Comparative feeding ecology and reproductive performance of ospreys in different habitats of southeastern British Columbia

CHRISTOPH STEEGER
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

HANS ESSELINK
Zoölogisch Laboratorium, Rijksuniversiteit Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

AND

RONALD C. YDENBERG
Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

Received January 30, 1991
Accepted October 18, 1991

STEEGER, C., ESSELINK, H., and YDENBERG, R. C. 1992. Comparative feeding ecology and reproductive performance of ospreys in different habitats of southeastern British Columbia. Can. J. Zool. **70**: 470–475.

We compared the general breeding and feeding ecology of ospreys (*Pandion haliaetus*) in the Creston and Nelson areas of southeastern British Columbia. In the Creston Valley, ospreys nested atop tall trees surrounding a shallow and productive warm-water marsh. Prey species taken by male ospreys included black bullhead (*Ictalurus melas*), pumpkinseed (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*). In contrast, near Nelson, ospreys nested on man-made structures along the narrow West Arm of Kootenay Lake. Osprey prey species in the Nelson area included longnose sucker (*Catostomus catostomus*), largescale sucker (*Catostomus macrocheilus*), and mountain whitefish (*Prosopium williamsoni*). Prey captured at Nelson were larger and contained significantly more energy than at Creston Valley, and hunting from a perch was used for 26% of all captures. All Creston Valley prey were caught by flight hunting. The strike success of foraging ospreys at Nelson was significantly higher than at Creston, and the net yield of flight hunting was 3 times higher. In spite of these differences, the breeding performance of ospreys in the two areas was very similar. Average clutch size was 2.8, brood size at hatching was 2.0, and the average pair fledged 1.4 young. The nest failure rate did not differ between the two areas. Most clutches were initiated in early May, with Nelson-area ospreys laying, on average, 4–7 days later. Egg volumes were smaller at Nelson (66.6 vs. 69.1 cm^3). However, the rate at which nestlings gained mass was significantly greater at Nelson. We discuss reasons why the breeding performance varies so little in spite of the great differences in feeding regime.

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Nous avons comparé l'écologie de la reproduction et de l'alimentation chez des Balbuzards (*Pandion haliaetus*) de deux régions de la Colombie-Britannique, Creston et Nelson. Près de Creston Valley, les Balbuzards nichaient au sommet de grands arbres entourant un marécage peu profond et très riche d'eau tiède. Les mâles capturaient notamment des Barbottes noires (*Ictalurus melas*), des Crapets-soleils (*Lepomis gibbosus*) et des Perchaudes (*Perca flavescens*). En revanche, les balbuzards de la région de Nelson nichaient sur des structures construites le long de l'étroit bras ouest du lac Kootenay. Les oiseaux de la région de Nelson capturaient des Meuniers rouges (*Catostomus catostomus*), des Meuniers à grandes écailles (*Catostomus macrocheilus*) et des Ménominis des montagnes (*Prosopium williamsoni*). Les proies capturées dans la région de Nelson étaient plus grosses et contenaient significativement plus d'énergie que les proies capturées près de Creston Valley et 26% des captures observées ont été faites par plongées à partir de perchoirs. Toutes les captures observées près de Creston Valley ont été faites par chasse au vol. Le succès des chasses s'est avéré significativement plus grand à Nelson qu'à Creston Valley et al production nette de la chasse au vol y était 3 fois plus élevée. En dépit de ces différences, la performance reproductrice des balbuzards des deux régions était semblable. Les couvées moyennes contenaient 2,8 oeufs et 2,0 oisillons au moment de l'éclosion et 1,4 oisillons atteignaient le stade d'envol chez un couple moyen. Le taux d'insuccès de la nidation était le même aux deux endroits. La plupart des couvées étaient entreprises au début de mai et les balbuzards de la région de Nelson pondaient en moyenne 4 à 7 jours plus tard. Le volume des oeufs était plus petit à Nelson (66,6 vs. 69,1 cm^3). Cependant la vitesse de croissance en masse des oisillons était significativement plus rapide à Nelson. Nous examinons les raisons qui peuvent expliquer pourquoi la performance reproductrice des deux espèces varie si peu alors que leurs habitudes alimentaires sont si différentes.

[Traduit par la rédaction]

Introduction

Extensive empirical work has linked many aspects of avian breeding behaviour with food supply. When food availability is high, birds generally breed earlier, lay larger clutches, and enjoy greater reproductive success (review in Martin 1987). The evidence is based on interannual and interhabitat comparisons, as well as experimental manipulations. These trends have also been documented among raptors (review in Newton 1979). With regard to interhabitat comparisons, the most extensive work is that of Newton (1976), who showed that sparrowhawks (*Accipiter nisus*) in good food habitats bred earlier, laid larger clutches, and had higher reproductive success than those in poor food habitats.

Little work has examined this question in ospreys (*Pandion haliaetus*). Poole (1982, 1989) reported that clutch and brood sizes are smaller in subtropical habitats, and that the rate of food delivery to nests is also lower there. Brood size and food delivery were also lower at one of two neighbouring breeding sites in New York. In neither of these comparisons could it be determined whether breeding success depended on food availability, or whether the delivery rate of food to the nest depended on brood size, which in turn may have varied due to other factors.

We studied ospreys in two different habitats in the Kootenay region of British Columbia. Early reports indicated that there were few ospreys in this area during the late 1940s (Munro 1950). However, an abundance of breeding pairs is now found in two distinct local nesting concentrations. One is situated in a large freshwater marsh along the Kootenay River in the Creston Valley; the other breeds near Nelson on the West Arm of Kootenay Lake, a cold productive lake. We compared the breeding and feeding ecology of ospreys in these two habitats. At both locations, the impoundment and control of water levels for hydro-electric power (Nelson) or marsh management (Creston) have enlarged the area of habitat suitable for osprey foraging by creating extensive shallows. We evaluated the feeding characteristics of the two habitats on the basis of measures of the osprey's hunting performance. We show that in spite of large differences in the food quality of the two habitats, breeding performance hardly differed.

Methods

The study area encompassed two valleys in southeastern British Columbia (Fig. 1). At the beginning of each breeding season, both areas were searched for breeding pairs by car and boat. A subset of easily accessible nests was checked on a weekly basis (39 in 1987, 41 in 1988). These closely monitored nests formed the basis of most of the analyses and demographic data. Most other nests monitored received a minimum of three visits per season, but a few were only visited during the fledging period. Thus, sample sizes varied among our analyses. Observers either climbed to the nests (using standard tree-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).

At each nest visit, egg size, clutch size, or brood size was determined. 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 backdating (subtracting the mean incubation period of 39 days) from hatching dates of first hatchlings. Hatching dates were determined either by direct observation or by assessing the age of chicks by means of a culmen length (x) − age (y) regression derived from known-age chicks ($y = -13.6 + 1.5x$, $r^2 = 0.96$, $n = 40$; cf. Poole 1984) as a predictor. Chick mass was measured using a 100-, 500- or 2000-g Pesola spring balance. To measure the rate of chick growth we used the rate of mass gain measured between the ages of 5 and 40 days. This represents the period of rapid and linear growth in ospreys. We derived an estimate for each nestling that survived, using the two most widely separated measurements made during this period. Hierarchies within broods were determined on the basis of chick age, and chicks were ranked as A, B, or C chick, accordingly. Chick mass or direct observations of chick interactions were used when age was not definitive.

During July 1988 we observed the flight-hunting activity of males from six selected nests on Kootenay Lake near Nelson. A total of 20.6 h of flight hunting was recorded during 288 h of observation. We used a portable computer to record the occurrence of all behaviours during flight hunting, as described in Machmer and Ydenberg (1990). Ospreys carry prey in their talons, so it was usually 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), judged accurate to within 5 cm (Stinson 1978). Although crude, this method was

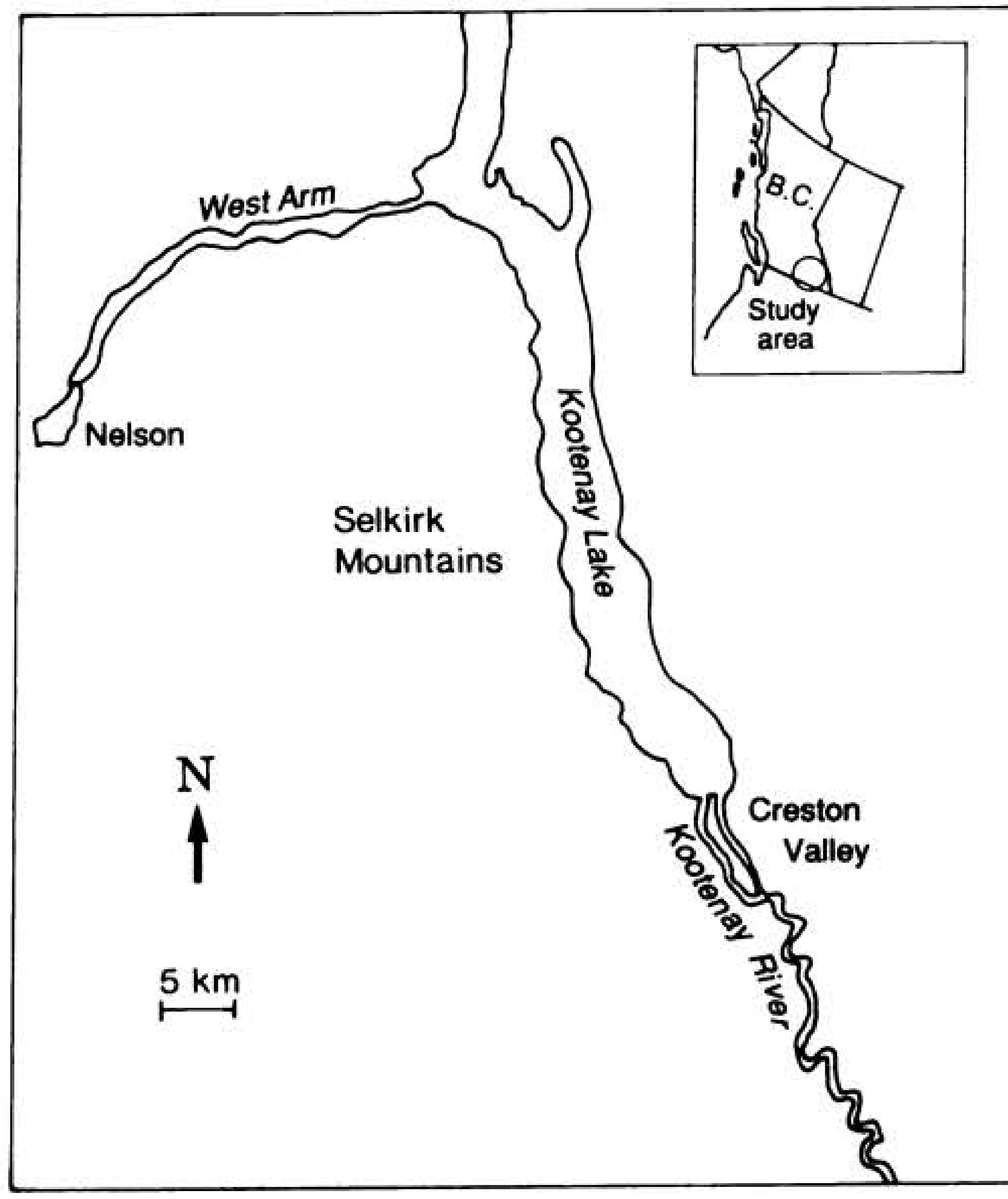

FIG. 1. The study area, showing the locations of Nelson (117°20′W, 49°30′N), the West Arm, Kootenay Lake, Kootenay River, and the Creston Valley.

sufficient to determine some large differences between Creston and Nelson. Biomass of fish was calculated using length−mass regressions for the various species (Forbes 1989), and energy equivalents were 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. The observations of fish species captured were compared with similar observations made at Creston (S. L. Forbes, unpublished data). From the behavioural records, we calculated the net rate of energy capture while flight hunting (method in Machmer and Ydenberg 1990). We compared the capture success (percentage of strikes) and the net energy capture rate measured in this study with those measured at Creston by Machmer and Ydenberg (1990). Although there are slight differences in the sampling protocol used at the two sites, the overall similarity of the methods permitted valid comparisons to be made.

Results

Status and productivity

The status and success of all osprey nests are summarized in Table 1. The total number of known nests increased by 21 from 1987 to 1988, due to the construction of new nests at the beginning of the 1988 breeding season. Twenty of these new nests were considered to be "alternate" nests (see Postupalsky 1977), built in response to occupation of the previous year's nests by Canada geese (*Branta canadensis*).

The proportion of successful nests (those rearing at least 1 fledgling) did not differ between Creston and Nelson but did differ between 2 years, with success being lower in 1988 (Table 1). Mean clutch size, brood size at hatching, and brood size at fledging in successful nests did not differ significantly between locations, nor did they change between years (Table 2).

TABLE 1. Status and success of all osprey nests surveyed

Nest status	1987 Creston	1987 Nelson	1987 Total	1988 Creston	1988 Nelson	1988 Total
No. of nests known	60	37	97	71	47	118
Occupied	45	37	82	49	40	89
Successful	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
% successful	78.6	75.7	77.2	63.0	59.5	61.4
Undetermined	3	0	3	3	3	6
Unoccupied	15	0	15	22	7	29

NOTE: The number of nests in each category is given.

Table 2. Summary statistics by year and location for each breeding parameter

	1987 Creston	1987 Nelson	1988 Creston	1988 Nelson	Total
Clutch-initiation date[a]	May10±2 d (15)	May14±2 d (24)	May6±2 d (21)	May13±2 d (20)	— (80)
Clutch size[b]	2.7±0.2 (15)	2.7±0.1 (27)	3.0±0.1 (24)	2.8±0.1 (21)	2.8±0.1 (87)
Brood size at hatching[b]	2.2±0.3 (15)	1.6±0.2 (27)	2.1±0.2 (24)	2.0±0.2 (21)	2.0±0.1 (87)
Brood size at fledging[b] (per successful nest)	2.0±0.1 (33)	2.2±0.1 (28)	2.0±0.1 (29)	2.1±0.1 (22)	2.1±0.1 (112)
Brood size at fledging[c] (per occupied nest)	1.6±0.2 (42)	1.7±0.2 (37)	1.2±0.2 (46)	1.2±0.2 (37)	1.4±0.1 (162)

NOTE: Statistics are presented as mean ± SE with sample size (n). Sample size increases for successive nesting stages as more nests could be included.
[a]Location: $P < 0.05$, year: ns (two-way ANOVA).
[b]Location: ns, year: ns (two-way ANOVA).
[c]Location: ns, year: $P < 0.05$ (two-way ANOVA).

Overall, clutch size averaged 2.8 eggs, brood size at hatching averaged 2.0 chicks, and productivity averaged 2.1 and 1.4 chicks in successful and occupied nests, respectively. The commonest clutch size in both areas was 3 eggs, and these nests were also the most productive (Table 3).

TABLE 3. Mean number of hatched and fledged young in relation to clutch size

Clutch size	n	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

NOTE: Represented here are 243 eggs in 87 clutches. Some of the nests reported in Table 1 are not included in this table because of egg chipping during handling, manipulation of clutches for experiments (Forbes 1989), nest failure due to excessive disturbance by local residents, or because the clutch size and brood size at hatching could not be determined.

Nest sites

In the Creston Valley, 59 (83%) of 71 nests were on the broken tops and dead trunks of tall black cottonwoods (*Populus trichocarpa*). The other 12 nests were located on pilings (3), power poles (6), and bridges (3). In the Nelson area, 45 (96%) of 47 nests were built on man-made structures such as pilings (29), navigation beacons (7), power poles (7), a telecommunication tower (1), and a power dam on the river draining the lake (1). Only two nests (4%) were built atop 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, thus the density of breeding pairs in this area depends on the availability of artificial nesting sites.

Breeding chronology

Ospreys returned to the Kootenay area at the beginning of April with males preceding females by 1–2 weeks. Initiation of clutches spanned 42 days in 1987 (30 April to 10 June, n = 39) and 38 days in 1988 (25 April to 1 June, n = 41). There was a significant difference in clutch-initiation dates between the two areas, but no difference between years (Table 2). For both years combined, the median clutch-initiation dates in the Creston Valley and Nelson area were May 8 and 12, respectively (Fig. 2). The frequency distributions of clutch-initiation dates showed different patterns for the two areas. In the Creston Valley, 61% of all clutches were initiated during the first 10 days of May, whereas Nelson-area ospreys showed a more even distribution over the entire laying period (Fig. 2). Based on five nests for which the laying date of the 1st egg and the hatching date of the 1st chick were known exactly, the mean (±SD) incubation period was 38.5±1.1 days. The minimum incubation period of seven other nests fell within the range 36–42 days.

In both years hatching commenced in the 1st week of June, and all chicks hatched by 8 July, except for 1 extremely late

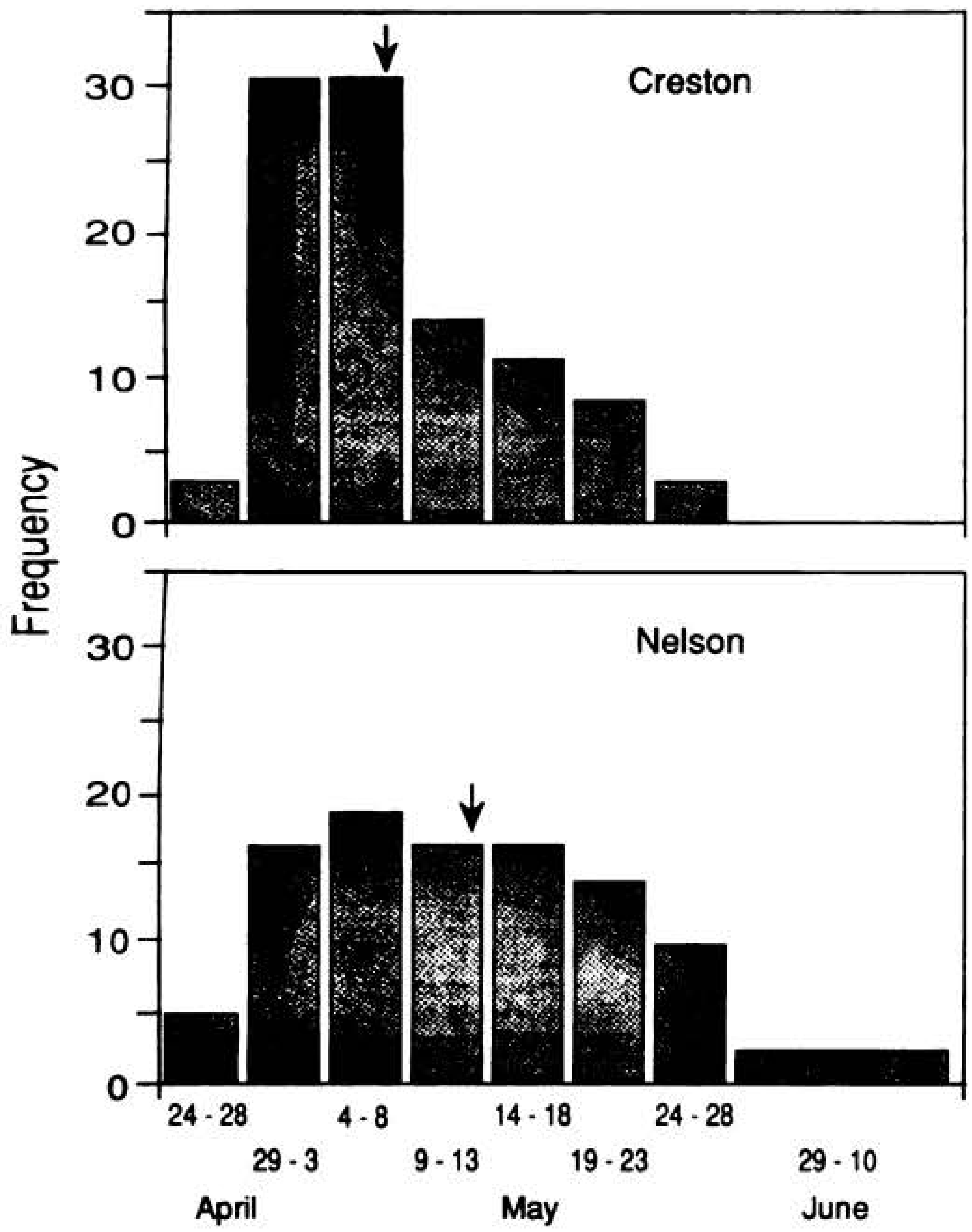

FIG. 2. Frequency distribution of clutch initiation dates (1987 and 1988 combined). The first period begins on April 24 and the last period ends on June 10. Arrows indicate medians: May 8 for Creston (n = 36) and May 12 for Nelson (n = 44).

singleton that hatched on 16 July 1987. No data could be collected on exact fledging dates. However, several chicks were observed practicing wing flapping on the nest, and some chicks fledged just before our last nest visits in early August. On the basis of these observations the nestling period was estimated at approximately 55 days.

Egg size

The volume (±SD) of Creston Valley osprey eggs measured, on average, 68.7 ± 5.7 cm^3 (n = 40) in 1987 and 69.4 ± 5.8 cm^3 (n = 68) in 1988. Eggs in the Nelson area measured 66.0 ± 5.2 cm^3 (n = 74) in 1987 and 67.2 ± 5.7 cm^3 (n = 67) in 1988. A two-way ANOVA indicated that location had a significant effect on egg volume (F = 10.96, P = 0.001); however, no significant difference was detected between years (F = 1.68, P = 0.196). Overall, the average egg volumes in the Creston Valley and Nelson area were 69.1 ± 5.9 cm^3 (n = 108) and 66.6 ± 5.6 cm^3 (n = 141), respectively.

Egg and chick mortality

Total egg mortality for the 2 years combined was 30% (83/276). This is based on 98 nests for which data could be obtained. Of these, 11 nests had to be excluded (Table 3). Natural egg mortality in the remaining 87 clutches, including 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).

TABLE 4. Rate of mass increase ($g \cdot d^{-1}$) of osprey nestlings between ages 5 and 40 d

	Location	
	Creston	Nelson
Rank		
A	46.7±8.0 (5)	51.9±6.1 (16)
B	47.7±13.4 (6)	50.3±5.9 (13)
C	40.2±5.9 (4)	49.7±3.6 (5)

NOTE: All measurements were made in 1987. The A chick is the oldest nestling in each nest. Statistics are presented as mean ± SD with sample size (n). Results of two-way ANOVA are as follows: location: $F_{[1,44]}$ = 15.48, P < 0.001; rank: $F_{[2,44]}$ = 4.21, P < 0.05, but see text.

Total chick mortality during the 2 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). Some chick mortality was most likely due to siblicide or selective starving of subordinate chicks. Several chicks were found dead in the nest, extremely emaciated or with severe wounds on the head and neck (cf. Poole 1982; Forbes 1989).

Chick growth

A two-way ANOVA revealed a significant difference in the rates of growth between birds from Nelson and Creston (Table 4). Nelson ospreys grew, on average, 5.7 $g \cdot d^{-1}$ more rapidly. We could not sex nestlings in our study, so this source of variation could not be accounted for.

There was also a significant, though much weaker, effect of chick rank on the growth rate (Table 4). We are not confident about this conclusion. The data reported here include nestlings from both locations, but nests at Nelson were much more accessible. We were therefore able to make more and more regular measurements of each chick there. Fitting a logistic growth curve over the entire nestling period and using the t_{10-90} measure to estimate growth rate (Ricklefs 1967), there was no effect of chick rank on the growth rate (Steeger 1989). It was possible that the effect became more pronounced when food was limited and hence was less detectable at Nelson. Nevertheless, at Nelson, A, B, and C chicks all grew faster (by 5.2, 2.6, and 9.5 $g \cdot d^{-1}$, respectively) than their counterparts at Creston.

Feeding behaviour

Diet composition differed markedly between locations (Table 5). In the Creston Valley, ospreys primarily captured black bullhead (*Ictalurus melas*), yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), and, to a lesser extent, rainbow trout (*Oncorhynchus mykiss*), longnose sucker (*Catostomus catostomus*), and largescale sucker (*Catostomus macrocheilus*). The diet of Nelson-area ospreys consisted primarily of largescale or longnose suckers, followed by mountain whitefish (*Prosopium williamsoni*), rainbow trout, and kokanee (*Oncorhynchus nerca*). In the Creston Valley, ospreys nesting in or near the marsh primarily fed on bullhead, perch, and pumpkinseed (Forbes 1989), but those at five nests close to Kootenay Lake typically captured suckers and trout.

Fish captured by Nelson-area ospreys were larger and contained significantly more energy (weighted mean = 1629 kJ) than Creston Valley prey (weighted mean = 472 kJ; Mann–Whitney U-test, U = 2477, df = 1, P < 0.001; Table 5). This difference was largely due to the greater number and size of

TABLE 5. Number, biomass (percentage of total), and estimated average energy content (kJ) of fish caught by male ospreys in the Creston Valley (Corn Creek Marsh) and in Nelson on the West Arm of Kootenay Lake

	Creston[a]			Nelson		
	No.	% biomass	kJ per fish	No.	% biomass	kJ per fish
Sucker spp.	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	—[d]	—	72	—[d]	—
Weighted avg.	—	—	472	—	—	1629

[a]Unpublished data from S. L. Forbes.
[b]Includes kokanee, northern squawfish, largemouth bass, and unidentified species at Creston; and unidentified species at Nelson.
[c]Estimated from average length–mass relationship of whitefish, trout, and kokanee. Suckers were very distinctive and extremely unlikely to be unidentifiable.
[d]Total biomasses of fish caught were 21 318 g in the Creston Valley and 28 533 g in Nelson.

suckers captured in the Nelson area (mean = 274 g, n = 7 and mean = 767 g, n = 29, respectively; Mann–Whitney U-test, $U = 36$, df = 1, $P < 0.01$). All fish caught in the Creston Valley were caught by flight hunting, whereas 26% (16/61) of all fish captures at Nelson were made by the energetically inexpensive method of hunting from a perch.

Capture success was higher at Nelson. Ospreys were successful on 47% of 128 observed dives, whereas at Creston they were successful on only 24% of 293 dives. Dive success was reduced by windy weather, and the samples differed in that observations made at Creston by Machmer and Ydenberg (1990) probably overrepresented the amount of poor weather, as they were attempting to measure its effect. When we included only dives made in good weather (wind speed $<1.2\ \mathrm{m \cdot s^{-1}}$) in the Creston sample, 31% of 135 dives were successful. The difference was therefore likely real (two-way contingency table comparing the conservative Creston sample with that at Nelson: one-tailed x^2-test = 7.55, $P < 0.025$).

The profitability of flight hunting was much lower at Creston than at Nelson. The net energy yield was $0.91\ \mathrm{kJ \cdot s^{-1}}$ (SD = 0.28; range of the 6 males = 0.63–1.43) at Nelson, whereas at Creston the net yield was only $0.23\ \mathrm{kJ \cdot s^{-1}}$ (based on 19.8 h of flight hunting; calculated as the weighted average of the data reported by Machmer and Ydenberg (1990)). As before, these observations might have overrepresented poor weather conditions. Considering only the calmest conditions, the estimated yield at Creston was $0.34\ \mathrm{kJ \cdot s^{-1}}$, or about one-third that of the Nelson rate. We had no way to estimate the variance in capture rate at Creston in a manner analogous to the estimate made at Nelson and could not test the difference in energy yield for significance. However, the difference was so large that even if the variance at Creston was larger than that at Nelson the difference would be significant.

Discussion

Creston Valley and Nelson-area ospreys differed 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 were warmer and shallower than the West Arm of Kootenay Lake, accounting for the differences in the fish fauna of these two areas. The difference in diet between Creston Valley and Nelson-area ospreys was therefore likely due to differences in prey availability. Along the shallow margins of the West Arm, Nelson-area ospreys were frequently able to hunt by perching on pilings in the shallows or from trees along the lakeshore. These perch sites were ideal for detecting large, slow-moving suckers. In contrast, ospreys in the Creston Valley captured all their prey by flight hunting. Thus, it appeared that the feeding situation in the Nelson area was more favourable than in the Creston Valley. Not only were individual prey items larger, they required less energy to capture. The greater capture success and net yield of flight hunting also indicated that the hunting habitat at Nelson was superior to that at Creston.

Breeding parameters, however, were almost identical between the two areas. A small difference in clutch-initiation dates was observed, with Nelson birds laying slightly later. Nelson-area ospreys also laid smaller eggs than their Creston Valley counterparts. Birds in the two areas were equally successful in rearing young that hatched, but Nelson nestlings grew faster.

Poole (1984; see also Newton 1979) found evidence that the egg size of female ospreys increased with age. In this study, we were not able to age adult ospreys. Considering that Nelson-area ospreys started laying later and laid smaller eggs than Creston Valley ospreys, it is possible that the Nelson-area nesting concentration consisted of younger birds. One possible reason is that new nesting opportunities had recently been created in the Nelson area. During the 2 years of this study, numerous man-made platforms were set up on the West Arm of Kootenay Lake. Many of these newly created nest sites were immediately occupied by an osprey pair. Presumably these were young birds. If the ospreys breeding at Nelson were truly younger, the better feeding habitat there may have compensated for their inexperience and may explain why ospreys in the two nesting areas did not differ in average clutch size, brood size at hatching, or number of young reared to fledging, despite great differences in the feeding regime.

An alternative, though not necessarily incompatible, hypotheis for the equivalent breeding performance is that the reproductive success of these ospreys was affected by factors unrelated to the food supply. Very different feeding situations may not affect breeding success if ospreys adopt a conservative breeding strategy to buffer their food-delivery ability against unpredictable but potentially devastating events (Forbes and Ydenberg 1992). One such factor is weather. It has a very strong correlation with breeding success at Creston (Forbes 1989), and is known to depress the foraging success of ospreys (Machmer and Ydenberg 1990). Observations by Forbes (1991) and Poole (1989) suggest that prolonged storms may be of special importance.

The results of this study show that although Nelson-area ospreys had a more favourable feeding situation than did Creston Valley ospreys, differences in measures of their breeding performance were minor. It is possible that younger, more inexperienced birds bred in the Nelson area, which would explain their slightly later clutch-initiation date and smaller eggs.

Acknowledgements

We thank the staff of the Creston Valley Wildlife Management Area and the Department of Fish and Wildlife in Nelson, in particular, B. Stushnoff, G. Woods, J. Krebs, J. Black, and L. Douglas for their help during the fieldwork for this study. L. Dill, D. Schluter, N. Verbeek, M. Machmer, and S. Forbes provided helpful comments on earlier drafts of the manuscript. Scott Forbes also shared some of his unpublished data with us. We thank West Kootenay Power and the City of Nelson for providing bucket-trucks to access nests, and the staff of the Canadian Pacific Railroad for their co-operation in granting access to their property and for their most valuable logistical support. The study was supported by an operating grant from the National Sciences and Engineering Research Council of Canada and a grant from the World Wildlife Fund, both to R.C.Y.

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