

The duration of the post-fledging dependence period of Ospreys *Pandion haliaetus* at Loch Garten, Scotland

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The post-fledging dependence period of Ospreys at Loch Garten, Scotland, lasted an average of 30.4 days (n = 35). During this time fledglings were observed playing with objects, chasing other raptors, practising flight movements related to fishing and trying to fish by themselves. Fish provisioning by the adult male was maintained during the post-fledging period and provisioning rate had no effect on the duration of the post-fledging dependence period. The adult female was usually the first individual to disappear from the nesting area, followed by the fledglings and then the adult male. Observations suggest that the adult male continued providing fish to the nest while the fledglings were in the area and did not promote fledgling independence by stopping fish delivery to the nest.

Although other aspects of the Osprey breeding cycle have been relatively well studied^{1,2} the post-fledging dependence period has received little attention. Stinson³ estimated the duration of the post-fledging dependence period of Ospreys at 12 nests in south-eastern Virginia (USA). Edwards^{4,5} studied the maturation of fishing behaviour in Osprey fledglings but did not indicate whether they were still dependent on their parents for food.

This study analyses the data on age at fledging, behaviour of fledglings and duration of the post-fledging dependence period, recorded at the Loch Garten Osprey nest, Scotland. Previous analyses of Loch Garten Osprey data have focused on the arrival, incubation and nestling periods, and on feeding ecology.⁶

STUDY AREA AND METHODS

Data come from a single nest at the Loch Garten RSPB Reserve, Badenoch and Strathspey, Scotland (57°15'N, 3°42'W), which has been monitored for 35 years since 1958. The nest is on the top of a tall Scots Pine *Pinus sylvestris* in an area of open forest, part of Abernethy forest, one of the best remnants of the original boreal forest. The data analysed come mainly from the period

1968–87 during which a standard recording scheme was followed by the observers, and observations were continued through the post-fledging period until the last Osprey had left the nesting area. Years in which breeding failed (1971, 1975, 1985, 1986 and 1987) were excluded.

Observations were made by different observers around the clock from a hide 250 m from the nest. Although occasional observations of the fledglings a few km away from the nest had been recorded in the logs, usually fledglings were not followed when they left the vicinity of the nest.

The exact hatching date of the first egg in the clutch was known from the change in the female's behaviour. The degree of hatching asynchrony in clutches of 2 or 3 eggs was not known, and for the estimates of nestling period duration it was assumed that all chicks from a clutch had hatched the same day. Fledging age is the age at the first flight. First flights were always witnessed, so the exact fledging date was known for each chick. Fledglings continued to feed on fish brought to the nest by the adult male while they were in the nesting area. It was considered that the post-fledging dependence period of a fledgling ended when it definitively abandoned the nesting area.

The daily feeding rates of at least 4 different males were analysed during 13 different years for the whole breeding cycle. The mean daily fish delivery rate was calculated each year in 4 distinct periods of the breeding cycle: (i) pre-laying, (ii) incubation, (iii) nestling (hatching to fledging of the first chick in the brood) and (iv) post-fledging (fledging of the first chick in the brood to independence of the last chick). In addition the delivery rate for the periods was examined: (v) 10 to 3 days before fledging of the first chick in the brood, (vi) during the last 3 days before fledging of the first chick in the brood, (vii) the interval between fledging of the first and the last chick in the brood, and (viii) the last 5 days of the post-fledging period. The mean delivery rate for each of these periods each year was calculated and the mean delivery rate for each period for each male then obtained as a mean of means. It was then tested whether the males increased or decreased their delivery rates in relation to a previous period (e.g. post-fledging period vs. nestling period) with a Student's *t*-test for paired samples.

RESULTS

Post-fledging dependence duration

Osprey chicks fledged at a mean age of 52.8 days (range 49–59, *sd* = 2.5, *n* = 46). In broods of more than 1 chick the second and the third chicks left the nest on average 1.6 days (*sd* = 1.4, *n* = 18) and 3.8 days (*sd* = 1.9, *n* = 7) after the first one. This is probably the effect of hatching asynchrony (estimated to be *c.* 2 days, R. Dennis pers. comm.) but could also be the effect of a different nestling period duration between male and female chicks. Unfortunately neither hatching sequence, hatching asynchrony nor chick sexes were known. Hatching date had no effect on fledging age (Pearson's $r_{44} = 0.076$, $P = 0.61$). Chicks from larger broods had significantly longer nestling periods, even after fledging ages had been corrected for differences in fledging sequence (fledging age of a chick—expected fledging age according to its fledging sequence within the brood; ANOVA $F_{2,43} = 5.94$, $P = 0.005$). The difference was only significant between 2-chick and 3-chick broods (Tukey test, $P < 0.05$).

Young Ospreys abandoned the nesting area on average 30.4 days after fledging (range 18–46, *sd* = 6.3, *n* = 35), at a mean age of 82.6 days (range 71–97, *sd* = 6.1, *n* = 35). There was no effect of fledging date on the duration of the post-fledging dependence period ($r_{33} = -0.029$, $P = 0.86$).

Larger broods tended to have shorter post-fledging dependence periods (1 chick = 42 days, *n* = 1; 2 chicks = 31 days, *n* = 22; 3 chicks = 27 days, *n* = 12; $F_{2,32} = 4.12$, $P = 0.026$) but as chicks of larger broods fledged on average when older the total dependence period was independent of brood size ($F_{2,32} = 2.41$, $P = 0.11$).

The adult female was usually the first to leave the family unit (9 out of 13 years), and on average did it 4.6 days (*sd* = 5.9, *n* = 14) before mean fledgling departure, the difference being significantly different from zero (Student's *t*-test, $t_{12} = 3.14$, $P = 0.008$). In contrast, the adult male was usually the last to leave, on average 3.3 days (*sd* = 3.2, *n* = 14) after mean fledgling departure ($t_{12} = 3.8$, $P = 0.002$) and frequently was the last individual recorded at the nest site (9 out of 13 years). The year 1979 was excluded because the adult male disappeared shortly after fledging, which was atypical for that male, and did not return the next year. All this suggested that the male might have died before migration.

No fledgling mortality was recorded during the post-fledging period (*n* = 35), although it cannot be excluded that some fledglings had disappeared due to death and not to dispersal.

Fledgling behaviour

Even though most of the observations were restricted to the nest surroundings, observations of behaviours related to training of foraging skills or maturation of foraging behaviour were frequent during the total of 401 days of observations of fledgling behaviour in the 13 years with adequate data (years 1970, 1972–74, 1976–84).

Fledglings played with objects (moss clumps, sticks and twigs), manipulated them, or transported them to and from the nest. Although it was frequently noted that fledglings were rearranging the nest material, it is doubtful whether their actions contributed to the maintenance of the nest structure, as they

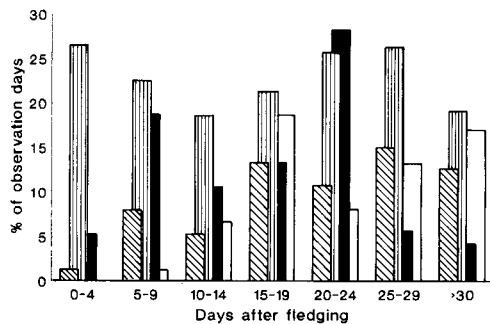


Figure 1. Percentage of observation days in which fledglings were observed chasing each other or other birds (▨), playing with objects (▤), practising foraging movements (▥), or trying to fish (□), in relation to days after fledging. All years pooled.

took material, with equal frequency, to and from the nest. This behaviour was observed in all years, on 27% of observation days, and on average started 4 days after fledging (Fig. 1).

Fledglings seemed to train their foraging skills, practising movements related to fishing, both over water and over the ground. Fledglings were observed diving towards the ground with extended talons and pulling out of the dive a few metres before touching the ground, snatching branches or clumps of pine needles from the tree crowns, or performing, what were described as acrobatic flights. These behaviours were recorded in all years, on 13% of observation days, and on average started 11 days after fledging (Fig. 1)

Occasionally fledglings were observed trying to fish at Loch Garten (1 km from the nest) before independence. Data were irregular because fledglings were not usually followed when leaving the vicinity of the nest. However, fledglings still dependent on their parents for food were observed trying to fish by themselves, on 15 different occasions. In only one instance did a fledgling catch a fish, that slipped from its talons a few seconds later. In 2 different years (1970, 1980) fledglings were recorded bringing fish to the nest. These may have been captured by the fledglings themselves, because adults were never seen using perches different from the nest to make prey transfers, and other perches used by adults and fledglings were in sight of the observers. Also, observations of fledglings with wet plumage returning to the nest, on days with no rain (11

instances) suggest that fledglings tried to fish before independence. One of these fledglings was followed by the observer and was later seen trying to fish in the loch. In 10 out of 13 years (9% of the observation days) behaviour was observed which suggested that the fledglings were trying to fish by themselves. Fishing behaviour was observed as early as 9 days after fledging, but on average started 16.6 days after fledging (Fig. 1).

Fledglings had variable reactions towards Osprey intruders coming near the nest. They frequently emitted alarm calls, and spread their wings if the intruder tried to perch on the nest; occasionally the juveniles would chase away the intruder by themselves or after joining the adults. Chases involving Osprey intruders were observed on 16 occasions, while on 14 occasions the fledgling mantled on the nest or fled from the intruder. Some intruders were ignored or the fledglings even begged food from them.

Chases by fledglings towards their siblings, and more frequently towards other raptors, were sometimes observed. Fledglings seemed to be playing more than trying to chase away the other bird, and frequently they were chased back. A total of 38 chases was observed towards Hooded Crows *Corvus corone*, Kestrels *Falco tinnunculus*, Sparrowhawks *Accipiter nisus*, Buzzards *Buteo buteo*, Merlins *Falco columbarius* and a Peregrine Falcon *Falco peregrinus* (Fig. 1).

Siblings frequently fought over fish delivered to the nest and took them to other perches. During fights or transport of fish to other perches, fish were sometimes dropped to the ground and never recovered. Fights over fish or its transport to other perches were observed on 58.6% of observation days, as soon as the first day after fledging and tended to increase over time (Fig. 2). One fledgling was observed tearing a fish and offering bits to its sibling (25 July 1981).

Adult behaviour, feeding by adults and prey transfers

Feeding of the fledglings was done almost exclusively by the male and all food transfers observed during the post-fledging period took place at the nest. In 10 out of 13 years with complete observations, the female also brought

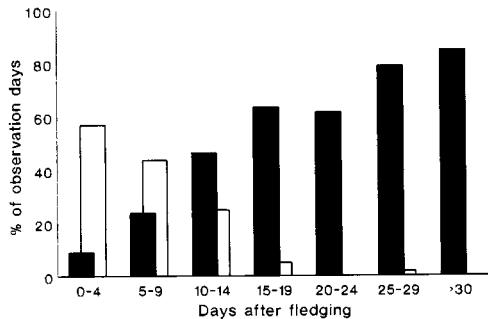


Figure 2. Percentage of observation days in which fledglings were observed fighting for the fish delivered to the nest or taking them to other perches ■, and percentage of days the female was observed tearing the fish and feeding the fledglings □, in relation to days after fledging. All years pooled.

a number of fish during the post-fledging period, but only in 1979, when the male disappeared shortly after fledging, did the female take on the duty alone of feeding the fledglings.

After fledging, the adult female sometimes still tore up the fish and offered small pieces to her offspring with her bill. This was observed on 25% of observation days during the post-fledging period (Fig. 2) and continued on average up to 14.2 days after fledging.

No behaviour was recorded that could be interpreted as the parents trying to lure the fledglings out of the nest, as described by Meinertzhagen.⁷ There was no decrease in the mean number of fish delivered to the nest when comparing the periods 10–3 days before fledging and the 3 days before fledging of the first chick in the brood (paired *t*-test, $t_3 = 0.10$, $P = 0.93$) (Fig. 3). However, fish delivery rate declined during the interval between the first flight of the first and last chick in a brood ($t_3 = 14.7$, $P = 0.0007$), and continued at a significantly lower rate during the post-fledging period compared to the rate during the nestling period ($t_3 = 3.99$, $P = 0.028$) (Fig. 3).

Mean fish delivery rate per fledgling during the post-fledging period had no effect on the mean duration of this period in a brood (Pearson $r_9 = 0.46$, $P = 0.48$). There was a significant final decrease in the rate that fish were delivered to the nest during the last 5 days of the post-fledging period compared

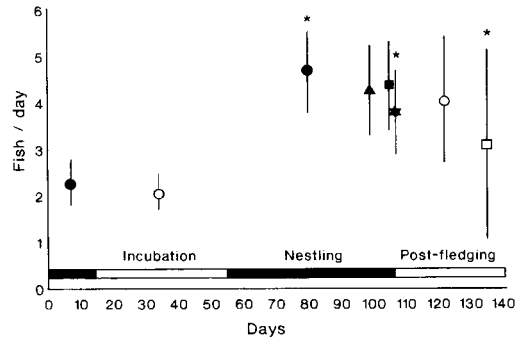


Figure 3. Mean number of fish per day ($\pm 95\%$ CI for individual means) delivered to the nest by the adults (mostly the male, as only during the post-fledging period did the female contribute a few fish), during different parts of the breeding cycle. The circle above each horizontal bar represents the mean value for that period. The triangle stands for the interval 10 days before fledging to 3 days before fledging of the first chick, the filled square stands for the last 3 days before fledging of the first chick, the star stands for the interval between the first and the last chick to fledge and the open square for the last 5 days of the post-fledging period. * indicates a significant change ($P < 0.05$) in feeding rate in relation to the previous period. Details of statistics are given in the text.

with the delivery rate in the previous part of the post-fledging period ($t_2 = 4.424$, $P = 0.047$).

DISCUSSION

The duration of the post-fledging dependence period in the Ospreys at Loch Garten (30.4 days) was very similar to that estimated by Stinson³ for North American Ospreys (32.5 days).

Larger Osprey broods fledged on average when older. Fledging age in raptors is affected by growth rate during the nestling period. In *Milvus* kites feeding hierarchies within the brood create an increase of fledging asynchrony in relation to initial hatching asynchrony.⁸ In species in which hierarchies at the nest are not well marked, as is the case with the Osprey,⁹ brood size has an effect on the average growth rate of chicks,⁹ and growth rate probably on fledging age.⁸

The gradual break-up of the family group suggests that the dependence period ended when the fledglings left the nesting area and that it did not continue elsewhere. Also, there

was no relation between average feeding rate per chick and post-fledging dependence duration. The observed decrease in feeding rate at the end of the post-fledging period seemed more likely to be following a decrease in demand by the offspring (the fledglings spent less and less time near the nest, were probably starting to fish by themselves and some had already dispersed) than the male trying to force the family break-up. The adult male was the last to disappear, and at least in 2 of the years he still brought fish to the nest after all the fledglings had left the nesting area. This suggests that there was no parent-offspring conflict¹⁰ (when offspring demand a longer period of parental care than parents are selected to give) at the end of the post-fledging period, and that the fledglings decided when to disperse rather than being forced to do so by a reduction in feeding by the adult male. The lack of clear parent-offspring conflict is similar to what has been found in the migratory Black Kite *Milvus migrans*;^{11,12} however, in Ospreys there is no relation between fledging date and post-fledging dependence period duration, in contrast to what was found in the Black Kite, in which migratory urgency seems to affect the timing of family break-up, and chicks fledged later in the season tend to have shorter post-fledging periods.^{12,13}

The behaviour of a chick feeding its sibling has also been observed in other raptors during the post-fledging period.¹⁴⁻¹⁶ Due to its infrequent occurrence it has been suggested that this is probably a behaviour out of context,¹⁴ rather than a gradual maturation of the behaviour of feeding the chicks after fledging.

The behaviour of the female feeding its offspring long after they can tear the fish by themselves is atypical in raptors. It could, possibly, help to reduce competition among siblings and reduce the amount of fish that is dropped to the ground during fights among siblings or during flights between perches.

Fish transport from the nest to other perches perhaps indicates increasing conflicts among the siblings, but it could, at the same time, be related to training in the ability to manipulate and transport prey, because this behaviour was also observed in a fledgling from a single brood.

Juvenile Ospreys at Loch Garten started their fishing trials on average 16.6 days after their

first flight. Edwards⁴ also observed the first fish captures among Osprey fledglings approximately 20 days after the first flight. All this suggests that fledglings start fishing by themselves 10-15 days before becoming independent from their parents for food. The frequency with which behaviours related to the gradual maturation of fishing skills were observed in the fledglings suggests that gradual learning during the post-fledging dependence period is important for survival after independence in the Osprey. Play with objects and gradual maturation of the foraging behaviour before independence has been observed in many species of raptors, but seems to be more important in species with specialized feeding habits and that feed on agile or 'difficult-to-catch' prey (e.g. *Falco* spp.,^{14,17,18} *Accipiter* spp.,^{19,20} *Circus cyaneus*,²¹ *Aquila* spp.,^{22,23} *Buteo* spp.,^{24,25} *Elanus caeruleus*²⁶) and relatively infrequent in those species feeding on insects or carrion, or with generalized feeding habits (e.g. *Milvus* spp.^{13,27} *Ictinia mississippiensis*²⁸, *Haliaeetus leucocephalus*,²⁹ *Neophron percnopterus*,¹⁶ *Falco naumanni*³⁰).

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