

**PROXIMATE AND ULTIMATE ASPECTS OF SEASONAL VARIATION IN
THE REPRODUCTIVE PERFORMANCE OF OSPREYS**

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PROXIMATE AND ULTIMATE ASPECTS OF SEASONAL VARIATION IN THE

REPRODUCTIVE PERFORMANCE OF OSPREYS

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ABSTRACT

The reproductive ecology of ospreys, *Pandion haliaetus*, breeding at two locations in the Kootenay region of British Columbia, was studied in 1987 and 1988. The types of nest sites used and the feeding ecology were very different at the two locations. The areas also differed slightly in breeding chronology and egg size, but clutch size, hatching success and fledging success did not differ. There was a marked seasonal decline in reproductive success, with later-breeding pairs fledging fewer young than early breeders. The decline was steeper in 1987 than in 1988, but in both years was almost entirely attributable to a seasonal decline in clutch size. In 1987 egg mortality also contributed.

As measured by growth rate and the number and intensity of fault bars in rectrices, the quality of fledglings did not decline during the season, and some evidence suggested that late-hatched chicks were fed more than early chicks. Weather records and measurements of male hunting performance indicated that food availability (influenced by weather) or male (and territory) quality could not explain the observed seasonal decline. The pattern is consistent with the hypothesis that late breeders reduce clutch size in order to be able to invest more in each chick to offset the inherent disadvantage that late fledglings have. The reasons for this, and mechanisms whereby variation in the timing of breeding could be maintained under selection, are discussed.

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To my parents

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CHAPTER I

GENERAL INTRODUCTION

The phenomenon of seasonal breeding trends has long intrigued ecologists interested in avian life histories (e.g. Lack 1947,1948; Klomp 1970; Slagsvold 1982, 1984; Toft et al. 1984). Breeding parameters such as clutch size, brood size, and the number of fledglings usually show a seasonal decline, resulting in lower reproductive output for late breeders. This trend seems to be universal among temperate zone, arctic, and antarctic breeding birds.

Most prominent among birds is seasonal variation in clutch size. Klomp (1970), in an extensive review on the determination of clutch size in birds, discerns two different patterns of intraseasonal change in clutch size. Many single-brooded species exhibit a monotonic decline in clutch size with progression of the breeding season. For multi-brooded species, a short initial increase followed by a later decline is most common. Similarly, inter-seasonal comparisons (e.g. Milne 1974; Korpimäki 1987; Perrins and McCleery 1989) show that when breeding is late, the average clutch size of the population is smaller than in early years. Furthermore, a decline in egg survival (Fisher 1971; Davis 1975; Poole 1984; Davis and McCaffrey 1986; Shaw 1986), in fledging success (see Daan et al. 1988), in recruitment (i.e. the number of survivors to breeding age; Perrins and McCleery 1989), or an increase in nest desertion (Southern 1954,1959; Cavé1968; Newton and Marquiss 1984; Davis and McCaffrey 1986) all have been shown to contribute to the lower reproductive success of late breeders.

The Study

The goal of this study is to describe and investigate seasonal breeding trends of a population of ospreys in the Kootenay region of British Columbia, and to explore factors that may be responsible. This thesis is divided into four chapters. This chapter (I) introduces seasonal breeding trends in birds, the study, and the Kootenay osprey population. I also discuss the various hypotheses proposed to explain seasonal breeding trends. Chapter II describes the general breeding biology and chronology of this population, with particular emphasis on measures of reproductive output. The extent and causes of nest failure, and egg and chick mortality are also discussed. In Chapter III, I document the occurrence of seasonal breeding trends in the Kootenay osprey population, and test predictions from three hypotheses to explain the observed trends. The hypotheses considered are food limitation, parental quality, and climatic factors. The final chapter(IV) discusses the findings within the framework of modern evolutionary theory.

The Osprey

Ospreys, *Pandion haliaetus*, are large, piscivorous birds of prey with a cosmopolitan distribution. They have bred in the Kootenay region for at least several decades (Munro, 1950), but only recently have they reached high local densities. My 1989 population census estimated the total number of active nests in the Creston Valley and Kootenay Lake regions at 150. Although ospreys are particularly concentrated along the Kootenay River in the Creston Valley and along the west arm of Kootenay Lake, these localized nesting concentrations are unlikely to be discrete populations. The overall number of breeding pairs in the region is increasing and young birds born at Creston are mixing with older, established pairs at Nelson. Furthermore, active nests have been found

interspersed between the two areas of highest density. Therefore, I regard the ospreys of the Kootenay region as part of a single breeding population. The separate nesting areas are relatively discrete patches of good breeding habitat within the population area, and therefore presumably filled up first as osprey populations all over North America recovered following the ban on DDT in the early '70s (see Chapter II).

The Kootenay osprey population is migratory and constitutes one of the most concentrated breeding populations in North America. Because the breeding habitat of this population is located relatively far north, the breeding season is much more restricted than that of more southern, non-migratory populations. The importance of this restriction becomes apparent when one considers that the minimum length of their breeding cycle is approximately 22 weeks (Chapter II).

Several characteristics make Kootenay ospreys a suitable subject for a behavioural study on seasonal breeding trends. Aside from the above-mentioned restriction on their breeding season, this population has very exposed and (for raptors) gregarious nesting habits, and conspicuous hunting and feeding behaviour. Furthermore, during the breeding season, ospreys have a well-defined division of labour with the male providing all the fish for the nestlings and the female. Females, on the other hand, spend most of the breeding season on the nest, where they incubate the eggs and brood and feed the chicks. Thus, one can easily discriminate between the individual contributions of males and females to the breeding success of particular pairs.

Ospreys spread their egg laying over several days, and, like most raptors (Newton 1979), begin incubation before they complete their clutches. This often results in eggs hatching over two or more days, creating a size and competitive hierarchy among the

nestlings. This, in turn, can lead to brood reduction or siblicide (Poole 1982). Asynchronous hatching can thus be regarded as an important feature of the breeding behaviour of ospreys.

To date, three studies have documented the existence of seasonal breeding trends in ospreys (Ogden 1977; Judge 1983; Poole 1984). All report a seasonal decline in one or several breeding parameters. However, only Poole tested hypotheses for the observed trends. The variables he examined were parental age, parental breeding experience and food availability, none of which could adequately explain the observed seasonal decline in reproductive success. Poole (1984, p. 98-99) suggests that "late-breeding pairs were either less 'efficient' in their ability to nurture eggs or young, or were less 'committed' to breeding". The results of his investigation suggest that a reduction in reproductive effort (Fisher 1930; Williams 1966) may be responsible for the poor success of late breeders. This thesis will expand on and corroborate Poole's investigation.

Existing Hypotheses

A large number of hypotheses have been proposed to explain avian seasonal breeding trends. In general, the hypotheses address the causal relationship between breeding date and measures of reproductive success on three levels.

PROXIMATE LEVEL OF CAUSATION.— The most common contention is that diminishing food supply during the breeding season energetically constrains egg formation and accounts for the widely observed seasonal clutch size decline (Lack 1966; Perrins 1970; Drent and Daan 1980, but see Meijer et al. 1989). Considerable empirical evidence indicates that females of high nutritional state breed early and have large clutches. Several

studies have shown a positive correlation between courtship feeding rates and female body weight (and hence laying date and clutch size; Brown 1967, Krebs 1970, Nisbet 1973, 1977) and supplemental feeding experiments resulted in advanced breeding dates and higher reproductive success in treatment groups (Drent and Daan 1980; Davies and Lundberg 1985; Arcese and Smith 1988). Studies not in support of the food limitation hypothesis show an inverse relationship between seasonal trends in breeding success and food availability. This has been demonstrated for shags, *Phalacrocorax aristotelis* (Coulson et al. 1969), Ural owls, *Strix uralensis* (Lundberg 1981), sparrowhawks, *Accipiter nisus* (Newton and Marquiss 1984), and five species of ducks in the genera *Anas* and *Aythya* (Toft et al. 1984). In all cases, food availability remained constant or even increased with season while clutch and brood size declined.

Other proximate factors that have been invoked to explain seasonal breeding trends (predominantly in waterfowl and passerines) include adverse weather conditions (Kendeigh 1934, 1941; Johnsgard 1973; Murphy 1986), deterioration of body condition (see Drent and Daan 1980), and reneating (Pinkowski 1977), all of which could result in energetic constraints on breeding. Recently, Meijer et al. (1989) found through field and laboratory food experiments on Eurasian kestrels, *Falco tinnunculus*, that food supply had a direct effect on laying date, but not on clutch size. Their results indicate that clutch size in kestrels is determined neither by food intake rate nor by condition of the female. It has also been suggested that a seasonal decline in hormone levels (Hilden 1964) or stimulation by photoperiod (Dane 1966) might account for reduced clutches in late breeders. Meijer (1988) shows that in the kestrel prolactin levels somehow influence the seasonal regulation of clutch size whereas daylength by itself does not.

ULTIMATE LEVEL OF CAUSATION.— A different class of hypotheses addresses the evolutionary significance of seasonal breeding trends. These hypotheses consider reduction in clutch and brood size in late breeders to be an adaptive response to, for example, diminishing food supply for nestlings and breeding females (Lack 1966), declining probability of breeding success (Trivers 1972; Drent and Daan 1980) or increasing cost of reproduction (Hussell 1972).

Furthermore, evidence for a genetic correlation between breeding date and clutch size (see references in Toft et al. 1984) suggests the existence of a genetic polymorphism. More than thirty years ago, Koskimies (1957) proposed that the tendency to breed early is genetically fixed and that genes for early breeding and large clutches are linked. However, Murphy (1986) argues that, in order to be maintained by natural selection, the genotypes early breeding/large clutch and late breeding/small clutch must have equal fitness and that this is unlikely in light of the many advantages of early breeding.

From yet another perspective, several theoretical models propose that predation pressure is one of the main selective forces that shape the evolution of clutch size in birds (Cody 1966; Perrins 1977; Ricklefs 1977; Slagsvold 1982, 1984; Lima 1987). With respect to seasonal trends, the nest predation hypothesis for passerine birds (Slagsvold 1982, 1984) states that variation in clutch size is an adaptive adjustment that reduces the risk of predation on nestlings and parents when predation pressures are predictably high. Empirical evidence for this hypothesis is very scarce (Slagsvold 1984).

ONTOGENETIC LEVEL OF CAUSATION.— Another category of explanation for seasonal decline in breeding success is based on the age or experience of the breeding

female. It has been well established that young, inexperienced birds breed later in the season and lay smaller clutches than older birds (De Steven 1978; Krapu and Doty 1979; Perrins and McCleery 1985). However, a seasonal decline in breeding success can occur even within a particular age-class (Batt and Prince 1979; Askenmo and Unger 1986).

It should be noted that the breeding experience of one partner could mask age-effects of the other. For example, in species in which the male provides parental care, a young female breeding with an older, more experienced male might lay earlier or lay a larger clutch than an old female paired with a young male (Newton et al. 1981). Another confounding factor in the relationship between female age and clutch size is that fecundity in birds has been shown to decrease with old age (e.g. Newton et al. 1981). Thus variation in the development of individuals, age of partners and pair-bond as well as effects of senescence all influence the ability to reproduce and have to be considered when age is invoked to explain seasonal breeding trends.

To summarize, many hypotheses on different levels of causation have been proposed to explain seasonal breeding trends. However, most are entirely proximate, are usually species or group specific, and thus cannot explain the universal nature of seasonal clutch and brood size decline. It is certain that proximate mechanisms are involved in the seasonal regulation of reproductive parameters, but without consideration of the underlying life history strategies the phenomenon cannot be fully explained. A general model that can provide a more parsimonious explanation for the observed trends is called for (cf. Toft et al. 1984).

CHAPTER II

BREEDING BIOLOGY OF THE KOOTENAY OSPREY POPULATION

Introduction

North American ospreys, *Pandion haliaetus carolinensis*, have received much attention since the 1960s when it was discovered that their populations were declining due to organo-chlorine pesticide pollution. Most field studies during the '60s and early '70s concentrated on assessing the status and productivity of osprey populations. Since then, the species has been considered a biological indicator of environmental problems (for review see Ogden 1977). Following this period, several investigations have examined osprey foraging behaviour (Ueoka and Koplín 1973; Häkkinen 1977; Swenson 1978; Szaro 1978), time and activity budgets (Green 1976; Stinson 1978; Levenson 1979; Jamieson et al. 1982) and the influence of environmental conditions on foraging and time budgets (Grubb 1977; Stinson 1978; Stinson et al. 1987; Machmer and Ydenberg 1989). Several behavioural studies on ospreys have recently addressed topics such as sibling aggression, siblicide, and brood reduction (Poole 1979, 1982; Judge 1980; Jamieson et al. 1983; Hagen 1986; Forbes 1989), but our understanding of the species' breeding adaptations is still in its infancy.

Poole (1982) stressed the importance of comparing breeding behaviour of ospreys in different parts of their range. He suggested that regional differences may be local adaptations since ospreys breed in a variety of ecologically distinct habitats. To date, only two studies have specifically addressed osprey behavioural differences in relation to geographical location and both of these were centered in coastal or southern habitats (Judge 1983, Poole 1984).

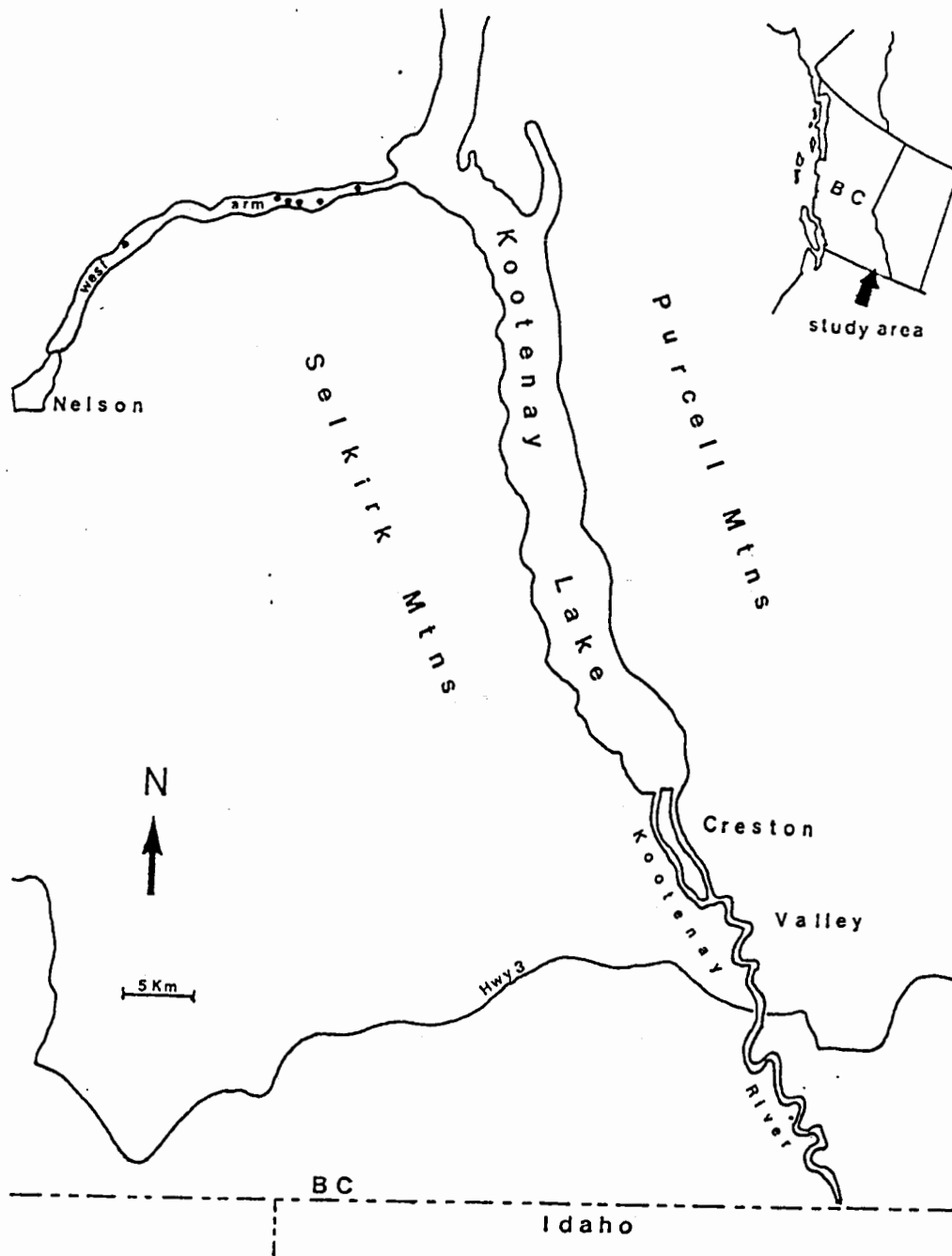
This chapter describes the general breeding biology and chronology of ospreys that breed annually from April to October in the Kootenay region of British Columbia. Early reports indicate that this population was small during the late 1940s (Munro 1950). However, a particularly high abundance of breeding pairs can now be found in two distinct local nesting concentrations: One is situated along the Kootenay River in the Creston Valley (60-65 pairs); the other (40-45 pairs) breeds on the west arm of Kootenay Lake near Nelson. These high numbers of breeding pairs, as well as their exposed and conspicuous nesting habits, offer an opportunity to investigate and compare local breeding characteristics. I have attempted a comparison between the two nesting concentrations within the Kootenay population. Also, on a larger scale, this population is contrasted with other North American populations. The investigation was conducted during the 1987 and 1988 breeding seasons.

Study Areas and Methods

The general study area encompassed two valleys in southeastern British Columbia (Figure 2.1). Although ospreys can be found throughout the entire region, I focused my efforts, for the purposes of this investigation, on the two largest nesting concentrations in the region: the Creston Valley and Nelson area. These two ecologically distinct habitats are separated by the Selkirk mountain range and breeding pairs differ in their nesting and feeding habits.

Ospreys of the Creston Valley nest primarily in riparian stands of black cottonwoods, *Populus trichocarpa*. Most nests are located on the broken tops and dead trunks of these tall trees (15-25 m high). The many shallow, eutrophic lakes, marshes, sloughs, and ponds of the area support an abundance of fish including black bullhead,

Figure 2.1 The study area. The locations of Nelson (117°20'W, 49°30'N), the west arm, Kootenay Lake, Kootenay River, and the Creston Valley are shown. Dots indicate the locations of the nests of the six focal males observed on the west arm during July 1988.



Ictalurus melas, yellow perch, *Perca flavescens*, pumpkinseed, *Lepomis gibbosus*, northern squawfish, *Ptychocheilus oregonensis*, longnose sucker, *Catostomus catostomus*, and largescaled sucker, *C. macrocheilus*. Water levels in the Creston Valley are controlled by the Creston Valley Wildlife Management Area authority. The effects of changing water levels on food availability for this osprey population have been described elsewhere (Forbes 1989).

In the Nelson area, ospreys nest along the west arm of Kootenay Lake and along the margins of the Kootenay River, usually atop man-made structures such as light beacons, pilings, and power poles. Most of these nests are only 5 to 10 m high. Osprey prey species in this area include largescaled sucker, mountain whitefish, *Prosopium williamsoni*, rainbow trout, *Oncorhynchus mykiss*, and kokanee, *O. nerka*.

Human interference is minimal in the Creston Valley. In contrast, along the west arm of Kootenay Lake many local residents and recreationists live in close proximity to breeding ospreys and numerous pilings and nest platforms have been set up that artificially increase the availability of nest sites. Although ospreys are generally very tolerant of human proximity, highway traffic and summer recreational activities (French and Koplín 1977), a total of seven nests failed due to excessive human disturbance. These nests were excluded from most analyses.

At the beginning of each breeding season, both areas were searched thoroughly for nests and breeding pairs. A subset of easily accessible nests was checked on a weekly basis (39 in 1987, 41 in 1988). These closely-monitored nests form the basis of most analyses and demographic data reported. Most other nests monitored received a minimum of three visits per season, while some were only visited during the fledging period. Thus sample

sizes vary among analyses. Observers either climbed to the nests (using standard tree and rock climbing equipment) or observed them with the aid of binoculars and spotting telescopes. Some nests located on powerline structures were accessed with bucket-trucks from local power supply companies. Status and productivity were determined following Postupalsky (1977).

Upon arrival at their breeding site, many Kootenay ospreys find their nest occupied by an incubating Canada goose, *Branta canadensis*. I surveyed all known nests in spring of 1988 to determine the extent of osprey nest occupancy by geese. Some ospreys responded to the temporary loss of their nests by building new nests. A nest was considered built in response to a goose, if it was located less than 200 m from the old nest and in the closest possible site. These nests were called 'alternate' nests (Postupalsky 1977).

At each nest visit, egg size, clutch size, or brood size was determined. Eggs were weighed with Pesola spring balances and egg length and breadth as well as chick culmen length were measured with Vernier calipers. Hoyt's (1979) equation was used to calculate egg volume. Clutch initiation dates were determined either from known dates of first eggs or by back-dating from hatching dates of first hatchlings. Hatching dates were determined either by direct observation or by assessing age of chicks using a culmen length(x)-age(y) regression derived from known-age chicks ($y = -13.6 + 1.5x$, $r^2 = .96$, $n = 40$; cf. Poole 1984) as a predictor.

During July 1988, I determined the composition of prey taken by ospreys on the west arm of Kootenay Lake. Males from six selected nests were observed for a total of 288 hours (see Chapter III). After a successful hunt, ospreys carry away prey in their talons. Thus, it was possible to identify the species of fish captured. Size of captured fish

was estimated as a proportion of the osprey's tail length (20 cm). Biomass of fish was calculated using length-mass regressions for the various species (Forbes 1989) and energy equivalents are based on values given in Watt and Merrill (1975). If a value could not be obtained for a particular species, that for the most closely related species was used.

Results

STATUS AND PRODUCTIVITY.— The status and success of all known osprey nests is summarized in Table 2.1. Overall nest success (proportion of nests with at least one fledgling) did not differ between the two areas, but did differ between years. The total number of known nests increased by 21 nests from 1987 to 1988. This increase resulted mainly from construction of new nests at the beginning of the 1988 breeding season. Twenty of these new nests were built in response to occupation of nests by Canada geese and are considered alternate nests (Postupalsky 1977). In the Creston Valley, during April and early May of 1988, geese occupied 26 (52%) of all osprey nests that were potentially available as nesting sites (i.e. located close to a body of water). In the Nelson area, 24 (60%) of the available osprey nests were occupied by geese.

NESTING SITES.— In the Creston Valley, 59 (83%) of 71 nests were on broken tops and dead trunks of tall black cottonwoods. The other 12 nests in the Creston Valley were located on pilings (3), power poles (6) and bridges (3). During 1987 and 1988, 24 nests disappeared due to strong winter storms that either blew down nests or caused cottonwood snags to fall. This combination of highly exposed nests on trees in advanced stages of decay, and violent windstorms is responsible for the high turnover rate of nests in this area. Similar results were obtained by Dunstan (1968) for a Minnesota population where 7% of 203 nests blew down from dead tree tops.

Table 2.1 Status and success of all osprey nests surveyed. The number in each category is given.

Nest Status	1987			1988		
	Creston	Nelson	Total	Creston	Nelson	Total
Known nests	60	37	97	71	47	118
Occupied	45	37	82	49	40	89
Successful ¹	33	28	61	29	22	51
1 fledgling	9	4	13	9	5	14
2 fledglings	14	14	28	12	10	22
3 fledglings	10	10	20	8	7	15
Unsuccessful	9	9	18	17	15	32
Undetermined	3	0	3	3	3	6
Unoccupied	15	0	15	22	7	29

¹location: ns; year: $\chi^2=4.72$, df=1, P<.05

In the Nelson area, the vast majority 45 (96%) of 47 nests were built on man-made structures. Twenty-nine of these nests were on pilings and seven on beacons located on the west arm of Kootenay Lake. Furthermore, seven nests were found on power poles, one on a tele-communication tower, and one on a power dam on Kootenay River. Only two nests (4%) were built on trees; one on a black cottonwood, the other on a broken-top Douglas fir, *Pseudotsuga menziesii*. In general, the Nelson area does not provide as many tall snags for nest sites as does the Creston Valley and thus the density of breeding pairs in this area depends on the availability of artificial nesting sites.

BREEDING CHRONOLOGY.— Ospreys return to their Kootenay breeding grounds at the beginning of April with the males preceding the females by one or two weeks. The population seems to overwinter in Central or South America as suggested by ring returns from Costa Rica (1988) and Ecuador (1989; Steeger, unpubl. data). These wintering locations are consistent with the findings of Melquist et al. (1978) and Melquist and Johnson (1984) for northern Idaho and eastern Washington ospreys. Before clutch initiation ospreys engage mainly in nest building or refurbishing, and in courtship displays and courtship feeding. Although no systematic observations were conducted during the pre-incubation period, the conspicuous 'sky dance' of males was observed on several occasions. It usually involved a series of about 10 to 15 (in one instance 45) rapid dives in mid-air accompanied by high-pitched vocalizations and presentation of a fish. Levenson (1979) reported that during the pre-incubation period, males are engaged in courtship flight 1.8 % of daylight time and 2.8 % is spent on supplying nest material. The activity levels of females during this period are significantly lower. In the Kootenay region, nest site disputes with Canada geese are frequent during April and attacks of 10 to 15 consecutive dives on nesting geese were observed on several occasions.

Initiation of clutches spanned 42 days in 1987 (April 30 - June 10, n=39 clutches) and 38 days in 1988 (April 25 - June 1, n=41 clutches). Most (87%) females started laying between April 29 - May 23. There was a significant difference in clutch initiation dates between the two areas, whereas no significant difference was observed between years (Table 2.2). For both years combined, median laying dates in the Creston Valley and Nelson area were May 8 and May 12, respectively (Figure 2.2). The frequency distributions of clutch initiation dates show different patterns for the two areas. In the Creston Valley, 61% of all clutches were initiated during 10 days around the beginning of May, whereas Nelson area ospreys show a much more even distribution over the entire laying period (Figure 2.2). Based on five nests for which laying date of first egg and hatching date of first chick was known exactly, the mean (\pm s.) incubation period was 38.5 ± 1.1 days. The minimum incubation period of seven other nests fell within the range of 36 -42 days.

In both years hatching commenced in the first week of June and all chicks had hatched by July 8, except for one extremely late singleton which hatched on July 16, 1987. No data could be collected on exact fledging dates. However, several chicks were observed practicing wing-flapping on the nest and some chicks had fledged before our last nest visit in early August. On the basis of these observations the nestling period was estimated at approximately 55 days. Adults leave on migration prior to their young. The last adults are usually seen in the Nelson area around mid- September, whereas young do not seem to depart until the end of September or beginning of October.

FEEDING HABITS.— Diet composition differed markedly between locations (Table 2.3). In the Creston Valley, ospreys primarily captured black bullhead, yellow perch, pumpkinseed, and, to a lesser extent, rainbow trout, and longnose and largescaled suckers (Forbes 1989). However, even within the Creston Valley, local abundance of different fish

Table 2.2 Summary statistics by year and location for each breeding parameter. Statistics presented are mean \pm S.E. (n). Sample size increases for successive nesting stages as more nests could be included.

	1987		1988		Total
	Creston	Nelson	Creston	Nelson	
Clutch initiation date ¹	May 10 \pm 2d (15)	May 14 \pm 2d (24)	May 6 \pm 2d (21)	May 13 \pm 2d (20)	- (80)
Clutch size ²	2.7 \pm 0.2 (15)	2.7 \pm 0.1 (27)	3.0 \pm 0.1 (24)	2.8 \pm 0.1 (21)	2.8 \pm 0.1 (87)
Brood size at hatching ³	2.2 \pm 0.3 (15)	1.6 \pm 0.2 (27)	2.1 \pm 0.2 (24)	2.0 \pm 0.2 (21)	2.0 \pm 0.1 (87)
Brood size at fledging ⁴ (per successful nest)	2.0 \pm 0.1 (33)	2.2 \pm 0.1 (28)	2.0 \pm 0.1 (29)	2.1 \pm 0.1 (22)	2.1 \pm 0.1 (112)
Brood size at fledging ⁵ (per occupied nest)	1.6 \pm 0.2 (42)	1.7 \pm 0.2 (37)	1.2 \pm 0.2 (46)	1.2 \pm 0.2 (37)	1.4 \pm 0.1 (162)

Two-way ANOVA results: ¹ location: P < .05, year: ns; ^{2,3,4} location: ns, year: ns; ⁵ location: ns, year: P < .05.

Figure 2.2 Frequency distribution of clutch initiation dates (1987 and 1988 combined). The first period begins on April 24 and the last period ends on June 10. Arrows indicate medians: Creston = May 8, Nelson = May 12.

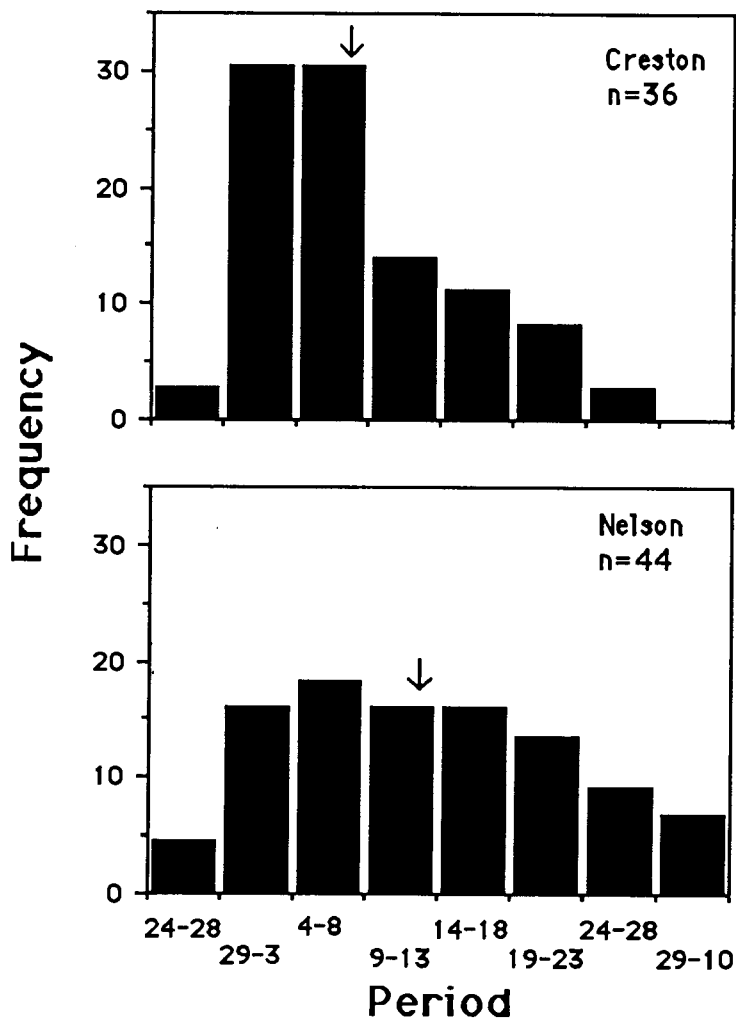


Table 2.3 Number, biomass (% of total), and estimated average energy content (kJ) of fish caught by male Ospreys in the Creston Valley and on the west arm of Kootenay Lake.

Species	CRESTON ^a (Corn Creek Marsh)			NELSON (Kootenay Lake)		
	No.	% biomass	kJ per fish	No.	% biomass	kJ per fish
Sucker sp.	7	9	1176	29	78	3210
Mountain whitefish	0	0	-	15	10	786
Rainbow trout	7	8	930	16	8	604
Kokanee	-	-	-	7	2	391
Black bullhead	59	44	569	0	0	-
Yellow perch	18	12	525	0	0	-
Pumpkinseed	54	21	275	0	0	-
Other ^b	9	6	-	5	2 ^c	-
Total	154	21318g	-	72	28533g	-
Weighted Average	-	-	472	-	-	1629

^a Forbes (unpubl. data)

^b Creston: includes kokanee, northern squawfish, largemouth bass, and unidentified; Nelson: unidentified

^c estimated from average length-mass relationship of whitefish, trout and kokanee. Suckers were very distinctive and extremely unlikely to be unidentifiable.

species varies considerably. While ospreys nesting in the vicinity of Corn Creek Marsh and Leach Lake primarily feed on bullhead, perch, and pumpkinseed (Forbes 1989), those nesting close to Kootenay Lake typically capture suckers and trout (pers. obs.).

The diet of Nelson area ospreys consisted primarily of largescaled or longnose suckers followed by mountain whitefish, rainbow trout, and kokanee (Table 2.3). The difference in diet between Creston and Nelson is therefore likely to be entirely due to differences in hunting habitat. On the west arm of Kootenay Lake, suckers are large (average size: 41 ± 8 cm, $n=29$) and abundant along the shallow shoreline. On several occasions ospreys captured suckers, but were unable to lift them out of the water (presumably because fish were too heavy). In these instances, the ospreys swam to shore and dragged the fish onto the beach. On one occasion, after taking only about 60 bites, the osprey abandoned its prey. Subsequent measurements revealed the fish was 50 cm long and the remains weighed 1050 g.

Fish captured by Nelson area ospreys contain significantly more energy (weighted mean = 1629 kJ) than Creston Valley prey (weighted mean = 472 kJ; $U=2477$, $df=1$, $P<.001$, Table 2.3). This difference is largely due to the greater number and size of suckers captured on Kootenay Lake. Suckers delivered to nests at Corn Creek Marsh in the Creston Valley weighed much less than their Nelson counterparts (mean = 274 g, $n=7$ vs mean = 767 g, $n=29$, respectively; $U=36$, $df=1$, $P<.01$). All fish caught in the Creston Valley were caught by flight-hunting, whereas 26% (16/61) of all observed fish caught on Kootenay Lake were captured by the energetically-inexpensive perch-hunting method.

REPRODUCTIVE PARAMETERS. — Mean sizes of Kootenay osprey eggs are presented in Table 2.4. A two-way ANOVA indicated that location had a significant effect on egg size, however no significant difference was detected between years. Overall, the average egg sizes in the Creston Valley and Nelson area were 69.1 ± 5.9 cm³ and 66.6 ± 5.6 cm³, respectively. To date, the only detailed investigation on the significance of egg size in ospreys has been conducted by Poole (1984). Using Poole's egg size data (Poole 1984, his Table 2.1), I compared the average egg size of three and four-egg clutches between coastal Massachusetts (Westport) ospreys and the Kootenay population. Egg size differed significantly between the two populations with larger eggs being laid in the Kootenay region (Westport: mean (\pm s.) = 64.9 ± 4.1 , Kootenay: mean (\pm s.) = 68.2 ± 5.1 ; $t=2.3$, $df=15$, $P < .05$).

Mean clutch size, brood size at hatching, and brood size at fledging (per successful nest) did not differ significantly between locations, nor did it change between years (Table 2.2). The average number of fledglings produced per occupied nest did differ between years, being lower in 1988. Overall, clutch sizes averaged 2.8 eggs, brood sizes at hatching averaged 2.0 chicks, and brood sizes at fledging averaged 2.1 and 1.4 chick per successful and occupied nest, respectively. The commonest clutch in both areas was three eggs, and this was also the most productive (Table 2.5). A comparison between one and two-egg clutches and three and four-egg clutches revealed that the larger clutches were significantly less likely to fail completely ($\chi^2=13.86$, $df=1$, $P<.001$). However, this trend was primarily due to the total failure of all one-egg clutches (Table 2.5).

EGG MORTALITY.— Total egg mortality for both years combined was 30% (83/276). This is based on 98 nests for which data could be obtained. Of these, 11 nests should be excluded for various reasons (see Table 2.5). Natural egg mortality in the remaining 87

Table 2.4 Summary statistics by year and location for egg volume. Statistics presented are mean \pm S.E. (n). Egg volume computed from length and width measures using Hoyt's (1979) formula. Not all eggs were measured for volume.

Location	Egg volume (cm ³) ¹	
	1987	1988
Creston	68.7 \pm 0.9 (40)	69.4 \pm 0.7 (68)
Nelson	66.0 \pm 0.6 (74)	67.2 \pm 0.7 (67)

¹Two-way ANOVA result: location: P = .001, year: ns.

Table 2.5 Mean number of hatched and fledged young in relation to clutch size.

Clutch size	n ¹	Percentage of all clutches	Mean No. of young hatched per clutch	Mean No. of young fledged per clutch
1	5	5.7	0.4	0
2	12	13.8	1.5	1.2
3	66	75.9	2.2	2.0
4	4	4.6	1.8	1.8

¹ The text (p. 21) reports 276 eggs in 98 clutches. Represented here are 243 eggs in 87 clutches. Eleven of the 98 nests are not included in this table because of egg chipping during handling, manipulation of clutches for experiments (Forbes 1989), or nest failure due to excessive disturbance by local residents.

clutches which includes the 80 closely-monitored nests was 22% (53/243). Causes of egg mortality were hatching failure (n=32), disappearance (n=40), breakage (n=5), and human disturbance (n=6). The exact causes of hatching failures could not be determined in every case. Five recovered eggs contained partially-developed embryos. Aside from these eggs, the nests contained one or two older chicks (approximate ages between 10 and 18 days) indicating that the females may have stopped incubating these five eggs, which would otherwise have hatched viable chicks. Another cause of hatching failures was lack of fertilization. Two eggs were found without partially developed embryos (i.e. they had not been fertilized). Most eggs that disappeared without leaving a trace (63%) were lost with entire clutches. Six of 10 lost clutches contained three eggs and one four-egg clutch also disappeared. Since all these clutches were lost early in the laying period, it seems unlikely that they were abandoned by the females. I think it likely that egg predation by, for example, racoons, *Procyon lotor*, crows, *Corvus brachyrhynchos*, ravens, *C. corax*, or gulls, *Larus sp.*, was responsible for the failure of these nests. Predation may also have been responsible for the failure of nests in which eggshell remains were found. Two nests in the Nelson area, both containing three eggs, failed due to constant human activity around the nest. These nests were either depredated while the female was disturbed, or were abandoned by the female.

CHICK MORTALITY.— Total chick mortality during the two years of this study was 10% (19/193). Chicks that died were either singletons (n=7), C-chicks (n=4), B- or C-chicks (n=6), or of unknown rank (n=2). All chick mortality was very likely due primarily to siblicide or selective starving of junior chicks (Forbes 1989). Several chicks were found dead in the nest, extremely emaciated or with severe wounds on head and neck. On one occasion, a brood of three young chicks (one, two and four days of age) was removed from their nest for measurements during a survey. We noticed fresh head wounds on the

C-chick. In our presence, the chicks began fighting. The A-chick continuously pecked at the head and neck of the C-chick until we separated them. When the nest was visited again a week later the C-chick had disappeared. An incidence of selective starving of a junior chick during a period of severe food shortage which resulted in the death of the chick is described in Forbes (1989).

The loss of a singleton is more enigmatic since no siblings could be responsible for its demise and parents should be able to provide sufficient food for a single chick. Lost singletons did not hatch later in the nestling period than did singletons that were reared successfully ($n=10$; $U=25$, $df=1$, $P>.05$). However, lost singletons came from significantly smaller clutches than singletons that survived to fledging ($n=10$; $U=13$, $df=1$, $P<.05$).

Discussion

STATUS AND PRODUCTIVITY.—Based on mortality rates from U.S. east coast banding data, Henny and Wight (1969) calculated that 0.95 to 1.30 fledged young per occupied nest are required to maintain a stable osprey population. During this study, the values obtained for the Kootenay population fell within or exceeded this range. At the beginning of the 1988 breeding season, many osprey pairs found their nests occupied by Canada geese and were forced to build new nests or to delay breeding. It is possible that this contributed to the low success rate in 1988. Unfortunately, no comparable information on goose interference is available for 1987. Nevertheless, the results indicate that this osprey population is stable or still increasing.

The increase in population size since the late 1940s and especially over the last 15 - 20 years (Guy Woods, B.C. Dept. of Fish and Wildlife, Nelson, pers. comm.) can largely be attributed to the management of water bodies and fish populations in the region, and to a general decrease in human persecution. Water levels are controlled in the Creston Valley by a series of dykes and culverts which have created numerous shallow ponds, sloughs, and marshes with healthy fish populations (Flook and Forbes 1983). In the Nelson area, the construction of several dams and the control of water levels have resulted in clearer water and many shallows along the shore of Kootenay Lake. In these shallow areas bottom-feeders such as suckers and mountain whitefish have become easy targets for ospreys. In addition, the fast growing black cottonwoods in the Creston Valley as well as the many nesting platforms on Kootenay Lake ensure a steady supply of nesting sites.

In general, the factors responsible for the well being of the Kootenay osprey population largely parallel those found for other inland populations in North America. Many populations have recently experienced the creation of new habitat or improvement of previously occupied habitat and have consequently increased in size (Van Daele and Van Daele 1982, and references therein).

BREEDING CYCLE.— Most Kootenay ospreys arrive at their breeding site by the second week of April. Egg laying begins in late April and by the end of May most females have initiated their clutch. The observed difference in clutch initiation dates between the two areas is surprising. Evidence suggests that young, inexperienced birds initiate clutches at a later date than older birds (review in Perrins 1970). Thus it might be possible that ospreys breeding in the Nelson area are on average younger than Creston Valley ospreys. Alternatively, differences in responses to Canada geese may explain the observed trend. While Creston Valley ospreys tended to build alternate nests when they found their old nest

occupied by geese, most Nelson area ospreys waited until geese vacated their nests. It was also found that those pairs that moved into a previously goose-occupied nest started breeding later than unaffected pairs (Steeger, unpub.data). More information is needed for a conclusive explanation.

Despite the fact that some pairs were delayed by geese, most females laid their clutches within a period of about four weeks. This narrow range of clutch initiation dates is characteristic of northern, migratory osprey populations (Kennedy 1977, Prevost et al. 1978). In contrast, sub-tropical, non-migratory populations exhibit an earlier and more protracted clutch initiation period. For an osprey population breeding in the Gulf of California, Judge (1983) reported a laying period of 9 - 10 weeks, from early January to early March. Similarly, Florida Bay ospreys initiate clutches over a three month period starting in late December (Ogden 1977). This latitudinal trend is not unique to ospreys. With an increase in latitude, birds lay later, more synchronous clutches and have shorter breeding seasons. For example, clutch initiation of peregrine falcons, *Falco peregrinus*, spans six weeks from late March in the southern temperate zone, five weeks from late April in the southern boreal zone, and only three to four weeks in the arctic where laying does not begin before late May (Newton 1979, p. 98). In addition, pre-incubation and post-fledging periods in peregrines are also shorter in more northern populations.

Given estimated periods of four weeks for pre-incubation, 5.5 weeks for incubation, 7-8 weeks for rearing of chicks, and a post-fledging period of five weeks, the breeding season of Kootenay ospreys totals approximately 22 weeks. No comparative data are available for more southern populations. However, considering that selection for shorter breeding cycles increases as one moves northward, I expect longer breeding seasons for more southern or non-migratory osprey populations.

FEEDING HABITS.— Creston Valley and Nelson area ospreys differ greatly in their feeding habits. There were differences in the species and size of fish caught, and in the methods used to catch them. The many eutrophic ponds, sloughs, and marshes in the Creston Valley are warmer and shallower than the west arm of Kootenay Lake which accounts for the differences in the fish fauna of these two areas. Due to the shallow margins of the west arm of Kootenay Lake and favourable perch sites, Nelson area ospreys frequently use the less energy-costly perch-hunting method. On the west arm, the males usually perch either on pilings in the shallows or on trees along the lakeshore. These perch sites are ideal for detecting the large, slow moving suckers which feed on the bottom vegetation along the shallow shore. In contrast, ospreys in the Creston Valley have rarely been observed perch-hunting which, at least in part, is due to the lack of perch sites close to the fishing grounds. Although it is difficult to assess how actively perching ospreys hunt, it is certain that much less energy is expended during perch-hunting than during flight-hunting. Thus, it appears that the feeding situation in the Nelson area is more favourable than in the Creston Valley: Not only are individual prey items larger, they also require less energy to capture.

EGG SIZE.— An interspecific comparison (Newton 1979) revealed that ospreys lay small eggs relative to their body size. This and the fact that fish are abundant in the Kootenay region suggests that egg size is not constrained by food availability in this population. Why, then, do Nelson area ospreys lay smaller eggs than their Creston Valley counterparts? Poole (1984) found evidence that egg size of female ospreys increases with age. In this study, I was not able to determine the ages of adult ospreys in the Kootenay population. However, in light of the evidence that laying date and egg size are correlated with age of female (see also Newton 1979) and, considering that Nelson area ospreys start

laying later and lay smaller eggs than Creston Valley ospreys, it is possible that the Nelson area nesting concentration consists of younger birds. This raises the question of why there should be a difference between the two areas in the average age of breeders. The most likely explanation is that new nesting opportunities for young ospreys have recently been created in the Nelson area. During the two years of this study, numerous man-made platforms were set up on the west arm of Kootenay Lake. Many of these newly created nesting sites were immediately occupied by an osprey pair. Furthermore, under favourable conditions birds tend to breed at a younger age than usual. For example, Newton (1976) found in Scottish Sparrowhawks that breeding by first year females was more common in valleys, where food was abundant, than on the hillsides, where food was scarce. Thus, the better feeding habitat on the west arm of Kootenay Lake (see earlier discussion), could explain why more younger ospreys would breed in the Nelson area.

Alternatively, the different feeding conditions in the Creston Valley might select for larger egg sizes. Since larger eggs give rise to larger, more resilient chicks (review in O'Connor 1979), large eggs might be an insurance against possible food shortage during the critical early nestling period. The fact that the Westport ospreys have smaller eggs than ospreys at either of the Kootenay locations suggests that age alone may not be responsible. The Westport ospreys were mature adults (i.e. not young breeding pairs, Poole 1989), but did exploit a completely different feeding situation than ospreys in the Kootenay region.

CLUTCH SIZE AND MORTALITY RATES.— The two osprey nesting areas of this study did not differ in average clutch size, brood size at hatching, or number of young reared to fledging. All one-egg clutches were laid late in the season and failed. This suggests these parents were either low quality or young, inexperienced birds.

Judge (1983) compared mean clutch sizes from different geographical regions in North America. Her results indicate that southern, non-migratory osprey populations tend to have smaller clutches than northern populations. Consistent with this notion are Poole's (1984) results from the U.S. east coast (Table 2.6). However, this study as well as an investigation on west-central Idaho ospreys (Van Daele and Van Daele 1982) found clutch sizes to be as low as those of southern populations (Table 2.6). It appears that an analysis of clutch size in isolation from other life history variables may be misleading. Although Table 2.6 indicates no obvious trend in hatching success among ospreys from the different geographical regions, nestling survival is clearly higher in northern populations.

The larger average clutch sizes of ospreys in the northeastern U.S. are due to the higher proportion of four-egg clutches in these populations. For example, Poole (1984) found 31% of 97 clutches in the Westport colony to contain four eggs. His evaluation of the pattern of egg and chick failure indicated that egg failure rates were equal for three and four-egg clutches, brood reduction was more severe in broods of four, and 20% of the fourth eggs laid produced fledglings. These results are consistent with the hypothesis that fourth eggs are "insurance eggs" (Dorward 1962, Mock 1984) against the loss of earlier produced eggs and chicks. If the probability of egg or chick loss varies among populations, one can expect the production of "insurance eggs" to vary accordingly, which, in turn, would result in different clutch sizes.

The results of this study show that although Nelson area ospreys apparently enjoy a more favourable feeding situation than do Creston Valley ospreys, only minor differences could be detected between measures of their breeding performance. These are perhaps attributable to differences in the age structure of the birds breeding in the two areas. It is possible that younger, more inexperienced birds breed in the Nelson area, and that this

Table 2.6 Geographic comparison of mean clutch size (\pm S.E.), percent hatching success, and percent nestling survival for North American Osprey populations. Where values for different years were reported, the mean was taken for all years combined. Reproductive values reported prior to 1977 were excluded (e.g. reports in Ogden 1977) because they are possibly confounded due to pesticide contamination.

Location	Latitude/Longitude	Mean Clutch Size	Percent Hatching Success	Percent Nestling Survival	Source
Florida Bay	25°08'N/80°55'W	2.7 \pm 0.06	80	53	a
Gulf of California	28°57'N/113°33'W	2.8 \pm 0.08	63	64	b
Westport	40°32'N/71°05'W	3.3 \pm 0.05	72	86	c
Eastern Long Island	41°N/72°30'W	3.2 \pm 0.06	69	88	a
Gardiners Island	41°N/72°30'W	3.2 \pm 0.06	61	72	a
West-Central Idaho	44°30'N/116°W	2.6	-	-	d
West Kootenay	49°30'N/117°20'W	2.8 \pm 0.06	78	90	this study

a = Poole 1982, Table 2; b = Judge 1983, Table 2; c = Poole 1984, Tables 4.2 and 4.3; d = Van Daele & Van Daele 1982, missing values were not available.

explains their slightly later clutch initiation date, and their smaller eggs. Birds in both areas were equally successful in rearing young that hatched, however.

With respect to the inter-population comparison, Kootenay ospreys have relatively small clutches with large eggs. These eggs have a high probability of hatching and the population exhibits the highest survival rate of nestlings of all North American osprey populations for which comparable data are available. There are much greater differences among North American osprey populations in aspects of their breeding behaviour than those observed between Creston and Nelson, and we are only beginning to understand the complex interactions of proximate mechanisms and life history strategies responsible for these observed differences. In the next chapter, I will address how seasonality affects the breeding performance of Kootenay ospreys and explore factors which may be responsible for the observed trends.

CHAPTER III

SEASONAL BREEDING TRENDS

Introduction

Over the last two decades, the seasonal decline in reproductive success of breeding birds has been well documented in the literature (Lack 1966, Klomp 1970, Hussell 1972, Toft et al. 1984, Daan et al. 1988). Klomp (1970) found 115 species from eight orders that exhibited seasonal clutch size variation, but he could not provide much data on the order Falconiformes. A review of the recent literature (Table 3.1) shows that seasonal declines in clutch size, brood size, and number of fledglings do occur in raptors as well (see also Newton 1979).

The main hypotheses that have been proposed to explain the existence of seasonal breeding trends in raptors include food availability, parental quality, parental age or experience, and climatic factors (Table 3.1, see also Chapter I). Few of these have been tested. The most extensive, long-term studies on wild-living raptors that have addressed causal factors for the observed trends are those conducted on the sparrowhawk (Newton and Marquiss 1984), the Eurasian kestrel (Daan et al. 1988), and the osprey (Poole 1984).

In sparrowhawks of southern Scotland, Newton and Marquiss (1984) found seasonal declines in clutch size and nest success in every year, habitat and age group during an 11 year study. Despite an increasing seasonal trend in food abundance, breeding performance of female sparrowhawks declined as egg laying was delayed. The success of females was correlated with body weight which, in turn, was based on the amount of food delivered by males. Poor hunters or individuals breeding in low quality habitats bred later and had the smallest clutches. Therefore, Newton and Marquiss suggest that local

Table 3.1 Seasonal decline in breeding parameters in raptors.

Species	Country	Clutch Size	Brood Size	Number of Fledglings	Hypotheses Proposed ¹	Source
<i>Falco tinnunculus</i>	France	d	-	-	FA, PA	Bonin & Strenna 1986
	Scotland	sd	-	sd	CF, PQ	Village 1986
	Netherlands	d	-	-	FA	Dijkstra et al. 1982
<i>Falco sparverius</i>	USA	sd	-	sd	CF, PQ	Cavé 1968
		-	sd	sd	FA, CF	Toland 1985
		sd	sd	sd	PQ, PA	Newton & Marquiss 1984
<i>Accipiter nisus</i>	Netherlands	sd	nsd	sd	FA	Schipper 1979
<i>Circus cyaneus</i>	Scotland	sd	d	sd	PQ	Picozzi 1984
<i>Circus pygargus</i>	Netherlands	nsd	sd	nsd	FA	Schipper 1979
<i>Circus aeruginosus</i>	Netherlands	sd	sd	sd	FA	Schipper 1979
<i>Pandion haliaetus</i>	USA	sd	sd	sd	PA, PQ	Judge 1983
<i>Hieraaetus spilogaster</i>	Zimbabwe	nsd	sd	nsd	FA, PA, PE	Poole 1984
<i>Buteo buteo</i>	Germany	-	-	sd	CF	Hustler & Howells 1988
		d	d	d	FA	Mebs 1964

¹ CF = climatic factors; PQ = parental quality; FA = food availability; PA = parental age; PE = parental experience
d = decline reported but significance level not reported
sd = significant decline;
nsd = non-significant decline

variations in prey availability and individual variations in male hunting efficiency (i.e. male quality) were responsible for the observed trends .

Similar results were obtained by Daan et al. (1988) in their exploration of the interrelationship between laying date, clutch size and food supply in the Eurasian kestrel. Clutch size and brood size in the kestrel also declined with progression of the season although food supply increased. Daan et al. (1988, their Fig.2) show that clutch initiation dates and male provisioning rates (courtship feeding as well as prey delivery after clutch initiation) are negatively correlated. They conclude that the declining seasonal trend in reproductive success is entirely caused by differences in male provisioning ability.

Poole (1984) reported a seasonal decline in reproductive success for a population of coastal Massachusetts ospreys. His examination of factors which may have been responsible for this decline showed that neither food availability, nor parental age or experience could explain the observed breeding trend. However, there was evidence that courtship feeding rates were lower in later breeding pairs. Poole proposed that the lower reproductive success of late breeders is caused by a seasonal decline in reproductive effort, rather than by worsening conditions or lower quality of those pairs. However, Poole did not assess parental quality directly by, for example, measuring the males' ability to provide food for females and nestlings.

This chapter investigates the extent of seasonal variation in egg size, clutch size, brood size, number of fledglings, hatching asynchrony, and nestling quality in the Kootenay osprey population. I attempt to test whether seasonal variation in a) food availability, b) paternal quality, or c) climatic factors influence reproductive success.

Finally, I discuss the possible evolutionary significance of seasonal breeding trends in ospreys.

Methods

The population studied is described in Chapter II. In early May of 1987 and 1988, the population was surveyed to determine egg sizes (for method see Chapter II) and clutch sizes. In order to minimize the possibility that predation events had occurred before clutch sizes were determined, nests were checked four or five days after onset of incubation. Whenever the possibility existed that a clutch was incomplete, the nest was visited again after a few days. Similarly, hatching success was determined after the last chick had hatched or when it was certain that remaining eggs were non-viable. Hatching dates were determined either through direct observations or through back-dating. For the latter, a culmen length-age regression equation (see Chapter II) was used to determine the age of individual chicks, and hence hatching date. Only culmen measurements less than 18.0 mm were used in the analysis.

Measures used to assess chick quality were growth rates, and number and intensity of fault bars. For the determination of growth rates a minimum of five to seven weight measurements were taken from each of 33 chicks. Chicks were weighed with 100, 1000, or 2000 g Pesola spring balances. All chicks were color-marked for identification of rank (i.e., A, B, and C-chicks). It was impossible to determine the sex of chicks. Growth rates of individual chicks were calculated using the t_{10-90} measure (Ricklefs 1967), which is the time interval required to grow from 10 to 90% of the asymptotic weight. The growth of nestlings in this population is best represented by the logistic equation (unpubl. data). For a

detailed description of the methodology see Ricklefs (1967). Growth rates for A, B, and C-chicks were calculated separately.

The plumage of many Kootenay osprey nestlings was found to contain fault bars. These points of improper barbule formation (King and Murphy 1984) potentially lead to feather breakage and thus are useful in assessing the quality of a fledgling's plumage. The method used to determine the number and intensity of fault bars is described in Machmer (1987).

In order to assess the influence of season on food availability and to determine whether late breeding males are poorer providers than early breeding males, six males on the west arm were each observed for three entire days during July, 1988. Males were chosen on the basis of clutch initiation dates and habitat. The latter was fairly homogeneous for all six males and fish abundance does not seem to differ among the six territories (Jay Hammond, B.C. Depart. of Fish and Wildlife, Nelson, pers. comm.). In fact, the hunting grounds of all males overlapped to some extent.

Males were followed by boat on every hunting trip and the following behaviours were recorded: occurrence and duration of flapping, gliding and hovering flight, as well as number of successful, unsuccessful and aborted dives. The species and length of fish captured were recorded, and the energetic value of fish estimated using the methods described in Chapter II. For each male, energy expenditure per flight-hunt was computed according to Machmer and Ydenberg (1989). Out of 288 observation hours, the six focal males spent a total of 20.5 hours flight-hunting, averaging (\pm s) $3.42 \pm .65$ hours per male. Of those 20.5 hours, males were out of sight 17% of the time. For estimation of the energy expended during out-of-sight flight-hunting periods, the average proportion of time each

male spent flapping, gliding, hovering and diving were used. Occurrence and duration of activities were recorded using a TRS-100 lap-top computer. In order to spread observation days on individual males evenly over the observation period (July 1-27), a rotating schedule starting with the earliest through to the latest male was used. During each of three rotations, each male was followed for a full day (ca. 16.5 hours).

From these data I calculated the net energy capture rate (energy in prey captured - energy expenditure, divided by flight-hunting time) and the hunting efficiency (energy in prey captured - energy expenditure, divided by energy expenditure) on each day for each male. These measures of hunting performance were compared between males, reasoning that if timing of breeding is influenced by access to good food (due either to male or territory quality) early males should show a better hunting performance than late-breeding males. The data were also used to assess whether any change in the availability of food occurred during July by examining the hunting performance measures for any consistent trend during the observation period.

Weather data were obtained from the Atmospheric Environment Service, Environment Canada at Castlegar Airport, British Columbia. This weather station is located 45 km southwest of Nelson.

Results

REPRODUCTIVE SUCCESS.— During the two years of this study, clutch size, brood size at hatching and number of fledglings steadily declined with progression of the breeding season (Figure 3.1, Table 3.2). This trend was significantly stronger in 1987 when clutch

Figure 3.1 Seasonal decline in breeding performance for 1987 and 1988. The regression lines shown are based on pooled data from Creston and Nelson. These do not differ significantly. Complete regression statistics are given in Table 3.2.

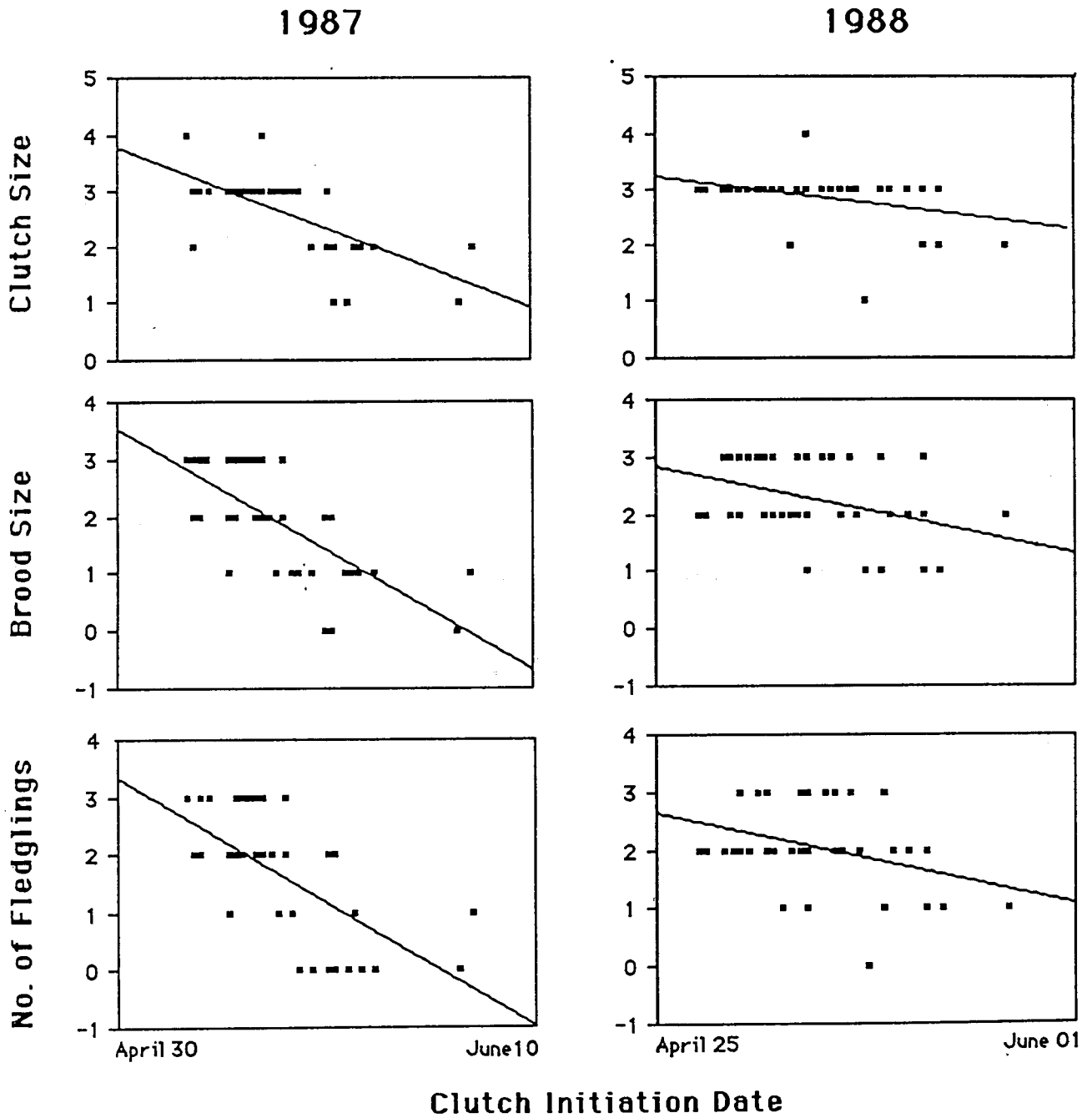


Table 3.2 Regression equations of clutch size, brood size, and number of young fledged (y) on clutch initiation date (x: January 1 = 1)¹. See also Figure 3.1. Q = 95% confidence limits on estimate of the slope.

	Clutch Size	Brood Size	Young fledged
1987	y = 9.14 - .049x r ² = .54, n = 39 P < .001, Q = .016	y = 11.21 - .070x r ² = .54, n = 39 P < .001, Q = .024	y = 11.20 - .072x r ² = .49, n = 39 P < .001, Q = .026
1988	y = 5.30 - .019x r ² = .17, n = 41 P < .05, Q = .016	y = 6.20 - .030x r ² = .15, n = 41 P < .05, Q = .024	y = 6.13 - .032x r ² = .16, n = 41 P < .05, Q = .024

¹ Regressions for 1987 and 1988 were computed as ANCOVAs, with location as a treatment effect. In none of the six cases was the effect of location significant. All interaction terms were also non-significant. A two-way ANCOVA including both the 1987 and 1988 data was computed with location and year as treatment effects. In all three cases (clutch size, brood size, and young fledged) neither the location effect nor the interaction terms were significant. However, the two-way ANCOVAs revealed that the slopes differed significantly between years (n = 80, clutch size: P = .018, brood size: P = .022, young fledged: P = .047).

size declined by $.049 \text{ egg d}^{-1}$ and brood size at hatching and fledging declined by $.070$ and $.072 \text{ chick d}^{-1}$, respectively (Figure 3.1, Table 3.2). The rates of decline in 1988 were $.019 \text{ egg d}^{-1}$, and $.030$ and $.032 \text{ chick d}^{-1}$. The declines in clutch size, brood size at hatching and brood size at fledging are not significantly different from one another, implying that the decline in reproductive success can be attributed entirely to the decline in initial clutch size. However, a comparison of osprey pairs that started breeding before and after the median clutch initiation date (May 8) showed that in 1987 late breeders experienced significantly greater partial and total clutch failure than did early breeders (Table 3.3). This trend was not significant in 1988; neither was there a difference in chick mortality between early and late broods (Table 3.3). Thus, while there may be a contribution of egg mortality to the seasonal decline in reproductive success, the effect seems small relative to that contributed by the clutch size decline.

During neither year were any complete nest failures observed for early breeders whereas 23% of all late breeders lost either their entire clutch or brood (Table 3.3). The exact proximate causes of complete nest failures were difficult to determine. Evidence suggests that predation was responsible in some cases (Chapter II), but nest desertion could have preceded predation events and thus might have been the primary cause of nest failures.

There is no trend for the average egg volume per clutch to decline with progressively later clutch initiation dates (Figure 3.2). A comparison between the average volume of eggs in three and four-egg clutches and one and two-egg clutches revealed that

Table 3.3 Loss of eggs and chicks of early and late breeding osprey pairs. Median clutch initiation dates are May 8 and May 12 for Creston Valley and Nelson area, respectively. n = total number of nests.

	1987		1988		Total	
	Early	Late	Early	Late	Early	Late
<u>EGGS</u>						
No. lost/nest ¹ (mean ± S.E.)	.39 ± .14	1.0 ± .17	.57 ± .15	.67 ± .18	.49 ± .11	.85 ± .12
% lost	13%	44%	19%	23%	16%	33%
% complete clutch failure ³	0%	14%	0%	0%	0%	8%
n	18	21	23	18	41	39
<u>CHICKS</u>						
No. lost/nest ² (mean ± S.E.)	.28 ± .11	.28 ± .11	.22 ± .09	.22 ± .10	.24 ± .07	.25 ± .07
% lost	11%	17%	9%	11%	10%	13%
% complete brood failure ³	0%	28%	0%	6%	0%	17%
n	18	18	23	18	41	36

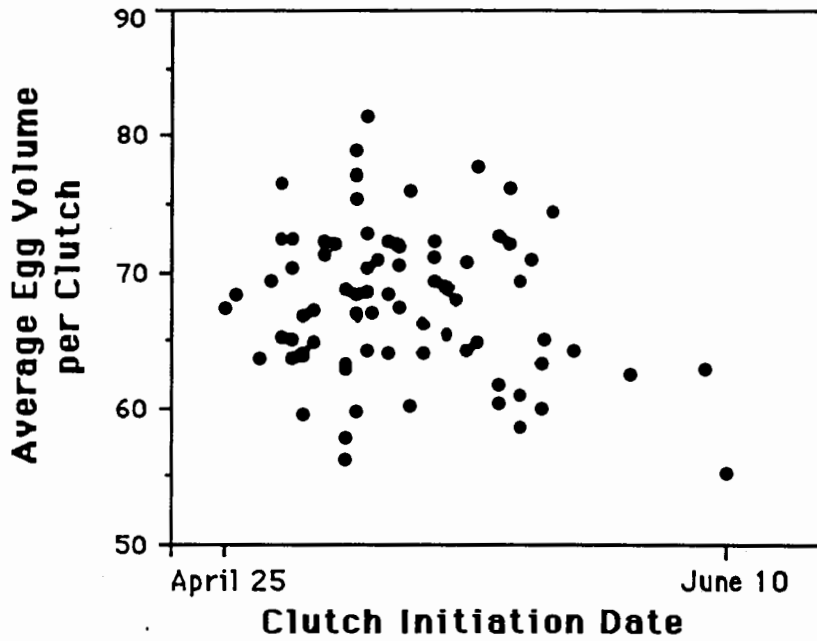
Mann-Whitney tests: ¹ 1987: U = 103, P = .008; 1988: U = 195, P = .661; Total: U = 582, P = .024

² 1987: U = 162, P = 1.00; 1988: U = 206, P = .971; Total: U = 773, P = .950

³ Comparing loss of entire clutches or broods between early and late breeders:

1987 and 1988 pooled: c2 = 10.6, df = 1, P < .01. Late breeders are more likely to fail completely.

Figure 3.2 Average egg volume (cm^3) per clutch for Creston and Nelson in 1987 and 1988 in relation to clutch initiation date. A two-way ANCOVA showed that neither the effects of location and year nor the interaction terms were significant. There is no seasonal trend apparent.



the latter contained significantly smaller eggs (three and four-egg clutches: mean (\pm s) = $68.2 \pm 5.7 \text{ cm}^3$, $n = 212$; one and two-egg clutches: mean (\pm s) = $64.8 \pm 5.6 \text{ cm}^3$, $n = 37$; $t = 3.4$, $df = 247$, $P = .001$).

HATCHING ASYNCHRONY.— All osprey chicks hatched asynchronously. The asynchrony between A and B-chicks (mean (\pm s) = 1.76 ± 1.28 days, $n = 23$) was significantly smaller than that between B and C-chicks (mean (\pm s) = 3.17 ± 1.51 days, $n = 22$; $t = 3.4$, $df = 43$, $P = .001$). There was a non-significant trend toward a seasonal decline in the asynchrony between B and C-chicks, but not between A and B-chicks (Figure 3.3). The asynchrony between B and C-chicks was reduced by approximately 1 day week⁻¹.

OFFSPRING QUALITY.— Nestling growth rates and average number and intensity of fault bars per brood were used as measures of offspring quality. Late-born nestlings did not grow significantly slower than did early ones (Figure 3.4). Similarly, no seasonal trend in the average number ($n = 30$, slope = 0.00, $P = .97$) or intensity ($n = 30$, slope = +0.01, $P = .56$) of fault bars was found. There is an indication that late breeding males tended to provide more food per chick than did early breeders (Figure 3.5); certainly they provide no less food to their chicks. Thus it appears that late breeding osprey pairs do not compromise the quality of the young they do rear.

SEASONAL CHANGES IN FOOD AVAILABILITY.— If late breeding pairs were disadvantaged by a lower food supply, this might account for the observed clutch and brood size declines. To avoid the problematic difference between measuring food abundance and availability (discussion in Daan et al. 1988), I measured the net energy capture rate and flight-hunting efficiency of male

Figure 3.3 Hatching asynchrony (in days) between a) A and B-chicks ($r^2 = .26$, $P = .16$) and b) B and C-chicks ($y = 20.71 - .14x$, $r^2 = .30$, $P = .095$) in relation to hatching dates of oldest chicks. A two-way ANCOVA showed that neither the effects of location and year nor the interaction terms were significant.

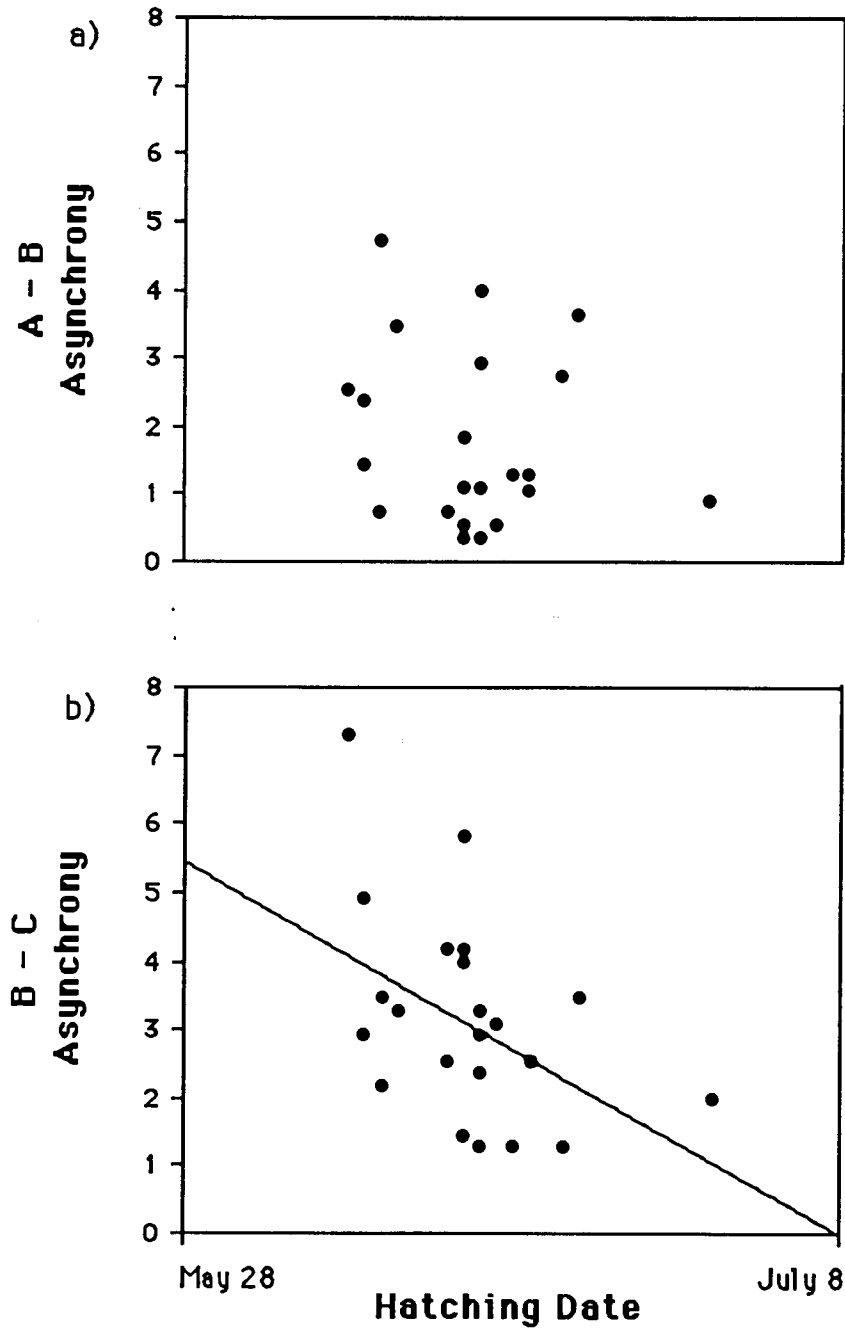


Figure 3.4 The growth rate (t_{10-90}) of A, B, and C-chicks, born in the Nelson area in 1987, in relation to clutch initiation dates (dots = A-chicks, diamonds = B-chicks, x = C-chicks). There is no significant tendency for the growth rate of any group to decline (A-chicks: $n = 14$, $r^2 = .04$, $P = .50$; B-chicks: $n = 12$, $r^2 = 0$, $P = 1.0$; C-chicks: $n = 5$, $r^2 = .22$, $P = .43$). Means and 95% confidence limits are shown in the figure.

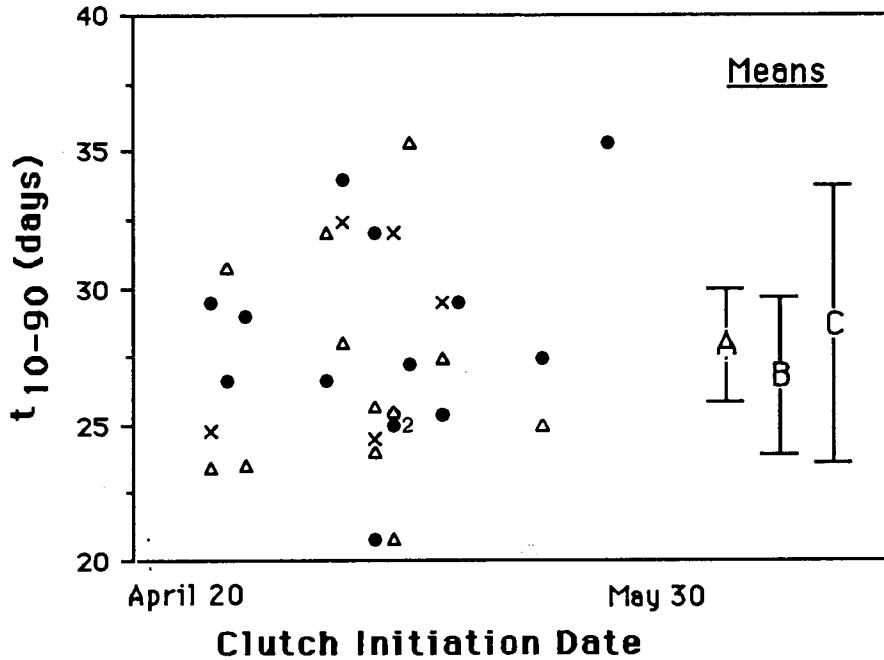
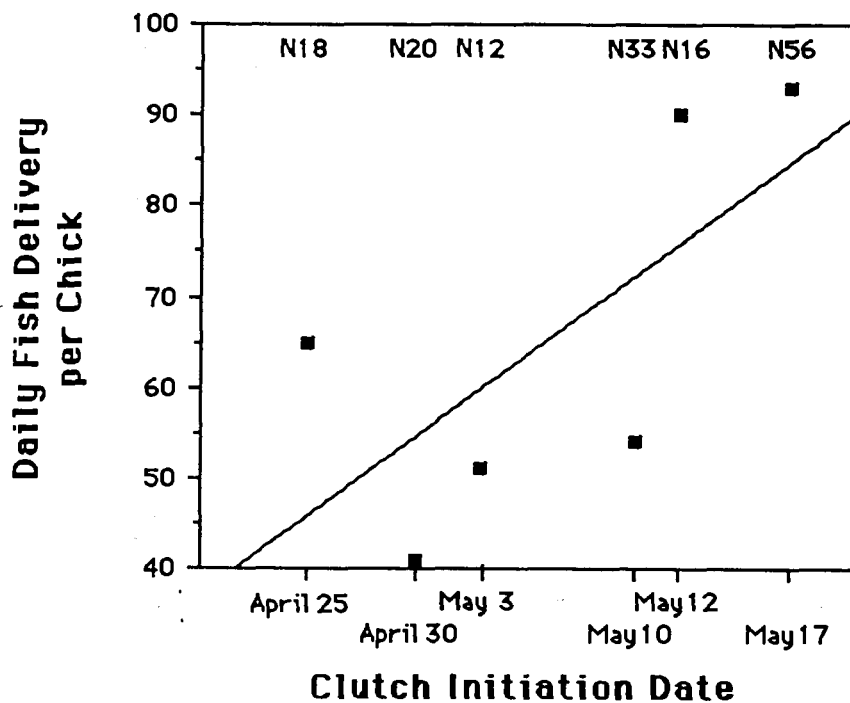


Figure 3.5 Total daily fish delivery (kJ) per chick of six focal males in relation to their clutch initiation dates. The total daily delivery was standardized by dividing by brood size and adjusting for brood age (Poole 1984, his Figure 4.5). Regression statistics: $n = 6$, $r^2 = .46$, $P = .14$. Male numbers are given at top of panel.



ospreys directly from behavioural observations. Over the observation period, the six focal males combined showed no significant trend in either measure of flight-hunting performance (Figure 3.6). The observation period included the time when energy requirements of nestlings were greatest. These results indicate that during this period of highest demand food availability does not decline. Female ospreys have a very low egg weight to body weight ratio (Poole 1984). Therefore, it is unlikely that earlier in the season egg production was energetically constrained by inadequate food supply. This suggests that food availability was not directly responsible for the observed decline in clutch size.

PARENTAL QUALITY.— Since the male osprey is the sole provider of food for the female and nestlings during most of the breeding season, the reproductive success of a pair largely depends on the hunting performance of the male. Hunting performance may be influenced by the male's intrinsic ability, as well as by the quality of his hunting territory. Thus, the parental quality hypothesis predicts that late clutch initiation and low reproductive success are correlated with poor provisioning ability of males. This prediction was tested by analysing the hunting performance of the focal males with respect to their clutch initiation dates. Figure 3.7 shows no apparent trend in net energy capture rate or hunting efficiency among the six males related to the time of clutch initiation.

Another measure of osprey hunting performance is the proportion of successful dives (Ueoka and Koplín 1973). This measure also did not differ among the focal males of this study (Table 3.4).

Although all females of the six males observed laid clutches of three eggs and experienced no chick loss, they differed considerably in their clutch initiation dates and to some extent in the number of young hatched (from the earliest through to the latest pair they

Figure 3.6 a) Net energy capture rate ($J_{in} - J_{out} / s$) and b) efficiency ($J_{in} - J_{out} / J_{out}$) during flight-hunting of six focal males in July, 1988. Each of three points per male represents the value for a full day's (16.5 hours) observation. Regression statistics: a) $n = 18$, $r^2 = .05$, $P = .39$; b) $n=18$, $r^2 = .03$, $P = .50$. There is no evidence of any decline in flight-hunting performance over this period.

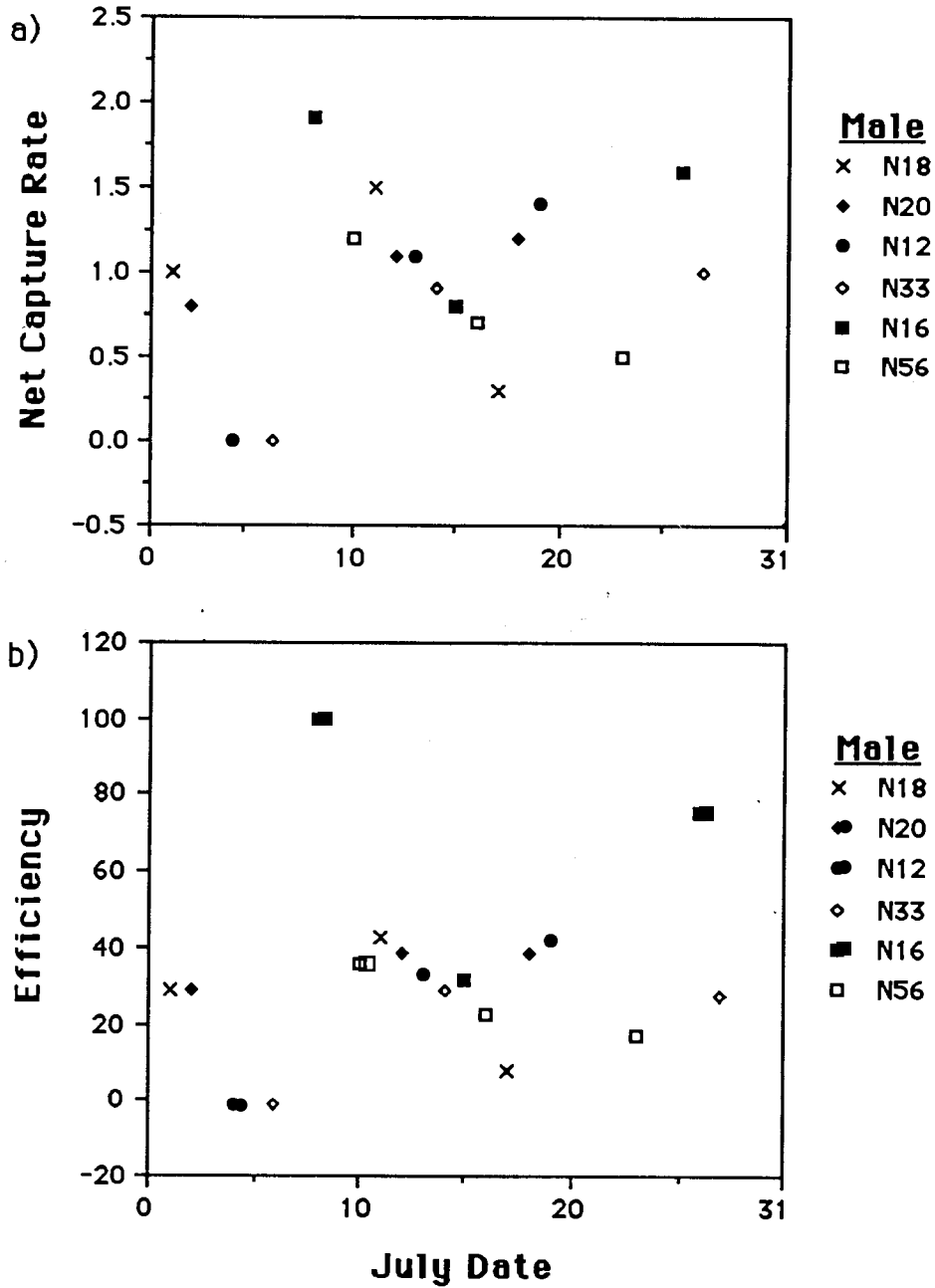


Figure 3.7 a) Net energy capture rate ($J_{in} - J_{out} / s$) and b) efficiency ($J_{in} - J_{out} / J_{out}$) during flight-hunting of six focal males in relation to their clutch initiation dates. x = mean of each of three days' observation, dot = overall mean of three observation days. Male numbers are given at top of panels. Regression statistics of overall means: a) $n = 6$, $r^2 = .00$, $P = .95$; b) $n = 6$, $r^2 = .04$, $P = .70$. There is no seasonal trend apparent.

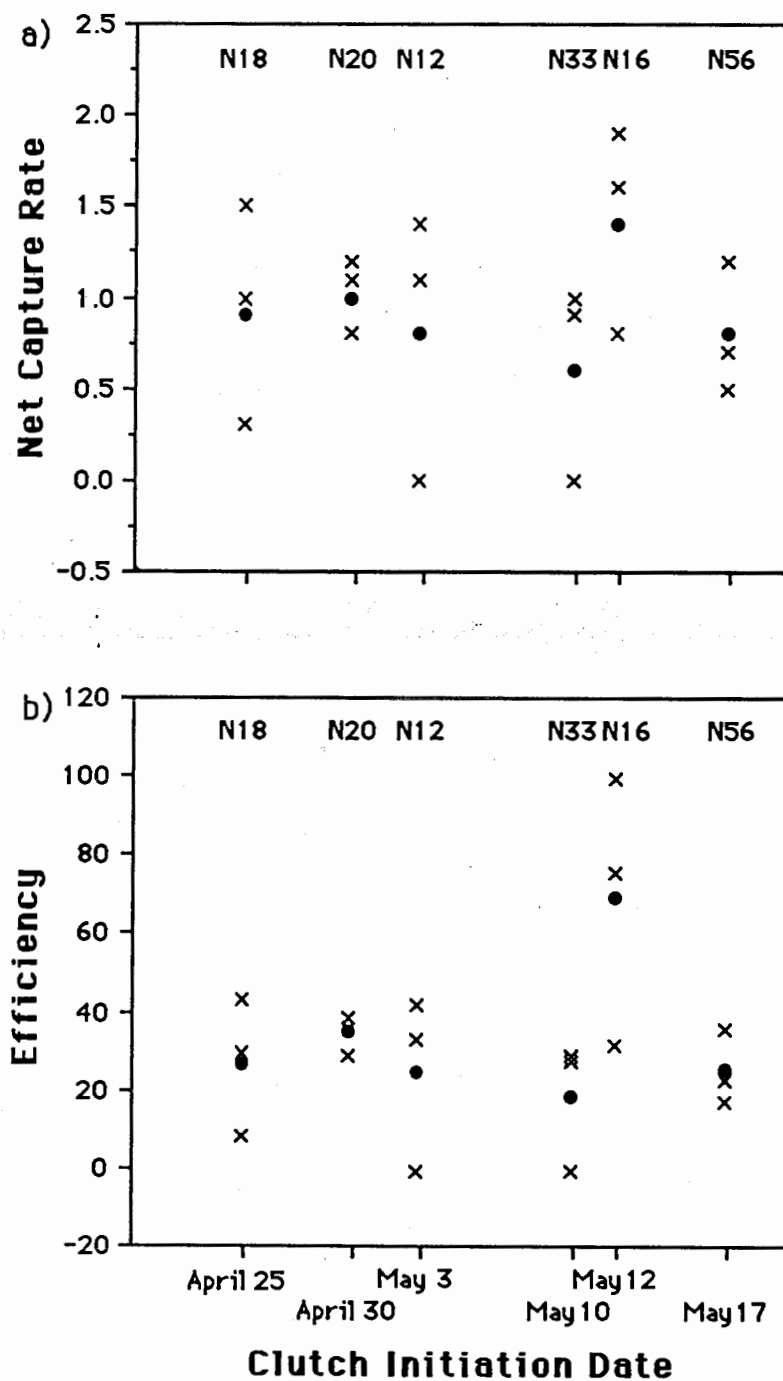


Table 3.4 Diving performance of six focal males on the west arm of Kootenay Lake during July 1988. Each male was observed for three entire days. The six males did not differ significantly in their diving performance.

Variable	Male No.					
	N18	N20	N12	N33	N16	N56
Total no. dives	62	67	41	25	27	38
No. aborted dives	28	37	22	11	15	19
No. completed dives	34	30	19	14	12	19
No. successful dives ¹	14	16	8	8	7	8
% successful dives	41%	53%	42%	57%	58%	42%

¹ $\chi^2 = 2.48$, $df = 5$, $P > .05$

hatched, in that order, two, two, three, three, two, and one chick). These differences do not appear to be related to corresponding differences in male hunting abilities.

CLIMATIC FACTORS.— Two climatic factors that potentially affect osprey breeding success are rain and wind. Poole (1982) reports that prolonged rain and winds were responsible for almost half of the nestling loss in the Eastern Long Island osprey population. Similarly, an inter-seasonal investigation on the effect of weather on reproductive success in Creston ospreys revealed that the average number of fledglings per nest was strongly negatively correlated with rainfall (Forbes 1989). Windspeed has also been shown to affect osprey hunting success negatively (Grubb 1977, Machmer and Ydenberg 1989). Table 3.5 summarizes the average monthly rainfall and windspeed for the two breeding seasons of this study. Overall, there is no evidence of worsening weather conditions with time during the two seasons which could account for the seasonal decline in osprey reproductive success. In fact, all variables considered show an improving seasonal trend (negative slopes).

Table 3.5 Monthly averages of number of rain days, total precipitation, and windspeed during 1987 and 1988 breeding seasons.

Variable	April	May	June	July	Aug.	Sept.	Oct.	r	Significance
1987									
No. rain days	10	14	8	12	5	2	5	.76	P < .05
Precipitation (mm)	44.4	49.8	35.6	89.3	16.2	29.2	5.0	.51	n.s.
Windspeed (km/h)	8.0	7.1	6.2	7.0	6.2	5.0	3.6	.92	P < .01
1988									
No. rain days	17	14	13	6	4	12	7	.69	n.s.
Precipitation (mm)	43.4	64.8	60.4	23.0	6.3	96.2	23.2	.13	n.s.
Windspeed (km/h)	10.1	8.2	7.0	6.5	9.9	6.5	6.8	.51	n.s.

Discussion

During the two years of this study, clutch size, brood size, and number of fledglings all declined as clutch initiation was delayed. In general, these results concur with the findings of other studies on osprey reproductive behaviour (Ogden 1977, Judge 1983, Poole 1984). None of the hypotheses I tested, namely food availability, parental quality or climatic factors, could explain the observed trends. Although number of fledglings declined with season, the quality of late-born young was not lower than that of early-born ones. In fact, the results of daily food delivery per chick suggest that later chicks may have received more food than earlier ones.

The investigation of hatching asynchrony revealed a marked difference in hatching date between A and B-chicks and B and C-chicks. Asynchrony predisposes the youngest chick to selective starvation if food supply is inadequate (Lack's (1954) brood reduction hypothesis). The asynchrony between A and B-chicks did not change with later hatching dates, suggesting no parental adjustment in laying and incubation behaviour with respect to the first and second egg. If the observed trend toward a seasonal decline in the B - C asynchrony is a real effect, it may be a parental tactic to increase sibling rivalry (cf. Hahn 1981) thereby promoting rapid brood reduction as opposed to gradual selective starvation. Late breeders that have neither reduced their clutch size nor their brood size at hatching may use the reduction in B - C asynchrony as an additional mechanism for adjusting their brood size. Alternatively, a more synchronous brood may compensate for a late start of the breeding season. In light of the great potential for siblicide or starvation mediated brood reduction, however, it seems more likely that ospreys adjust the hatching asynchrony between chicks to influence chick behaviour rather than to save time.

One perplexing aspect of the results is the difference in the rate of clutch size decline between the two years of the study (Figure 3.1), the rate being more than twice as high in 1987 than in 1988. The most likely suggestion - that in 1987 later breeding osprey parents laid smaller clutches due to greater deterioration of the weather - can be rejected because Table 3.5 shows that 1988 was the year of poorer weather later in the season. The hypothesis that the faster rate of decline in 1987 is an outcome of later laying dates overall can also be discounted (Table 2.2). The possibility of some sort of interaction between these two factors seems unlikely, but cannot be ruled out.

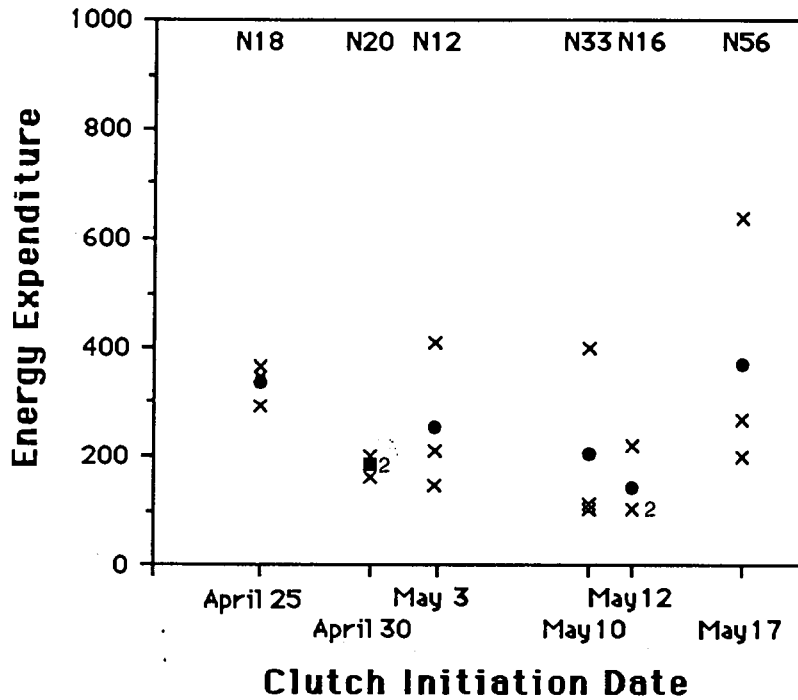
In a study on the adaptive significance of laying date in coastal Massachusetts ospreys, Poole (1984) demonstrated that reproductive success declined with season. This was mainly the result of increased egg loss in late breeders. Testing for causation, Poole found no conclusive evidence that parental age, parental experience or food availability could account for this trend. In short, neither the hypotheses tested by Poole nor those tested in this study can adequately explain the observed trends.

What, then, causes this declining seasonal trend in osprey reproductive success? As pointed out by Poole (1984), two possibilities exist: first, late-breeding pairs may have poorer ability to perform essential breeding tasks, or second, they may be less 'committed' to breeding than birds which initiate clutches earlier in the season (i.e. they were less prepared to expend reproductive effort *sensu* Williams 1966). My study does not support the notion that inferior ability causes low reproductive success in late breeders. Furthermore, I observed that the activity levels and hence energy expenditures of the six focal males were well below capacity. According to Kirkwood's (1983) allometric formula for maximum metabolizable energy intake ($ME_{max} = 1200 \text{ kJ/kg} \cdot 72$, maintenance metabolism discounted), a male osprey weighing 1428 g (Cramp and Simmons 1977)

would have 1551 kJ per day available for work, provided food is not limited. The six males observed spent on average (\pm s) 253 ± 140 kJ per day, or just 16% of maximum work capacity. Only half of this energy expenditure was used for foraging-flight. The rest was used for territory and nest defense and for the supplying of nest material. Considering that these values were obtained during the period of highest energy requirements of chicks and that total daily energy expenditure was not correlated with clutch initiation date (Figure 3.8), it seems that late breeding males should be able to forage at a much higher rate and to provide food for more young than observed.

It has previously been proposed (Poole 1984, Toft et al. 1984) that an adaptive adjustment of reproductive effort may be responsible for the low reproductive success of late-breeding pairs. In particular, two observations of this study are consistent with this contention. (1) The seasonal decline in reproductive success in Kootenay ospreys was caused primarily by a decline in clutch size, and to a much lesser extent by increased egg loss, but not by higher chick mortality in late breeders. This result is explicable if one considers that in order to minimize wastage, a reduction in reproductive effort, if desirable, should occur early in the annual breeding cycle. (2) Of 276 eggs laid during the two breeding seasons of this study, 32 (12%) remained unhatched in the nest (Chapter II). Most of these eggs belonged to late breeders. As indicated by five partially-developed unhatched chicks (Chapter II), females may have stopped incubation of the last egg if one or two chicks have hatched already and if the survival chances of those chicks are predictably high. These observations both suggest that parents 'decide' to commit less reproductive effort if they start breeding late in the season.

Figure 3.8 Daily energy expenditure (kJ) of six focal males in relation to their clutch initiation dates. x = total energy expended per observation day, dot = mean of three observation days. Male numbers are given at top of panels. Regression statistics of means: $n = 6$, $r^2 = .02$, $P = .81$. There is no trend apparent.



This raises the question of why commitment should be reduced when breeding is late. The most likely answer is that parents reduce commitment because late-born offspring have lower reproductive value (Fisher 1958) than early-born ones. Osprey fledglings in the Kootenay region remain with their parents for approximately 6 - 8 weeks after leaving the nest (Chapter II). During this time they acquire essential foraging skills before they begin their first migration. Since this population breeds relatively far north, the correct timing of migration must be an important factor of the annual cycle. Therefore, one would expect that late fledglings, who have less time to acquire foraging skills, are of lower reproductive value than early fledglings. Daan et al. (1988) calculated the reproductive value of Eurasian kestrel eggs in relation to laying dates and found that late eggs had lower reproductive value than earlier ones. Poole (1988, p. 133) provides evidence that survival of late-born osprey young between fledging and first breeding is lower than that of early-born ones. These reduced survival chances of late fledglings are likely a critical factor in the seasonal allocation of reproductive effort.

If reducing commitment when breeding is late is adaptive in ospreys, it must involve a tradeoff. There are two basic possibilities:

(1) LIFE HISTORY TRADEOFF HYPOTHESIS.— The existence of a cost of reproduction for parents has been shown for several species of birds (review in Nur 1988). Usually, this cost is measured in terms of reduced parental survival or future fecundity and could be caused by, for example, physiological deterioration, injury or predation. If reproducing ospreys incur such a cost, reduced commitment (i.e., reproductive effort) may increase survival or future fecundity and, in turn, lifetime reproductive success. To explain seasonal clutch size decline, this hypothesis demands that late breeding birds must pay a higher cost than early breeding birds.

(2) OFFSPRING QUALITY-QUANTITY TRADEOFF HYPOTHESIS.— Late young are disadvantaged by virtue of being late. Thus parents breeding late (for whatever reason) do better to reduce clutch size or brood size at hatching in order to be able to invest more per chick. This could offset, at least in part, the lateness-disadvantage if chicks in such broods can be better nourished. The results of this study suggest that late-born osprey chicks may indeed receive more food.

These two hypotheses are not mutually exclusive. Both may hold, but either hypothesis by itself may be sufficient to explain reduction in reproductive commitment when breeding is late.

In summary, Kootenay ospreys show a significant seasonal decline in reproductive success consistent with that observed in other osprey populations. Although no direct tests of the tradeoff hypotheses were possible, the results of this study suggest that ospreys reduce reproductive commitment as clutch initiation is delayed. All surviving nestlings developed without apparent deficiencies, and I conclude that late breeding Kootenay ospreys compromise the quantity more than the quality of their young.

CHAPTER IV

SUMMARY AND GENERAL DISCUSSION

Productivity values obtained during the two years of this study indicate that the Kootenay osprey population is healthy, stable, and likely still growing. This is consistent with the general trend observed for this and most other osprey populations over the last 15 to 20 years. The main reasons for the population increase in the Creston Valley and Nelson area are the creation of several artificial water reservoirs, the maintenance of large fish populations, and the general decrease in human persecution.

No significant differences were found between Creston Valley and Nelson area ospreys in the average clutch size, brood size or number of fledglings. However, the two nesting concentrations did differ in several aspects of their breeding ecology. In the Creston Valley, ospreys primarily nest in trees, whereas their Nelson counterparts use man-made structures such as pilings and power poles as nesting sites. Creston Valley ospreys mainly capture black bullhead, yellow perch, and pumpkinseed almost exclusively by flight-hunting, while Nelson area ospreys prey mainly on largescaled and longnose suckers, mountain whitefish, rainbow trout, and kokanee, often using the perch-hunting method. These local preferences largely reflect availability of resources. With regard to their reproductive biology, clutches in the Creston Valley were laid slightly but significantly earlier and showed a more clumped distribution in time than those laid in the Nelson area. In addition, Creston Valley eggs were slightly larger than Nelson area eggs.

A comparison of the Kootenay population with other North American osprey populations revealed that Kootenay ospreys lay relatively small clutches with large eggs. This result does not support Judge's (1983) finding of a trend towards larger clutches in

more northern populations. Furthermore, no latitudinal trend was found in osprey hatching success, although nestling survival seems to be higher in northern populations.

The Kootenay osprey population exhibits a significant seasonally declining trend in reproductive success. This is consistent with the results of breeding studies conducted on other North American osprey populations (Ogden 1977, Judge 1983, Poole 1984). The trend in Kootenay ospreys is mostly attributable to seasonal clutch size decline and, to a much lesser extent, to an increase in egg mortality of late breeders. This latter trend was more pronounced in 1987. Neither nestling quality nor nestling survival differ between early and late breeding pairs. In fact, the results indicate that late nestlings may receive more food than early-born ones. The declining seasonal trend in reproductive success could not be attributed to food availability, parental quality, or climatic factors.

As suggested by Poole (1984), two possibilities exist to explain the seasonal decline in osprey reproductive success: late-breeding pairs are either unable to produce more eggs or raise more young, or, alternatively, they are less committed to breeding than are early-breeding pairs. The results of my study suggest that lack of ability can be discounted and that parents reduce reproductive effort (i.e. commitment) when breeding is late. By reducing clutch size or brood size, parents may be able to compensate for the inherent disadvantage that late fledglings face (see Chapter III) by nourishing each nestling better while at the same time reducing the overall commitment. This does not require that a cost of reproduction exists for the parents, but it is not inconsistent with such a cost. It is possible that both contribute to a strategic lowering of reproductive commitment contingent on clutch initiation date. Such an ultimate explanation for the seasonal decline in osprey reproductive success is not incompatible with the proximate mechanisms described by Poole (1984) and by this study. Proximate, ultimate, and ontogenetic explanations for

behavioural phenomena such as seasonal variation in reproductive performance (see Chapter I) are simply explanations on different levels of causation and are not mutually exclusive.

Several studies have shown that laying date (among other breeding parameters) is heritable in bird populations (van Noordwijk et al. 1981; Findlay and Cooke 1982; O'Donald 1983). As the reproductive success of late-breeders is low, an interesting question is: Why doesn't breeding date evolve? That is, why doesn't selection advance the breeding date so that all birds breed early? There seem to be three main possibilities.

The first, suggested by Toft et al. (1984), is that early and late breeders have equal fitness, because late breeders enjoy more breeding seasons to balance their lower success in each. Under this scenario each breeding date-clutch size combination is a 'support' (Bishop and Cannings 1978) of a mixed evolutionary stable strategy (mESS). Breeding date does not evolve because all breeding dates are equally fit. Although not impossible, it seems unlikely to me that breeding success and longevity would balance in the way required by this idea (Murphy 1986).

The set of possible reproductive decisions available to ospreys that could be responsible for the observed seasonal breeding pattern include adjustments of clutch size, laying asynchrony, hatching asynchrony (via incubation tactics), and brood size (via feeding tactics). If, together, these decisions constitute a breeding strategy that is contingent on the timing of breeding, it would read: "if early, commit; if late, restrain". The second hypothesis to explain the failure of breeding date to evolve is that due to non-heritable factors, some birds are of low quality and hence are prevented from breeding early. Given their later breeding date, reduction of clutch or brood size is the best they can do. This

would result in lower fitness of late breeders and the 'early/commit-late/restrain' strategy would be a conditional evolutionary stable strategy (cESS). Breeding date does not evolve because the lower quality of later breeders is not heritable. I call this the 'random ontogenetic factors' hypothesis (ROF); "random" because the relevant factors must be random with respect to the genotype (else breeding date would evolve), and "ontogenetic" because events during ontogeny seem the most likely to have such profound and long-lasting effects.

The third possibility, suggested by Price et al. (1988), is that events prior to breeding each year (e.g. during winter, on migration, Canada geese in the nest) delay randomly selected pairs during each breeding season. The key is that pairs are delayed in breeding at random. The lowered clutch size of later breeders is a conditional response, and this is also a conditional evolutionary stable strategy. Again, breeding date does not evolve. I call this the 'random annual factors' (RAF) hypothesis.

My data do not give a way to evaluate the mESS hypothesis, but I can test predictions from the two cESS hypotheses. The ROF hypothesis predicts that the same individual birds will always be relatively late-breeders, while the RAF hypothesis predicts that late-breeders will be a random subset of breeders. I could not identify individual ospreys, but I can use the fact that ospreys are highly philopatric, and breed in the same nests year after year (Poole 1989). This is very common in raptors (Newton 1979). If it is accepted that the same nests are very likely to contain the same breeders in successive seasons, a test of the hypotheses can be made by comparing the successive dates of clutch initiation. The ROF hypothesis predicts a high correlation, while the RAF hypothesis predicts no correlation.

The relation between breeding dates in successive years is shown in Figure 4.1. The figure includes one nest later by 16 days than any other nest observed in that year. Excluding this outlier produces a highly significant relationship. Although not entirely conclusive, due to the small sample size and the small number of years considered, these results support the random ontogenetic factors hypothesis - that some birds are habitually late breeders due to non-heritable events during ontogeny.

The results of my study support indirectly the idea that seasonal decline in osprey reproductive performance is an outcome of the strategic lowering of clutch size by late-breeding birds. This is a conditional ESS, depending on the quality of individuals. The strategic lowering is made due to the relatively lower fitness value of late-born young, and may involve a cost of reproduction for the parents, a partial compensation for the disadvantages late-born young face, or both.

An appealing feature of this idea is its potential generality. As I outlined in Chapter I, seasonal clutch size decline is an ubiquitous feature of temperate, arctic, and antarctic avian breeding patterns. The basic notion is that, by virtue of their birthdate, late-born young in a seasonal environment are disadvantaged because of the reduced amount of time they have for development before the onset of winter, and because they face a greater number of more skillful competitors than early-born young. These effects would seem to be very general, although the natural history details will of course vary greatly. Several possible mechanisms have been described in the literature (Table 4.1).

This hypothesis predicts that the pattern of seasonal clutch size decline should vary with seasonality, being strong in the arctic and antarctic, absent in the aseasonal tropics but present in the wet/dry tropics. In areas with more than one seasonal cycle per year (e.g.

Figure 4.1 Correlation of breeding dates in successive years of individual nests whose dates could be determined. The figure includes 21 nests from 1987/1988 and a further 8 nests from 1988/1989. Correlation statistics (two-way ANCOVAs with location and year as treatment effects): $n = 29$, slope = .44, $r = .33$, $P = .12$. This correlation includes the point in the lower right of the figure (open circle), a nest later by 16 days than any other nest observed in 1987. Excluding this point, the correlation is: $n = 28$, slope = .47, $r = .59$, $P = .01$. The line given is the significant line.

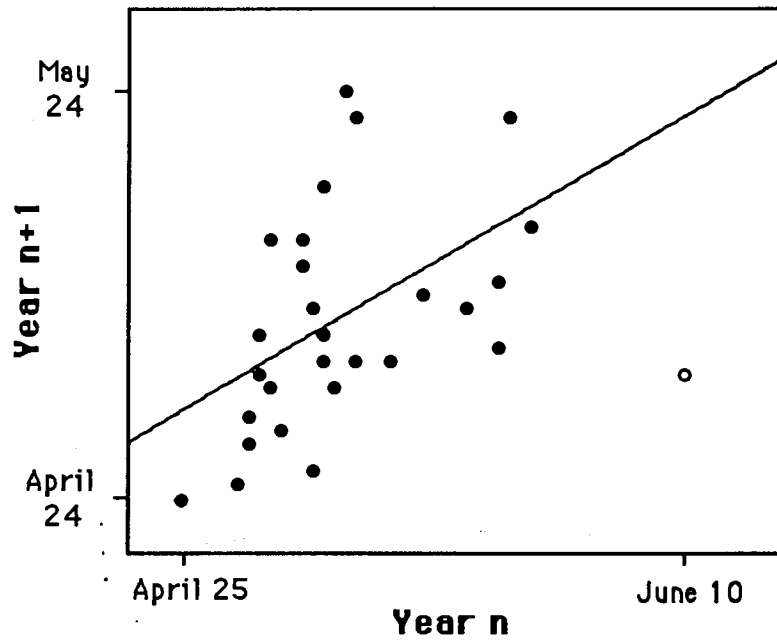


TABLE 4.1 Juvenile attributes negatively affected by late fledging.

Species	Variable	Source
<i>Sitta europaea</i> (nuthatch)	- territory establishment	Mathysen 1987
<i>Parus palustris</i> (marsh tit)	- establishment on wintering grounds	Nilson & Smith 1985
<i>Accipiter nisus</i> (sparrowhawk)	- acquisition of hunting skills - habitat settlement	Newton & Marquiss 1984
<i>Aegolius funereus</i> (Tengmalm's owl)	- post-juvenile moult - acquisition of hunting skills - accumulation of energy and nutrients before winter	Korpimäki 1987
<i>Melospiza melodia</i> (songsparrow)	- juvenile survival - territory establishment	Arcese & Smith 1985
<i>Zosterops lateralis</i> (silveryeyes)	- dominance status - winter survival	Kikkawa 1980

Ghana has two wet seasons annually and some birds breed twice) seasonal clutch size declines should be observed in each seasonal cycle. The hypothesis seems to be flexible enough to accommodate most of the known facts about seasonal clutch size decline, and is capable of generating new and testable predictions. It therefore has merit as a scientific hypothesis, but it remains to be tested rigorously.

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