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THE RELATIONSHIP BETWEEN MALE COURTSHIP FEEDING,
MALE PROVISIONING, AND REPRODUCTIVE DECISIONS IN
THE OSPREY (PANDION HALIAETUS)

by

David J. Green

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTERS OF SCIENCE

in the Department

of

Biological Sciences

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THE RELATIONSHIP BETWEEN MALE COURTSHIP FEEDING, MALE PROVISIONING, AND REPRODUCTIVE DECISIONS IN THE OSPREY (PANDION HALIAETUS)

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Abstract

This study examined the relationship between male courtship feeding, male provisioning, and reproductive decisions in ospreys on the West Arm of Kootenay Lake, British Columbia. The courtship feeding rates of pairs that laid eggs were significantly higher than those that failed to lay, in both 1991 and 1992. For pairs that initiated a clutch, the duration of the courtship period was negatively correlated with male courtship feeding rate. The suggestion that the food supplied to females during the courtship period plays a role in determining both whether and when a female initiates a clutch was supported by a supplementary feeding experiment; a greater proportion of the females in the "fed" group initiated a clutch and their laying date was advanced by an average of 2.5 days. Male courtship feeding rate was also correlated to both male delivery rate to the nest when chicks were one to two weeks of age, and mean brood growth rate. Female ospreys may therefore be able to evaluate male parental performance using courtship feeding rates. Direct and indirect evidence suggest that female ospreys use the information gained from male courtship feeding rate to manipulate hatching patterns, maximizing the reproductive value of their brood given the predicted levels of food availability.

The daily energetic expenditure (DEE) of male ospreys, provisioning nestlings and providing post-fledging parental care, was estimated using detailed time-energy budgets. There was no seasonal pattern to male DEE. Males provisioning large broods had a higher mean DEE than males provisioning small broods. However, male ospreys did not respond to brood size manipulations by altering their energetic expenditure, indicating that male DEE is not causally linked to brood size. It is argued that male age or condition may determine both brood size and DEE. The mean DEE of male ospreys was well below the maximum they are able to sustain. Physiological constraints are therefore unlikely to restrict ospreys to broods of three chicks. The conservative strategy of male ospreys is consistent with the idea that males trade-off the benefits resulting from increased effort in the current year, against future reproductive potential, and thus forage at an optimum rather than maximum capacity.
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Chapter 1
General Introduction

Birds face two major decisions at the start of the breeding season: when to initiate a clutch, and how many eggs to lay. Lack (1954, 1966) argued that birds should breed when food is most available and rear as many young as they can nourish. These breeding decisions were thought to have a genetic basis, with the availability of food, especially to the young, and to a lesser extent the laying female, acting as the main selective pressures shaping the timing and extent of reproduction in birds. Lack's theory suggested that, on average, both early and late laying pairs should produce fewer surviving offspring than birds laying at an average date. However, population studies subsequently revealed that the earliest clutches produced the most surviving offspring (Perrins 1965, Cave 1968, Perrins and Moss 1975). These results were reconciled with Lack's optimal-timing theory by the suggestion that most females were prevented from laying at the optimal time because of a lack of energetic reserves (Perrins 1965, 1970; Lack 1968). Individual breeding optima were thus thought to result from an interaction between local environmental conditions and the state of the parent (Drent and Daan 1980).

Drent and Daan (1980) advocated studying the link between environmental conditions, such as local food supply, and individual reproductive performance. They suggested that this would elucidate individual breeding decisions, and allow interpretation of the broad pattern of breeding behaviour seen at the population level. Furthermore, they posed three questions aimed at understanding the proximate control exerted by local food supply on avian reproductive performance. Firstly, what evidence exists to suggest that shortage of energy, or a specific nutrient, results in failure of some females to lay eggs? Secondly, to what extent does energy, or a specific nutrient, impose a limitation on laying date? Finally, does the foraging capacity of the parents, itself determined by some interplay between time and energy, subsequently set the upper limit to brood size?
Evidence that food supply plays a role in determining avian reproductive performance, at least at a crude level, is available for several species of raptors. The density of the breeding population, timing of laying, and reproductive success of Eurasian kestrels *Falco tinnunculus* (Cave 1968), rough-legged buzzards *Buteo lagopus* (Hagen 1969), tawny owls *Strix aluco* (Southern 1970), northern harriers *Circus cyaneus* (Simmons et al. 1986), and Tengmalm's owls *Aegolius funereus* (Hornfeldt and Eklund 1990), are all tied to the population cycles of microtine rodents, their primary prey. Female body mass of Eurasian kestrels is also correlated with several indices of vole abundance (Dijkstra 1988). Study of the detailed pattern of female body mass change in Eurasian kestrels during surplus feeding experiments has suggested that females have to reach a threshold condition before initiating a clutch (Meijer et al. 1988). Similarly, Alisauskas and Ankney (1985) have argued that American coots *Fulica americana* require a minimum lipid reserve before initiating reproduction.

The role of female body condition, or energetic intake, in determining the timing of laying has prompted renewed interest in courtship feeding, the transfer of food from the male to the female prior to egg-laying. Studies of several species have shown that females depend on courtship feeding for a substantial part of their energetic intake (e.g.: blue tit *Parus caeruleus* Krebs 1970, lesser black-backed gull *Larus fuscus* Brown 1967, common tern *Sterna hirundo* Nisbet 1973). The suggestion that the food supplied during courtship feeding plays a role in determining the timing of laying is supported by supplementary feeding experiments, which have consistently advanced laying date (for reviews see Davies and Lundberg 1985, Daan et al. 1988). Further studies will reveal whether food supply, acting through female condition, generally imposes a limitation on the timing of avian breeding.

Although there is mounting evidence which suggests that food supply influences the timing of laying, the period of nestling care has traditionally been viewed as the bottleneck in the reproductive cycle. Drent and Daan (1980) have postulated that the optimal level of parental care should be associated with a level of energetic expenditure that represents the maximum that can be sustained without deterioration of the parents' condition. They argued that physiological
constraints would set the limit to sustainable working capacity. They also presented evidence from five avian species which suggested that the "optimal working capacity" (Royama 1966a) of a "prudent parent" involves a daily energetic expenditure that does not exceed four times their basal metabolic rate. Their seminal paper prompted a rapid growth of interest in physiological constraints on animal energy budgets. Ecophysiologists now agree that the upper limit to sustainable energy budgets is likely to be set by the digestive tract's capacity to assimilate nutrients or energy from food (Wiener 1992). The question of whether or not parental energetic expenditure is indeed limited by this physiological constraint, however, still invites further investigation.

In this thesis I follow the approach advocated by Drent and Daan in an attempt to determine the role of food supply, and energetic limitation, in the reproductive decisions of ospreys Pandion haliaetus. Ospreys are especially suited for studies which require detailed examination of foraging energetics because of their visibility and sexual task differentiation. In ospreys, as in many raptors, the male is responsible for providing almost all of the food to the female and nestlings from pair initiation until the fledging of young. The analysis of food limitation prior to egg laying, and parental performance while provisioning nestlings, is therefore concerned primarily with the foraging behaviour of male ospreys.

In Chapter 2 I use both natural variation in male courtship feeding rate and a supplementary feeding experiment to assess the influence of food supplied by male ospreys during courtship on whether and when females lay. In Chapter 3 I examine how male ospreys allocate their time and energy while provisioning nestlings and providing post-fledging parental care. I estimate the daily energetic expenditure of male ospreys using detailed time-energy budgets, analyze which factors affect daily energetic expenditure, and ask whether physiological constraints may limit male parental effort.
Chapter 2
Courtship feeding: a functional analysis

Introduction

Courtship feeding, the provisioning of females by their mates, is a widespread avian phenomenon (Lack 1940, Smith 1980). Traditionally, such provisioning was considered to serve only a symbolic function in strengthening the pair bond (Lack 1940, Kluijver 1950). Recent studies, however, have found that courtship feeding can provide females with an important source of energy, that may improve their condition, and influence the timing of reproduction (Royama 1966b, Krebs 1970, Nisbet 1973, Newton 1979). This hypothesis has been widely supported by supplementary feeding experiments which have consistently shown that experimentally fed birds advance their laying date (for a review see Daan et al. 1988), and occasionally lay larger clutches (Newton and Marquis 1981, Carlson 1989, Korpimaki 1989, Hornfeldt and Eklund 1990). However, two further, but not mutually exclusive, hypotheses have been put forward to explain the significance of male courtship feeding. Firstly, it has been suggested that courtship feeding may help induce females to copulate, and a temporal relationship between courtship feeding and copulations has been found in a number of bird species (Calder 1967, Stokes and Williams 1971, Tasker and Mills 1981). In addition, it has been suggested that females may use courtship feeding to evaluate male parental ability (Nisbet 1973, Simmons 1988, Korpimaki 1989). Several studies have established a link between male courtship feeding rate and the quality of subsequent paternal care (Nisbet 1973, Niebuhr 1981, Wiggins and Morris 1986, Donazar et al. 1992), but few studies have assessed whether females use information gained from courtship feeding rate in making breeding decisions (but see Palokangas et al. 1992).

The timing of courtship feeding, and the quantity of food offered by males varies considerably between species. In some species, the majority of courtship feeding takes place
after egg-laying has begun (e.g., eastern bluebird *Sialia sialis* Krieg 1971; European robin *Erithacus rubecula* East 1981). In others, like the osprey *Pandion haliaetus*, females are also fed almost exclusively by their mate between pair formation and egg laying, a two to six week period. Poole (1985), however, argued that the food supplied by male ospreys during courtship plays a limited role in the timing of breeding in this species, because females gained little weight during the courtship period, and experimentally fed birds neither advanced laying date nor laid larger clutches. Unfortunately, male ospreys responded to Poole's experimental food supplements by reducing their own delivery rate to the female, which may have confounded the experimental treatment.

Male ospreys continue to provision females during incubation, and provide the great majority of food items eaten by the female and chicks prior to fledging. Female ospreys may therefore be able to use courtship feeding rate to predict the quality of male parental care, allowing them to adjust breeding decisions in response to the expected levels of food availability at the nest. Hatching asynchrony is a highly variable trait among ospreys; three chick broods can hatch over 2-10 days (Steeger et al. 1992). Magrath (1989) suggested that optimal hatching patterns may be dependent on food availability during the nestling period, after finding that asynchronous blackbird *Turdus merula* broods were more productive than synchronous broods when food was limited, but less productive when food was abundant. If female ospreys can predict male chick provisioning rates using male courtship feeding rate, it may therefore be expected that females with low courtship feeding rates produce relatively asynchronous broods, while females with high courtship feeding rates produce relatively synchronous broods.

This study examines the courtship behaviour of ospreys, and assesses: (1) whether courtship feeding acts to induce copulations; (2) the effects of food supply on the timing and extent of reproduction, using both natural variation in male courtship feeding rate and a supplementary feeding experiment; and (3) whether females can use courtship feeding rate to predict male parental performance, and if so, whether they use this information to adjust hatching asynchrony.
**Methods**

This study was conducted in the Kootenay region of British Columbia in 1991 and 1992. Approximately 50 pairs of ospreys breed along the West Arm of Kootenay Lake near Nelson. The study area and the general breeding ecology of this population are described by Steeger et al. (1992). Ospreys begin to return to the Kootenays from their Central American wintering grounds in early April, and pairs re-form at nest sites from mid-April onwards. Females initiate clutches in May, hatch chicks in June, and fledge offspring in August. Adults continue to provision fledglings until they leave the breeding grounds in October.

**Breeding biology**

Surveys of the study area were conducted every one to two days from early April until the end of egg laying in late May to establish date of pair formation at each nest site, and the duration of the courtship period. The first day that both members of a pair were seen at, or in close proximity to the nest defined the date of pair initiation unless surveys were separated by more than one day, in which case the date between surveys was used. The onset of incubation was also established from surveys, and was used to define clutch initiation date, and courtship period (the number of days from pair initiation to laying of the first egg). Clutch initiation dates were later confirmed by back dating from the date of hatch. One week following the onset of incubation, clutch sizes were determined using a mirror on an extendable pole or by climbing to the nest. Nests were revisited three to four days later if clutches contained one or two eggs, and were therefore potentially incomplete. Hatching success was determined after the last chick had hatched, or when it became certain that the remaining eggs were not viable (i.e. depredated, broken, or unhatched when the youngest chick was 10 days old). Hatching dates and brood hatching asynchrony were determined during the first visit to nests after hatch using a culmen length-age regression established for known-aged chicks (y=1.41x - 13.75, r²=0.91, n=49; cf. Poole 1984, Steeger et al. 1992). Chick masses were determined during regular visits to the
nests, conducted from hatching until the oldest chick was approximately 40 days of age. Individually colour marked chicks were weighed with 100, 1000, or 2000 g Pesola spring balances. Growth rates of individual chicks were then calculated from the four to five measurements taken during the period of linear growth (7-30 days; Machmer 1992).

Courtship

Courtship behaviour of 43 pairs of ospreys (20 in 1991, 23 in 1992) was observed from pair initiation until completion of laying, or until members of a pair no longer regularly attended the nest. Pair initiation dates and subsequent reproductive data were obtained for a further 23 pairs (10 in 1991, 13 in 1992). In 1991, nest watches of five hours duration were conducted during three periods of the day (roughly 0500-1000, 0930-1430, 1400-1900). Nest watches were conducted by two observers, watching a maximum of two pairs, on a rotating basis so that each pair was observed every four to seven days. Each pair was observed for a total of approximately 30 hours (range 20-40), with watches equally distributed throughout the day. In 1992, the protocol was altered slightly to allow for a supplementary feeding experiment. Each pair was again observed for approximately 30 hours (range 24-40) with watches taking place every five to seven days, but watches were of eight hours duration and started at first light.

In both years prey species captured were identified and their size was estimated by visual comparison to the tail length of adult ospreys (20 cm), a method which is accurate to within 5 cm (Stinson 1978). Levels of male courtship feeding were determined by counting the number of "bites" a female ripped and consumed from each fish delivered (Poole 1985). Bite size was calibrated by counting the number of bites required by six females to consume a fresh fish of known mass, left at their nests during the supplementary feeding experiment (average bite size ± se = 1.03 ± 0.96 g). Courtship feeding rate (kJ/h) was then calculated by converting the number of bites into energetic equivalents for each fish species (Watt and Merrill 1975) using an estimate of 80% assimilation efficiency (Kushlan 1977).
Temporal patterns in male courtship feeding rate were examined within a day, in relation to three stages of the courtship period (early: one to two weeks before clutch initiation, late: less than one week before clutch initiation, and during laying: one to five days after clutch initiation), and with respect to year.

*Courtship feeding and copulations*

The timing and success of all copulation attempts were recorded during nest observations. Copulations were classified as successful if a female tipped forward following mounting and her mate appeared to achieve cloacal contact (see Cramp and Simmons 1980). The association between male courtship feeding and copulation rate was examined at two levels. Firstly, it was determined whether a pair's copulation rate, or the relative success of copulation attempts, increased during, or in the hour following, the delivery of a fish. Secondly, it was determined whether a pair's copulation rate prior to egg-laying was correlated with male courtship feeding rate.

*Courtship feeding rate, the timing of laying, and breeding success*

Individual differences in male courtship feeding rates were used to evaluate the importance of food supplied by males during courtship in determining whether a pair initiated a clutch, and the duration of the courtship period. The relationship between male courtship feeding rate and three measures of breeding success (clutch size, brood size, and fledging success) was investigated.

*Supplementary feeding experiment*

In April and May 1992, a supplementary feeding experiment was conducted to determine the effects of food provided during the courtship period on the timing of reproduction. As pairs formed at nest sites in the study area in 1992 they were matched on the basis of pair initiation date, and fledging success in the previous year, and then randomly
assigned to the control or experimental group. This continued until both groups had 10 pairs. After allowing each pair five days to establish, approximately 400g of fish was placed on each experimental nest each day between 1700 and 1900 hours (12-14 hours after first light). As male courtship feeding rate was low after 1700 hours in 1991, providing food supplements at the end of the day aimed to increase the amount of food available to females, without causing males to reduce their provisioning rate (as was observed in Poole's (1985) experiment). This was tested by comparing the courtship feeding rate of males in control and fed pairs. The birds quickly returned to the nest following our visits, accepted, and ate the fish provided. Feeding supplements stopped when clutches were initiated, as ospreys have been reported to be more sensitive to disturbance during laying (Poole 1989). Control nests were visited during the experimental period, but received no fish. One experimental pair failed to lay and feeding supplements in this case were stopped after 20 days. The influence of food supplements on clutch size and the duration of courtship was assessed. Length of the courtship period was used in preference to laying date, because the wide range of pair initiation dates in both the control and fed group would mask any effect of supplementary food given the relatively small sample size of this experiment. A pair's courtship feeding period was unknown if they did not initiate a clutch. When comparing the courtship feeding period of pairs in the fed and control group a rank test was used, with pairs that did not initiate a clutch being ranked equal and last.

Courtship feeding rate, male parental performance, and hatching asynchrony

Two measures of male quality were used to test the hypothesis that male courtship feeding rate can predict later parental performance. (1) Male delivery rate to the nest when chicks were one to two weeks old (when the majority of brood reduction occurs in this population; Machmer 1992). Food delivery rate (kJ/h), and the intake rate per chick (kJ/chick/h) were determined for 15 different pairs (5 in 1991, 10 in 1992) during 10 hour focal watches which started at first light. Delivery and intake rates were determined, after calibrating the bite size of females feeding chicks aged one to two weeks (mean bite size ± se = 0.35 ±
0.08 g; n=6), using the methodology described for establishing courtship feeding rates.

(2) Mean brood growth rates (g/day), an indirect measure of male provisioning rate when chicks are 7-30 days old.

If female ospreys were able to use male courtship feeding rate to predict the quality of subsequent paternal care, I expected a negative relationship between courtship feeding rate and degree of hatching asynchrony. To test whether courtship feeding rate was negatively correlated with hatching asynchrony, I examined the relationship between these variables in the 12 pairs of ospreys with known courtship feeding rate that hatched three eggs. This prediction was also evaluated indirectly, by determining whether mean brood growth rate, a measure of male parental performance, was negatively correlated with hatching asynchrony. The mean brood growth rate and hatching asynchrony of all complete broods that fledged three chicks between 1987-1992 were available for the latter analysis (Ydenberg, unpub. data).

Statistical analysis

Non-parametric statistics were used when sample sizes were too low to determine how variables were distributed, or when variables had distributions that were not normal. All tests are two-tailed unless otherwise stated.

Results

Temporal patterns

There was a pronounced diurnal pattern to male courtship feeding; fish delivery peaked in the early morning and late afternoon (Fig. 2.1). The rate at which males delivered fish did not differ between early, late, and egg laying stages of the courtship period (Fig. 2.2a), and individual courtship feeding rates were therefore calculated using the mean of all observation periods. Male courtship feeding rates did not differ significantly between 1991 and 1992 (Table 2.1). As there were also no differences in the courtship period, mean brood growth rate, and
Fig. 2.1  Diurnal variation in male delivery rate (kJ/h) to females during courtship. Data presented are based on the mean delivery rate, at each hour, of 13 males that initiated a clutch in 1991. The bold horizontal line indicates the time period 1700-1900 when supplementary food was added to nests in 1992.
Fig. 2.2  (a) Courtship feeding rate (kJ/h) and (b) Copulation rate (/h) during early\textsuperscript{a}, late\textsuperscript{b}, and laying stages\textsuperscript{c} of the courtship period. Data presented are for all 22 pairs observed during all three stages of courtship in 1991-1992, that were not fed food supplements.

a) Courtship feeding rate, Friedman’s test: $M_{3,22}=0.98$, $p=0.61$

b) Copulation rate, Friedman’s test: attempts, $M_{3,22}=12.18$, $p=0.002$; successful, $M_{3,22}=10.96$, $p=0.004$

Dunn’s multiple comparisons: attempts, $T_{a,b}=0.08$, $p>0.2$, $T_{a,c}=2.79$, $p<0.05$, $T_{b,c}=2.87$, $p<0.05$; successful, $T_{a,b}=0.15$, $p>0.2$, $T_{a,c}=2.64$, $p<0.05$, $T_{b,c}=2.79$, $p<0.05$
Table 2.1  Mean courtship feeding rate and mean reproductive parameters (± SD) for the osprey population on the West Arm of Kootenay Lake in 1991 and 1992. Sample sizes are indicated in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>1991</th>
<th>1992</th>
<th>Mann-Whitney test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Courtship feeding rate (kJ/h)</td>
<td>54.1±36.1 (13)</td>
<td>55.1±28.1 (18)</td>
<td>U=121, p=0.87</td>
</tr>
<tr>
<td>Clutch size</td>
<td>2.24±0.83 (17)</td>
<td>2.67±0.68 (27)</td>
<td>U=294, p=0.08</td>
</tr>
<tr>
<td>Brood size / active nest</td>
<td>1.63±1.26 (16)</td>
<td>2.15±0.82 (27)</td>
<td>U=261.5, p=0.23</td>
</tr>
<tr>
<td>Brood size / successful nest</td>
<td>2.36±0.67 (11)</td>
<td>2.23±0.71 (26)</td>
<td>U=157, p=0.61</td>
</tr>
<tr>
<td>Fledging success/ active nest</td>
<td>1.5±1.16 (16)</td>
<td>2.04±0.85 (27)</td>
<td>U=270.5, p=0.15</td>
</tr>
<tr>
<td>Fledging success/ successful nest</td>
<td>2.18±0.60 (11)</td>
<td>2.11±0.77 (26)</td>
<td>U=148, p=0.86</td>
</tr>
<tr>
<td>Mean brood growth rate (g/day)</td>
<td>57.1±6.9 (8)</td>
<td>58.0±5.5 (17)</td>
<td>U=74.5, p=0.7</td>
</tr>
</tbody>
</table>
fledging success of pairs in 1991 and 1992 (Table 2.1), the two years have been combined for most analyses.

_Courtship feeding and copulation rates_

Copulation rates did not differ between the early and late stages of the courtship period, but declined significantly following clutch initiation (Fig. 2.2b). Approximately 60% of all copulations were successful, during all three stages of the courtship period. Male courtship feeding had no apparent impact on copulation rate. The mean copulation rate of a pair, during, and in the hour following feeds, did not differ from their mean copulation rate during other periods of the day (t=-1.574, df=27, p=0.13). Furthermore, only 9% of the 385 copulation attempts observed were associated with feeds. The copulation attempts associated with feeds were also not more likely to be successful than those not associated with feeds (Chi²=0.067, df=1, p=1.0). The copulation rate of a pair prior to egg-laying tended to be correlated with the male's overall courtship feeding rate (r_p=0.31, n=34, p=0.08). However, this relationship occurred due to the low courtship feeding and copulation rates of pairs that failed to lay, relative to pairs that succeeded. Courtship feeding rate was not correlated with copulation rate when only pairs that laid eggs were considered (r_p=0, n=22, p=1.0).

_Courtship feeding rate, the timing of laying, and breeding success_

The courtship feeding rates of unmanipulated pairs that laid eggs were significantly higher than those that failed to lay eggs in both 1991 and 1992 (Fig. 2.3). Male courtship feeding rate was also negatively correlated with the duration of the courtship period, for pairs that initiated a clutch (Fig. 2.4a). This relationship may have arisen as a consequence of variation in the age and breeding experience of pairs, factors which are known to affect both courtship feeding rate and the duration of the courtship period (Poole 1985). Although birds in this study were unmarked, pair initiation dates may be used as an indicator of mean pair age and experience (Poole 1985). Pair initiation dates of those pairs that failed to initiate a clutch were
Fig. 2.3  Relationship between courtship feeding rate and the initiation of a breeding attempt in 1991 and 1992. Sample sizes are indicated above the bars. 1991, Mann-Whitney $U_{7,13}=84.5$, $p<0.005$; 1992, Mann-Whitney $U_{4,10}=37$, $p<0.05$. 
Fig. 2.4  Relationship between (a) courtship feeding rate (kJ/h), and (b) pair initiation date (julian date, Jan 1=1), and the courtship period (d:ys).

a) \( y=25.06-0.06x \), \( r^2=0.21 \), \( n=22 \), \( p=0.031 \)

b) \( r^2=0.01 \), \( n=34 \), \( p=0.64 \)
no different from those that succeeded (1991, Mann-Whitney $U_{13,17}=120$, $p=0.69$; 1992, Mann-Whitney $U_{8,18}=103.5$, $p=0.08$). The duration of the courtship period was also unrelated to pair initiation date (Fig. 2.4b). This suggests that variation in courtship feeding rate and the duration of the courtship period are not explained solely by differences in a pair's age and breeding experience.

Although courtship feeding rate affected the duration of courtship, there was no relationship between courtship feeding rate and any measure of breeding success: clutch size ($r_p=0.17$, $n=23$, $p=0.44$), brood size ($r_p=0.17$, $n=22$, $p=0.46$), or fledging success ($r_p=0.11$, $n=22$, $p=0.63$). The clutch of one pair was lost due to human interference and was therefore dropped from subsequent analyses.

**Supplemental feeding experiment**

The food supplements did not cause male ospreys to significantly reduce their own courtship feeding; the courtship feeding rate of males in the control and experimental groups did not differ significantly (Table 2.2). The experimental females gained a food supplement equivalent to 49kJ/h on days they were fed, or 30 kJ/h if the effect of supplements is averaged over the whole courtship period (Table 2.2). A greater proportion of females in the experimental group initiated a clutch. The courtship period of pairs in the experimental group was significantly shorter, by an average of 2.5 days, than that of pairs in the control group (Table 2.2). Even when the pairs that did not initiate a clutch were removed from the analysis, the courtship period still tended to be shorter in the experimental group ($U_{7,9}=45.5$, 1-tailed $p=0.07$). The food supplements did not affect clutch sizes (Table 2.2).

**Courtship feeding rate, male parental performance, and hatching asynchrony**

Male courtship feeding rate correlated positively with male delivery rate to the nest when chicks were one to two weeks old (Fig. 2.5). Male courtship feeding rate was also correlated with mean brood growth rate (Fig. 2.6). The courtship feeding rate of male ospreys
Table 2.2 Feeding rates and breeding performance (± SE) of ospreys provided with supplementary food during 1992, compared to control pairs that were not fed. Mann-Whitney tests are all one-tailed.

<table>
<thead>
<tr>
<th></th>
<th>Control Group</th>
<th>Fed Group</th>
<th>Mann-Whitney</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Pair initiation date</td>
<td>April 18 ± 1.5</td>
<td>April 18 ± 2</td>
<td></td>
</tr>
<tr>
<td>CFR(^a) (kJ/h)</td>
<td>52.2 ± 11.0</td>
<td>43.2 ± 9.1</td>
<td>U(_{10,10}=58) p=0.29</td>
</tr>
<tr>
<td>Supplement (kJ/h)</td>
<td>0</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>Adj. supplement(^b) (kJ/h)</td>
<td>0</td>
<td>29.7 ± 3.1</td>
<td></td>
</tr>
<tr>
<td>Number of pairs that failed to lay</td>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Courtship period (days)</td>
<td>22.0 ± 1.2</td>
<td>19.4 ± 1.7</td>
<td>U(_{10,10}=74) p=0.034</td>
</tr>
<tr>
<td>Clutch size / pair</td>
<td>2.0 ± 0.47</td>
<td>2.5 ± 0.31</td>
<td>U(_{10,10}=58.5) p=0.24</td>
</tr>
<tr>
<td>Clutch size / active nest</td>
<td>2.86 ± 0.26</td>
<td>2.77 ± 0.15</td>
<td>U(_{7,9}=33) p=0.43</td>
</tr>
</tbody>
</table>

a) Courtship feeding rate by male

b) The adjusted supplement is calculated as follows: \(\text{Number of days fed} \times \frac{49}{\text{Duration of courtship period}}\)
Fig. 2.5  Relationship between courtship feeding rate (kJ/h) and (a) total delivery rate (kJ/nest/h) and (b) delivery rate per chick (kJ/chick/h), when chicks are one to two weeks old.

a) $y = 0.34x + 34$, $r^2 = 0.27$, $n = 15$, $p = 0.049$

b) $y = 0.11x + 5.3$, $r^2 = 0.47$, $n = 15$, $p = 0.005$
Fig. 2.6 Relationship between courtship feeding rate (kJ/h) and mean brood growth rate (g/day).

\[ y = 0.09x + 52.6, \quad r^2 = 0.27, \quad n = 21, \quad p < 0.05 \]
was therefore correlated with the quality of parental care they subsequently provided.

As predicted, courtship feeding rate was negatively correlated with brood hatching asynchrony (Fig. 2.7). However, as this relationship is strongly affected by the removal of one data point, it is difficult to draw any conclusions from this result. Mean brood growth rate, a measure of male parental performance, was also negatively correlated with brood hatching asynchrony (Fig. 2.8). This relationship is not a consequence of seasonal patterns to hatching asynchrony or mean brood growth rate, as there is no relationship between hatching asynchrony or mean brood growth rate and clutch initiation date (Fig. 2.9).

**Discussion**

*Courtship feeding and copulation behaviour in ospreys*

The delivery of fish by male ospreys did not affect either copulation rate, or the likelihood that copulation attempts achieved cloacal contact. Furthermore, only 9% of the copulation attempts observed were associated with food deliveries. This is consistent with other studies, which have also failed to find any association between courtship feeding and copulation in ospreys (Poole 1985, Birkhead and Lessels 1988). It therefore appears unlikely that courtship feeding is required to induce female ospreys to copulate.

The copulation rate of ospreys in this study was high, with pairs copulating successfully approximately 90 times before clutches were initiated. The success rate of copulations (60%) was higher than that recorded in other osprey studies (46% Levenson 1979, 47% Poole 1985, 39% Birkhead and Lessels 1988). The high copulation rate observed is common in species in which males are unable to guard their mates, and is argued to have evolved primarily in response to sperm competition (Moller 1987, Birkhead et al. 1989).

*Courtship feeding rate, laying date, and clutch size*

Females that failed to initiate a clutch were provisioned at a significantly lower rate than
Fig. 2.7  Relationship between courtship feeding rate (kJ/h) and brood hatching asynchrony (days) for three-chick broods in 1991 and 1992.

$r_s = -0.505$, $n=12$, one-tailed $p=0.047$
Fig. 2.8  Relationship between mean brood growth rate (g/day) and brood hatching asynchrony (days) for three-chick broods in 1987-1992.

\[ y = 12.0 - 0.14x, \quad r^2 = 0.26, \quad n = 24, \quad \text{one-tailed p} = 0.007 \]
Fig. 2.9  Relationship between clutch initiation date (julian date, Jan 1=1) and (a) brood hatching asynchrony (days), and (b) mean brood growth rate (g/day) for three-chick broods in 1987-1992.

a) \( r^2 = 0.001, \ n = 63, \ p = 0.78 \)

b) \( r^2 = 0.068, \ n = 25, \ p = 0.21 \)
females that succeeded, which suggests that the food supplied by male ospreys plays an important role in determining whether females are willing or able to breed. The duration of the courtship period was also negatively related to courtship feeding rate, providing correlative evidence for an association between male provisioning and the timing of reproduction. Poole (1985) found a similar relationship for an osprey population in Massachusetts. However, he argued that food had no independent effect on the courtship period because the rate of food consumption by females during courtship was also related to a pair's age and their previous breeding experience. The supplementary feeding experiment conducted during this study provides evidence for an independent and causal role of food supply. The 2.5 day reduction in the courtship period resulting from the food supplement approximates that predicted from the regression of natural courtship feeding rate on courtship period (y=25.06-0.06x; Fig. 2.4a).

Thus, while age-related improvement in foraging efficiency (Curio 1983, Nol and Smith 1970), or age-specific reproductive effort (Gadgil and Bossert 1970, Pianka and Parker 1975) may influence courtship feeding rate, it is the food transferred that has a proximate effect on laying date. This conclusion is generally supported by other supplementary feeding experiments, to which seven out of eight multiple-brooded passerine species responded with a significant advance in laying date (reviews in Davies and Lundberg 1985, Meijer et al. 1988). Among six single-brooded species, carrion crows Corvus corone (Yom-Tov 1974), Eurasian kestrels Falco tinnunculus (Meijer et al. 1988), and Tengmalm's owls Aegolius funereus (Korpimaki 1989, Hornfeldt and Eklund 1990) showed significant advances in laying date, while the black-billed magpie Pica pica (Hogstedt 1981, Hochachka and Boag 1987), sparrowhawk Accipiter nisus (Newton and Marquis 1981), and red-backed shrike Lanius collurio (Carlson 1989) all showed slight but non-significant advances.

Although food supply affected the timing of reproduction in this study, no relationship was observed between courtship feeding rate and clutch or brood size. The experimental addition of food also had no effect on clutch size. As advancing the laying date by 2.5 days would only be expected to enlarge clutch size by 0.05 of an egg (based on a clutch size decline
of 0.02 egg/day; Steeger and Ydenberg submitted), it is not surprising that no change in clutch size was detected. Other supplementary feeding experiments have rarely shown date-independent increases in clutch size (for a review see Daan et al. 1988, but see Carlson 1989, Korpimaki 1989, Hornfeldt and Eklund 1990). The idea that laying date determines clutch size, independent of food supply, is also supported by other experimental studies. The best direct evidence that clutch size is linked to calendar date is provided by Meijer et al. (1990), who successfully manipulated the clutch sizes of captive Eurasian kestrels by altering the photoperiod. Steeger and Ydenberg (submitted) found that ospreys who are forced to delay clutch initiation reduced clutch size, and that the magnitude of the reduction reflected the seasonal clutch size decline seen in the unmanipulated population.

The data currently available on the effects of food supply on the timing and extent of reproduction in ospreys support the general framework proposed by Drent and Daan (1980), and establishes that food availability during courtship primarily affects laying date, and that laying date in turn determines clutch size. Drent and Daan (1980) distinguished two alternative pathways by which food supply can affect the timing of reproduction. The "capital" model assumes that laying is induced and clutch size determined by the female's condition when she reaches a seasonally decreasing threshold condition. In contrast, the "income" model assumes that the rate of change of condition determines clutch size. The capital model predicts no difference between fed birds and controls laying on the same date, while the income model predicts larger clutches by fed birds. While the supplementary feeding experiment in this study did not follow the protocol suggested by Drent and Daan (1980) to distinguish between the two alternatives, the results appear inconsistent with the income model. Whether condition determines laying date in osprey is still open to investigation, and the distinction between rate of food intake and body reserves as triggers for the onset of reproduction requires more detailed analysis of energetics in female ospreys during the breeding season.
Courtship feeding rate, male parental performance, and hatching asynchrony

This study found that male courtship feeding rate was correlated with male delivery rate when chicks were one to two weeks old. Courtship feeding rate was also correlated with mean brood growth rate, suggesting that females can use courtship feeding rate to predict male delivery rates for at least the first 30 days of the nestling period. Several other studies, in a variety of species, have found similar results. Niebuhr (1981) found that the courtship feeding rate by male herring gulls Larus argentatus was positively correlated with time spent incubating, the time spent in the territory during the chick stage, and the frequency of chick feeding by males. Courtship feeding rates of common terns Sterna hirundo in Ontario (Wiggins and Morris 1986), and lesser kestrels Falco naumanni in southern Spain (Donazar et al. 1992) were also correlated with later chick-feeding rates. Females, in a variety of avian species, may therefore be able to use courtship feeding rate to predict the quality of subsequent paternal care.

Although previous studies have shown that rates of male food delivery to the nest are seasonally autocorrelated, no studies have been able to show that females use information gained from courtship feeding rates in making breeding decisions. Simmons (1988) has suggested that female northern harriers may select mates principally on their provisioning performance. However, he did not measure courtship feeding rates directly. In contrast, Palokangas et al. (1992) found that female Eurasian kestrels did not use male courtship feeding rates as a basis for mate choice.

Mate choice on the basis of courtship feeding rate is unlikely in ospreys due to the limited number of single males with a nest or potential nest site, and the costs associated with delaying reproduction in this species (Poole 1985). However, female ospreys might be expected to facultatively manipulate hatching patterns if parental performance during the nestling period can be predicted from courtship feeding rate, as the costs and benefits of hatching asynchrony are likely dependent on food availability during the nestling period (Magrath 1989, Pijanowski 1992, Wiebe submitted). Specifically, females who predict their male will deliver
food at a high rate should reduce hatching asynchrony. This will reduce the competitive asymmetry in the brood and minimize the probability of brood reduction. Alternatively, if females predict that their mate will provision poorly, they should increase hatching asynchrony. The resulting competitive asymmetry will lead to rapid brood reduction if inadequate food is delivered for the entire brood. If female ospreys are using courtship feeding rate to evaluate male parental performance, courtship feeding rate should therefore be negatively correlated with hatching asynchrony.

Courtship feeding rate in this study was negatively correlated with hatching asynchrony, but, as this relationship was weak, it requires confirmation before any conclusions can be drawn. However, this study found convincing evidence that courtship feeding rate can be used to predict male parental performance. Furthermore, mean brood growth rate, a measure of male parental performance, was negatively correlated with hatching asynchrony. Although indirect, these results suggest that female ospreys can use courtship feeding rate to evaluate male parental performance, and do use the information gained to adjust hatching asynchrony.

Intra-specific variation in hatching patterns may also be interpreted as the proximate result of individual differences in food availability (Pierotti and Bellrose 1986, Sydeman and Elmslie 1992). However, egg-laying does not place the same demands on all avian species (Ricklefs 1974). The eggs of larids, for example, weigh approximately 16% of female body mass (Ricklefs 1974), whereas those of the osprey weigh only 3.5% (Poole 1985). Energetic constraints during laying are therefore unlikely to explain the wide range of hatching spreads observed in this species.

The suggestion that female ospreys manipulate hatching patterns to individual optima, by adjusting the timing of egg-laying or start of incubation, however, is supported by other studies that have examined intra-specific variation in hatching asynchrony. The best evidence that hatching asynchrony can be facultatively manipulated is provided by a study on American kestrels *Falco sparverius* (Wiebe and Bortolotti submitted). Parents provided with food supplements prior to laying hatched their eggs more synchronously, but fledged fewer young
than control pairs, perhaps because they adjusted hatching asynchrony to food levels that were not representative of actual prey abundance in the territory. Other studies provide further evidence that hatching asynchrony is phenotypically plastic, and can be facultatively manipulated. Older parents have more synchronous broods than younger parents in blue-eyed shags *Phalacrocorax atriceps* (Shaw 1985), and western gulls *Larus occidentalis* (Sydeman and Elmslie 1992) suggesting that asynchrony is plastic, while the fact that older birds with greater foraging experience, or birds with higher provisioning rates have more synchronous broods is consistent with the idea of facultative manipulation (Nisbet and Cohen 1975, Bryant 1978, Shaw 1985, Sydeman and Elmslie 1992).

This study has shown that while the primary function of courtship feeding may be to improve a female's nutritional state, thereby advancing laying date, females can also use courtship feeding rates to evaluate their male's parental performance and appear to use this information to fine-tune hatching asynchrony. However, further work is needed to clarify the adaptive value of intra-specific variation in hatching asynchrony, and to determine the importance of information gained from courtship feeding rates in manipulating breeding decisions.
Chapter 3
Energetic expenditure and intake of male, female, and nestling ospreys

Introduction

Time and energy constraints have been proposed by many ecologists as critical factors determining the foraging capacity, and hence reproductive rates of altricial birds (Royama 1966, Drent and Daan 1980, Daan et al. 1988). The consequences to parents and offspring of raising more or fewer young than present in the natural brood have often been evaluated using brood size manipulations. The majority of brood manipulation experiments have demonstrated that altricial birds are able to raise more offspring than present in their natural brood (Ydenberg and Bertram 1989, VanderWerf 1992), but that this is often at the expense of the condition (usually body mass) or survival of individual fledglings (for reviews see Dijkstra et al. 1990, Lessels 1991). Studies attempting to measure reproductive costs to parents associated with brood size have been more equivocal, although reduced adult survival or lowered fecundity in subsequent years have been found in 9 of 14 studies (Dijkstra et al. 1990). As manipulation of brood size does not directly manipulate parental effort, equivocal results may be due to the "unwillingness" or inability of parents to increase their energetic expenditure when given enlarged broods.

Ecophysiologists agree that the upper limit to sustainable energy budgets is likely to be set by the digestive tract’s capacity to assimilate nutrients or energy from food (for a review see Wiener 1992). This upper limit ($A_{max}$) can be predicted using an allometric relationship based on empirical measurements of the maximum energy intake of birds exposed to low ambient temperatures (Karasov 1992). Measurement of energetic expenditure by parents during the breeding season, while provisioning natural and manipulated broods, allows the effects of brood size on the energetic expenditure of parents
to be quantified, while also allowing an assessment of whether parents are working at close to their estimated physiological limit.

The osprey *Pandion haliaetus* is a large, sexually dimorphic raptor with marked division of parental duties during the breeding season. Males capture the great majority of prey eaten by the female and chicks prior to fledging, while females feed, brood, and protect the young. Despite their seemingly demanding role, male ospreys spend between 65% and 85% of their day perched at or near the nest (Poole 1989), hardly suggestive of time or energetic constraints to parental effort. Wilson (1975), however, suggested that parental effort may be far higher during occasional stringent periods. Time or energetic constraints during these rare periods may limit parental foraging capacity, restricting brood size, while at other times parental effort is relaxed. Alternatively, ospreys may balance the potential benefits of increased reproductive success resulting from increased effort in the current year against future reproductive potential (Williams 1966), and consequently forage at a level below their maximum capacity.

This study examines how male ospreys allocate their time and energy while provisioning nestlings and providing post-fledging parental care. The daily energetic expenditure (DEE) of male ospreys is estimated using detailed time-energy budgets collected over the whole breeding season in a variety of weather conditions. Factors affecting DEE are investigated, and comparison between DEE and *A*<sub>max</sub> are used to determine whether physiological constraints limit reproductive effort at any point in the breeding season. Short term brood manipulations are used to assess the impact of raising more or fewer young than the natural brood on male energetic expenditure, and the intake rates of males, females, and nestlings.

**Methods**

This study was conducted in the Kootenay region of British Columbia during the summers of 1991 and 1992. Approximately 50 pairs of ospreys breed along the West Arm
of Kootenay Lake, near Nelson. The majority of nest sites are located on man-made structures such as light beacons, pilings and power poles, and are easily observed from the shore or from a boat. Females initiate clutches in May, chicks hatch in June, and offspring fledge in August. Males provision both the female and the chicks with fish during the nestling period, with most fish being captured within a kilometre of the nest. After fledging, both adults provision young until they leave the breeding grounds in October.

Breeding biology

Surveys of the study area were conducted every one to two days following the return of osprey from their wintering grounds in early April. One week following the onset of incubation, clutch sizes were determined using a mirror on an extendable pole or by climbing to the nest. Nests were revisited three to four days later if clutches contained one or two eggs, and were therefore potentially incomplete. Hatching success was determined after the last chick hatched, or when it became certain that the remaining eggs were not viable (i.e., depredated, broken, or unhatched when the youngest chick was 10 days old). Precise hatching dates were determined during the first visit to nests after hatching, using a culmen length-age regression established for known-aged chicks \( y=1.41x - 13.75, r^2=0.91, n=49 \); cf. Poole 1984, Steeger et al. 1992). Chicks were individually marked, and their mass was determined during regular visits to the nest, conducted from hatch until the oldest chick was approximately 40 days of age. Chicks were weighed with 100, 1000, or 2000 g Pesola spring balances. Growth rates of individual chicks were then calculated from the four to five mass measurements taken during the period of linear growth (7-30 days; Machmer 1992). The lengths of the culmen, wing, tail, and third primary of each chick were also determined during each visit to the nest.
During 1991 and 1992, detailed time budgets were collected for 11 individual males provisioning broods at three stages of nestling development (1-2, 3-4, and 6-7 weeks). Post-fledging time budgets were also collected for five of these males in 1992. Time budgets of six additional males were collected only when these males were provisioning chicks of one to two weeks (these data were collected as part of a broader study on male parental care). Time budgets were collected during 98 days between 16 June and 2 September, for 17 males, with brood sizes ranging from one to three. These time budgets were based on 10-hour focal watches, where the male's activity was known for at least 80% of the time (mean 95.2%; range 82.2%-100%). All focal watches started at first light. Eighteen time-budgets were collected for the entire day to test for possible biases in the estimates of energetic expenditure and intake rates determined using time budgets collected over the first 10 hours of the day.

During focal watches, males were followed on every flight by boat or using binoculars. Flight activity was partitioned into flaps, glides, and dives, with dives being classified as successful, unsuccessful, or aborted (i.e., not resulting in contact with the water). The sequence of these three types of flight activity, their duration, and the outcome of all dives were recorded directly onto an event recorder. The apparent purpose of each flight (hunt, chase intruder, collect nest material, unknown), the male's position at the end of a flight, and the duration of non-flight activities (feeds and perching) were also recorded.

Weather conditions

During all focal watches the following weather variables were recorded at 30 minute intervals using a portable weather station: temperature (°C), wind speed (km/h at 2 m above the ground), water surface conditions (0-calm to 5-rough), rainfall (mm), and the number of minutes of direct sunlight in the half-hour. Total rainfall, hours of direct sunlight, hours
with calm water surface conditions, and mean daily temperature, and wind speed were then used as variables in regression analyses to evaluate the impact of weather conditions on DEE and daily prey capture rate.

Energetic estimates

A. Energetic intake rates

Nest watches were conducted concurrently with all male focal watches to determine the energetic intake of males, females, and chicks. Prey species captured were identified and their size was estimated by visual comparison to the adult osprey's tail length (20 cm), a method which is accurate to within 5 cm (Stinson 1978). The mass of each fish captured was determined by counting the number of "bites" ripped and consumed from each prey item (Poole 1985). Adult bite size was calibrated by counting the number of bites taken to consume a fresh fish of known mass placed on the nest of six pairs during the courtship period. As the size of bites that females fed to chicks appeared to change with chick age, bite size was also calibrated at three stages of nestling development (Table 3.1). Intake rates (kJ/h) for males, females, and chicks were then calculated by converting the number of bites into energetic equivalents for each fish species (Watt and Merrill 1975) using an estimate of 80% assimilation efficiency (Kushlan 1977). Fledgling intake rate was determined by estimating prey mass using species-specific length-mass regressions, and converting them into energetic equivalents, since the relatively long time period required for fledglings to consume prey items made it impossible to count bites while at the same time collecting time activity budgets on males.

B. Flight costs

Ospreys have a variety of flight styles, ranging from gliding to continuous flapping, that are used in differing circumstances and that vary in energetic cost. Gliding is the least expensive; an estimate of 10.6 Watts (2 BMR; Baudinette and Schmidt-Nielson 1974) was used in this study. Powered flight in ospreys can be sub-divided into continuous flapping
Table 3.1. Bite size calibration for adults during courtship, and for adults feeding chicks at three stages of nestling development. Bite size was determined by counting the number of bites taken to consume fish of known mass. \( N = \) number of trials conducted.

<table>
<thead>
<tr>
<th>Adults feeding</th>
<th>N</th>
<th>Bite size (grams) ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults self-feeding</td>
<td>6</td>
<td>1.03 ± 0.06</td>
</tr>
<tr>
<td>Adults feeding 1-2 week old chicks</td>
<td>6</td>
<td>0.35 ± 0.08</td>
</tr>
<tr>
<td>Adults feeding 3-4 week old chicks</td>
<td>6</td>
<td>0.87 ± 0.05</td>
</tr>
<tr>
<td>Adults feeding 6-7 week old chicks</td>
<td>6</td>
<td>0.82 ± 0.08</td>
</tr>
</tbody>
</table>
and undulating flight, which consists of bursts of active flapping flight interspersed by gliding phases. The energetic savings of undulating flight are poorly understood. Some authors argue that the energetic costs are equivalent to those of continuous flapping (Ward-Smith 1984, Kerlinger 1989), while others argue that modes: savings may be made (Videler et al. 1983, Rayner 1985). As any savings are likely to be small, I have assumed that undulating flight costs are the same as those for sustained horizontal flapping flight. Ospreys also mix gliding with bouts of flapping flight, in what has been termed power glides (Kerlinger 1989). Power glides are expected to result in energetic savings though no empirical study has measured its energetic cost. Power glides and undulating flight do not appear to be fundamentally different flight styles, and, as the frequency distribution of glide duration is not bimodal (Fig. 3.1), I arbitrarily defined power glides as those with glide phases longer than four seconds. The cost of powered glides was then calculated by partitioning flight time into flaps and glides, and multiplying by the costs of powered or gliding flight. A sensitivity analysis found that doubling or halving the glide duration used to define flight styles resulted in changes to DEE estimates of +1.6% and -1.4%, respectively. The magnitude of these changes is likely to be small relative to the error associated with using allometric relationships to determine energetic costs.

Curves of power consumption against speed for powered flight, and estimates of maximum range speed and minimum power speed, were calculated using Program 1 of Pennycuick (1989). This program incorporates the most recent modifications in the theory of bird flight. Modified versions of Program 1 also enabled power curves to be calculated for osprey carrying fish of 100-600 grams (Table 3.2, Fig. 3.2). When calculating powered flight costs, ospreys were assumed to travel at maximum range speed (the speed which minimizes flight costs per metre) when chasing intruders, collecting nest material, or moving between perches. Foraging ospreys, however were assumed to minimize flight costs per second, as they waited for prey to approach the surface of the water, and therefore to travel at minimum power speed. Ospreys were also assumed to travel at minimum power speed when
Fig. 3.1  Frequency distribution of glide duration during osprey flight. Data presented are from all time-activity budgets collected during July 1991 and 1992.

N = 5660 individual glide events.
Table 3.2 Additional drag used to modify Program 1 of Pennycuick (1989) when calculating the flight costs of male ospreys carrying fish of varying mass.

<table>
<thead>
<tr>
<th>Fish mass (g)</th>
<th>Additional $S_bC_d^*$ (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>600</td>
<td>0.0040</td>
</tr>
<tr>
<td>400</td>
<td>0.0032</td>
</tr>
<tr>
<td>200</td>
<td>0.0026</td>
</tr>
<tr>
<td>100</td>
<td>0.0023</td>
</tr>
</tbody>
</table>

$S_bC_d^*$ = (additional body frontal area due to the fish and position of legs) x (drag coefficient)
Fig. 3.2  Power curves generated using Program 1 of Pennycuick (1989) for a male osprey weighing 1428 grams, flying unloaded, and carrying fish of 100, 200, 400, and 600 grams.
carrying fish, as the estimated flight costs at maximum range speed exceeded the predicted amount of power available in their flight muscles (Pennycuick 1989). Flight types and costs are described in Table 3.3.

The additional energetic costs required to accelerate to a given flight speed and altitude were calculated as a gain in kinetic and potential energy (Oster 1976), as given by the following equation.

\[
\text{Cost} = \frac{(0.5mV^2 + mgh)}{E}
\]

where

\[m = \text{mass in kg}\]
\[V = \text{airspeed (m/s)}\]
\[g = \text{acceleration due to gravity (9.81 ms}^{-2}\)
\[h = \text{height gained in metres}\]
\[E = \text{metabolic efficiency (0.23; Pennycuick 1975)}\]

This equation was also used to calculate the costs of take-offs, and of regaining altitude and speed after successful and unsuccessful dives (Table 3.3).

C. Daily energetic expenditure (DEE)

DEE was estimated using the detailed time-energy budgets and weather records collected during focal watches, using the methodology of Koplin et al. (1980). DEE estimates calculated from time-energy budgets have been validated for raptors by comparison with observed food consumption in wild birds of constant weight (Koplin et al. 1980) and with estimates derived using doubly-labelled water techniques (Masman et al. 1988).

The calculation of DEE is summarized in equation 2.

\[
\text{DEE} = \text{NFA} \left( \frac{\text{EM}_{Ta} - \text{(1-P)SM}_{TNa}}{\text{PL}} \right) + \sum \text{FA}_i (\text{FC}_i) + (1-P)\text{SM}_{TNa}
\]

where:

\[\text{NFA} = \text{duration of diurnal non-flight activity (s)}\]
\[\text{FA}_i = \text{duration of flight type } i \text{ (s)}\]
\( FC_i = \text{cost of flight type } i \) (see Table 3.3 for details)

\[ EM_{Ta} = \text{existence metabolism of non-passerine birds during the} \]
\[ \text{summer as a function of average daily air temperature (Ta)} \]
\[ = EM_{0^\circ C} + Ta \cdot b \quad \ldots 3 \]
\[ \text{where } b = (EM_{30^\circ C} - EM_{0^\circ C})/30 \]
\[ EM_{30^\circ C} = 4.472W^{0.6637} \quad \ldots 4 \]
\[ EM_{0^\circ C} = 17.343W^{0.5444} \quad \ldots 5 \]
\[ W = \text{body mass (g)} \]

\[ SM_{Tna} = \text{standard metabolism of non-passerine birds during the} \]
\[ \text{summer at night, as a function of average night time} \]
\[ \text{temperature (Tna)} \]
\[ = SM_{0^\circ C} - b \cdot Tna \quad \ldots 6 \]
\[ \text{where } SM_{0^\circ C} = 10.987W^{0.5705} \quad \ldots 7 \]
\[ b = 0.270W^{0.5886} \quad \ldots 8 \]

but at the lower critical temp. \( (T_{lc}) \);
\[ SM = BM \]
\[ T_{lc} = 47.17W^{-0.1809} \quad \ldots 9 \]

\[ BM = \text{basal metabolism} \]
\[ = 2.1873W^{0.7347} \quad \ldots 10 \]

\[ P = \text{photoperiod as a proportion of the 24-h day} \]

\[ L = 86400 \text{ and converts } \text{kJ/day} \text{ to } \text{kJ/sec} \]
Table 3.3  Flight types, costs, and speeds used in calculating the daily energetic expenditure of male ospreys.

<table>
<thead>
<tr>
<th>Flight type</th>
<th>Cost (J/s)</th>
<th>Flight speed (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hunting</td>
<td>70.4</td>
<td>9.8</td>
</tr>
<tr>
<td>Chasing</td>
<td>93.9</td>
<td>16.2</td>
</tr>
<tr>
<td>Collecting nest material</td>
<td>93.9</td>
<td>16.2</td>
</tr>
<tr>
<td>+ fish of 600g</td>
<td>151.3</td>
<td>9.4</td>
</tr>
<tr>
<td>+ fish of 400g</td>
<td>126.5</td>
<td>9.2</td>
</tr>
<tr>
<td>+ fish of 200g</td>
<td>104.8</td>
<td>9.0</td>
</tr>
<tr>
<td>+ fish of 100g</td>
<td>94.3</td>
<td>8.8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Additional cost (J)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Take-off: Nest to Hunt</td>
</tr>
<tr>
<td>Nest to Chase</td>
</tr>
<tr>
<td>Tree to Hunt</td>
</tr>
<tr>
<td>Tree to Chase</td>
</tr>
<tr>
<td>Diving: Fail</td>
</tr>
<tr>
<td>Catch 100g fish</td>
</tr>
<tr>
<td>Catch 200g fish</td>
</tr>
<tr>
<td>Catch 400g fish</td>
</tr>
<tr>
<td>Catch 600g fish</td>
</tr>
</tbody>
</table>
DEE, BM and all expressions of SM and EM are in kJ/day. Equation (3) is a linear interpolation to Ta of the allometric equations (4) and (5) of Kendeigh et al. (1977).

Equations (6)-(10) are also from Kendeigh et al. (1977) and apply to non-passerine birds during the summer and at night. There are two components to $EM_{Ta}$: diurnal non-flight activity and nocturnal rest. The expression $(EM_{Ta} - (1-P)SM_{Ta})/PL$ calculates the cost of diurnal non-flight activity by compensating for the lower energetic costs of nocturnal rest.

**Brood manipulations**

Brood size was manipulated at 16 nests. Eight broods were enlarged by adding one chick of intermediate size 26-28 days after hatching, with the foster chick coming from one of eight reduced broods. Prior to the manipulation, half the enlarged and reduced broods had two chicks, and half had three chicks. Male energetic expenditure and the intake rates of males, females, and nestlings were determined for four consecutive days, two control days prior to, and two experimental days following brood enlargement. There were insufficient observers to also determine male energetic expenditure and intake rates for the reduced broods. However, all chicks were weighed and measured three times: two days before the brood manipulation, at the time broods were enlarged or reduced, and after the two day treatment. Chick growth rates in this population are linear between 7-30 days (Machmer 1992), so changes in levels of parental care associated with brood reductions or enlargements could be evaluated by comparing mean brood growth rates before and after experimental manipulation. Although the foster chicks were all between three and four weeks of age during this experiment, because of a shortage of potential donors, two of the reduced broods had chicks that were older than 30 days following the manipulation. These two reduced broods were dropped from the analyses.

**Statistical analysis and data handling**

Non-parametric statistics were used when sample sizes were small or when variables had distributions that deviated from normality and could not be normalized using standard
transformations. Dunn’s non-parametric multiple range tests were employed to identify groups that differed significantly in Kruskall-Wallis and Friedman’s tests. Since probabilities are "shared" between groups in these tests, two groups are considered to be significantly different at p values greater than 0.05, depending on the number of groups being tested (Neave and Worthington 1988). Multiple range tests with three and four groups were therefore considered significantly different at 0.20.

Friedman’s test was employed to analyse the effect of chick age on DEE, male capture rate, and the intake rates of males, females, and chicks. Time budgets were collected for individuals provisioning nestlings of 1-2, 3-4, and 6-7 weeks, and fledglings of 9-10 weeks. Analyses were performed using both the full data set, which includes the fledging period (N=5), and the first three age categories (N=11). The results of the two analyses were consistent, except where specifically stated, and for simplicity the statistics and graphs presented refer to the full data set.

Variation in the patterns of capture and consumption of food within a day were examined using the 18 time budgets collected over the entire day. Friedman’s test was used to determine whether intake rates for each pair differed across five roughly equal periods of the day (0-4, 4-7, 7-10, 10-13, and 13-17 hours after first light).

Multiple regression analysis was used to examine the impact of weather, Julian date, year, early morning perch-hunting success (a stochastic event), and three reproductive parameters relating to individual males on prey capture rate and daily energetic expenditure. Capture rate and daily energetic expenditure were first normalized using a square root transformation. Stepwise regression analysis with alpha to enter and remove of 0.15 was used to select the sub-set of variables that were then used in multiple regressions (for rationale see Wilkinson 1989). The reproductive parameters considered were date of hatching, brood size, and mean brood age.
Results

Validation of methodology

Estimates of male DEE, daily capture rate, and male energetic intake determined using time budgets collected over the entire day did not differ from estimates based on the first 10 hours of the same time budgets (Table 3.4). Furthermore, energetic expenditure in the first 10 hours of a day was not negatively correlated with energetic expenditure in the remaining portion of the day ($r_s=+0.333$, $n=18$, $p=0.169$). Males evidently did not compensate for high levels of expenditure early in the day by reducing expenditure later. Female and chick intake rates were not estimated as accurately; female intake rate was consistently over-estimated, and chick intake rates underestimated (Table 3.4). This pattern suggests that females may "feed-up" chicks in anticipation of nightfall, by reducing their self-feeding rate. Patterns of female and chick intake rates presented in this paper should therefore be interpreted cautiously.

Time allocation

Male ospreys provisioning nestlings spent approximately 82% of their active day perched, and allocated only 8-9% of the active day to flight hunting (Table 3.5). Other flight activities, such as chasing intruders or collecting material for nest maintenance, accounted for the remaining 9% of their time (Table 3.5). Although male time allocation did not change over the first seven weeks of the breeding season, the proportion of time males spent in flight increased when providing post-fledging parental care (Table 3.5).

Activity patterns were unevenly distributed through the day, at least when chicks were three to four weeks of age. Capture rate was highest in the first hour of the morning, and a second peak occurred 13-14 hours after first light (Fig. 3.3). Diurnal variation in male, female, and chick feeding rates had a similar bimodal pattern, although only chick intake rates were significantly reduced in the middle of the day (Fig. 3.4).
Table 3.4  Estimates (mean ± SE) of male daily energetic expenditure, daily capture rate, and the energetic intake rates of males, females, and chicks determined using 18 time budgets collected over the entire day, compared with estimates derived from the first 10 hours of these 18 time budgets.

<table>
<thead>
<tr>
<th></th>
<th>Entire day</th>
<th>First 10 hours</th>
<th>Wilcoxon test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily energetic expenditure (kJ/day)</td>
<td>1302 ± 47</td>
<td>1316 ± 54</td>
<td>Z=0.457, p=0.65</td>
</tr>
<tr>
<td>Daily capture rate (kJ/day)</td>
<td>4146 ± 428</td>
<td>4352 ± 594</td>
<td>Z=0.544, p=0.59</td>
</tr>
<tr>
<td>Male intake rate (kJ/day)</td>
<td>1005 ± 175</td>
<td>1001 ± 246</td>
<td>Z=0.152, p=0.88</td>
</tr>
<tr>
<td>Female intake rate (kJ/day)</td>
<td>530 ± 65</td>
<td>839 ± 111</td>
<td>Z=3.72, p=0.0002</td>
</tr>
<tr>
<td>Chick intake rate (kJ/chick/day)</td>
<td>848 ± 70</td>
<td>773 ± 101</td>
<td>Z=1.85, p=0.064</td>
</tr>
</tbody>
</table>

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Table 3.5  

Hours (mean ± SE) spent in various activities by male osprey provisioning chicks of four ages (nestlings of 1-2, 3-4, and 6-7 weeks, and fledglings of 9-10 weeks). The figures in parentheses are the percentage of daylight hours spent by males in each activity.

<table>
<thead>
<tr>
<th>Activity</th>
<th>1-2</th>
<th>3-4</th>
<th>6-7</th>
<th>9-10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hunt</td>
<td>1.41±0.18  (8.5)</td>
<td>1.53±0.22 (9.3)</td>
<td>1.27±0.22 (8.1)</td>
<td>2.47±0.52 (16.1)</td>
</tr>
<tr>
<td>Chase Intruder</td>
<td>0.62±0.14  (3.7)</td>
<td>0.92±0.14 (5.6)</td>
<td>0.69±0.10 (4.4)</td>
<td>1.09±0.15 (7.4)</td>
</tr>
<tr>
<td>Collect stick</td>
<td>0.39±0.08  (2.3)</td>
<td>0.20±0.05 (1.2)</td>
<td>0.21±0.03 (1.3)</td>
<td>0.06±0.03 (0.4)</td>
</tr>
<tr>
<td>Other/unknown</td>
<td>0.44±0.05  (2.6)</td>
<td>0.62±0.14 (3.8)</td>
<td>0.38±0.06 (2.4)</td>
<td>0.39±0.12 (3.3)</td>
</tr>
<tr>
<td>Perch</td>
<td>13.79±0.06 (82.7)</td>
<td>13.17±0.32 (80.0)</td>
<td>13.06±0.22 (83.6)</td>
<td>10.71±0.69 (72.8)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>N</th>
<th>17</th>
<th>11</th>
<th>11</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hrs of daylight</td>
<td>16.67±0</td>
<td>16.47±0.04</td>
<td>15.62±0.09</td>
<td>14.72±0.05</td>
</tr>
</tbody>
</table>
Fig. 3.3 Daily pattern of prey capture from perch and flight hunts while provisioning chicks of 3-4 weeks of age. Data presented are based on the mean capture rates of 11 males during each hour from 0 to 10 hours after dawn, and for 5 males during each hour thereafter.
Fig. 3.4  Daily pattern of prey consumption (kJ/h ± SE) for a) nestlings, b) females, and c) males during 5 periods of the day (0-4^a, 4-7^b, 7-10^c, 10-13^d, and 13-17^e hours after dawn). Data presented are from 5 pairs, observed for 18 complete days when chicks were 3-4 weeks of age.

Friedman's test: chick, M=10.06, p<0.05; female, M=4.98, p=0.29; male, M=9.09, p<0.10

Dunn's multiple range test: chick, T_{a,b}=0.9, p>0.2; T_{a,c}=3.23, p<0.05; T_{a,d}=0.26, p>0.2; T_{a,e}=0, p>0.2; T_{b,c}=2.33, p<0.2; T_{b,d}=1.16, p>0.2; T_{b,e}=0.9, p>0.2; T_{c,d}=3.4, p<0.05; T_{c,e}=3.23, p<0.05; T_{d,e}=0.26, p>0.2.
a) nestlings

![Intake rate (kJ/h) for nestlings](chart)

b) females

![Intake rate (kJ/h) for females](chart)

c) males

![Intake rate (kJ/h) for males](chart)
**Patterns of DEE, capture rate, and energetic intake rates during the breeding season**

There was no significant seasonal pattern to the DEE of provisioning male ospreys (Fig. 3.5). The amount of energy males allocated to hunting also showed little variation (Fig. 3.5). Capture rate, however, varied significantly over the breeding season, and peaked when chicks were three to four weeks of age (Fig. 3.6). The increase in hunting efficiency, presumably due to greater food availability, coincided with a significant increase in chick intake rates (Fig. 3.7). Chick intake rates also appeared to rise after they fledged, but females hunted consistently during this period, capturing approximately one-third of all prey items (Fig. 3.6). Adult intake rates did not change significantly during the breeding season, although males tended to consume less, and females to consume more as chicks aged (Fig. 3.7).

**Natural variation in DEE**

During 1991 and 1992 there was considerable variation in male DEE (range 829-1936 kJ/day, N=82; Fig. 3.8). Some of this variation could be attributed to variation in brood size; males with large broods had a significantly higher mean daily energetic expenditure than males with small broods (Fig. 3.9a). This increased expenditure resulted in more fish being delivered to nests with more nestlings (Fig 3.9b). Consequently, mean brood growth rate was independent of brood size (1-chick broods: 54.7±2.9 g/day; 2-chick broods: 58.8±1.9 g/day; 3-chick broods: 58.2±1.6 g/day; Kruskall-Wallis test, H=2.11, p=0.35). Although males provisioning large broods expended greater amounts of energy, their intake rates did not differ significantly from males provisioning small broods (Fig. 3.9c). Presumably, males with three-chick broods therefore lost a greater proportion of their body mass during the breeding season.

The multiple regression model explained 29% of the variation in DEE (Table 3.6). Weather conditions had a small affect on DEE; male ospreys had a lower DEE when the water surface was calm for a greater proportion of the day. Stochastic events also affected male energetic expenditure; DEE was reduced if males successfully perch hunted a fish in the first
Daily energetic expenditure (DEE; kJ/day ± SE), and the amount of energy expended hunting (kJ/day ± SE) by male ospreys provisioning broods at four stages (nestlings of 1-2, 3-4, and 6-7 weeks; fledglings of 9-10 weeks of age). Numbers above bars indicates sample size at each brood age, although statistical tests presented below are for the 5 males observed at all 4 ages (see Methods for rationale).

Friedmans' test: DEE, $M=4.84$, $p=0.18$; Hunts, $M=2.52$, $p=0.47$. 

Fig. 3.5
Fig 3.6

Capture rate (kJ/h ± SE) for male and female ospreys provisioning broods of four ages (nestlings of 1-2<sup>a</sup>, 3-4<sup>b</sup>, and 6-7<sup>c</sup> weeks; fledglings of 9-10<sup>d</sup> weeks) Data presented graphically are for 11 pairs during the nestling stages, and five pairs following fledging. Statistics presented below are for the five pairs observed at all four brood stages (see Methods for rationale).

Friedmans' test: male, M=7.8, p=0.05; female, M=13.9, p<0.005

Dunn's multiple range tests: male, T<sub>a,b</sub>=2.21, p<0.2; T<sub>a,c</sub>=0.74, p>0.2; T<sub>a,d</sub>=0.74, p>0.2; T<sub>b,c</sub>=0.74, p>0.2; T<sub>b,d</sub>=2.69, p<0.05; T<sub>c,d</sub>=1.72, p>0.2; female, T<sub>a,b</sub>=0, p>0.2; T<sub>a,c</sub>=0.37, p>0.2; T<sub>a,d</sub>=2.57, p<0.1; T<sub>b,c</sub>=0.37, p>0.2; T<sub>b,d</sub>=2.57, p<0.1; T<sub>c,d</sub>=2.2, p<0.2.
Fig. 3.7 Intake rates (kJ/h ± SE) of males, females, and chicks at four stages of the breeding season (nestlings of 1-2\textsuperscript{a}, 3-4\textsuperscript{b}, and 6-7\textsuperscript{c} weeks; fledglings of 9-10\textsuperscript{d} weeks of age). Data presented graphically are for 11 pairs during the nestling stages, and five pairs following fledging. Statistical tests are presented for both the five pairs observed at all four stages, and for the 11 pairs observed at the three nestling stages before fledging (see Methods for rationale).

Friedmans' test- all 4 groups: male intake, $M=5.88$, $p=0.18$; female intake, $M=6.12$, $p=0.11$; chick intake, $M=6.84$, $p=0.08$.

Friedmans' test- 3 nestling groups: male intake, $M=0.55$, $p=0.76$; female intake, $M=3.82$, $p=0.15$; chick intake, $M=11.46$, $p<0.005$.

Dunn's multiple range tests: chick intake, $T_{a,b}=2.26$, $p<0.1$; $T_{a,c}=1.81$, $p>0.2$; $T_{b,c}=0.45$, $p>0.2$. 

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Fig. 3.8  Daily energetic expenditure (kJ/day) of male ospreys vs. Julian date (Jan. 1 = 1) in 1991 and 1992. Symbols denote individual males, and these symbols are filled when broods were experimentally enlarged. Different males were observed in 1991 and 1992 although some symbols are re-used. The solid line, $A_{\text{max}}$, is the predicted upper limit to sustainable energetic expenditure for a male osprey weighing 1428 grams (Karasov 1992).
Fig. 3.9  The relationship between brood size and a) mean daily energetic expenditure (kJ/day ± SE), b) mean delivery rate to the nest (kJ/day ± SE), and c) mean male intake rate (kJ/day ± SE). Sample size is denoted above the bars in a).

Kruskall-Wallis tests: DEE, $H=5.32$, 1-tailed $p<0.05$; Delivery rate, $H=4.73$, 1 tailed $p<0.05$; Male intake rate, $H=0.55$, $p=0.76$.

Dunn's multiple range tests: DEE, $T_{1,2}=1.23$, $p>0.2$; $T_{1,3}=2.26$, $p<0.1$; $T_{2,3}=1.32$, $p>0.2$; Delivery rate, $T_{1,2}=1.13$, $p>0.2$; $T_{1,3}=2.12$, $p<0.15$; $T_{2,3}=1.27$, $p>0.2$
a) Mean DEE (kJ/day)

b) Mean delivery rate (kJ/day)

c) Mean intake rate (kJ/day)

Brood size
Table 3.6  Results of multiple regression analysis examining variation in male daily energetic expenditure \(^{a}\). The variable early perch hunt is a dummy variable indicating the success or failure to capture a fish by perch hunting in the first hour of the day.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>R(^{b})</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early perch hunt</td>
<td>+0.277</td>
<td>2.65</td>
<td>0.010</td>
</tr>
<tr>
<td>Brood size</td>
<td>+0.262</td>
<td>2.50</td>
<td>0.015</td>
</tr>
<tr>
<td>Julian date</td>
<td>-0.239</td>
<td>2.41</td>
<td>0.019</td>
</tr>
<tr>
<td>Calm water surface conditions (h)</td>
<td>-0.238</td>
<td>2.36</td>
<td>0.021</td>
</tr>
<tr>
<td>Direct sunlight (h)</td>
<td>+0.135</td>
<td>1.40</td>
<td>0.167</td>
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</table>

\(^{a}\) Coefficient of determination (R\(^2\)) = 0.29, df = 4,78, p<0.0001

\(^{b}\) Standardized regression coefficient
hour of the day. The multiple regression analysis also confirmed that DEE was linked to brood size, and suggested that DEE decreased as the season progressed.

Weather conditions, at least within the range experienced in the Kootenays during 1991 and 1992, had no statistically detectable effect on the daily prey capture rate of male ospreys. None of the variables considered explained any of the variation in daily capture rate.

**Brood size manipulations**

Males provisioning experimentally enlarged broods did not increase their DEE significantly, and also did not increase their energetic expenditure hunting at the expense of other flight activities (Table 3.7). Of the eight males provisioning enlarged broods, four increased and four decreased their DEE. There was also no indication that males adjusted their food allocation decisions in response to brood enlargements; male intake rates went down in only three of eight trials (Table 3.7). In contrast, females reduced their own intake rate when feeding enlarged broods in six of eight trials (Table 3.7). This non-significant change in female food allocation did not compensate for the additional chick and nestling intake rates per capita decreased significantly, by approximately 20% (Table 3.7). The original brood size at enlarged nests did not appear to influence any of the above results (Table 3.7).

Male energetic expenditure and patterns of food allocation were not determined for reduced broods. However, the relative level of parental provisioning to reduced, natural, and enlarged broods can be assessed by comparing the mean weight gain, and mean primary growth of a brood before and after the experimental treatment. Mean weight gain and mean primary growth of a brood tended to increase when brood size was experimentally reduced (Fig. 3.10). In enlarged broods, mean brood weight gain and mean brood primary growth rate decreased, although only the former was altered significantly (Fig. 3.10). Both mean brood weight gain and mean brood primary growth were significantly higher in reduced compared to enlarged broods (Fig. 3.10).
Table 3.7 Male energetic expenditure, and the energetic intake rates of male, female, and nestling ospreys in the two days before and after experimental brood enlargements at eight nests. Means ± se are shown, as are brood sizes prior to manipulation, and the results of Wilcoxon signed-rank tests.

<table>
<thead>
<tr>
<th>Nest</th>
<th>Brood</th>
<th>Expenditure (kJ/day)</th>
<th>Male intake (kJ/h)</th>
<th>Female intake (kJ/h)</th>
<th>Chick intake (kJ/h)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Daily Natural</td>
<td>Hunting Natural</td>
<td>Hunting Enlarged</td>
<td>Male Natural</td>
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<td></td>
<td></td>
<td>Enlarged</td>
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<tr>
<td>13</td>
<td>2</td>
<td>1071</td>
<td>212</td>
<td>33</td>
<td>52</td>
</tr>
<tr>
<td>16</td>
<td>2</td>
<td>1120</td>
<td>177</td>
<td>996</td>
<td>32</td>
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<tr>
<td>38</td>
<td>2</td>
<td>1314</td>
<td>371</td>
<td>398</td>
<td>29</td>
</tr>
<tr>
<td>93</td>
<td>2</td>
<td>1102</td>
<td>165</td>
<td>639</td>
<td>57</td>
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<tr>
<td>10</td>
<td>3</td>
<td>1242</td>
<td>467</td>
<td>424</td>
<td>59</td>
</tr>
<tr>
<td>11</td>
<td>3</td>
<td>1104</td>
<td>244</td>
<td>591</td>
<td>142</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td>1471</td>
<td>535</td>
<td>424</td>
<td>31</td>
</tr>
<tr>
<td>54</td>
<td>3</td>
<td>1248</td>
<td>178</td>
<td>102</td>
<td>0</td>
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Mean ± se

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<tr>
<td>1209±43</td>
<td>1343±91</td>
<td>294±46</td>
<td>451±96</td>
<td>50±15</td>
<td>46±19</td>
<td>29±5</td>
<td>25±5</td>
<td>50±4</td>
<td>41±5</td>
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Wilcoxon test

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</thead>
<tbody>
<tr>
<td>Z = -0.7, p = 0.48</td>
<td>Z = -0.7, p = 0.58</td>
<td>Z = 0, p = 1.0</td>
<td>Z = -0.7, p = 0.48</td>
<td>Z = -1.96, p&lt;0.05</td>
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Fig 3.10  Mean brood weight gain ± SE (g/day), and mean brood primary feather growth ± SE (mm/day) of experimentally enlarged (E) or reduced (R) broods in comparison to their growth rates prior to manipulation (C).

Mean brood weight gain:  E vs C, Wilcoxon Z=-2.38, one-tailed p<0.01, N=8;  R vs C, Wilcoxon Z=-1.57, one-tailed p<0.1, N=6;  E vs R, Mann-Whitney U_{6,8}=39, one-tailed p<0.05.

Mean primary feather growth:  E vs C, Wilcoxon Z=-1.10, one-tailed p>0.1, N=8;  R vs C, Wilcoxon Z=-1.48, one-tailed p<0.1, N=6;  E vs R, Mann-Whitney U_{6,8}=41.5, one-tailed p<0.05.
Discussion

Time and energetic constraints

Even when the food demands of nestlings were high, male ospreys devoted a large proportion of their day to activities unrelated to provisioning. Male ospreys in this study spent an average of 82% of daylight hours perched at or near the nest during the nestling period. This figure is substantially higher than the 38% and 44% reported for ospreys in Virginia and Washington (Stinson 1978, Stinson et al. 1986). However, since male ospreys frequently perched for long periods at distances greater than 100 m from the nest, figures based on nest watches may underestimate the amount of time male ospreys spend perched. Regardless of the exact figure, male ospreys spend only a small proportion of daylight hours in flight. Wilson (1975) suggested that parents are only forced to spend most of their time foraging during rare stringent periods and as a consequence appear "lazy" at other times. However, although brood reduction occurs in approximately 20% of three-chick broods in this population (Machmer 1992), there were no environmental conditions during the two years of this study which induced males to spend all their time provisioning. The longest a bird was observed to flight hunt during 82 days of observation was 4.7 hours, 31% of the active day.

Physiological constraints also do not appear to limit energy budgets of ospreys during the breeding season. While the upper limit to sustainable energy expenditure for a male osprey weighing 1428 grams is predicted to be 1913 kJ/day (Karasov 1992), the mean daily energetic expenditure of male ospreys provisioning three-chick broods during this study was only 1317 kJ/day. Furthermore, the daily energetic expenditure of male ospreys rarely came within 20% of this upper limit, and only exceeded it once in 82 days of observation. These results suggest that if stringent periods occur, they are extremely rare, supporting the claim of Weathers and Sullivan (1989), and Dykstra and Karasov (1992), that physiological constraints do not generally limit reproduction in birds.
This study found that male ospreys have a DEE that is far lower than their physiological maximum, but this still poses the question of whether male ospreys work at similar levels to other avian species during the breeding season. The daily energetic expenditure of 30 species during the most active period of reproduction is related to body mass \((W)\) by the allometric function \(13.82W^{0.65}\) (Masman et al. 1989), and predicts that male ospreys should expend \(1553 \pm 367 \text{ kJ/day}\) during the breeding season. Male ospreys therefore work at a similar level to other avian species, but at a rate well below their supposed physiological maximum.

**Natural variation in DEE**

Weather conditions did not explain any of the variation in the daily prey capture rate of male ospreys in this study. Osprey capture rates in Scotland (Green 1976), Virginia (Stinson 1978), and Washington (Stinson et al. 1986) were also found to be unaffected by weather conditions. Weather conditions also explained relatively little of the variation in the DEE of male ospreys in this study, although wind speed, water surface conditions and sunlight are all known to influence the duration and success of individual foraging bouts in this species (Grubb 1977, Stinson et al. 1986, Machmer and Ydenberg 1990). This apparent contradiction is likely a result of the time scale inherent to the two analyses. As males only have to hunt for a limited amount of time each day to provision their brood, they can generally avoid hunting during poor conditions. If inclement weather is rare and of short duration, as it was during this study, weather conditions will have little impact on DEE. In years with prolonged periods of high winds and heavy rain, reduction in foraging success may force males to increase their DEE to maintain delivery rate to the nest. Alternatively, males may stop hunting completely if it becomes unprofitable in these conditions (Machmer and Ydenberg 1990), which would explain the poor condition and reduced survival of chicks following prolonged storms (Poole 1989, Forbes 1991).

Brood size explained some of the variation in the daily energetic expenditure of male ospreys. Male ospreys provisioning three chicks broods expended more energy hunting, but
were no more efficient at foraging, than males provisioning singletons. The increased parental
effort of males with large broods resulted in the delivery of a greater amount of food, and
brood size therefore had no affect on chick growth rates. In contrast, energetic expenditure of
male Eurasian kestrels *Falco tinnunculus* does not vary with brood size (Masman et al. 1989).
Eurasian kestrels, however, defend resource-based territories, and males with large broods
have territories with higher hunting yields than the territories of males with small broods
(Masman et al. 1989).

The positive relationship between brood size and daily energetic expenditure found in
this study does not necessarily imply that the two are causally linked. A third variable such as
male age or condition may set both brood size and daily energetic expenditure. Monitoring
male DEE before and after brood enlargement can determine whether brood size has a direct
affect on DEE.

*Brood size manipulations*

Male ospreys neither increased energetic expenditure nor reduced food intake when
provisioning experimentally enlarged broods. Brood size manipulations in other raptors have
also failed to elicit a parental response (e.g.: Coopers' hawks *Accipiter cooperii* Snyder and
Snyder 1973; sparrowhawks *Accipiter nisus* Geer 1981; African red-breasted sparrowhawks
*Accipiter rufiventris* Simmons 1986; Tengmalm's owls *Aegolius funereus* Korpimaki 1988;
cf. Eurasian kestrels Masman et al. 1989). In my study, this failure lead to chicks gaining
weight at a slower rate following experimental brood enlargement. It is therefore likely that if
the experimental treatment had continued nestlings in enlarged broods would have fledged later
and/or at lower weights, reducing post-fledging survival and recruitment (Perrins 1965, Moss
1972, Nur 1984, Poole 1989). There is no evidence to suggest that the energetic expenditure
of male ospreys is physiologically constrained. Male ospreys in this study are therefore
apparently "unwilling" rather than unable to increase their reproductive effort. A conservative
strategy in a single year is perhaps not unexpected in long lived species, such as the osprey,
given the importance of longevity in determining an individual's lifetime reproductive success (Clutton-Brock 1988). The results of this study are consistent with the idea that male ospreys trade off the potential benefits of increased reproductive success, resulting from increased effort in the current year, against future reproductive potential, and thus forage at an optimum rather than at maximum capacity. Biologists studying Eurasian kestrels have come to similar conclusions; Masman et al. (1989) found that the mean daily energetic expenditure of male Eurasian kestrels provisioning nestlings was well below the maximum they are able to sustain. In contrast to ospreys, however, male Eurasian kestrels responded to brood manipulation experiments by increasing their energetic expenditure (Masman et al. 1989). The increased parental effort, however, appeared costly as parental survival was reduced in experimentally enlarged broods (Dijkstra et al. 1990).

In contrast to male ospreys, females have been shown to reduce their food consumption and suffer increased weight loss when provisioning experimentally enlarged broods (Poole 1989). The results of this study (although non-significant, likely due to small sample size) support the conclusion that females do alter their behaviour and incur an energetic cost when provisioning enlarged broods. Female ospreys weigh 30% more than males, and lose a substantially higher proportion of their body mass during the breeding season (Poole 1989). Weight loss may therefore not have the same fitness consequences in male and female ospreys, which could explain the sex-specific response to brood enlargement.

The optimal level of energetic expenditure and intake rate during the breeding season may be influenced by individual differences in age or current condition, as these factors could affect an individual's residual reproductive value, and the magnitude of the costs associated with various levels of reproductive effort. Further work on state-dependent reproductive effort, and condition-dependent survival in both sexes, is required to further elucidate the life history decisions of this species.
Chapter 4
General conclusions

Examination of the role food supply plays in osprey breeding decisions has provided the principal focus of this thesis. Male ospreys provide almost all the food eaten by females and nestlings from the time a pair becomes established at a nest site until nestlings fledge. I have therefore assessed the importance of male courtship feeding rate in determining whether and when females lay, and determined the extent to which male foraging capacity subsequently limits brood size.

In Chapter 2 I showed that the failure of female ospreys to initiate a clutch was associated with low male courtship feeding rates. Furthermore, male courtship feeding rate was negatively correlated with the duration of the courtship period for pairs that did lay. This provided correlative evidence linking the food supplied to the female by the male during the courtship period with the timing of laying. The supplementary feeding experiment, which significantly reduced the courtship period of "fed" females, confirmed the role food supply plays in determining laying date. The suggestion that a lack of energy reserves constrains most females from laying earlier in the breeding season is supported by supplementary feeding experiments, which have consistently advanced laying date (for reviews see Davies and Lundberg 1985, Daan et al. 1988), and studies which have shown that members of a population which are in better condition breed earlier (e.g., Meijer et al. 1988, Hamann and Cooke 1989).

Drent and Daan (1980) have suggested two alternative mechanistic models to explain how food supply can affect the timing of reproduction; the "capital" and "income" models. Further study is required to distinguish between seasonally declining condition thresholds, and the rate of change of condition with respect to date, as triggers for the onset of reproduction. This may require better indices of body condition than total body mass, such as levels of fat or protein reserves. Timing of laying in red-billed quelea *Quelea quelea*, for example, has been
found to be closely tied to changes in body protein reserves that are stored in the pectoralis muscle (Jones and Ward 1976). Clutch initiation in American coots *Fulica americana*, on the other hand, is thought to be dependent on lipid reserves (Alisauskas and Ankney 1985).

In Chapter 2, I also show that female ospreys may be able to use male courtship feeding rate to evaluate their male's later parental performance, as male delivery rates to the nest are seasonally autocorrelated. The limited number of single males with a nest, or good potential nest site, and the costs associated with delaying reproduction in this species make it unlikely that female ospreys select mates on the basis of courtship feeding rates (Poole 1985). However, in Chapter 2, I present both direct and indirect evidence that suggests that female ospreys may use information gained from male courtship feeding rates, and manipulate hatching asynchrony in response to predicted food availability. Further work is needed to clarify the adaptive value of intra-specific variation in hatching asynchrony, and to determine the importance of female mate assessment in the facultative manipulation of hatching patterns.

In Chapter 3, I examined how males allocated their time and energy while provisioning nestlings and providing post-fledging parental care. I found that male ospreys spent approximately 80% of their active day perched, and that their mean daily energetic expenditure was well below the maximum they are able to sustain. This suggests that time and energetic constraints do not limit male foraging capacity, and hence brood size in ospreys. The majority of brood manipulation experiments which have demonstrated that altricial birds are able to raise more offspring than present in their natural brood (Ydenberg and Bertram 1989, VanderWerf 1992), and other detailed studies of energetic expenditure in free-living birds (e.g., Masman et al. 1989, Weathers and Sullivan 1989), support the conclusion that physiological constraints do not limit avian reproductive effort.

The daily energetic expenditure of male ospreys was linked to the size of the brood they were provisioning; males raising large broods expended more energy hunting than males raising small broods, thereby maintaining equal chick growth rates. The failure of male ospreys to respond to brood size manipulations, however, indicates that the daily energetic
expenditure of male ospreys is independent of brood size. It therefore appears likely that factors such as male age and condition, which are likely to affect laying date, and hence brood size in ospreys, also determine a male's mean daily energetic expenditure. The influence of age and condition on male parental effort could be determined experimentally by monitoring parental effort of known-age individuals, following manipulation of male condition (perhaps by providing supplementary food during the incubation period).

The conservative strategy of male ospreys is consistent with the idea that male ospreys trade off the potential benefits of increased reproductive success, resulting from increased effort in the current year, against future reproductive potential, and thus forage at an optimum rather than at maximum capacity. This hypothesis has been supported by brood manipulation experiments in other species where increased parental effort has been found to reduce parental survival (Askenmo 1979, Dijkstra et al. 1990), or future reproductive potential (Roskaft 1985, Tinbergen 1987, Tinbergen et al. 1987, Gustaffson and Sutherland 1989). However, this hypothesis can only be evaluated using brood manipulation experiments in species which respond to manipulations with changes in parental effort. Further work on state-dependent reproductive effort, and condition-dependent survival, is therefore required to clarify osprey reproductive strategies.
Literature cited


Wiebe, K.L. (submitted) Intra-specific variation in hatching asynchrony: should birds manipulate hatching spans according to food supply?

Wiebe, K.L. & G.R. Bortolotti (submitted) The role of food in determining hatching spans of birds: energetic constraints or facultative manipulation?


