ENERGETIC EXPENDITURE OF MALE OSPREYS PROVISIONING NATURAL AND MANIPULATED BROODS

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ABSTRACT   This study examined the relationship between brood size and energetic expenditure of male Ospreys. The daily energetic expenditure (*DEE*) of male Ospreys, provisioning nestlings and providing post-fledging parental care, was estimated using detailed time-energy budgets. Factors affecting *DEE* were investigated, and *DEE* and the maximum rate of energy assimilation were compared to determine whether physiological constraints limit energetic expenditure. The *DEE* of male Ospreys was independent of brood age, but increased linearly with brood size. Males provisioning three-chick broods had a mean *DEE* of 1336 kJ/day, significantly more than the mean of 1084 kJ/day expended by males provisioning single-chick broods. Male Ospreys, however, did not respond to brood size manipulations by altering their energetic expenditure, indicating that male *DEE* is not directly determined by brood size. Male Ospreys also did not alter their intake rates when provisioning enlarged broods and the mean brood growth rate following brood enlargement was consequently reduced. Weather conditions had a small affect on *DEE*; male Ospreys had a lower energetic expenditure on days when the water surface was calm for a longer time. The *DEE* of male Ospreys in this study was estimated to be well below the maximum they are able to sustain. Physiological constraints therefore appear unlikely to limit brood size in Ospreys. It is suggested that individual differences in age or current condition may influence both brood size and the level of energetic expenditure of male Ospreys as these factors could affect an individual's residual reproductive value and the magnitude of the costs associated with various levels of reproductive effort.

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INTRODUCTION

Time and energetic constraints have been argued to be critical factors determining the foraging capacity and hence brood size of altricial birds (Royama 1966, Drent & Daan 1980, Daan *et al.* 1988). The majority of brood size manipulation experiments, however, have demonstrated that altricial bird are able to raise more offspring than present in their natural brood (Ydenberg & Bertram 1989, VanderWerf 1992). This discrepancy may be explained if nestlings in larger broods have reduced fledging survival, or the increased costs of parental care threaten the parents prospects for future reproduction. Drent & Daan (1980) have therefore argued that the optimal level of parental care is associated with a daily energetic expenditure (*DEE*) that represents the maximum that can be sustained without deterioration of the parents condition.

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). Data currently available on *DEE* during parental care suggest that small avian species (ca 25 g) may work at close to the maximum rate of energy assimilation (A_{max}), but that larger species have a *DEE* below their physiological maximum (Masman *et al.* 1989). However, the question of whether or not parental energetic expenditure and

hence brood size, is determined by A_{max} invites further investigation.

In the Osprey *Pandion haliaetus*, as in many raptors, males capture the majority of prey eaten by the female and chicks prior to fledging, while females feed, brood and protect young. Despite their seemingly demanding role, male Ospreys spend between 65% and 85% of their day perched at or near the nest (Poole 1989). This suggests that time constraints on foraging are relatively unimportant for Ospreys. We therefore evaluate whether energetic constraints limit the capacity of male Ospreys to provision nestlings or provide post-fledgling care. *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_{max} is used to determine whether physiological constraints limit energetic expenditure at any point in the breeding season. We also examine the consequences of variation in brood size for both parents and young. 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 study area and general breeding ecology of this population are described by Steeger *et al.* (1992). The majority of nest sites are located on 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 1-2 days following the return of Ospreys from their wintering grounds in early April. One week following the onset of incubation, clutch size was determined at each nest using a mirror on an extendable pole or by climbing to the nest. Nests were revisited 3-4 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., predated, broken, or unhatched when the youngest chick was 10 days old). 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). Individually colour-marked chicks were weighed (using 100, 1000, or 2000 g Pesola spring balances) during regular visits to the nest, from hatching until the oldest chick was about 40 days old. Growth rates of individual chicks were then determined using the slope of the regression through 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.

Time budgets

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 provisioning chicks of 1-2 weeks were also collected. Time budgets were collected on a total of 98 days between 16 June and 2 September, for 17 males, with brood sizes ranging from one to three. Most of 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. On 18 of the watches data was collected for the entire daylight period 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.

While collecting time budgets male Ospreys were followed by boat or kept in sight 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

Weather conditions in the vicinity of the male Osprey under observation were recorded during all focal watches 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 were recorded every 30 minutes. 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

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

Table 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. In each trial a fish of 200-400 g was supplied to a nest, and its consumption observed.

	n	Bite size (g) ± 95% C.I.
Adults self-feeding	6	1.03 ± 0.12
Adults feeding 1-2 week old chicks	6	0.35 ± 0.16
Adults feeding 3-4 week old chicks	6	0.87 ± 0.10
Adults feeding 6-7 week old chicks	6	0.82 ± 0.16

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. The size of bites that females fed to chicks was calibrated at three stages of nestling development as bite size appeared to change with chick age (Table 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 & Merrill 1975) using an estimate of 80% assimilation efficiency (Kushlan 1977). Fledgling intake rates were determined by estimating prey mass using species-specific length-mass regressions and converting them into energetic equivalents. The long time period required for fledglings to completely consume prey items made it impossible to count bites while also collecting time budgets on males.

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 & Schmidt-Nielson 1974) was used in this study. Powered flight in Ospreys can be sub-divided into continuous flapping and undulating flight. Undulating flight consists of bursts of ac-

tive flapping flight interspersed by short gliding phases, arbitrarily defined in our study as being $\leq$ 4 sec. 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 modest savings may be made (Videler et al. 1983, Rayner 1985). As energetic savings are likely to be small we assumed that undulating flight costs were equivalent to those of continuous flapping. A sensitivity analysis found that doubling or halving the glide duration used to define undulating flight 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.

When calculating flight costs, Ospreys were assumed to travel at maximum range speed (Vmr; the speed which minimises flight costs per metre) when chasing intruders, collecting nest material, or moving between perches. Foraging Ospreys, however, were assumed to minimise flight costs per second as they waited for prey to approach the surface of the water and therefore to travel at minimum power speed (Vmp). The costs of powered flight at Vmr and Vmp were calculated using Program 1 of Pennycuick (1989). This program incorporates the most recent modifications in the theory of bird flight. The additional energetic costs required to take-off, or regain altitude and speed after successful and unsuccessful dives were calculated as a gain in kinetic and potential energy (Oster 1976).

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 methodology used to calculate DEE is described in the Appendix.

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 each had two chicks, and half 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 determine male energetic expenditure and intake rates for the reduced broods while the enlarged broods were observed. However, all chicks were weighed and measured three times: 2 days before the brood manipulation, at the time broods were enlarged or reduced, and after the 2 day treatment. All transfers and measurement of chicks took place at the end of the active day. Chick growth in this population is 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 rate before and after the experimental manipulation. Although the foster chicks were all between 3-4 weeks of age during this experiment, because of a shortage of potential donors, chicks were older than 30 days following the manipulation in two of the reduced broods. 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 normalised 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 signifi-

cantly different at p values greater than 0.05, depending on the number of groups being tested (Neave & Worthington 1988). Multiple range tests with three and four groups were therefore considered significantly different at $p = 0.20$.

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 and for brevity the statistics presented refer to the full data set.

Multiple regression analysis was used to examine the impact of weather, Julian date, year and three reproductive parameters relating to individual males on prey capture rate and *DEE*. Capture rate and *DEE* 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 laying date, brood size and mean brood age. Means in the text are presented with 95% confidence intervals.

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 2). 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 ($r_s = +0.333, n = 18, p = 0.17$). 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 tended to be underestimated (Table 2). Patterns of female and chick intake rates are therefore not presented in this paper.

Energetic expenditure, capture rate and intake rate during the breeding season

Male Ospreys provisioning nestlings spent 1.34 ± 0.38 h or approximately 8% of their active day flight-hunting (Fig.1a). Other flight activities, such as chasing intruders or collecting material for nest maintenance, accounted for a further 1.49 ± 0.54 h or 9% of their day (Fig. 1a). Although the amount of time males allocated to flight hunting did not change over the first seven weeks of nestling development (Fig. 1a; Friedman's test: $M = 1.64, n = 11, p = 0.44$), males did spend a greater proportion of their day foraging when providing post-fledging parental care (Fig.1a; Wilcoxon signed-rank test: $Z = -2.02, n = 5, p = 0.04$). Male energetic expenditure was, however, independent of brood age (Fig. 1b; Friedman's test: $M = 5.4, n = 5, p = 0.14$). Male energetic expenditure did not increase during the post-fledging period, de-

Table 2. Estimates (mean ± C.I.)of male daily energetic expendure, daily capture rate and the energetic intakes 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.

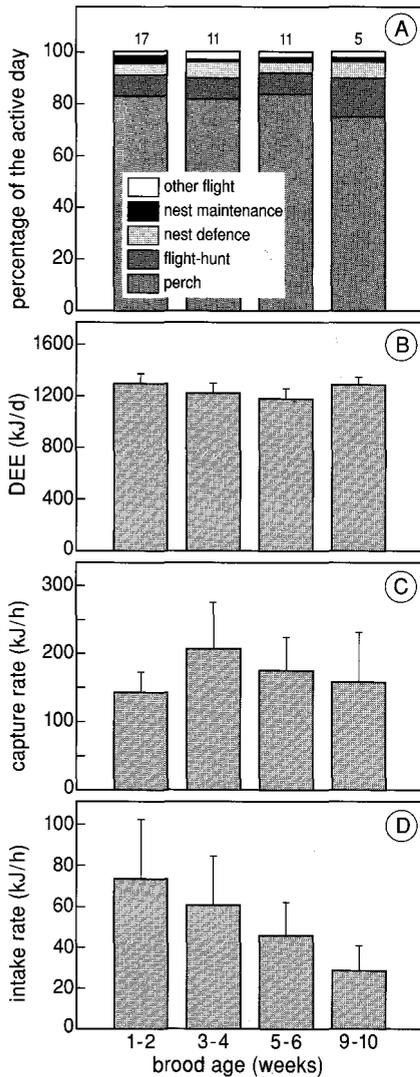|	Entire day	First 10 hours	Wilcoxon test
DEE (kJ/day)	1302 ± 94	1316 ± 108	$Z = 0.46, p = 0.65$
Daily capture rate (kJ/day)	4146 ± 856	4352 ± 1188	$Z = 0.54, p = 0.59$
Male intake rate (kJ/day)	1005 ± 350	1001 ± 492	$Z = 0.15, p = 0.88$
Female intake rate (kJ/day)	530 ± 130	839 ± 222	$Z = 3.72, p < 0.001$
Chick intake rate (kJ/chick/day)	848 ± 140	773 ± 202	$Z = 1.85, p = 0.06$

Fig. 1. Variation in the (a) time budgets, (b) daily energetic expenditure (*DEE*; kJ/day), (c) capture rate (kJ/h) and (d) intake rate (kJ/h) of male Ospreys provisioning broods of four ages (nestlings of 1-2, 3-4 and 6-7 weeks; and fledglings of 9-10 weeks). Means are presented with 95% C.I. Sample sizes are presented at the on top of the bars in (a).

spite the increase in flight-hunting activity, as males tended to spend a greater proportion of their time foraging in low cost gliding flight (nestling care: 22 ± 1% gliding; fledgling care 33 ± 6%

gliding; Wilcoxon signed-rank test $Z = -1.84$, $n = 5$, $p = 0.07$).

Although male energetic expenditure was independent of brood age, the capture rate of male Ospreys increased significantly when chicks were between 1-2 and 3-4 weeks of age (Fig. 1c; Friedman's test: $M = 7.8$, $p = 0.05$; Dunn's multiple range tests: $T_{1-2,3-4} = 2.21$, $p < 0.2$). Male intake rates did not increase during this period (Fig. 1d; Friedman's test: $M = 5.88$, $p = 0.18$), suggesting that chicks obtained more food as a result of the increased hunting yield.

Individual variation in energetic expenditure, capture rate and intake rate

There was considerable variation in the *DEE* of male Ospreys, both between individuals and within an individual between days (Fig. 2). Energetic expenditure was influenced by brood size; males provisioning large broods spent a greater amount of time flight-hunting, and had a significantly higher mean *DEE* than males with small broods (Fig. 3a, b; Kruskall-Wallis tests: Flight-hunting, $H = 7.74$, one-tailed $p = 0.01$; *DEE*, $H = 5.96$, one-tailed $p = 0.025$; Dunn's multiple range tests: Flight-hunting, $T_{1,2} = 0.78$, $p > 0.2$; $T_{1,3} = 2.42$, $p < 0.05$; $T_{2,3} = 2.20$, $p < 0.1$; *DEE*, $T_{1,2} = 1.23$, $p > 0.2$; $T_{1,3} = 2.26$, $p < 0.1$; $T_{2,3} = 1.32$, $p > 0.2$). The increased energetic expenditure of males provisioning large broods resulted in more fish being delivered to their nests (Fig. 3c; Kruskall-Wallis test: $H = 5.90$, one-tailed $p = 0.029$; Dunn's multiple range test: $T_{1,2} = 2.20$, $p < 0.1$; $T_{1,3} = 2.42$, $p < 0.05$; $T_{2,3} = 1.27$, $p > 0.2$). Consequently, mean brood growth rate was independent of brood size (1-chick broods: 54.7 ± 10.6 g/day; 2-chick broods: 58.8 ± 7.2 g/day; 3-chick broods: 58.2 ± 6.0 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. 3d; Kruskall-Wallis test: $H = 0.55$, $p = 0.76$).

The multiple regression model explained 22% of the variation in *DEE* (Table 3). Weather conditions had a small affect on *DEE*; male Ospreys

Table 3. Results of multiple regression analysis examining variation in male daily energetic expenditure [a]. A stepwise procedure was used to select the variables used in the multiple regression analysis, with non-significant factors being excluded. ΔR^2 indicates change in the R^2 following removal of one independent variable.

Independent variable	ΔR^2	R[b]	t	p
Brood size	0.12	+0.36	3.51	0.001
Calm water conditions (h)	0.05	-0.23	2.24	0.028
Julian date	0.04	-0.21	2.03	0.046

[a]: Coefficient of determination (R^2) = 0.22, df = 3,78, p=0.0002
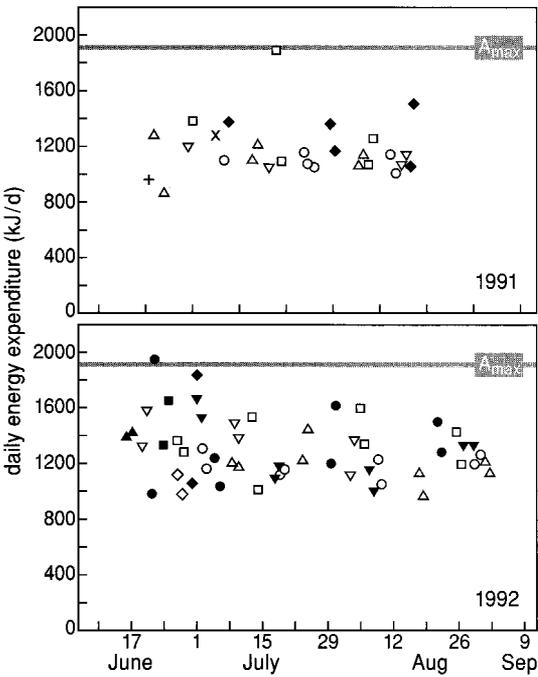[b]: Standardized regression coefficient

Fig. 2. Daily energetic expenditure (kJ/day) estimated from time energy budgets for male Ospreys provisioning natural broods in 1991 and 1992. Symbols denote individual males. Different males were observed in 1991 and 1992 although some symbols are re-used. The solid line, A_{max}, is the predicted upper limit to sustainable energetic expenditure for a male Osprey weighing 1428 grams (Karasov 1992).

Fig. 3. The relationship between brood size and (a) amount of time spent flight hunting (h/day), (b) *DEE* (kJ/day), (c) delivery rate (kJ/nest/h) and (d) intake rate (kJ/h) of male Ospreys. Means are presented with 95% C.I. Sample sizes are presented above the bars in (a).

had a lower *DEE* when the water surface was calm for a greater proportion of the day. The multiple regression analysis also confirmed that *DEE*
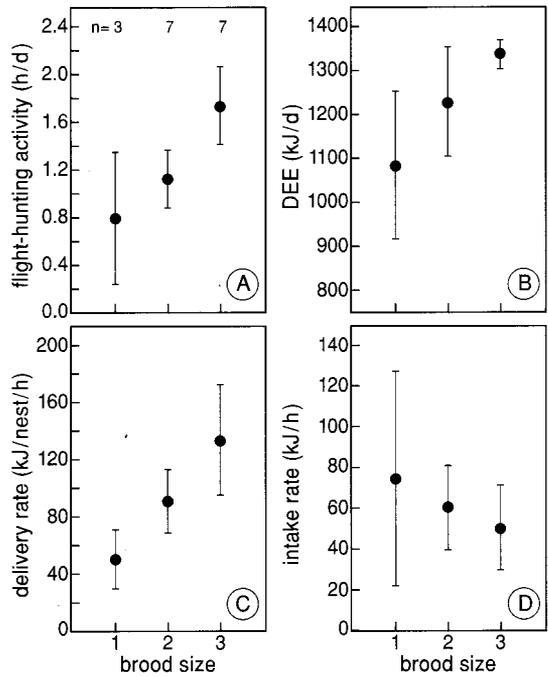
was influenced by brood size and suggested that *DEE* decreased as the season progressed.

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 weather variables considered explained any of
the variation in daily capture rate.

Brood size manipulations

Male Ospreys did not respond to brood size
enlargements by increasing their *DEE* (control:
1231 ± 94 kJ/day; enlarged: 1364 ± 198 kJ/day;
Wilcoxon signed-rank test, $Z = -0.7$, $n = 8$, $p = 0.48$). Of the eight males provisioning enlarged
broods, four increased and four decreased their
DEE (Fig. 4). Furthermore, males provisioning
enlarged broods did not increase the amount of
time they allocated to hunting (control: 1.28 ±
0.44 h/day; enlarged: 1.89 ± 0.89 h/day; Wilcox-
on signed-rank test, $Z = -0.56$, $n = 8$, $p = 0.58$) and
male capture rate did not increase (control: 186 ±
87 kJ/h; enlarged: 223 ± 94 kJ/h; Wilcoxon
signed-rank test, $Z = -1.01$, $n = 8$, $p = 0.31$). There
was also no indication that males adjusted their
food intake in response to brood enlargements;
male intake rates went down in only three of eight
trials (Table 4). Females, in contrast, reduced
their own intake rate when feeding enlarged
broods in six of eight trials (Table 4). However,
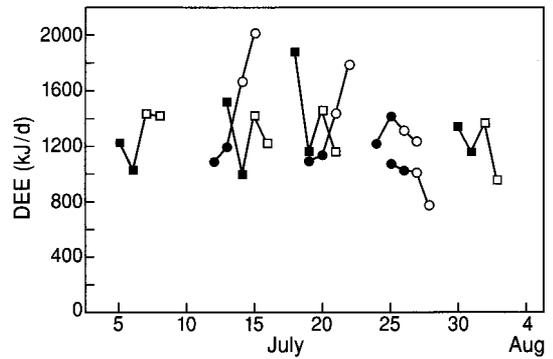nestling intake rates were still reduced by approx-

Fig. 4. Effect of brood enlargement on the *DEE* of
male Ospreys. Days with brood enlargements are indi-
cated by open symbols, closed symbols indicate days
males are provisioning their natural brood. *Lines* con-
nect the four days of each trial. Circles denote males
with a natural brood size of two, squares denote males
with a natural brood size of three. The solid line, Amax,
is the predicted upper limit to sustainable energetic ex-
penditure for a male Osprey weighing 1428 grams
(Karasov 1992).

Table 4. Energetic intake rates of male, female and nestling Ospreys in the two days before and after experimen-
tal brood enlargements at eight nests. Means ± 95% C.I. are shown, as is the brood size prior to manipulation and
the results of Wilcoxon signed-rank tests.

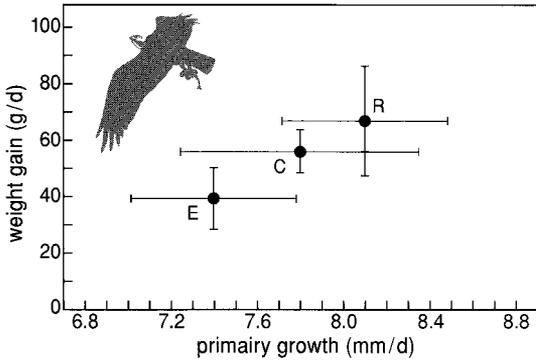| Nest	Brood Size	Male intake (kJ/h)		Female intake (kJ/h)		Chick intake (kJ/h)	
		Natural	Enlarged	Natural	Enlarged	Natural	Enlarged
13	2	52	34	38	31	39	23
16	2	32	87	11	44	51	60
38	2	29	40	24	17	50	48
93	2	57	87	44	17	46	45
10	3	59	38	37	30	66	54
11	3	142	33	43	22	67	38
12	3	31	51	13	25	44	37
54	3	0	0	20	11	37	23
Mean ± 95% C.I.		50 ± 29	46 ± 37	29 ± 10	25 ± 10	50 ± 8	41 ± 10
Wilcoxon test		$Z = 0, p = 1.0$		$Z = -0.7, p = 0.48$		$Z = -1.96, p = 0.05$	

Fig. 5. Mean brood weight gain (g/day) ± 95% C.I. and mean brood primary feather growth (mm/day) ± 95% C.I. of experimentally enlarged (E) or reduced (R) broods in comparison to their growth rates prior to manipulation (C).

imately 20% (Table 4). The original brood size at experimental nests did not influence any of the above results (Fig. 4, Table 4).

Male energetic expenditure and patterns of food allocation were not determined for reduced broods. The relative level of parental provisioning to reduced, natural and enlarged broods were instead 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. 5; Wilcoxon signed-rank tests: weight gain, $Z = -1.57$, $n = 6$, one-tailed $p = 0.06$; primary growth, $Z = -1.48$, $n = 6$, one-tailed $p = 0.07$). In enlarged broods, mean brood weight gain and mean brood primary growth rate decreased, although only the former was altered significantly (Fig. 5; Wilcoxon signed-rank tests: weight gain, $Z = -2.38$, $n = 8$, one-tailed $p = 0.01$; primary growth, $Z = -1.10$, $n = 8$, one-tailed $p = 0.14$). Both mean brood weight gain and mean brood primary growth were significantly higher in reduced compared to enlarged broods (Fig. 5; Mann-Whitney tests: weight gain, $U_{6,8} = 39$, one-tailed $p = 0.03$; primary growth, $U_{6,8} = 41.5$, one-tailed $p = 0.01$).

DISCUSSION

Time and energetic constraints

Male Ospreys provisioning nestlings in this study spent only 1.34 h/day flight-hunting and were inactive for approximately 13 of the 16 hours of daylight. Brown (1980) suggested that parents may only be forced to spend most of their time foraging during rare stringent periods and as a consequence appear "lazy" at other times. However, there were no environmental conditions during the two years of this study which induced male Ospreys to spend all their time provisioning. The longest a male was observed to flight hunt during 82 days of observation was 4.7 hours, 31% of the active day. Time constraints to foraging therefore appear unlikely to limit brood size in this population of Ospreys.

The digestive tract's capacity to assimilate nutrients or energy from food also do not appear likely to limit brood size in the Osprey. 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 *DEE* of male Ospreys during this study was only 1248 kJ/day. Furthermore, the *DEE* of male Ospreys only came within 20% of the maximum they are predicted to be able to sustain on 8 of the 82 days they were observed, exceeding A_{max} only once. However, in this study, male Ospreys could avoid hunting during poor conditions and still maintain their delivery rate to the nest as inclement weather was both rare and of short duration. Wind speed, water surface conditions and sunlight are all known to influence the duration and success of individual flight-hunts (Grubb 1977, Stinson *et al.* 1986, Machmer & Ydenberg 1990). In years with prolonged periods of high winds and heavy rain male Ospreys may therefore be forced to increase their *DEE* to levels approaching A_{max} in order to maintain their delivery rate to the nest. Alternatively, males may stop hunting completely if it becomes unprofitable in bad weather (Machmer & Ydenberg 1990), which might explain the poor condition and reduced survival of chicks following prolonged storms (Poole 1989, Forbes 1991).

The *DEE* of male Ospreys in this study can also be compared with that of other breeding birds using an allometric relationship derived by Masman *et al.* (1989). This allometric function, which relates body mass to *DEE*, predicts that a male Osprey weighing 1428 g should expend 1553 kJ/day during the breeding season. Male Osprey in this study therefore worked at a level close to that predicted for a bird of their mass, but at a rate well below their supposed physiological maximum.

Energetic expenditure and natural brood size

The energetic expenditure of male Ospreys appeared to be dependent upon the number of chicks in their brood. Males provisioning three chicks spent significantly longer in flight and had a higher energetic expenditure, than males provisioning one or two chicks. The increased workload 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. Although male Ospreys provisioning large broods expended more energy, their intake rates were no different, than males with smaller broods. Presumably males with large broods therefore lost a greater proportion of their body mass during the breeding season. This suggests that the condition of male Ospreys at the start of the breeding season may influence their energetic expenditure. Individual differences in either age or current condition might be expected to influence the energetic expenditure of male Ospreys as these factors could affect an individuals residual reproductive value and the magnitude of the costs associated with various levels of reproductive effort. Although adult birds in this study were of unknown age, pair initiation dates can be used as an indicator of mean pair age (Poole 1985). There was no relationship between pair initiation date and mean male *DEE* ($r_s = -0.167$, $n = 17$, $p = 0.48$), suggesting that male condition is more likely to be able to explain individual differences in *DEE* than male age.

While it might be expected that parents adjust *DEE* and brood size to individual optima, result-ing in a positive relationship between *DEE* and brood size, several studies have found *DEE* to be independent of natural brood size (egs: Bryant & Westertep 1983, Masman *et al.* 1989). Brood size, in these cases, appears to be adjusted to food availability, or individual differences in foraging efficiency, such that parents with different brood sizes work at similar rates.

Energetic expenditure and experimental manipulation of brood size

The results of the brood size manipulation experiment suggest that, despite the positive relationship between natural brood size and male *DEE*, brood size does not have a direct affect on *DEE*. Male Ospreys neither increased their energetic expenditure nor reduced their food intake when provisioning experimentally enlarged broods. As a consequence chick intake rates were significantly reduced and chicks gained 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 (Poole 1989). Brood size manipulations in other raptors have also failed to elicit a parental response (egs: Coopers' Hawks *Accipiter cooperii* Snyder & Snyder 1973; Sparrowhawks *Accipiter nisus* Geer 1981; African Red-breasted Sparrowhawks *Accipiter rufiventris* Simmons 1986; Tengmalm's Owls *Aegolius funereus* Korpimaki 1988). In contrast, male Eurasian Kestrels responded to short-term brood manipulation experiments by increasing their energetic expenditure (Masman *et al.* 1989). The increased parental effort, however, appeared costly as parental survival was reduced when provisioning experimentally enlarged broods for an extended period (Dijkstra *et al.* 1990). The failure of male Ospreys to respond to manipulation of brood size, when there is no evidence to suggest that the energetic expenditure of male Ospreys is physiologically constrained, could therefore be interpreted as an "unwillingness" to pay the costs associated with increased energetic expenditure.

Unlike male Ospreys, females have been found to reduce their food consumption and suffer increased mass loss when provisioning experimentally enlarged broods (Poole 1989). The results of this study (although not statistically significant) 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 while caring for nestlings (Poole 1989). The sex-specific response to brood enlargements may therefore result because mass loss does not have the same consequences for male and female Ospreys. Alternatively, female Ospreys may respond to brood enlargements as they are able to regain mass lost during the nestling period while caring for fledglings, an opportunity that males, who continue to capture the majority of fish eaten by fledglings, probably do not have.

This study has shown that the mean *DEE* of male Ospreys, to which brood size is apparently adjusted, is unlikely to be limited by either time or energetic constraints. The failure of Ospreys to respond to brood enlargements, even when their mean *DEE* was well below the maximum they are predicted to be able to sustain, suggests that there are costs associated with an increase in workload. Individual differences in age or current condition may affect the magnitude of the costs associated with various levels of energetic expenditure. Further work on state-dependent energetic expenditure and condition dependent survival, is therefore required to elucidate the life history decisions of this species.

ACKNOWLEDGMENTS

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SAMENVATTING

Centraal in dit artikel staat het verband tussen broedselgrootte en energie-spendering van mannetjes Visarenden in zuidwestelijk Canada. De dagelijkse energiebesteding tijdens de verzorging van jongen in het nest, maar ook daarna, werd geschat aan de hand van nauwkeurige waarnemingen van de tijdsbesteding van de mannetjes (Fig. 1, Tabel 2), literatuurgegevens over de kosten van vliegen en ander gedrag, en gegevens over de weersgesteldheid.

De baten van alle inspanningen (vis voor de jongen, voor het wijfje en voor hemzelf) konden worden gekwantificeerd aan de hand van het aantal happen waarmee de buit op het nest geconsumeerd werd (Tabel 1). De inspanningen van het mannetje blijken niet samen te hangen met de leeftijd van de jongen en slechts in geringe mate met de kalenderdatum (Fig. 2, Tabel 3). Ook de weersomstandigheden hadden betrekkelijk weinig invloed op de energiebesteding van de mannetjes. De energiebesteding bleef wat lager wanneer er gedurende geruime tijd weinig golfslag was.

De inspanningen hingen wel duidelijk samen met de broedselgrootte (Fig. 3). Experimentele manipulatie daarvan had echter geen aantoonbaar effect op de energiebesteding (Tabel 4, Fig. 4). Dit suggereert dat er geen *directe* invloed is van broedselgrootte op het inspanningsniveau.

Mannetjes visarenden brachten ook niet meer of

minder vis aan bij manipulaties met de broedselgrootte (Tabel 4), hetgeen duidelijke gevolgen had voor de groeisnelheid van de jongen (Fig. 5). De mannetjes bleken onder hun maximale inspanningsniveau te werken. Daarom is het onwaarschijnlijk dat de broedselgrootte door fysiologische factoren wordt beperkt.

Gesuggereerd wordt dat zowel broedselgrootte als de mate waarin energie wordt geïnvesteerd, beïnvloed worden door individuele verschillen in leeftijd en conditie. Het inspanningsniveau is kennelijk niet aangepast op het grootbrengen van zoveel mogelijk jongen per seizoen, maar wellicht wel op een maximaal voortplantingsresultaat in de nog resterende levensjaren.

JvR

APPENDIX

The calculation of *DEE* is summarised in equation 1.

$$DEE = NFA((EM_{Ta}-(1-P)SM_{Tna})/PL)+\sum_{i=1}^{7}(FA_i \cdot FC_i) + ADD + (1-P)SM_{Tna} \qquad (1)$$

where: *NFA* = duration of diurnal non-flight activity (s)
EM_{Ta} = existence metabolism of non-passerine birds during the summer as a function of average daily air temperature (*Ta*) (kJ/day)
P = photoperiod as a proportion of the 24-h day
L = 86400 and converts kJ/day to kJ/sec
FA_i = duration of flight type i (s)
FC_i = cost of flight type i (see Table 5 for details)
ADD = additional take-off and dive costs (see Table 5 for details)
SM_{Tna} = standard metabolism of non-passerine birds during the summer at night, as a function of average night time temperature (*Tna*) (kJ/day)

$$EM_{Ta} = EM_{0°C} + Ta \cdot b \qquad (2)$$
where: $b = (EM_{30°C} - EM_{0°C})/30$
$$EM_{30°C} = 4.472 \cdot W^{0.6637} \qquad (3)$$
$$EM_{0°C} = 17.343W^{0.5444} \qquad (4)$$
W = body mass = 1428 g

$SM_{Tna} = SM_{0°C} - b \cdot Tna$ for Tna below the lower critical temperature (T_{lc}) $\qquad (5)$
SM_{Tna} = basal metabolism (*BM*) for Tna above the lower critical temperature
where: $SM_{0°C} = 10.987W^{0.5705} \qquad (6)$
$b = 0.270W^{0.5886} \qquad (7)$
$Tlc = 47.17W^{-0.1809} \qquad (8)$
$BM = 2.1873W^{0.7347} \qquad (9)$
W = body mass = 1428 g

Allometric equations (2)-(9) were derived by Kendeigh *et al.* (1977) for non-passerine birds during the summer and at night. Daily measurements of photoperiod and ambient temperature were used to calculate *DEE*, EM_{Ta} and SM_{Tna}. Variation in photoperiod and temperature observed during the breeding season is presented in Figure 6. Male Ospreys in this study were not weighed. Flight costs, *EM* and *SM* for each bird were therefore calculated using a body mass of 1428 g, the average mass for male Osprey during the breeding season (Cramp & Simmons 1980). There are two components to EM_{Ta}: diurnal non-flight activity and nocturnal rest. The expression $(EM_{Ta} - (1-P)SM_{Tna})/PL$ calculates the cost of diurnal non-flight activity by compensating for the lower energetic costs of nocturnal rest.
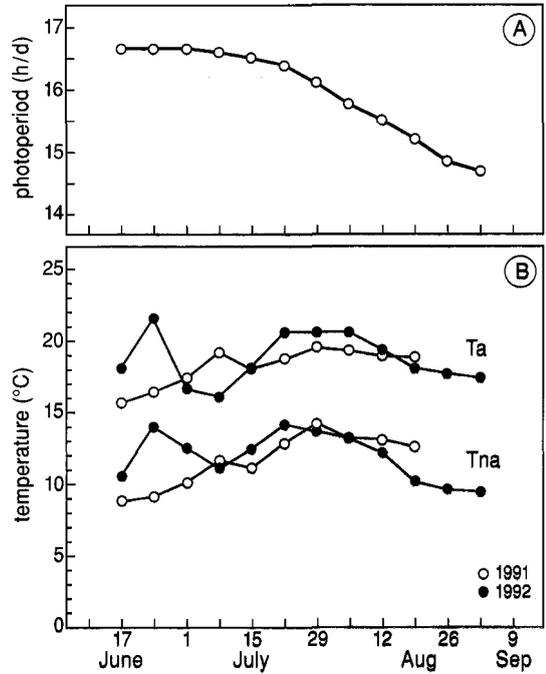

Fig. 6. Weekly variation in (a) photoperiod and (b) ambient temperature during the breeding season at Nelson, British Columbia in 1991 and 1992. The temperature in 1991 and 1992 differed so weekly averages are presented separately.

Table 5. Flight types and costs used in calculating the daily energetic expenditure of male Ospreys. Powered flight costs were calculated from Program 1 of Pennycuick (1989). Take-off and dive costs were calculated from the gain in kinetic and potential energy.

Flight type		Cost(J/s)
1. Gliding		10.6
2. Powered flight at *Vmr*		70.4
3. Powered flight at *Vmp*		93.9
4.	+ fish of 100g	94.3
5.	+ fish of 200g	104.8
6.	+ fish of 400g	126.5
7.	+ fish of 600g	151.3

		Additional cost (J)
Take-off:	from nest to *Vmp*	1029
	from nest to *Vmr*	1546
	from tree to *Vmp*	298
	from tree to *Vmr*	815
Diving:	fail	1516
	catch 100g fish	1561
	catch 200g fish	1675
	catch 400g fish	1896
	catch 600g fish	2120