they were known to exhibit hatching asynchrony and facultative brood reduction (Fitzner 1978; Bechard 1983). In addition, breeding densities of this species in southern Alberta (Rothfels and Lein 1983) are adequate to provide the sample sizes necessary to carry out manipulative experiments. Finally, Swainson's Hawks nest in accessible locations and are relatively tolerant of human intrusion. Swainson's Hawks in southern Alberta thus constitute an ideal subject (from both ecological and logistic points of view) for an investigation of hatching asynchrony in a raptor species with facultative brood reduction.

The general objectives of this study were:

(1) To assess the frequency of brood reduction in a breeding population of Swainson's Hawks.

(2) To investigate the effects of annual variation in climate and food availability on the breeding success of Swainson's Hawks.

(3) To determine the timing, proximal cause and usual victim of brood reduction in this species.

(4) To test, using manipulation experiments, Lack's

Brood Reduction Hypothesis of hatching asynchrony.

CHAPTER 2

STUDY AREA AND GENERAL METHODS

1. Study Area

This investigation was carried out in two adjacent study areas in southern Alberta. The first area (50°35' N, 114°5'W), approximately corresponding to the Mixed Area of Rothfels (1981), is located 20 km south of Calgary, Alberta and has an area of 320 km^2. The region lies immediately northwest of the town of High River, is characterized by rolling and flat agricultural land, and is located in Aspen Parkland and Fescue Grass ecoregions (Strong and Leggat 1984). The second, and larger (860 km^2) area (50°40' N, 113°30' W) is 25 km southeast of Calgary and includes the Swainson's Area of Rothfels (1981). This area is immediately east and northeast of the town of High River and is located in the Fescue Grass ecoregion (Strong and Leggat 1984). Rothfels (1981) gives a more detailed description of the entire area.

Both areas are devoted primarily to agricultural activity with grain production, particularly wheat and barley crops, accounting for approximately 60% of land use (Rothfels 1981). Pasture and hay production account for

approximately 35% of land use while less than 5% of the land
in either area is wooded (Rothfels 1981). More land in the
Swainson's Area is involved with grain production than is
the case in the Mixed Area (Rothfels 1981), but Swainson's
Hawks tend to nest in very similar habitat in each area.
Torrance (1984) was unable to demonstrate a significant
difference in the reproductive success of Swainson's Hawks
as a function of the area in which they bred and therefore
this study will make no distinction between the two areas.

Suitable nest sites within the study area are usually
located in windbreaks, farmyards, ditches alongside section
roads, and in small clumps of trees surrounding sloughs or
dugouts (Torrance 1984). Species used include willows
(_Salix_ spp.), trembling aspen (_Populus tremuloides_), balsam
poplar (_P_. _balsamifera_), cottonwoods (_Populus_ spp.), white
spruce (_Picea glauca_), Manitoba maple (_Acer negundo_) and
common caragana (_Caragana arborescens_) (Torrance 1984).
Most nests are located 2 - 10 m above the ground and may be
re-used for several years in succession.

Other raptors that breed regularly in the area include
Red-tailed Hawks (_Buteo jamaicensis_), Northern Harriers
(_Circus cyaneus_), Short-eared Owls and Great Horned Owls
(_Bubo virginianus_) (Torrance 1984). Ferruginous Hawks
(_Buteo regalis_) (pers. observ.), Prairie Falcons (_Falco
mexicanus_) and Long-eared Owls (_Asio otus_) (M. R. Lein,
pers. comm.) are also known to breed in the study area.

2. Meteorological and Soil Moisture Data

Because annual variation in environmental factors may
affect reproductive performance it is important to determine
if environmental conditions experienced by breeding
Swainson's Hawks differed greatly over the three years of
the study. Meteorological records from High River (a
meteorological station located on the edge of the study
area) indicate that within each breeding season, mean daily
temperatures (calculated on a monthly basis) in all three
years were similar to, or slightly higher than, long-term
norms (Table 1). Precipitation was lower than normal in
April, May and June of each year of the study but was
similar to long-term norms in July and August. An exception
to this pattern occurred in July of 1987 when precipitation
was 2-3 times the long-term norm (Table 1). Total
precipitation over the breeding period was similar among the
three years of the study and was lower than the long-term
average (Table 1).

The soil moisture conditions on cultivated lands in
Alberta are determined by Alberta Agriculture each spring
(May) and fall (October). Soil moisture conditions on the
study site ranged from Medium to High in the fall of 1987
and from Medium to Low in the fall of 1989. However,
moisture conditions in the fall of 1988 were designated Very
Low, indicating little or no subsoil moisture below a depth

Table 1. Temperature and precipitation data for High River,
Alberta during the Swainson's Hawk breeding
season in 1987, 1988, and 1989, along with long-
term norms based on data from 1951 – 1980 (Source:
Environment Canada).

Month	Mean Daily Temperature (^{o}C)				Total Precipitation (mm)			
	1987	1988	1989	Norm	1987	1988	1989	Norm
April	7.0	5.8	4.1	2.7	22	18	36	46
May	10.8	11.0	8.2	8.5	11	24	47	58
June	15.4	15.2	13.7	12.4	50	70	54	93
July	14.5	15.8	16.7	15.3	123	54	52	54
August	12.1	14.5	14.9	14.3	72	82	52	63
Total	----	----	----	----	278	248	241	314

of 15 cm (Table 2). Measures of soil moisture were not available for the spring of 1987 but were similar (Medium) in the springs of 1988 and 1989 (Table 2).

3. Data Collection

The entire study area is criss-crossed by a series of paved or gravel roads and road allowances. These section roads run in a north to south direction at 1 mile (1.6 km) intervals and in a east to west direction at 2 mile (3.2 km) intervals. Beginning in late April of 1987, 1988 and 1989, roads and trails were traveled by vehicle in an effort to locate nests known to have been used by Swainson's Hawks in the past (Rothfels 1981; Torrance 1984) as well as any new nests not already recorded. Because most nests were located by driving through the study area rather than by searching on foot, some nests were almost certainly missed and measures of breeding density were not obtained. Suspected nests in areas that were difficult to reach were not investigated and accessible wooded areas were searched by foot only when there was reason to believe that they contained an active Swainson's Hawk nest. The opportunity to monitor active nests was also subject to obtaining permission from landowners to travel on their property.

A nest was designated as "active" if a Swainson's Hawk was observed on the nest cup in the incubation posture. To

Table 2. Soil moisture conditions on the study area in each
year of the study (Source: Alberta Agriculture).
Soil moisture is categorized as being High
(subsoil moist beyond 75 cm), Medium (subsoil
moist to about 45-75 cm), Low (subsoil moist to
about 45 cm), or Very Low (little or no available
water below 15 cm).

Year	Season	
	Spring	Fall
1987	----	Medium/High
1988	Medium	Very Low
1989	Medium	Medium/Low

minimize the risk of desertion by adults (Fyfe and Olendorff 1976), nests were not approached closely during the incubation period. Rather, nest status was checked every 3-4 days from a safe distance using binoculars or a spotting scope. The only exceptions to this practice involved nests located in ditches next to roads. These were checked by merely driving past at normal speed (30-40 km/hour) and checking for the presence of an incubating female. Nests were no longer considered active if an incubating bird was absent on two consecutive nest visits or when the complete failure of a clutch or brood was observed directly. Incubating Swainson's Hawks seldom leave the nest (Fitzner 1978) and the absence of an incubating female on two consecutive visits is a strong indicator of breeding failure.

Physical characteristics of nest sites, including the species of nest tree, approximate tree height, and approximate nest height, as well as distances from road, habitation, and water were recorded. The location of each nest was plotted on air-photo mosaic maps and 1:50,000 scale topographical maps.

Nests were first visited late in the incubation period (late June) in each year. Nest contents were determined by climbing the nest tree or with the aid of a mirror attached to a long aluminum pole. In cases where landowners denied access to their property or where the nest tree was judged

to be unsafe to climb, contents could not be determined. However, these nests were monitored from a distance and their eventual success or failure was recorded.

Beginning with the onset of hatching, most accessible active nests were visited every two days to permit accurate aging of nestlings. Eggs showed obvious pipping on the day prior to hatching and newly-hatched young remained damp and unable to lift their heads for several hours after emerging from the egg. These characteristics, along with size comparisons to known-age chicks (Torrance 1984), allowed aging of chicks to within one day. Nestlings were individually marked with a temporary, non-toxic, commercial hair dye at the time of hatching. These markings were renewed as necessary until the young were banded with U. S. Fish and Wildlife Service aluminum leg bands at approximately three weeks of age.

Following the completion of hatching and the brood manipulations (described in Chapter 4), nests were monitored until the fledging of the last chick or the failure of the entire brood. In 1988 all accessible broods were visited every 2-4 days. In 1987 and 1989 it was not logistically possible to visit all nests on a regular basis, therefore only those nests which originally contained broods of 3 were visited every 2-4 days. Nests with broods of other sizes were visited less regularly. During each visit young were removed from the nest and various measurements were taken.

These measurements included: mass (to the nearest 1 g for chicks < 200 g and to the nearest 5 g for chicks $\geq$ 200 g), wing chord, tail length, length of primaries 4 and 7, tarsus length and culmen length (all length measurements were taken to the nearest 1 mm). The presence and identity of freshly-captured ($\leq$ 24 hours old) prey or cannibalized young were noted on each visit, as was the behaviour of the parents.

Incubating and brooding females usually did not leave the nest until someone approached to within 2 m of the nest tree or until climbing of the nest tree was begun. Adults remained in the vicinity and generally returned to the nest within 2-3 minutes of the departure of observers from the nest area. Data were collected as quickly as possible and most nest visits were less than 30 minutes in duration.

CHAPTER 3

REPRODUCTIVE PERFORMANCE

1. Introduction

A knowledge of the factors affecting the reproductive performance of Swainson's Hawks will contribute to an understanding of the effect of hatching asynchrony on the biology of this species. The purpose of this chapter is to provide information relating to the overall reproductive performance of the study population.

Measures of reproductive performance used commonly in studies of raptor biology include: (1) nest success, expressed as the proportion of occupied territories producing at least one fledgling; (2) mean brood size, expressed as the number of young per active nest late in the nestling period, and (3) fledging success, expressed as the number of young fledged per successful nest (Postupalsky 1974). In many cases these measures are calculated on the basis of two visits to the nest, one early in the breeding season and one late in the nestling period (Postupalsky 1974). The logistical difficulties associated with censusing widely-dispersed breeding populations on a regular basis, together with the threat of desertion inherent in

visiting nests during the incubation period (Fyfe and
Olendorff 1976), preclude more detailed measures of
reproductive performance in many studies.

Nevertheless, the protocol described above provides only
a crude estimate of a population's reproductive performance
and is unsatisfactory for a number of reasons. First, any
nests that fail prior to, or that are initiated following,
the first census are not included in measures of nest
success. Second, clutch size and hatching success are not
measured. Third, measures of brood sizes obtained late in
the nestling period ignore all nestling mortality (including
brood reduction) that may have occurred earlier in the
nestling period. Fourth, fledging success, as defined
above, fails to take into account broods in which all chicks
died. Finally, all these measures of reproductive success
will vary greatly as a function of the number and timing of
nest visits.

To avoid confusion and to ensure that between-study
comparisons are appropriate, it is important to define
clearly all measures of reproductive performance and to
indicate the type of data (i.e. the number of nest visits)
on which they are based. The following measures of
reproductive performance were used in the current study:

(1) Clutch Size: This was measured as the number of
eggs present per active nest (defined in Chapter 2 as a nest
where a Swainson's Hawk was observed in the incubation

posture) late in the incubation period (i.e. within 7 days of hatching). Clutches deserted or destroyed earlier in the incubation period are not included in this measure.

(2) Hatching Success: Clutches were assigned to one of three categories of hatching success according to the proportion (all, some, or none) of the eggs within a clutch that hatched. As with measures of clutch size this measure does not take into account eggs that were deserted or destroyed earlier in the incubation period.

(3) Brood Size: This was measured as the number of nestlings per nest of known clutch size (as defined above). This differs from Postupalsky's (1974) measure of mean brood size in that it is calculated at the time of hatching rather than at some point later in the nestling stage.

(5) Brood Success: Broods were assigned to one of three categories of brood success according to the proportion (all, some, or none) of the chicks within a brood that survived the nestling period.

(4) Mean Fledging Success: This was measured as the average number of fledglings produced per brood. This measure does not focus exclusively on nests that produce at least one chick, nor does it assume there is no mortality during the latter part of the nestling period.

(6) Nest Success: This was measured as the proportion of active nests that produced at least one fledgling. The number of active nests may have been underestimated if

breeding attempts failed before they were censused or if some breeding attempts were missed all together. Since the entire study area was censused every four days during the early part of the breeding season, some active nests which failed within four days of initiation would be excluded from measures of nest success. The failure to include breeding attempts that failed soon after being initiated may have resulted in an overestimation of nest success.

2. Methods

Methods used in determining the measurements of reproductive success are given in Chapter 2. Broods that were manipulated with respect to size or hatching asynchrony (Chapter 4) are not included in measures of mean fledging success, brood success, nestling mortality, brood reduction or nest success.

Statistical analyses were performed using SAS (SAS Institute 1988a) or Statistix (Analytical Software 1989) statistical packages. Nonparametric tests were employed when the data (despite being transformed) did not conform to a normal distribution. The test statistic for all Mann-Whitney U-Tests is a "Z" score with a continunity correction of 0.5 (SAS Institute 1988a). This statistic approximates a "T" value when there are few ties but is superior when ties

are common (Conover 1980.) Variation is reported as mean $\pm$ standard error unless stated otherwise. A Type I error rate of $\alpha = 0.05$ was used throughout this study. Statistical power analyses were performed when analyses yielded marginal probability values (i.e. $0.05 < P < 0.1$). Statistical power analysis calculates the percent chance of correctly rtejecting the null hypothesis (i.e. not committing a Type II Statistical Error).

3. Results

A. Nest Location

Because of the methods used to locate active nests (Chapter 2), nests positioned close to roads may be over-represented in the population sample. If reproductive performance of breeding attempts closer to roads differs from that of those farther away, then measures of population reproductive performance may be biased.

Previous studies of Swainson's Hawks in the same area (Rothfels 1981; Torrance 1984) employed searches on foot, as well as from vehicles, in an effort to locate all active nests on the study area. However, the distribution of nests (relative to a road) in those studies did not differ significantly from that observed in the current study (G =

10.26, d.f. = 6, P = 0.116; Table 3). It appears, therefore, that breeding attempts located near roads were not significantly over-represented in this study.

B. Incubation Period

Totals of 103, 83, and 104 nesting attempts were observed in 1987, 1988, and 1989, respectively. Of these attempts, 32%, 38%, and 27% were abandoned prior to the hatching period in 1987, 1988, and 1989, respectively. The proportion of nest attempts that failed during the incubation period did not differ significantly among years (G = 2.86, d.f. = 2, P = 0.240).

Because nests were not approached until late in the incubation stage, it was difficult to determine causes of breeding failure. In a few cases nests were tipped, or blown out of trees, during high winds. In one case a male was killed (by a vehicle) a few days prior to his mate's desertion of the nest, suggesting that the female abandoned the attempt when the male ceased to provide her with food. Predation on eggs, especially by corvids (Fitzner 1978, Torrance 1984), was a possible cause of reproductive failure, but the fact that female Swainson's Hawks attend the eggs almost continually during incubation suggests that predation was not a significant source of egg mortality.

Breeding pairs that experienced reproductive failure

Table 3.   The distances of active Swainson's Hawk nests from
           roads in previous (Rothfels 1981; Torrance 1984)
           and current studies conducted on the same study
           area.

| Distance From | Number of Nests | |
Road (m)	Previous Studies	Current Study
< 10	52	72
11 - 50	27	41
51 - 100	26	30
101 - 200	32	35
201 - 500	46	38
501 - 1000	33	22
> 1000	12	7
Total	228	245

during the incubation period did not attempt replacement clutches. However, these pairs did continue to occupy and defend territories for the remainder of the breeding season.

C. Clutch Size

Clutch sizes were determined approximately one week prior to hatching in each year. Clutch sizes ranged from 1 to 5 (Table 4) while modal clutch size ranged from 2 (1989) to 3 (1987, 1988). The overall distribution of clutch sizes did not differ significantly on a yearly basis (X^2 = 12.34, d.f. = 6, P > 0.05, Power > 70%; clutch sizes of 4 and 5 pooled for this and subsequent analyses). There was however, a significant difference in the distribution of clutch sizes between 1987 and 1989 (X^2 = 10.96, d.f. = 3, P < 0.05) because of the fact that clutches of 2 were relatively more common, and clutches of 3 relatively less common, in 1989 than in 1987. Clutch sizes did not differ significantly between 1987 and 1988 (X^2 = 1.85, d.f. = 3, P > 0.10) or between 1988 and 1989 (X^2 = 4.32, d.f. = 3, P > 0.10).

D. Hatching Asynchrony

Inter-hatch intervals were estimated for clutches of 3

Table 4. Clutch sizes of Swainson's Hawks in each year of
          the study.

| Year | Clutch Size | | | | | | | Number of |
	1	2	3	4	5	Mean	Median	Clutches
1987	6	15	38	10	1	2.8	3	70
1988	3	15	28	5	0	2.7	3	51
1989	6	35	30	5	0	2.4	2	76
Total	15	65	96	20	1	2.6	3	197

in each year of the study (Table 5). The period over which all eggs in a clutch hatched did not differ significantly among years (one-way ANOVA, F = 1.45, d.f. = 2,61, P = 0.241). In addition, the interval between the hatching of the first (a-egg) and second (b-egg) eggs did not differ significantly with year (one-way ANOVA, F = 2.226, d.f. = 2,61, P = 0.116), nor did the interval between the hatching of the second and third (c-egg) eggs (one-way ANOVA, F = 0.321, d.f. = 2,61, P = 0.726).

E. Hatching Success and Brood Size

The proportion of nests in which all, some, or no eggs hatched differed significantly among years (Table 6, G = 16.13, d.f. = 4, P = 0.003). In 1989, 29% of the clutches failed to produce any young while all eggs hatched in the remaining 71% of the clutches. No clutches experienced partial hatching success in 1989. These proportions differed significantly from those observed in 1987 (Fisher's Exact Test, P = 0.001) and 1988 (Fisher's Exact Test, P = 0.038). The proportions did not differ significantly between 1987 and 1988 (G = 2.27, d.f. = 2, P = 0.321). Partial hatching of a clutch was relatively rare and occurred in 9% or less of the clutches in each year.

Unlike clutch size, brood size varied significantly among years (Table 7, G = 16.28, d.f. = 8, P = 0.038).

Table 5. Inter-hatch intervals (in days) of Swainson's Hawk
clutches of 3 in each year of the study.

Year	Number of Broods	Hatch Interval		
		Between a-egg and b-egg ($\bar{X} \pm$ SE)	Between b-egg and c-egg ($\bar{X} \pm$ SE)	Total ($\bar{X} \pm$ SE)
1987	22	2.0 ± 0.24	2.0 ± 0.19	4.0 ± 0.32
1988	22	2.0 ± 0.24	2.2 ± 0.24	4.2 ± 0.33
1989	23	1.5 ± 0.14	2.1 ± 0.15	3.6 ± 0.15

Table 6.   Frequency of complete and partial hatching failure
and complete hatching success in Swainson's Hawk
clutches in each year of the study.

Year	Complete Hatching Failure (%)	Partial Hatching Failure (%)	Complete Hatching Success (%)	Total
1987	7 (10)	6 (9)	56 (81)	69
1988	10 (20)	4 (8)	36 (72)	50
1989	20 (29)	0 (0)	50 (71)	70
Total	37 (20)	10 (5)	142 (75)	189

Table 7.   Brood size of Swainson's Hawks in each year of the study.

Year	Brood Size							Number of
	0	1	2	3	4	Mean	Median	Broods
1987	7	3	16	34	9	2.5	3	69
1988	10	4	10	22	4	2.1	3	50
1989	20	1	22	24	3	1.8	2	70
Total	37	8	48	80	16	2.2	3	189

Brood sizes in 1987 were larger than those recorded in 1989 (X^2 = 12.92, d.f. = 4, P < 0.05). However, the distribution of brood sizes in 1988 did not differ from that recorded in 1987 (X^2 = 3.61, d.f. = 4, P > 0.05) or in 1989 (X^2 = 6.72, d.f. = 4, P > 0.05).

F. Brood Success and Nestling Mortality

The proportions of nests in which all, some, or no chicks survived the nestling period (Table 8) differed significantly among years (G = 20.62, d.f. = 4, P < 0.001). Proportions in 1989 differed significantly from those observed in 1987 (X^2 = 6.39, d.f. = 2, P < 0.05) and in 1988 (X^2 = 20.20, d.f. = 2, P < 0.0001) largely as a result of a decrease in total brood reduction and an increase in complete brood success in 1989 (Table 8). The proportions did not differ significantly between 1987 and 1988 (X^2 = 5.56, d.f. = 2, P > 0.050). However, the power of this test (approximately 50%) is relatively low.

The proportions of broods in which at least one chick survived the nestling period (i.e. brood success) were 79%, 55%, and 95% in 1987, 1988 and 1989 respectively. All pairwise comparisons of years differed significantly (G > 4.75, d.f. = 1, P < 0.03 for all comparisons). The proportion of broods which experienced a partial size reduction was relatively constant among the years and ranged

Table 8.   Frequency of complete and partial brood reduction
           and complete brood success in Swainson's Hawk
           broods in each year of the study.

Year	Complete Brood Failure (%)	Partial Brood Failure (%)	Complete Brood Success (%)	Total
1987	9 (21)	18 (42)	16 (37)	43
1988	14 (45)	11 (36)	6 (19)	31
1989	2 (5)	14 (36)	23 (59)	39
Total	25 (22)	43 (38)	45 (40)	113

from 36% (1988 and 1989) to 42% (1987).

Overall nestling mortality was highest in 1988 when only 37% of the chicks survived to fledging. In 1987, 57% of the chicks fledged, while in 1989, 76% of the chicks survived the nestling period. These differences in survival were significant for all pairwise comparisons of years (G > 6.73, d.f. = 1, P < 0.004 for all comparisons).

As discussed above (Chapter 2), nests containing three chicks were visited more frequently than other nests in 1987 and 1989. If frequent visits to the nest influenced nestling survival one would expect higher survival among nestlings in broods of two than among nestlings in broods of three, provided that nestling survival is not dependent on brood size. In 1987, 50% of the chicks in broods of two, and 51% of the chicks in broods of three, survived the nestling period. This difference was not statistically significant (G = 0.009, d.f. = 1, P = 0.92). In 1989, 79.5% and 64.1% of young in broods of two and three, respectively, survived to fledge. As in 1987, this difference was not significant (G = 2.46, d.f. = 1, P = 0.116). This test does not constitute a proper control because it does not control for any differences in nestling survival as a function of brood size. However it does indicate that survival among chicks that were handled frequently was not significantly different from those which were handled only a few times.

G. Fledging and Nest Success

The mean number of young fledged per brood ranged from
0.96 in 1988 to 1.87 in 1989 (Table 9). Fledging success
varied with year (Kruskal-Wallis Test, X^2 = 21.04, d.f. = 2,
P = 0.002); in 1987 and 1989 significantly more young
fledged per brood than in 1988 (Mann-Whitney U-Test, Z < -
2.08, P < 0.038 for both comparisons). Fledging success did
not differ significantly between 1987 and 1989 (Table 9,
Mann-Whitney U-Test, Z = 1.61, P = 0.108).

Overall nest success varied significantly between years
(G = 11.06, d.f. = 2, P = 0.004). The proportion of
breeding attempts which successfully fledged at least one
young was significantly smaller in 1988 (27%) than in 1987
(45%; G = 4.74, d.f. = 1, P = 0.029) or 1989 (55%; G =
10.85, d.f. = 1, P = 0.001). Nest success did not differ
significantly between 1987 and 1989 (Table 10, G = 1.57,
d.f. = 1, P = 0.210).

The mean number of fledglings produced per breeding
attempt also varied with year (Table 10, Kruskal-Wallis Test
X^2 = 11.33, d.f. = 2, P = 0.004); in 1987 and 1989
significantly more young fledged per brood than in 1988
(Mann-Whitney U-Test, Z < -2.20, P < 0.029 for both
comparisons). The number of fledglings produced per
breeding attempt did not differ significantly between 1987
and 1989 (Table 10, Mann-Whitney U-Test, Z = 1.31, P =

Table 9. Fledging success of Swainson's Hawks in each
year of the study. Values with the same
superscript are not significantly different from
one another.

Year	Fledging Success $\overline{X} \pm SE$	Number of Broods
1987	1.53 ± 0.18^a	43
1988	0.96 ± 0.19^b	31
1989	1.87 ± 0.15^a	39
Overall	1.48 ± 0.11	113

Table 10. Number of fledglings produced per breeding
attempt by Swainson's Hawks in each
year of the study. Values with the same
superscript are not significantly different from
one another.

Year	Number of Fledglings per Breeding Attempt $\bar{X} \pm SE$	Number of Breeding Attempts	Number of Breeding Attempts Producing Young
1987	0.86 ± 0.13^a	76	34
1988	0.47 ± 0.11^b	63	17
1989	1.09 ± 0.14^a	67	37
Overall	0.82 ± 0.08	206	88

0.189).

4. Discussion

In any examination of year-to-year changes in reproductive performance within a breeding population, it is important to determine not only differences in overall measures of productivity, such as fledging success and nest success, but also to determine the cause of such differences. Clutch size, hatching success, and nestling mortality can vary independently of one another and thus an examination of these measures can provide insights into the ecology of a population that could not be gained from an examination of overall measures of productivity.

In 1987 relatively large clutch sizes (Table 4) and high hatching success (Table 6) resulted in a large mean brood size (Table 7). These conditions, together with moderate (relative to the other two years) levels of nestling mortality, produced high levels of mean fledging success and nest success. In 1988, clutch sizes were also relatively large and hatching success relatively high. However, very high nestling mortality resulted in the lowest levels of mean fledging success and nest success observed in the study. In 1989, clutch size was smaller than in previous years and hatching success was lower, mainly as a result of an increase in the complete failure of clutches. However,

as a result of very low levels of nestling mortality, mean fledging success was the highest recorded in the study. It appears, therefore, that the factors which ultimately determine nest success varied from year to year (Table 11).

Clutch size is obviously one of the most important factors in determining reproductive performance and yet the determinants of clutch size itself are difficult to identify (Murphy and Haukioja 1986). Several food-supplementation experiments in raptors (Newton and Marquis 1981; Dijkstra et al. 1982) have demonstrated that clutch size is positively correlated with food availability during the pre-laying and laying periods, and that food availability during these periods may also act as a predictor of food availability during the nestling period. Swainson's Hawks in southern Alberta feed primarily on Richardson's ground squirrels during both the egg-laying and nestling periods (Schmutz et al. 1980) and it is possible that the observed variation in clutch size may be related to differences in ground squirrel abundance early in the breeding season. Unfortunately, I lack the information on ground squirrel densities required to investigate this possibility.

Alternatively, clutch size may be constrained not by food availability on the breeding ground, but by energy reserves available to breeding adults when they first arrive in the spring (Winkler and Walters 1983). Under this hypothesis, smaller clutch sizes in 1989 may have been

Table 11.   A summary of relative clutch size, hatching
success, nestling success and nest success of
Swainson's Hawks in each year of the study.

Variable	Year		
	1987	1988	1989
Clutch Size	High	High	Low
Hatching Success	High	High	Low
Fledging Success	Moderate	Low	High
Nest Success	High	Low	High

caused by poor conditions on the wintering ground
(Argentina) or an energetically-expensive migration to the
breeding grounds, either of which would reduce the amount of
energy reserves available to breeding females at the time of
egg formation and laying.

Clutch size may also be influenced by energetic
expenditures experienced in the previous breeding season.
Roskaft (1985) experimentally enlarged brood size in Rooks
(Corvus frugilegus), thereby forcing experimental birds to
invest more energy in breeding than they would have
otherwise. He found that experimental birds had a lower
reproductive success in the following season when compared
to control birds. Gustafsson and Sutherland (1988)
manipulated investment levels in the Collared Flycatcher
(Ficedula albicollis) and also found that reproductive costs
incurred in one season can affect future fecundity and
reproductive success. If the costs associated with breeding
in 1988 were quite high (see below and Chapter 4 for
detailed description of nestling period) and if parents were
unable to recover completely, these costs may have been
expressed in the form of smaller clutch sizes in 1989. An
adequate test of this hypothesis was beyond the scope of
this study.

Hatching success was lower in 1989 than in the two
previous years, primarily as a result of complete clutch
failure (Table 6). Breeding failure of this type may be

caused by the desertion of viable clutches by one or both members of the breeding pair or by the presence of infertile clutches which are abandoned when they fail to hatch.

Schmutz et al. (1980) found that nesting in close proximity to conspecifics may lead to desertion of the clutch and reproductive failure in Swainson's Hawks. However, this effect was noted only when Swainson's Hawks attempted to breed within 100 m of the nest of a conspecific. I never observed Swainson's Hawks to nest within 100 m of a conspecific's nest, suggesting that interference from conspecifics was not a major cause of breeding failure in any year of this study.

Weather, particularly cold temperatures or wet conditions, may lead to an increase in breeding failure among raptors (Newton 1979). However, as pointed out in Chapter 2, temperatures and precipitation levels observed during the incubation period (May) were similar over the three years of the study and were also comparable to long-term averages for this area.

Pesticide contamination may also lead to egg mortality (Newton 1979). Data relating to pesticide levels in the eggs of Swainson's Hawks belonging to this population are not available but the possibility of pesticide contamination does exist. This is particularly true in a species such as the Swainson's Hawk which winters in areas where the use of pesticides is not well-regulated.

Nestling mortality differed among years; the highest values were observed in 1988, the lowest values in 1989 while intermediate values were observed in 1987.

In 1988 much of western Canada, including the study area, experienced drought conditions. Soil moisture conditions on the study area were classified as very low in the fall of 1988 (Chapter 2) and yields of wheat averaged only 19 bushels/acre compared with yields of 31 and 29 bushels/acre in the same area in 1987 and 1989, respectively (P. Woloshyn, Alberta Agriculture, pers. comm.)

While it was not possible to determine directly the effect of this drought on the abundance and availability of prey of Swainson's Hawks (particularly Richardson's ground squirrels), drought conditions may have reduced food availability and led to an increase in nestling mortality. Evidence for year to year changes in food availability will be discussed in more detail in Chapter 4.

It is difficult to compare measures of reproductive performance obtained in this study with those reported in other studies of Swainson's Hawks for several reasons. First, data from different studies may not be comparable because of differences in methodology. In some studies (e.g. Gilmer and Stewart 1984; Bednarz 1988; Schmutz and Hungle 1989) nests were visited only two or three times during the breeding season. As discussed above, infrequent visits to active nests may bias estimates of reproductive

performance. In particular, lack of visits early in the
breeding season may result in underestimation of the number
of breeding failures. Second, some studies (Schmutz et al.
1980; Bednarz 1988; Schmutz and Hungle 1989) measured
reproductive performance in terms of the number of young
fledged per successful breeding attempt. A similar analysis
of the data collected in this study shows little yearly
variation in the number of young fledged per successful nest
(1.9, 1.8, 2.0 fledglings per nest in 1987, 1988 and 1989,
respectively). These values fall within the range (1.8 -
2.2) reported in other studies but they obviously fail to
capture significant differences in reproductive performance
experienced by the population over the three years of the
study.

CHAPTER 4

MANIPULATION EXPERIMENTS

1. Introduction

Although the majority of altricial bird species hatch their eggs asynchronously (Clark and Wilson 1981), the adaptive significance of this characteristic remains unclear. This uncertainty can be attributed primarily to two factors. First, there have been few attempts to define clearly, and to test experimentally, the underlying assumptions and predictions of the hypotheses proposed to explain the adaptive significance of hatching asynchrony (Chapter 1). Properly-designed manipulative experiments will permit rigorous tests of predictions derived from the hypotheses. Second, the selective factors that act to maintain hatching asynchrony are very likely to differ from species to species (and possibly within species). Rates of nestling predation, the viability and aggressiveness of older chicks, the mating strategies of adults, the relative length of the breeding season, and relative food availability vary among species, among populations, and within single populations over time. These factors will strongly affect the costs and benefits of hatching

asynchrony. Any test of the hypotheses concerning the adaptive significance of hatching asynchrony must therefore consider the relevant ecological characteristics of the species and population being studied. The results of any such test would be fully applicable only to species and populations known to possess similar ecological characteristics.

A. Additional Hypotheses

The most obvious and well-documented consequence of hatching asynchrony is a reduction in the growth and survival of the last-hatched chick in the brood relative to its siblings. Reduced growth and/or survival of the youngest (or younger) brood member(s) has been documented not only in raptors (see Chapter 1) but also in members of the Pelecaniformes (Shaw 1985; Cash and Evans 1986; Drummond 1987; Anderson 1989), Ciconiiformes (Werschkul 1979; Fujioka 1985a, b; Mock et al. 1987a, b), Charadriiformes (Hahn 1981; Braun and Hunt 1983; Hebert and Barclay 1986), and Passeriformes (Howe 1976, 1978; Richter 1984; Haydock and Ligon 1986; Husby 1986; Gibbons 1987; Magrath 1989).

Loss of the youngest brood member has usually been considered to be evidence in support of Lack's Brood Reduction Hypothesis, but at least fifteen different

hypotheses have been put forth to explain hatching asynchrony (Chapter 1) and each can account for the loss of the youngest, smallest sibling (Lessells and Avery 1989). What follows are brief descriptions of each hypothesis (except for the Brood Reduction Hypothesis) and the evidence supporting it as well as an assessment of its applicability to Swainson's Hawks.

a. Adaptive Explanations

(1) The <u>Nest Failure Hypothesis</u> (Clark and Wilson 1981, 1985) argues that females begin incubation prior to laying the last egg because this reduces the period between the laying of the first egg and the fledging of the first chick. This reduces the time over which the entire clutch or the entire brood is susceptible to predation. Clark and Wilson (1981, 1985) and Slagsvold (1986) have reviewed published accounts of incubation patterns, hatching asynchrony and risk of predation, and have found a correlation between the risk of predation and the degree of hatching asynchrony among many passerine species. However, as pointed out by Magrath (1988), more information on the frequency and timing of predation is required to test this hypothesis properly.

Swainson's Hawk nestlings are sometimes preyed upon (Fitzner 1978). However, in my study, only 7 of the 152 broods observed over the three breeding seasons showed

evidence of mortality as a result of predation (i.e. sudden disappearance of the entire brood, evidence of predator on nest). This suggests that predation is unlikely to play a significant role in maintaining hatching asynchrony in this population.

(2) The Hurry-Up Hypothesis (Clark and Wilson 1981) suggests that parents begin incubation before the clutch is complete because it results in earlier hatching of the first chick(s) and allows the parents to better exploit declining food resources. This hypothesis may also apply to those species constrained by the length of the breeding season (Magrath 1990). In this case parents benefit by producing fledglings as far in advance of the end of the breeding season as possible.

The availability of Richardson's ground squirrels does decline over the Swainson's Hawk's breeding season (Schmutz et al. 1980; Michener and Koeppl 1985). However, it is not clear if advancing the onset of hatching by two to four days (less than 10% of the nestling period) provides a benefit to parents. I am unable to test this hypothesis with the information available.

(3) The Sexual Conflict Hypothesis (Slagsvold and Lifjeld 1989a, b) is based on the assumption that the male will begin to feed the young shortly after the first egg hatches in species in which the female performs all the incubation duties. The female, by beginning incubation

prior to the laying of the last egg, produces the first nestling sooner than if she had hatched the clutch synchronously. The female can thus "manipulate" the male into provisioning the nestlings earlier, and over a longer period, than he otherwise would. An additional advantage would accrue to the female if this "advanced start to nestling feeding" also reduced the male's opportunities to obtain additional mates, since any additional mates might reduce the quality or quantity of male care provided to the first brood.

Slagsvold and Lifjeld have found some support for this hypothesis in the Pied Flycatcher (Ficedula hypoleuca) and have also argued that their hypothesis applies to hawks and owls. There is, however, little evidence for this type of sexual conflict in raptors in general, and in Swainson's Hawks in particular. First, in Swainson's Hawks (Fitzner 1978) and other raptors (Newton 1979), females usually stop foraging during the egg-laying period. The male thus provides the female with all her food during the incubation period and provides all food to the female and nestlings through at least the first half of the nestling period. There is no advantage to the female in using hatching asynchrony to "manipulate" the male into advancing the start of nestling feeding because the male, at the time of hatching, has already been supplying all the food for 4-5 weeks.

Second, with rare exceptions (Cash 1989), Swainson's Hawks are thought to be strictly monogamous. Any additional female attracted by a male at the time the first clutch hatched (late June - early July) would lack sufficient time to rear a brood to the fledging stage before the end of the breeding season (mid to late August). Thus, in the Swainson's Hawk at least, there is no evidence for the type of sexual conflict which is a basic assumption of the Sexual Conflict Hypothesis.

(4) The Insurance Egg Hypothesis (Dorward 1962) argues that hatching asynchrony serves to establish a hierarchy in size and dominance within the brood that permits a quick and efficient elimination of the youngest chick should the older nestling(s) prove viable. The Insurance Egg Hypothesis maintains that the last egg is essentially an "extra" egg and that the chick resulting from such an egg will die within a few days unless an earlier-laid egg fails to hatch or an older sibling dies soon after hatching. Experimental evidence in support of the Insurance Egg Hypothesis has been obtained for American White Pelicans (Pelecanus erythrorhynchos) (Cash and Evans 1986) and Masked Boobies (Sula dactylatra) (Anderson 1989, 1990). An insurance function for the last-laid egg has also been suggested as an explanation for hatching asynchrony and brood reduction in raptors with obligate brood reduction (Stinson 1979; Mock 1984a).

The hypothesis predicts that, if the last-laid egg acts primarily as insurance, earlier-laid eggs commonly fail to hatch or, in the event that all eggs in a clutch hatch, brood reduction will take place shortly after the completion of hatching. If the last-laid egg acts primarily as insurance, then brood size at the time of fledging will rarely, if ever, match clutch size. In the current study 20% of the clutches experienced complete hatching failure, 5% had partial hatching success and 75% experienced complete hatching success (Chapter 3). The entire brood was raised to the fledging stage in from 19% (1988) to 59% (1989) of the nests (Chapter 3). Bechard's (1983) data indicate that brood reduction usually occurs 3-4 weeks after hatching. These observations are contrary to predictions of the hypothesis, suggesting that the last-laid egg in Swainson's Hawk clutches does not function chiefly as an insurance egg.

(5) The Brood Parasitism Hypothesis (Power et al. 1989) argues that hatching asynchrony and the resulting size hierarchy allows for adjustment of brood size in the event of intra- or interspecific brood parasitism. This hypothesis may apply to species which typically experience brood parasitism (Magrath 1990). However, in Swainson's Hawks (Fitzner 1978; Torrance 1984), as in most raptors (Newton 1979), almost constant nest attendance during the egg-laying and early incubation periods provide little opportunity for brood parasitism. Furthermore, in a recent

review of intraspecific nest parasitism, Rohwer and Freeman (1989) did not list Swainson's Hawks (or any other raptor) as a species subject to intra-specific brood parasitism.

(6) The Brood Sex Ratio Hypothesis (Slagsvold 1990) argues that, in sexually-dimorphic species, the sex ratio of the brood and hence its total food requirement may be unpredictable at the time of clutch formation. Hatching asynchrony permits adjustment of brood size thereby adjusting the brood's total food requirement to prevailing conditions. Sexual size dimorphism is pronounced in many species of raptors (Newton 1979) and sex ratio within a brood may well affect total food demand (Magrath 1990). However, Swainson's Hawks do not display significant size dimorphism as nestlings (Torrance 1984) and thus brood sex ratio in this species is unlikely to affect total food demand significantly.

(7) The Sex-Ratio Manipulation Hypothesis (Howe 1976, 1978; Bortolotti 1986; Burley 1986; Magrath 1990; Bednarz and Hayden 1991). A sex-dependent hatching sequence may serve to compensate partially for competitive imbalances resulting from nestling size dimorphism (Magrath 1990). In other words, by hatching the smallest sex first, parents can compensate for nestling size differences resulting from sexual-dimorphism. This would not only promote equal investment among nestlings but minimize the risk of "maladaptive brood reduction" (i.e. a disproportionate loss

of the smaller, presumably less competitive sex, Bednarz and Hayden 1991) and could facilitate the loss of the larger, more expensive sex in times of food shortage (Magrath 1990). Bednarz and Hayden (1991) provide evidence in support of this hypothesis for Harris' Hawks (Parabuteo unicinctus). However, as described above, Swainson's Hawks show little sexual size dimorphism as nestlings and the degree of nestling size dimorphism and competitive size asymmetries assumed by the hypothesis may not exist in this species.

(8) The Peak-Load Reduction Hypothesis (Hussell 1972, 1985) argues that hatching asynchrony ensures that all nestlings within a brood do not reach their peak energy demand at the same time, thus reducing the peak energy demand of the entire brood. Lessells and Avery (1989) tested the Peak-Load Reduction Hypothesis in European Bee-eaters (Merops apiaster) and found that hatching asynchrony reduced the peak load by less than 1%. This was primarily because individual chicks did not attain a sharp peak in energy demand. Similarly, nestling Swainson's Hawks do not appear to attain a sharp peak in energy demand. Olendorff (1971) raised wild-hatched Swainson's Hawks in captivity and found that food consumption rose until the young were approximately 20 days old. Thereafter food consumption remained high until the pre-fledging period when the young were about 35 days old. If the "peak" energy demand in Swainson's Hawks lasts approximately 15 days, an inter-hatch

interval of 2 days probably does not significantly reduce the maximum daily food consumption of an entire brood. Mock and Schwagmeyer (1990) have constructed an analytical model to test this hypothesis and have shown that the conditions necessary for peak load reductions as small 5% are rarely, if ever, found in nature.

(9) The Dietary Diversity and Food Supply Hypothesis (Snow 1960; O'Connor 1978) argues that hatching asynchrony serves to reduce the number of nestlings that require a scarce, small food type at any one time (Magrath 1990). Young Swainson's Hawk nestlings do not feed directly on whole prey items. Rather, the female, by directly feeding young for the first three weeks of the nestling period (Fitzner 1978), determines the size of food items delivered to the chicks. Foraging Swainson's Hawks would thus not be constrained by the need to forage for small food items. Furthermore, as pointed out by Schmutz et al. (1980) the diet of Swainson's Hawks does not change greatly over the nestling period. It seems unlikely, therefore, that nestling Swainson's Hawks are constrained by the need to consume only small prey during part of their development. The ability to monopolize access to a parent willing to feed young or to the prey delivered to the nest (when young are old enough to feed themselves) may be important in determining the manner in which food is distributed within the brood (Mock et al. 1987a, b)

(10) The <u>Sibling Rivalry Hypothesis</u> (Hamilton 1964; Hahn 1981) suggests that the size and competitive differences generated by asynchronous hatching result in a dominance hierarchy among brood members. This hierarchy serves to reduce the number and intensity of aggressive encounters among siblings at an energetic saving to both offspring and parents. By creating a stable competitive hierarchy, hatching asynchrony also promotes efficient distribution of food within the brood. Hahn (1981) found support for this hypothesis in the Laughing Gull (<u>Larus atricilla</u>), but some of its strongest evidence comes from studies of egrets and herons (Fujioka 1985a, b; Mock and Ploger 1987; Mock <u>et al.</u> 1987a, b). In these species, the frequency and intensity of aggressive encounters among siblings increases with increasing hatching synchrony (Fujioka 1985a, b; Mock and Ploger 1987) but is independent of the amount of food brought to the brood (Mock <u>et al.</u> 1987a). Sibling aggression is, however, dependent upon the ability of the chicks to monopolize access to food delivered to the nest (Mock 1985; Mock <u>et al.</u> 1987b).

Nestling Swainson's Hawks certainly have the ability to inflict serious injury on nestmates. Although sibling aggression is known in other raptors (Stinson 1979), there was little evidence of direct aggression in the current study (see below). However, the absence of direct sibling aggression is not, in itself, evidence against the

hypothesis. A true test of the Sibling Rivalry Hypothesis requires a comparison of the frequencies of aggressive encounters in broods with normal asynchrony and in broods in which the effects of asynchrony have been removed.

(11) The Nestling Identification Hypothesis (Gottlander 1987) suggests that hatching asynchrony facilitates rapid parental recognition of individual nestlings which, in turn, allows one parent (usually the female) to feed different brood members selectively while the second (usually the male) merely feeds the closest (or loudest) begging nestling. In this way the female can "fine tune" the way in which food is distributed within the brood while the male, freed from the need to distribute food equally among all nestlings, can spend more time foraging. This hypothesis has been invoked for Budgerigars (Melopsitticus undulatus, Stamps et al. 1985) and Pied Flycatchers (Ficedula hypoleuca, Gottlander 1987). In both cases there is biparental feeding of the young and the female tends to feed the smallest chick while the male feeds the closest or loudest begging chick. In the Swainson's Hawk the male provides almost all food to the nest during most of the nestling period (Fitzner 1978), but does not feed the young directly. The time available for foraging is therefore not constrained by the male's need to distribute food among the nestlings.

(12) The Larder Hypothesis (reviewed in Magrath 1990)

argues that females lay an extra egg to provide the older chick(s) with a "larder", in the form of a younger sibling. In other words, the last chick acts as a food source for its older sibling(s). Magrath (1990) dismisses this hypothesis for several reasons: (1) the cost of producing and maintaining the "larder" reduces the proposed benefits, (2) the younger chick often disappears early in the nestling period when there is little need for a "larder", and (3) the energy provided by the "larder" is likely to be small compared to the total food demands of the brood over the entire nestling period. This hypothesis will not be considered further.

b. Nonadaptive Explanations

(1) The Constraints on Incubation Hypothesis (Slagsvold 1986) argues that the foraging needs of females during the egg-laying period act as a constraint on the onset of full incubation. Under favourable conditions (e.g. higher ambient temperatures) females will enjoy higher foraging success, spend less time foraging, and be capable of beginning full incubation earlier in the egg-laying period. Higher ambient temperatures may also result in greater hatching asynchrony if they serve to keep eggs above physiological zero (that temperature above which

embryological development is possible) during the egg laying period (Magrath 1990). Thus the observed levels of hatching asynchrony are determined by the female's ability to initiate full incubation and not by selection for some optimum level of hatching asynchrony. In most raptors (Newton 1979), including Swainson's Hawks (Fitzner 1978), females remain on the nest during the egg-laying period while the male provides all the food. Under these circumstances the female would be free to begin full incubation as soon as the first egg is laid.

(2) The <u>Constraints on Egg Laying Hypothesis</u> argues that poor feeding conditions can influence egg size and quality (reviewed in Magrath 1990) and, in aerial insectivores such as Swifts (<u>Apus apus</u>, O'Connor 1979) and House Martins (<u>Delichon urbica</u>, Bryant 1978), can also influence the egg-laying interval and thus the degree of observed hatching asynchrony. As with the previous hypothesis, conditions during the egg-laying period, rather than direct selection on the onset of full incubation, are thought to determine the observed degree of hatching asynchrony. In the current study, food availability was not measured during the egg-laying period and its affects on the egg-laying interval are unknown. However, inter-hatch intervals in this study (Chapter 3) were similar among years and were also similar to hatching intervals reported in other studies of Swainson's Hawks (Parker 1976; Fitzner 1978; Pilz and

Seibert 1978; Bechard 1983). This suggests that hatching interval is fairly constant in this species. Nevertheless, the constraints on egg-laying hypothesis cannot be ruled out completely for this population. Unfortunately I lack the data to test this hypothesis.

(3) The Phylogenetic Constraints Hypothesis (Mead and Morton 1985) argues that hatching asynchrony is an epiphenomenon generated by physiological constraints related to hormonal changes in the switch from egg-laying to incubation behaviour. These authors suggest that because prolactin controls both the termination of egg laying and the initiation of incubation, incubation will begin with the laying of the penultimate egg. In this event hatching asynchrony is not adaptive and its effect on reproductive success would not be a result of natural selection.

Magrath (1990) reviewed the literature on incubation patterns and rejects Mead and Morton's hypothesis for several reasons. First, contrary to the hypothesis, the onset of incubation is actually quite variable. Many species begin full incubation prior to the laying of the penultimate egg and, in some species, the female gradually increases the proportion of time spent incubating over the egg-laying period. Second, within a population the observed degree of hatching asynchrony can vary both among seasons and among different females breeding at the same time. Third, hatching asynchrony often increases with increasing

clutch size.

These observations suggest that while hormonal factors may represent a constraint on incubation behaviour there is still considerable variation in incubation patterns. If some of this variance is genetically based then it may be subject to natural selection (Magrath 1990).

B. Predictions

Some researchers (e.g. Amundsen and Stokland 1988; Skagen 1988) have attempted to test the Brood Reduction Hypothesis by comparing the numbers of young fledged from asynchronous and synchronous broods of the same size. These authors have argued that support for the hypothesis is provided if significantly more young are produced in asynchronous broods. However, as pointed out by Magrath (1990), fledging success may not provide the best estimate of eventual recruitment to the breeding population if there is differential survival during the post-fledging period. Slagsvold (1986) has argued that asynchronous broods may fledge fewer, higher-quality, young than do synchronous broods and thus satisfy the predictions of the Brood Reduction Hypothesis despite a lower fledging success relative to synchronous broods. In addition, the benefits of hatching asynchrony may vary with environmental conditions. Magrath (1989) varied both the degree of

hatching asynchrony and the amount of food available to
breeding Blackbirds (Turdus merula). He found that under
poor conditions asynchronous broods were more productive (a
greater number of young survived until four weeks after
fledging) than were synchronous broods. When food was
abundant, asynchronous and synchronous broods did not differ
in productivity.

Thus, I favour an approach that attempts to identify the
major fitness effects of hatching asynchrony rather than
merely examining differences in reproductive success in any
one season.

Predictions of the Brood Reduction Hypothesis tested in
this study include:

(1) Mortality attributable to brood reduction will most
often involve the loss of the youngest chick. Hatching
asynchrony places the youngest, smallest chick at a
competitive disadvantage relative to its nestmates. If food
supplies become restricted the youngest chick will be the
first to starve. As discussed above, a reduction in the
growth and survival of the last-hatched chick is a well-
documented consequence of hatching asynchrony.

(2) Asynchronous broods will be more productive than
synchronous broods under poorer breeding conditions. This
prediction has been supported by Magrath (1989) in the first
study that manipulated both food availability and hatching
asynchrony. Haydock and Ligon (1986) and Skagen (1987)

found that synchronous broods fledged more young than asynchronous broods, while Shaw (1985), Gibbons (1987), Amundsen and Stokland (1988) and Skagen (1988) were unable to show any difference in the number of young fledged in synchronous and asynchronous broods.

(3) Brood reduction will occur earlier in asynchronous broods than in synchronous broods. If hatching asynchrony promotes efficient elimination of the smallest nestling, then brood reduction will be more common in asynchronous broods. In asynchronous broods a size, and presumably dominance, hierarchy exists by the time the youngest chick hatches. If young compete for access to a limited amount of food, then the youngest chick will be at a disadvantage and may eventually starve. Within a synchronous brood there is initially less discrepancy in the size, and presumably competitive abilities, of the nestlings. If food is in short supply differences in competitive abilities will determine which chick dies but, because initial size differences are slight, the process will take longer.

Haydock and Ligon (1986), Gibbons (1987), and Magrath (1989) all found that brood reduction occurred significantly earlier in asynchronous broods. I am not aware of any study that has tested, but failed to support, this prediction.

(4) The oldest nestling from an asynchronous brood will fledge at a higher mass than will nestlings from synchronous broods of the same initial size, particularly during times

of food shortage. Hatching asynchrony promotes efficient distribution of food among the nestlings as well as brood reduction if food resources are insufficient to support the entire brood. Under these conditions the oldest nestling in a brood will enjoy competitive advantages which should enable it to fledge at a higher mass than its siblings or chicks from synchronous broods. Data in support of this prediction have been provided by Shaw (1985), Haydock and Ligon (1986), Skagen (1988) and Magrath (1989). However, Gibbons (1987), Skagen (1987), and Amundsen and Stokland (1988) were unable to demonstrate a difference in fledgling mass in chicks from asynchronous versus synchronous broods. Differences in mass at fledging may have implications for survival in the post-fledging period and beyond. Birds that fledge at heavier weights are believed to have a survival and/or breeding advantage over smaller fledglings (Perrins 1988; Skagen 1988; Richner et al. 1989).

The purpose of these eeperiments was therefore to test these predictions in a breeding population of Swainson's Hawks.

2. Methods

General methods used to locate and monitor active

Swainson's Hawk nests and to obtain growth and survival data
nestlings were given in Chapter 2.

A. Manipulation Procedures

Beginning with the onset of hatching in each year, all
accessible nests were visited every two days to permit
accurate aging of nestlings (Chapter 2). As hatching
proceeded, the mass (to the nearest g), and wing chord (to
the nearest mm) of newly-hatched young were recorded, and
each nestling in a brood was marked uniquely with a small
amount of nontoxic dye to allow individual identification.

Nests with clutch sizes of three, complete hatching
success, and with young of similar age and size were
selected to act as experimental nests. Newly-hatched young
were moved among these nests to create broods of three in
which all the young were of similar size (i.e. differences
in nestling mass and size within experimental broods were
about 10%). Young within experimental (SYN) broods had
usually hatched on the same day and, at most, over a 36-hour
period. In contrast, unmanipulated broods of three
generally hatched over a four-day period (Chapter 3). All
manipulations involved nestlings up to four days old. All
experimental broods were created over a period of 7-10 days
in each field season. Experimental nests were not
subsequently used as either control or experimental nests if

they were occupied in the next breeding season.

Young were transported between nests in a grass-lined styrofoam container to minimize the danger of excessive heating or cooling. None of the nestlings transported in this manner displayed any obvious signs of stress. The most common reaction of chicks transported in this way was to sleep or to direct begging behaviour toward the experimenter.

Experimental broods usually contained non-siblings, one of which had actually hatched in the nest containing the experimental brood. In a few cases experimental nests contained two siblings and a third chick from another nest. In similar manipulations in the Cattle Egret (<u>Bubulcus ibis</u>), Mock and Ploger (1987) found no evidence that newly-hatched nestlings were capable of distinguishing between actual and "foster" siblings.

Because it was necessary to obtain measurements on young from several broods before manipulations could be carried out, some nests were visited as often as three times on the day that the manipulations took place. In all cases, brooding females were quick to return to the nest once the researchers left the immediate vicinity and in no instance did a breeding pair desert the nest during the manipulation period or in the five-day period immediately thereafter. There was no evidence that breeding adults could discriminate between actual and "foster" offspring and in no

instance could chick mortality be attributed to rejection by the parent. Control (ASYN) broods were also visited and measured during this period to ensure that all broods were subjected to similar levels of disturbance and that chicks in ASYN and SYN broods were handled to the same extent.

Control broods consisted of natural broods of three that hatched from clutches of three. These do not constitute true controls because they were not created artificially by moving chicks between nests. If transportation of chicks between nests influenced their growth and survival, then data from SYN broods may be somewhat biased (Magrath 1990).

In 1987, in an attempt to determine if parents attempted to rear the maximum number of young possible during each breeding season, one "foster" chick was added to each of eight broods of three (each brood was produced from a clutch of three) to create artificially-enlarged broods of four. The "foster" chicks were obtained from broods of two or four and were positioned at random in the size hierarchy of enlarged broods. The range of chick sizes in enlarged broods of four fell within the range of chick sizes recorded in nonmanipulated, natural broods of four. All breeding pairs involved in the manipulation accepted and fed all members of the enlarged brood.

Fledgling age and mass were defined as the age (in days) and the mass (in grams) at which the young were first capable of sustained flight (i.e. > 50 meters). In

most cases young left the nest between visits. However, in a few cases fledging age or mass could not be determined accurately. Only those young whose fledging age (within 1 day) and mass (measured within 2 days of fledging) could be accurately estimated are included in analyses of growth and age at fledging.

In order to assess the interactions of young within a brood, one brood in 1988 and six broods in 1989 were observed for a total of 65 hours. Broods were observed from a blind positioned approximately 75 m from the nest (n = 3) or from a vehicle parked approximately the same distance away. Nestlings were marked with a small amount of nontoxic dye to permit individual identification and were observed with the aid of a spotting scope. Observation periods varied from 1-7 hours in duration. Young in observed broods were from 5-28 days old.

B. Analyses

The traditional approach to the quantitative study of avian growth has involved a graphical method of fitting growth data to one of three models (logistic, Gompertz, or von Bertalanffy) (Ricklefs 1967, 1983). More recently, White and Brisbin (1980) have described a reparameterized version of the Richards sigmoid growth function (Richards

1959). This model, as employed by Brisbin et al. (1986a, b), utilizes nonlinear least-squares curve-fitting techniques with the result that the models listed above are included in, and become special cases of, the Richards sigmoid growth function (Brisbin et al. 1987a, b, c). In other words, the Richards sigmoid growth function can take a number of forms including those described by the logistic, Gompertz and von Bertalanffy models.

The Richards model describes three parameters: (1) the asymptotic size, (2) the growing time, an indicator of growth rate, and (3) the Richards shape parameter, a quantitative measure of the trajectory of the growth process (Brisbin et al. 1987a). The specific model employed in this study is from Brisbin et al. (1986a, b) and takes the form:

$$\frac{W_{i+1} - W_i}{t_{i+1} - t_i} = \frac{2(m+1)}{T(1-m)} (W^{1-m} W_i^m - W_i) + e_i$$

where: W_i is the size at time t_i,

 W is the asymptotic size,

 T is the growing time, (i.e. the period over which the chick grows from 10% to 90% of its asymptotic size),

 m is the Richards shape parameter, and

 e_i is the stochastic error at time t_i.

Specific parameters describing the growth of individual nestlings were obtained using the DUD option of the PROC NLIN Procedure of SAS (SAS Institute 1988a). These parameters were then used as dependent variables in uni- and multivariate analyses of variance.

The timing of brood reduction was examined using failure time analysis (Lee 1980; Muenchow 1986). This nonparametric approach uses the product-limit method (SAS Institute 1988b) to construct survival distribution functions for whole broods. In other words, a partial brood (one which has experienced brood reduction) is considered to have "failed" in this analysis. The distribution of these failures over time is used to construct a survival distribution for all the broods. Different covariates, such as experimental treatment, can then be identified and the strength of their association with the overall survival function can be measured. In addition, a sequence of test statistics can be derived that examine the joint effect of two or more covariates on the survival function. All analyses relating to the timing of brood reduction were performed using the PROC LIFETEST Procedures of SAS (SAS Institute 1988b).

All other statistical analyses were performed using SAS (SAS Institute 1988a) or Statistix (Analytical Software 1989) statistical packages. Nonparametric tests were employed when the data (despite being transformed) did not conform to a normal distribution. The test statistic

for all Mann-Whitney U-Tests is a "Z" score with a
continuity correction of 0.5 (SAS Institute 1988a). This
statistic approximates a "T" score when there are few ties
but is superior when ties are frequent (Conover 1980).
Variation is reported as mean ± standard error unless stated
otherwise. A Type I error rate of $\alpha = 0.05$ was used
throughout this study. Statistical power analyses were
performed when analyses yielded marginal probability values
(i.e. $0.05 < P < 0.1$).

3. Results

The growth and survival of nestlings were monitored in
40 ASYN, 26 SYN, and 8 enlarged broods over the three years
of the study. In 1987 14 ASYN, 8 SYN, and 8 enlarged broods
were studied while in 1988, and again in 1989, 13 ASYN and 9
SYN broods were monitored.

A. The Timing of Hatching and Initial Size Differences Between Oldest and Youngest Chicks in ASYN Broods.

Schmutz et al. (1980) have shown that in Swainson's
Hawks nestlings, mass is negatively correlated with hatch
date. In the current study the initiation of hatching in
three-egg clutches did not vary significantly among

experimental treatments (two-factor ANOVA, F = 2.23, d.f. = 2,60, P = 0.116), nor was there any significant interaction between year and treatment level (two-factor ANOVA, F = 2.38, d.f. = 2,60, P = 0.102). However, hatch date of the first egg in three-egg clutches did vary significantly among years (Table 12, two-factor ANOVA, F = 18.71, d.f. = 2,60, P < 0.001). Hatching commenced significantly earlier in 1987 than in 1988 or 1989 and significantly earlier in 1989 than in 1988 (Tukey's Studentized Range Test, P < 0.05 for all comparisons).

As discussed above (Chapter 3), clutches of three generally hatched over a four-day period regardless of year. Within ASYN broods, differences in mass between first- and last-hatched chicks at the time when the youngest chick hatched did not vary significantly among years (one-way ANOVA, F = 0.46, d.f. = 2,27, P = 0.634) and averaged 80 g (S.E. = 6.3 g, n = 30). The average hatching mass of the youngest chick in ASYN broods was 48.2 g (S.E. = 1.2 g, n = 30).

B. Frequency and Usual Victim of Brood Reduction in ASYN Broods

The frequency of brood reduction in ASYN broods was similar to that recorded for the population as a whole (Chapter 3). In 1987, 64.3% of ASYN broods experienced

Table 12. Mean hatch date (Julian date) of the oldest chick
from three-egg clutches of Swainson's Hawks in
each year of the study.

Year	Mean Hatch Date ($\overline{X} \pm$ S.E.)	Number of Clutches
1987	174 ± 0.86	22
1988	181 ± 0.93	22
1989	178 ± 0.73	23

brood reduction, while 92.3% and 61.5% of ASYN broods did so in 1988 and 1989, respectively. The proportion of ASYN broods which experienced at least one instance of brood reduction did not differ significantly among the three years (Fisher's Exact Test, P > 0.16 in all cases).

Within each season the youngest or c-chick, was the usual first victim of brood reduction (Table 13). The second (b-) chick was the first victim in 15% of all brood reductions, and in no instance was the first-hatched or a-chick the first victim of brood reduction (Table 13). The proportion of ASYN broods in which the c-chick was the first chick to die or disappear varied from 67% (n = 6) in 1989, to 100% (n = 11) in 1988, but did not vary significantly from year to year (Fisher's Exact Test, P > 0.11 in all cases).

Clear evidence of sibling aggression (i.e. wound marks on the head or shoulders) directed toward the eventual victim of brood reduction was recorded in only 5 (19%) of 26 cases of brood reduction. In 4 (15%) of these cases direct sibling aggression was the apparent proximal cause of nestling mortality (i.e. the nestling appeared to die from its wounds rather than as a result of starvation or exposure). In the fifth the nestling apparently died of starvation after its wounds had healed.

In 23 of the 26 cases of brood reduction listed in Table 13, the nests were visited within 3 days prior to the

Table 13. Identity of the first victim of brood reduction in control (ASYN) Swainson's Hawk broods in each year of the study. The young in three ASYN broods could not be individually identified and are not included in this analysis.

Year	a-chick (%)	b-chick (%)	c-chick (%)	Total
1987	0 (0)	2 (22)	7 (78)	9
1988	0 (0)	0 (0)	11 (100)	11
1989	0 (0)	2 (33)	4 (67)	6
Total	0 (0)	4 (15)	22 (85)	26

occurrence of brood reduction. In 18 (78.3%) of these

cases, the second-lightest nestling was at least 50% heavier

than the eventual victim, suggesting that starvation was the

proximal cause of brood reduction (Table 14). Victims of

brood reduction usually disappeared from the nest between

visits, but in some cases were cannibalized by their

siblings. Cannibalism itself provides no information on the

proximate cause of death because it was not clear if

nestlings merely scavenged on the remains of dead siblings

or actually killed and consumed their weaker nestmates.

In general, brood reduction was preceded by a period

during which the eventual victim gained little or no mass

relative to its sibling. Changes in chick mass over time

for the members of a randomly-selected ASYN brood are given

in Figure 1. In this instance, the c-chick died, apparently

as a result of starvation, when the brood was 18 days old.

The a-chick and b-chick both survived the nestling period

but the b-chick was found dead near the nest shortly after

fledging.

C. Frequency of Brood Reduction in ASYN versus SYN Broods

Multi-dimensional contingency table analysis indicated

that the proportion of nests (Table 15) that experienced

brood reduction was significantly dependent on experimental

treatment (G = 7.93, d.f. = 1, P < 0.005) and year (G =

Table 14. Probable causes of Swainson's Hawk nestling
losses among first victims of brood reduction in
control (ASYN) Broods.

Year	Number of nestlings lost to		
	Starvation	Siblicide	Unknown
1987	6	1	2
1988	7	2	2
1989	5	1	0
Total	18	4	4

Figure 1.   Patterns of growth by a- (- ● -), b- (- ▼ -),
and c- (- ■ -) chicks in a randomly-selected
control (ASYN) brood.
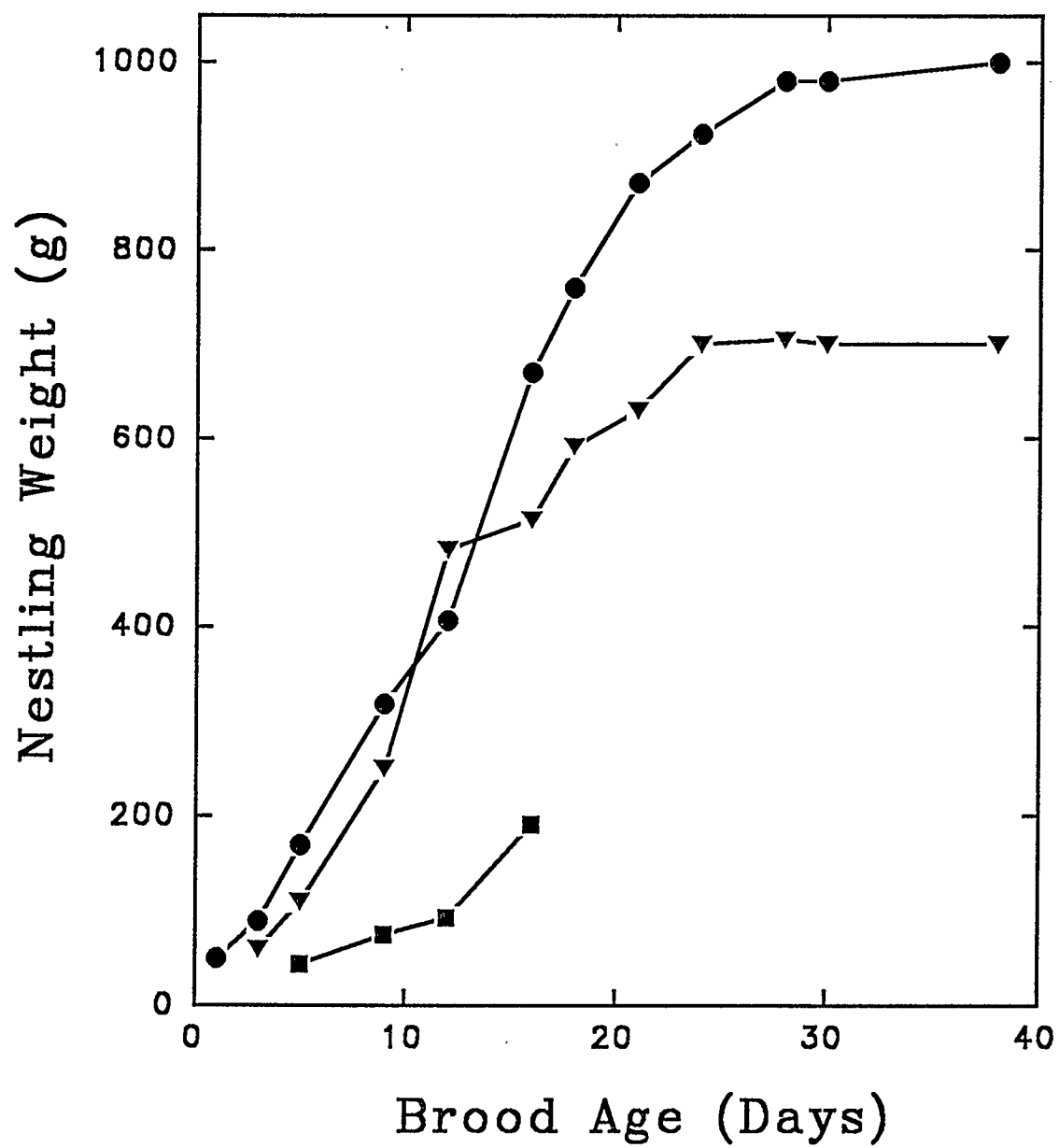
Table 15. Numbers of control (ASYN) and experimental (SYN) Swainson's Hawk nests that experienced brood reduction in each year of the study.

Year	Brood Type	Brood Reduction	No Brood Reduction
1987	ASYN Broods	9	5
	SYN Broods	3	5
1988	ASYN Broods	12	1
	SYN Broods	8	1
1989	ASYN Broods	8	5
	SYN Broods	2	7
Total	ASYN Broods	29	11
	SYN Broods	13	13

13.76, d.f. = 2, P < 0.005). However there was no evidence that brood reduction was dependent on any year and experimental treatment interaction (G = 1.56, d.f. = 2, P > 0.250). Overall, brood reduction occurred more often in ASYN broods than in SYN broods independent of year, while brood reduction was more common in 1988 than in other years independent of treatment.

Brood size of SYN broods at fledging was larger than that of ASYN broods in 1987 and 1989 (Table 16). In 1988, when overall nest success was very low (Chapter 3), there was no significant difference in the number of young produced in ASYN and SYN broods (Table 16).

D. Timing of Brood Reduction in ASYN versus SYN Broods

The survival distribution functions differed between SYN and ASYN broods in each year (Figures 2 - 4). In each year the distribution of ages of brood reduction within SYN broods falls to the right of that for ASYN broods (brood age is measured in days and begins with the hatching of the first chick in the brood). In other words, there was a tendency for brood reduction to occur earlier in ASYN broods. The median ages of ASYN broods at brood reduction were 12, 13 and 12 days in 1987, 1988, and 1989, respectively. The corresponding ages among SYN broods in 1987, 1988, and 1989 were 25, 17 and 29 days, respectively.

Table 16. Number of young fledged from control (ASYN) and experimental (SYN) Swainson's Hawk broods in each year of the study.

Year	ASYN Broods ($\tilde{X} \pm$ SE)	SYN Broods ($\tilde{X} \pm$ SE)	P*
1987	1.36 ± 0.27	2.38 ± 0.32	P < 0.05
1988	0.84 ± 0.30	0.78 ± 0.36	ns
1989	1.92 ± 0.29	2.67 ± 0.24	P < 0.05

* Results of one-tailed Mann-Whitney U-Tests comparing treatments within each year.

Figure 2. Temporal distribution of brood reduction for
control (ASYN) (- △ -) and experimental (SYN)
(- O -) broods in 1987.
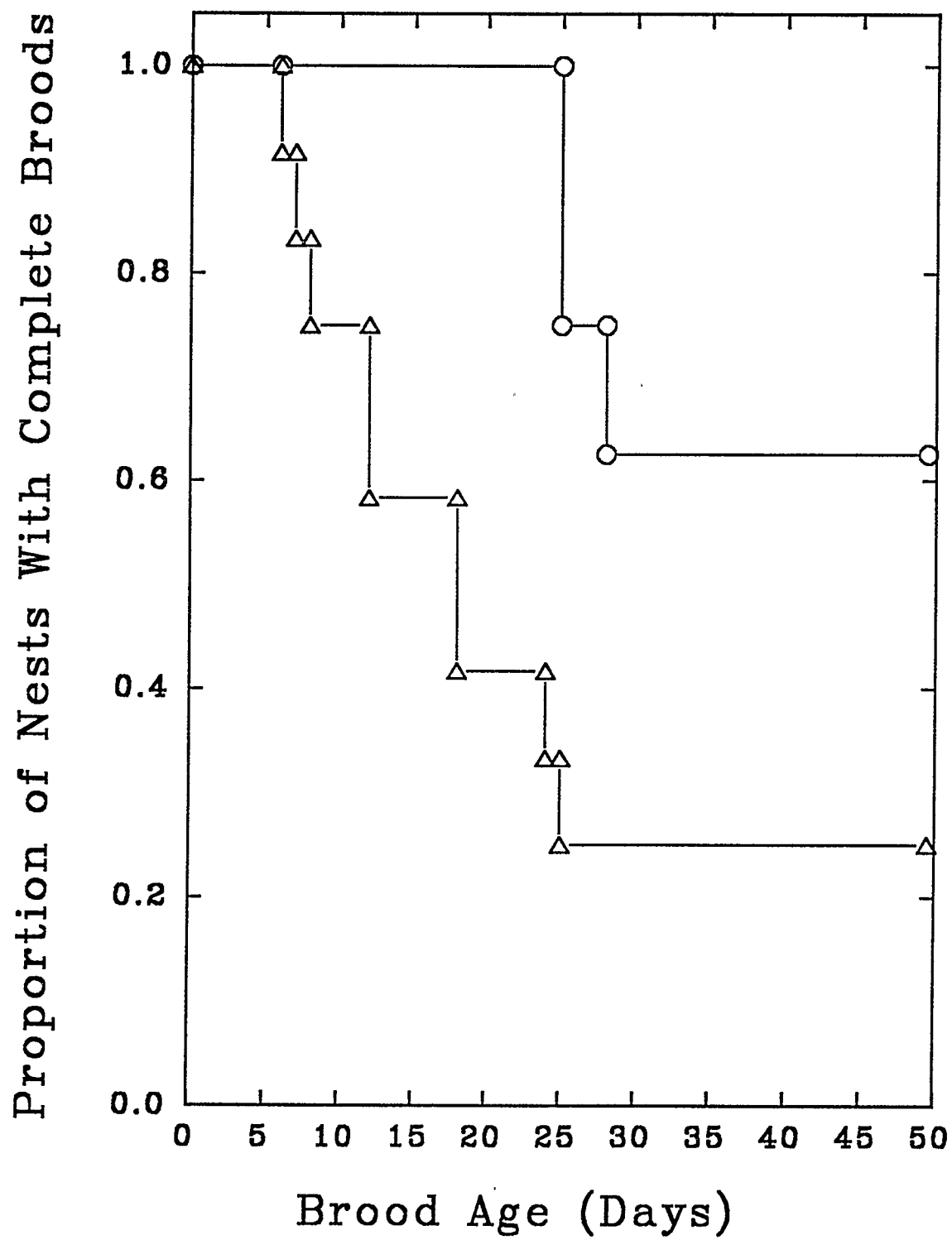
Figure 3. Temporal distribution of brood reduction for
control (ASYN) (- △ -) and experimental (SYN)
(- O -) broods in 1988.
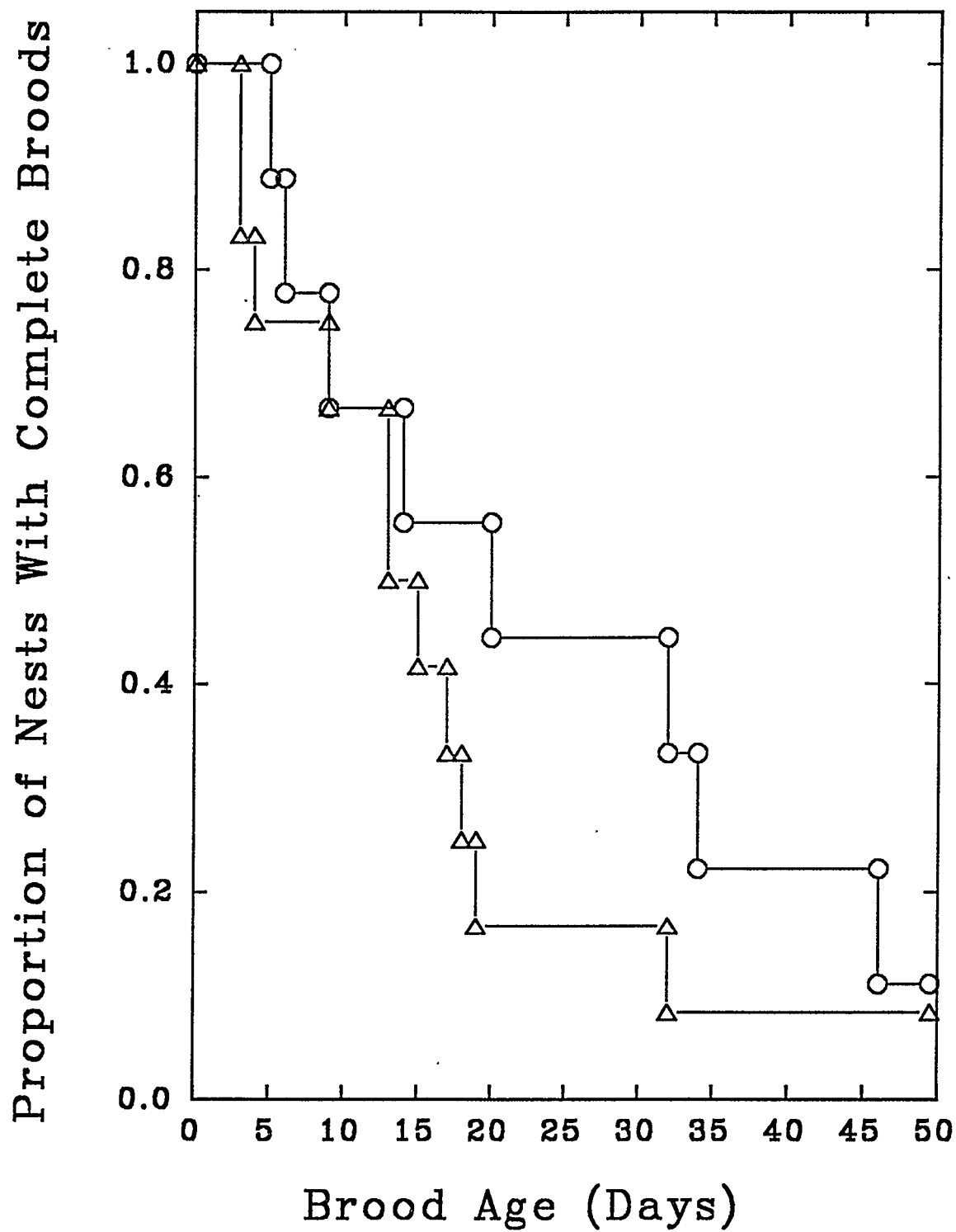
Figure 4. Temporal distribution of brood reduction for
          control (ASYN) (- △ -) and experimental (SYN)
          (- O -) broods in 1989.
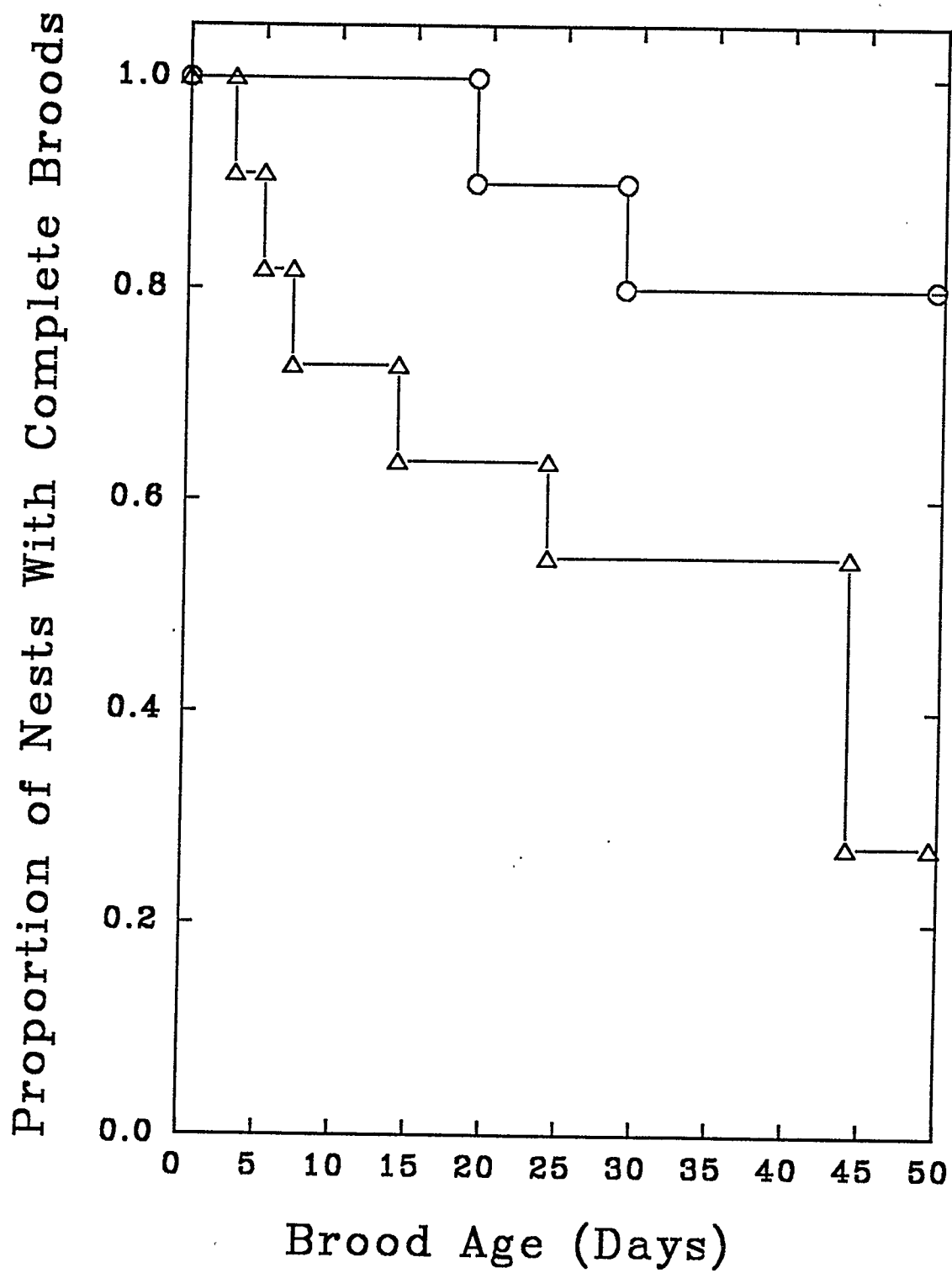
The effects of year and experimental treatment on the overall survival function were examined by defining experimental treatment in each year as a different covariate. A forward stepwise sequence Wilcoxon test indicates that experimental treatment significantly affected the overall survival function in 1987 (X^2 = 4.15, d.f. = 1, one-tailed P = 0.020) and in 1989 (cumulative X^2 = 6.95, d.f. = 2, one-tailed P = 0.047). The addition of experimental treatment in 1988 as a third covariate did not increase the strength of association between the covariates and the survival distribution function (cumulative X^2 = 8.69, d.f. = 3, 1-tailed P > 0.108). Therefore, treatment significantly affected the overall survival function in 1987 and 1989 but not in 1988.

E. Age at Fledging

Nestling Swainson's Hawks fledged 34 - 53 days after hatching. Over 80% of young first flew when 40 - 46 days old. Within a brood, chicks fledged asynchronously, usually over a period of 2 - 4 days, although in a few cases up to 10 or more days passed between the fledging of the first and last chicks. Within ASYN broods, a nestling's position within the brood's size hierarchy had no effect on its fledging age (one-way Anova, F = 0.36, d.f. = 2,19, P = 0.705).

Table 17. Age (in days) at fledging of Swainson's Hawks in
control (ASYN) and experimental (SYN) broods in
each year of the study.

Year	ASYN Broods $\bar{X} \pm$ SE (n)	SYN Broods $\bar{X} \pm$ SE (n)	All Broods $\bar{X} \pm$ SE (n)
1987	41.4 $\pm$ 0.51 (17)	43.2 $\pm$ 0.48 (19)	42.3 $\pm$ 0.04 (36)
1988	45.0 $\pm$ 1.06 (11)	47.1 $\pm$ 1.30 (7)	45.8 $\pm$ 0.84 (18)
1989	40.1 $\pm$ 0.45 (24)	41.0 $\pm$ 0.66 (26)	40.5 $\pm$ 0.40 (50)
Total	41.5 $\pm$ 0.43 (62)	42.6 $\pm$ 0.50 (52)	

Fledging age was significantly affected by experimental treatment (Table 17). Chicks in ASYN broods fledged earlier (41.5 $\pm$ 0.43 days) than did chicks from SYN broods (42.6 $\pm$ 0.50 days; 2-factor Anova, F = 4.59, d.f. = 1,60, P = 0.036). Age at fledging was also significantly affected by year (2-factor ANOVA, F = 12.50, d.f. = 2,65, P < 0.001), and the mean fledging age differed significantly among years (Tukey's Studentized Range Test, P < 0.05 for all comparisons). The mean fledging age (pooled over treatments) was lowest in 1989 (40.5 $\pm$ 0.40 days), highest in 1988 (45.8 $\pm$ 0.84 days), and intermediate in 1987 (42.3 $\pm$ 0.04 days). There was no significant interaction between year and experimental treatment (2-factor ANOVA, F = 1.11, d.f. = 2,58, P = 0.338).

F. Nestling Growth

The Richards growth function was used to calculate three parameters of nestling growth: (1) asymptotic size, (2) a measure of growing time (i.e. the time over which a chick grows from 10% to 90% of its asymptotic size), and (3) a measure of the shape of the growth curve.

Because wing chord length had not reached a definite asymptote by the time the young left the nest I was unable to fit the data to the Richards growth model. Thus only mass was used in the analyses of nestling growth.

Table 18. Asymptotic mass, in grams, (as calculated by
the Richards growth model) of Swainson's Hawks in
control (ASYN) and experimental (SYN) broods in
each year of the study.

Year	ASYN Broods $\bar{X} \pm$ SE (n)	SYN Broods $\bar{X} \pm$ SE (n)
1987	884.21 ± 30.16 (13)	791.77 ± 20.99 (13)
1988	879.14 ± 46.50 (6)	888.59 ± 69.59 (5)
1989	950.32 ± 30.49 (22)	862.69 ± 22.01 (23)

Table 19. Duration (in days) of growth between 10 and 90%
of asymptotic size (T as calculated by the
Richards growth model) of Swainson's Hawks in
control (ASYN) and experimental (SYN) broods in
each year of the study.

Year	ASYN Broods $\bar{X} \pm$ SE (n)	SYN Broods $\bar{X} \pm$ SE (n)
1987	28.6 ± 1.49 (13)	26.5 ± 1.15 (13)
1988	30.3 ± 1.64 (6)	33.5 ± 2.75 (5)
1989	32.7 ± 1.79 (22)	28.3 ± 1.07 (23)

Table 20. Shape parameter (m) of the Richards growth model
for Swainson's Hawks in control (ASYN) and
experimental (SYN) broods in each year of the
study.

Year	ASYN Broods $\overline{X} \pm SE$ (n)	SYN Broods $\overline{X} \pm SE$ (n)
1987	1.39 $\pm$ 0.15 (13)	1.48 $\pm$ 0.16 (13)
1988	1.59 $\pm$ 0.15 (6)	1.74 $\pm$ 0.32 (5)
1989	1.42 $\pm$ 0.13 (22)	1.51 $\pm$ 0.14 (23)

Mean values for each of the parameters are given in Tables 18 - 20. Multivariate analyses of variance failed to demonstrate a significant effect of experimental treatment (MANOVA, F = 1.02, d.f. = 3,33, P = 0.394) or year (MANOVA, F = 0.87, d.f. = 6,66, P = 0.519) on these parameters.

Univariate analyses (ANOVA) of weighted values (i.e. each parameter estimate was weighted by the inverse of its own standard error) revealed that in 1987, chicks from ASYN broods achieved heavier asymptotic mass than did those from SYN broods (F = 5.56, d.f. = 1,16, P = 0.031). There were no significant differences in asymptotic mass between chicks from ASYN and SYN broods in 1988 (F = 1.05, d.f. = 1,6, P = 0.346) or 1989 (F = 0.89, d.f. = 1, 23, P = 0.355).

Within ASYN broods, position in the hatching order significantly affected asymptotic mass (F = 12.61, d.f. = 2,33, P = 0.001). A-chicks achieved higher asymptotic mass than did b-chicks, who in turn were heavier than c-chicks (Table 21, Tukey's Studentized Range Test, P < 0.05 for all comparisons). Asymptotic mass did not vary significantly among years (F = 0.29, d.f. = 2,33, P = 0.749), nor was there a significant interaction between year and hatch position (F = 0.87, d.f. = 3,33, P = 0.465).

First-hatched chicks in ASYN broods attained significantly heavier asymptotic mass than did chicks in SYN broods (Table 21, F = 9.25, d.f. = 1,53, P = 0.004). As

Table 21. Weighted mean asymptotic mass, in grams, of nestling Swainson's Hawks in control (ASYN) and experimental (SYN) broods in each year of the study.

Year	ASYN Broods			SYN Broods	
	a-chick	b-chick	c-chick	Heaviest Brood Member	Mean
1987	887.7	827.7	759.0	808.6	803.7
1988	975.7	798.0	---	876.9	862.4
1989	910.5	834.5	784.4	906.9	804.5
Total	915.2	818.4	782.4	871.3	809.2

with ASYN broods, asymptotic mass of young in SYN broods did not vary significantly with year (F = 1.34, d.f. = 2,53, P = 0.270). Asymptotic mass achieved by nestlings in SYN broods did not differ significantly from those achieved by b-chicks (F = 0.01, d.f. = 1,47, P = 0.924) or c-chicks (F = 0.50, d.f. = 1,47, P = 0.481).

I also compared the asymptotic mass of chicks in ASYN broods to that of the heaviest fledging in each of the SYN broods. The heaviest fledgings in SYN broods were significantly lighter than a-chicks in ASYN broods (F = 5.21, d.f. = 1,37, P = 0.029). Asymptotic mass did not vary significantly among years in this analysis (F = 3.25, d.f. = 2,37, P = 0.052, Power > 95%), nor was there a significant interaction between year and and experimental treatment (F = 1.53, d.f. = 2,37, P = 0.231).

The asymptotic mass of the heaviest nestlings in each SYN brood were not significantly heavier than those of b-chicks in ASYN Broods (F = 2.61, d.f. = 2,26, P = 0.118), but they were heavier than those of c-chicks in ASYN broods (F = 7.66, d.f. = 2,26, P = 0.010). There was no significant year effect (F < 2.1, P > 0.14, for both tests) or interaction between year and experimental treatment (F < 1.4, P > 0.250, for both tests) in these analyses.

Univariate analyses of the type conducted on asymptotic mass were also carried out on the remaining two shape parameters. However, these parameters did not vary

significantly with year, treatment, or relative position in the hatch order.

G. Behavioural Observations

Limited observations suggest that direct sibling aggression is relatively rare among nestling Swainson's Hawks. In 37 hours of observations on four ASYN broods, eight instances of sibling aggression were noted. All aggressive encounters lasted less than 2 minutes and generally occurred when the female was off the nest. In seven of eight encounters the c-chick was pecked about the head and shoulders by the a- (6 times) or b-chick (once). In the last case a c-chick pecked at an a-chick. The object of aggression was never observed to fight back and generally moved away from its sibling, thus ending the encounter.

I observed 24 feedings at ASYN nests. In 9 of these cases only one chick positioned itself in front of the female while the remaining chick(s) apparently slept. In the 15 cases in which two chicks begged at once, the older chick received almost all the food offered by the female until it appeared satiated and ceased begging. Thereafter the smaller chick was fed until it too stopped begging. I never observed more than two chicks beg at one time.

In 28 hours of observations on 3 SYN broods we noted 5 aggressive encounters. The rate, context, and duration of

these encounters were similar to those observed in ASYN broods. Of 16 feedings observed at SYN broods, more than one chick begged on only two occasions. In both cases the female fed the chick closest to her before feeding the second nestling.

These observations suggest that the frequency of direct aggression was similar in ASYN and SYN broods. Observations also indicate that, within ASYN broods, older chicks were fed preferentially when two chicks begged simultaneously.

H. Brood Enlargement Experiments

Of the eight broods selected for enlargement experiments in 1987, five (62.5%) experienced brood reduction. The frequency of brood reduction among nine natural broods of four observed in the same year was 55.6% and did not differ significantly from that recorded among experimental broods (Fisher's Exact Test, P = 1.000). Nor did the average number of young fledged in enlarged (2.4 $\pm$ 0.56 chicks/brood) and natural (2.7 $\pm$ 0.50 chicks/brood) broods differ significantly (Mann-Whitney U-Test, Z = -0.351, P = 0.725). It was not logistically possible to visit broods of four often enough to collect growth data.

I. Food Availability

Food availability was not assessed directly. However, as described above (Chapter 2), the presence or absence of fresh prey was noted during each nest visit, providing a crude measure of food available to the brood itself (Table 22). Only data from those broods that were visited from 6 - 16 times were included in this analysis. Analysis of transformed (i.e. arcsin square root) data indicates a significant effect of year on the proportion of nest visits during which fresh prey was present (2 factor ANOVA, F = 7.42, d.f. = 2,49, P < 0.001). More specifically, fresh prey was significantly less common in 1988 than in 1987 or 1989 (Tukey's Studentized Range Test, P < 0.05 for both comparisons). The proportion of visits during which fresh prey was noted did not differ significantly between 1987 and 1989 (Tukey's Studentized Range Test, P > 0.05). The proportion of visits during which fresh food was found on the nest did not vary significantly between SYN and ASYN broods (2 factor ANOVA, F = 2.77, d.f. = 1,49, P = 0.103), nor was there a significant interaction between year and experimental treatment (2 factor ANOVA, F = 0.27, d.f. = 2, 49, P = 0.763).

Table 22. Proportion of visits during which fresh prey was found at the nests of control (ASYN) and experimental (SYN) broods in each year of the study (n = number of nests).

Year	% of Visits With Fresh Prey	
	ASYN Broods $\overline{X} \pm$ SE (n)	SYN Broods $\overline{X} \pm$ SE (n)
1987	36.5 ± 3.28 (8)	49.5 ± 6.96 (9)
1988	22.4 ± 3.86 (8)	27.4 ± 5.63 (9)
1989	39.6 ± 5.07 (12)	44.5 ± 6.06 (9)

4. Discussion

A. Predictions

Results of the manipulation experiments generally support the predictions of Lack's Brood Reduction Hypothesis. What follows is a brief restatement of each prediction and an assessment of the evidence for and against each hypothesis.

(1) Mortality attributable to brood reduction will most often involve the loss of the youngest chick. The c-chick in ASYN broods was the usual first victim of brood reduction in each year of the study (Table 13). When all years are considered together, 85% of the first victims of brood reduction were c-chicks. These results thus provide strong support for the prediction.

(2) Asynchronous broods will be more productive than synchronous broods under poorer breeding conditions. This prediction, although critical to the hypothesis, has been rarely tested because few studies actually measure breeding conditions (Magrath 1990) and only one study (Magrath 1989) has directly manipulated food availability.

Although I did not directly measure food availability I do have evidence that breeding conditions in 1988 were poor relative to 1987 and 1989. First, soil moisture conditions

were very low in the fall of 1988 (Chapter 2). Second,
agricultural yields in that year were lower than in 1987 or
1989 (Chapter 3). These observations indicate that the
study area experienced drought conditions in the summer of
1988. Indeed much of western North America experienced a
drought in 1988 (Trenberth et al. 1988). Third, fresh prey
was present at the nest significantly less often in 1988
than in 1987 or 1989 (Table 22). A reduction in the
presence of fresh prey at Swainson's Hawk nests during a
drought suggests that the prey availability is lower during
those periods. If this is the case, 1988 may represent a
"poor" year.

Schmutz and Hungle (1989) have argued that the
reproductive performance of Swainson's Hawks is unaffected
by drought or by ground squirrel densities (as measured by
sales of "gopher" poison). However, they measured the
reproductive performance only of pairs which produced at
least one fledgling. A similar analysis of the data in this
study would indicate that the number of young fledged per
nest was 1.9 in 1987, 1.8 in 1988, and 2.0 in 1989.
Obviously these values fail to capture significant year to
year variation in reproductive performance as described in
Chapter 3. These observations also illustrate the
importance of detailed measurements of reproductive
performance in multi-year studies of breeding populations.

In 1988 ASYN and SYN broods did not differ significantly

in the number of fledglings produced. However, a-chicks in
ASYN broods were significantly heavier at fledging than were
the heaviest fledglings in SYN broods. If post-fledging
survival is positively correlated with fledging mass, then
survival of a-chicks from ASYN broods would be higher than
that of the heaviest chicks in SYN broods and ASYN broods
(in accordance with the prediction) would produce more young
which survived to breed.

A positive correlation between fledging mass and
survival has been recorded in a number of species
(Gustafsson and Sutherland 1988; Nur 1988b; Richner et al.
1988; Tinbergen and Boerlijst 1990). However, Newton and
Moss (1986) failed to find any such correlation in European
Sparrowhawks. These authors found that post-fledging
survival was not significantly affected by fledging mass,
sex or brood size, but they also argued that very high food
availability at the time of fledging allows young
sparrowhawks to compensate for low fledging weights. Young
Swainson's Hawks fledge at the same time that Richardson's
ground squirrels are entering hibernation (Michener and
Koeppl 1985) and although parents may provide fledglings
with some food (Fitzner 1978), young have only a few weeks
to develop the flight and foraging skills required to
undertake the longest of raptor migrations. Under such
circumstances even small advantages in fledging mass may
be important in surviving the early post-fledging period.

(3) <u>Brood reduction will occur earlier in asynchronous broods than in synchronous broods</u>. This prediction was supported in 1987 and 1989 (Figures 2, 4) but not in 1988 (Figure 3). This suggests that in 1988, when conditions (relative to 1987 and 1989) were poor, hatching asynchrony did not facilitate early brood reduction. In contrast, hatching asynchrony facilitated efficient (i.e. earlier) brood reduction in years with higher food availability.

(4) <u>The oldest nestling from an asynchronous brood will fledge at a higher mass than will nestlings from synchronous broods of the same initial size, particularly during times of food shortage</u>. This prediction was supported in each year of the study. Not only did the a-chick attain a significantly heavier asymptotic mass than did b- and c-chicks in ASYN broods, but a-chicks were also significantly heavier than were the heaviest fledglings in SYN broods.

Results of this study thus indicate (1) that the effect of hatching asynchrony varies from year to year as a function of changing food availability, and (2) that the results of manipulation experiments, viewed in light of this variation, provide support for Lack's Brood Reduction Hypothesis.

Two recent studies, one a field study of the Shag (Amundsen and Stokland 1988), and the second a laboratory study of the Zebra Finch <u>Poephila guttata</u> (Skagen 1988),

employed experimental techniques similar to those used in this study but, in each case, the results failed to support Lack's hypothesis. I would argue that these studies attempted to test the hypothesis under conditions of relatively high food availability when hatching asynchrony would be expected to have little, if any, affect on the growth and survival of nestlings. In their study of Shags, Amundsen and Stokland (1988) did find some evidence of starvation, but overall productivity measures suggested that rates of starvation and nestling mortality were low. Skagen (1988) controlled the amount of food available to broods, but the difference in the amounts delivered to broods under food-restricted and non-restricted conditions was approximately 10%. As discussed above, hatching asynchrony is predicted to affect growth and survival only under certain conditions, and any test of the hypothesis must take place under those conditions. A lack of support for the predictions under conditions of high food availability does not constitute rejection of the hypothesis.

B. Costs and Benefits of Hatching Asynchrony

In 1987 and 1989, parents of SYN broods produced more fledglings than did parents of ASYN broods. If the number of fledglings produced was the only factor determining parental fitness, then clearly hatching asynchrony would not

be an adaptive strategy. However, parents of SYN broods may have incurred greater costs than those rearing ASYN broods and these costs may well outweigh the advantage of producing additional young.

There was a significant tendency, in each year of the study, for nestlings from ASYN broods to fledge at an earlier age than nestlings from SYN broods. However, the differences in fledging age were small (1-2 days, Table 17) and the biological importance of such differences is difficult to determine. Differences in fledging age may result from a more efficient distribution of food among ASYN broods. However, if this was the case one would expect faster growth within ASYN broods and there was no evidence of such a difference.

Data relating to the timing of brood reduction in Swainson's Hawks indicate that brood size was adjusted much more efficiently (i.e. earlier in the nestling period) in ASYN broods. If feeding conditions do not permit the rearing of the entire brood, selection should favour an early adjustment of brood size. Maintaining young that will not survive to fledge represents an energetic cost to parents and surviving siblings. Energetic savings resulting from efficient brood reduction have also been proposed as an advantage of hatching asynchrony in studies of Chihuahuan Ravens (Corvus cryptoleucus, Haydock and Ligon 1986), Jackdaws (C. monedula, Gibbons 1987), and Blackbirds

(Magrath 1989).

In addition to gaining the energetic benefits of efficient brood reduction, adults rearing ASYN broods may be able to distribute food more efficiently within the brood (Magrath 1990). This strategy assures them of producing large, presumably healthy a-chicks in all but the most severe feeding conditions. As pointed out by Nur (1984a, b, 1988a) in a study of Blue Tits (Parus caeruleus), and by Richner (1989) in a study of Carrion Crows (Corvus corone), even small differences in fledging size and mass can strongly influence survival, recruitment and eventual breeding success. Thus, despite producing fewer fledglings, parents that adopt a strategy of hatching asynchrony may actually experience higher reproductive success than those that hatch their clutch asynchronously. It is important to note that the efficient distribution of energy within the brood that is facilitated by hatching asynchrony not only facilitates productivity as predicted by the Brood Reduction Hypothesis but is also consistent with the Sibling Rivalry Hypothesis.

Finally, a possible additional cost incurred by parents of SYN broods relates to a potential reduction in survival and future reproductive success as a result of being forced to provide more parental care than would have been the case had the manipulations not been carried out. This argument is based on two assumptions: (1) Swainson's Hawks are

capable of increasing their breeding effort in response to manipulations and, (2) any increase in breeding effort takes place at a cost to future survival and fecundity.

Evidence that Swainson's Hawks are capable of increasing their reproductive effort comes from the fact that pairs that had produced a clutch of 3 were as capable of raising 4 young as were pairs which had naturally produced clutches of 4. This argument ignores the cost of producing a fourth egg, a cost which may be particularly important if there is a constraint on the ability of Swainson's Hawks to form additional eggs. However the experiment did indicate that breeding pairs are capable of adjusting their levels of parental investment during the nestling period. Schmutz et al. (1980) also performed brood enlargement experiments on Swainson's Hawks. They did not compare survival of same-size experimental and control broods but compared the survival of manipulated broods of three or less to those of four or five (three was the maximum natural brood size recorded in their study). They found that 88% of the enlarged broods produced at least one young but that larger broods (4 - 5 young) produced at least one young less often than did smaller broods (1 - 3 young). Schmutz et al. (1980) do not state how many young were added to broods or the initial size of broods subject to manipulation, information which is needed to properly interpret their results. In addition, as pointed out by Nur (1988b)

enlarging brood sizes beyond the range normally experienced by the population may not be an adequate test of parents ability to adjust their reproductive effort.

Although the amount of fresh prey at nests of SYN broods was not significantly greater than that discovered during visits to nests of ASYN broods, an increase in the amount of food delivered to SYN broods (presumably as a result of an increase in begging) has been noted in Herring Gulls (Graves et al. 1984) and Cattle Egrets (Fujioka 1985b; Mock and Ploger 1987) and may have also occurred in this study. This suggests that, in at least some species, parents must forage more to provision synchronous as opposed to asynchronous broods. Finally, parents of SYN broods raised more chicks (in 1987 and 1989) than did parents of ASYN broods and thus invested more energy in the brood than they would have had they been left undisturbed.

Unfortunately, it was beyond the scope of this study to determine the long-term cost of the increase in breeding effort experienced by the parents of SYN broods. However, life history theory (Murphy and Haukioja 1986; Nur 1987) assumes a trade-off between breeding effort in one year and subsequent survival and fecundity. Evidence for such trade-offs has been provided for several species (Roskaft 1985; Gustafsson and Sutherland 1988; Nur 1988b; Dijkstra et al. 1990). It is important to recognize, therefore, that the manipulations of hatching asynchrony carried out in this

study also had the effect of manipulating the amount of parental care provided to SYN broods, presumably at a cost to the parents of those broods.

C. The Sibling Rivalry Hypothesis

The results of the manipulation experiments provide support for the contention that hatching asynchrony in Swainson's Hawks may be explained by Lack's Brood Reduction Hypothesis. As discussed above, alternative explanations for the adaptive significance of hatching asynchrony are not generally supported by data from the Swainson's Hawk. The one exception to this is the Sibling Rivalry Hypothesis. Nestling Swainson's Hawks in this study did show evidence of the type of sibling aggression assumed by the hypothesis and advantages in fledging mass observed in older brood members are also consistent with the hypothesis. Bechard (1980, 1983) argued that aggression and siblicide were important in the ecology of nestling Swainson's Hawks. However, his argument was based on the presence of cannibalized chicks which he assumed to be the victims of siblicide. Cannibalism was also common in this study but the evidence indicates that most victims of cannibalism died as a result of starvation rather than direct sibling aggression.

An appropriate test of the Sibling Rivalry Hypothesis
would involve detailed behavioural observations on the
frequency of sibling aggression in ASYN and SYN broods.
Limited observations did not suggest that sibling aggression
was more common in SYN than in ASYN broods; however, the
data are quite limited. The Sibling Rivalry Hypothesis may
still apply in Swainson's Hawks if the establishment of a
stable feeding hierarchy permits the efficient distribution
of food within the brood, but once again the data required
to test this hypothesis were not collected. Thus the Brood
Reduction and Sibling Rivalry hypotheses may act in concert
to maintain hatching asynchrony in the Swainson's Hawk.

D. Conclusions

The results of this study appear to be consistent with
the predictions of the Brood Reduction Hypothesis and may
also support the Sibling Rivalry Hypothesis, but several
questions remain unanswered. I have assumed that fledging
mass is positively correlated with survival and eventual
recruitment to the breeding population. Evidence for such a
correlation exists for some species (Gustafsson and
Sutherland 1988; Nur 1988b; Richner et al. 1988; Tinbergen
and Boerlijst 1990) but not for others (Newton and Moss
1986). As pointed out by Magrath (1990), such information is
essential to any definitive test of the Brood Reduction

Hypothesis but is lacking not only for Swainson's Hawks but for most species in which the degree of hatching asynchrony has been manipulated.

A second area which merits further investigation relates to the costs of reproduction. There is evidence from this, and from other studies, (e.g. Fujioka 1985a,b; Haydock and Ligon 1986; Gibbons 1987; Mock and Ploger 1987) that parents of synchronous broods invest more energy in the breeding effort than do parents of asynchronous broods. However, the costs, in terms of future survival and reproduction, of raising a synchronous brood have yet to be assessed in any species.

Finally, as pointed out by Magrath (1990) there is a need for the development of more quantitative models to test the adaptive significance of hatching asynchrony. Such models allow for the development of explicit, testable predictions but also require detailed information on the biology of the species under study. In addition, the development of models may indicate the type of experiments required to distinguish among complementary hypotheses concerning the adaptive significance of hatching asynchrony.

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