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Post-fledging dependence and dispersal in hacked and wild Montagu's Harriers *Circus pygargus*

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We compared the post-fledging dependence period, dispersal patterns and resighting rates of captive-raised and hacked Montagu's Harriers *Circus pygargus* with those of wild reared and naturally fledged Montagu's Harriers, in order to assess the validity of hacking as a release technique for this species. Among hacked birds, we found significant relationships between the length of the dependence period and both hatching date and body condition (birds hatched later in the season had shorter periods of dependence; birds in poorer condition had longer periods of dependence). The condition index increased with the amount of time spent in captivity. The length of the dependence period did not differ significantly between released and naturally fledged birds, when hatching dates were accounted for. Observation rates of wing-tagged fledglings in years after marking were higher for released birds (15.5–20.9%) than for naturally fledged birds (9.4–9.9%). Released birds also tended to be resighted closer to their released location than did the naturally fledged birds. We suggest that the differences in resighting data are related to the better condition of the released birds, compared with their wild counterparts. We conclude that hacking is apparently a good release technique for captive-reared Montagu's Harriers, and that comparisons of behaviour at the post-fledging period may be a valid method for evaluating the success of release techniques.

Bird conservation programmes are increasingly focused around captive propagation and release, either for reintroducing species that have become locally extinct (McGrady *et al.* 1994, Love & Ball 1979) or for supplementing dwindling populations (Wiemeyer 1981, Meyers & Miller 1992, Cade & Temple 1995). More recently, methods of artificially manipulating natural nests have also been employed (Pomarol 1994, Watson *et al.* 1996). However, the extent of success of release is difficult to evaluate and is thus rarely estimated (Csermely & Corona 1994).

Success of wildlife releases has often been assessed by the subsequent survival and reproduction of the released individuals (McGrady *et al.* 1994, Evans *et al.* 1994). This has been achieved through various forms of post-release monitoring, such as the use of radio-tracking (Meyers & Miller 1992, Csermely & Corona 1994) and recognition markers (Newton *et al.* 1987, Martell *et al.* 1994). However, such assessment methods may prove difficult with species that undergo long-distance dispersal or migration and/or which do not subsequently display philopatric behaviour. In such cases, a method of assessing success indirectly could be through comparing certain behavioural patterns of released animals with those of their wild counterparts: detection of any abnormalities may indicate that time spent in captivity has had an effect on their behaviour, and thus, their probability of survival (see also Meyers & Miller 1992). In birds, the post-fledging dependence period (hereafter termed simply the dependence period) and the subsequent initial independence from parents is a critical life-history stage, when young develop foraging skills essential to survival (Weathers & Sullivan 1989). Its importance is reflected by the high mortality rates witnessed during this time (Lack 1954, Henry 1972, Sullivan 1989). This period, therefore, seems meaningful for use in these comparisons.

Hacking is a method for releasing captive raptors into the wild, with food provided at a known locality – the hack site – until the young no longer return there for food (Cade & Temple 1977). It has been used to release many species of captive-bred raptors into the wild (Newton 1979), including Montagu's Harriers

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(Pomarol 1994). For raptors released by this method, the time they remain dependent on the hack site for food can be considered as equivalent to the dependence period of wild fledged birds. The only investigations of this period for released raptors come from Meyers and Miller (1992) and Pomarol (1994). Pomarol studied length of the dependence period for released Montagu's Harriers *Circus pygargus*. He did not, however, make any comparisons with wild birds. We investigated the factors influencing the length of the dependence period in released Montagu's Harriers, and compared it with that of birds which fledged naturally. Additionally, the resighting rates and location of naturally fledged and released birds, marked with patagial tags, were examined for differences in important movement patterns such as migration and philopatry (Reed *et al.* 1993).

METHODS

Study areas, captive rearing and hacking

Since 1994, we have monitored Montagu's Harriers breeding in three study areas (Deux-Sèvres, Baie de l'Aiguillon and Rochefort), located approximately 50–60 km around La Rochelle (central western France) and covering between 20 000 and 30 000 ha each (for details see Butet & Leroux 1993, Arroyo *et al.* 1998). We systematically searched for all nests in each study area. As a conservation measure, we removed eggs and very young chicks from nests located in crop fields due for immediate harvesting. These were then raised in captivity and subsequently released by the method of hacking (Pomarol 1994). Nests that contained large young (> 15 days old) at the time of harvesting, or that were located in natural vegetation, did not require such intervention.

Eggs were artificially incubated until hatching in two captive rearing centres, one located in Deux-Sèvres, the other in Baie de l'Aiguillon. Chicks were housed in small boxes in groups of two to six birds, approximately of the same age but not necessarily siblings, and were fed *ad libitum* on a diet of dead one-day-old chickens and mice. At Deux Sèvres, the hack site was situated on the border of a wheat field and was about 13 km from the rearing centre, whereas at Baie de l'Aiguillon, the hack site was in the suburbs of a village and next to the rearing centre. In both localities, the surrounding crops were mainly cereals, sunflowers and pasture. In 1995 and 1996, there were nesting pairs of Montagu's Harriers in these adjacent fields, which had either large nestlings or dependent fledglings at the time when hacking began. The location in Deux-Sèvres was thought suitable because of the presence of wild birds and also because there was a large traditional roosting site nearby (about 300 m). The hacking shed consisted of a three-sided wire enclosure with the fourth side being made up by a small farm building. The wire enclosure was roofless to allow the birds to fly out at will, but had a small roof to protect them from any severe rain and heat. Pomarol (1994) fully described details of a hack site design for Montagu's Harriers. Releases (i.e. translocation from rearing centre to hack site) commenced on 4 July with the last release occurring on the 19 August in Deux-Sèvres. Birds were usually released at the hack site in groups with an average size of seven (range 1–11). Because there were no birds already present at the hack site, the first release consisted of the largest group; for subsequent releases, previously released birds were still found around the hack site and, therefore, group size was thought less important in ensuring a smooth transition to the release state (Evans *et al.* 1994). After the first release, one-day-old chickens were placed each day within the hacking enclosure and on the roof of the adjacent farm building. The quantity of food placed each day was in excess of the amount eaten, but was not theoretically enough to fulfil the energetic needs of all released birds.

Hatching success at the rearing centre was 62% (n = 54 eggs) and fledging success was 64% (from the 33 hatchlings). Hatching success was significantly lower at the rearing centre compared to the wild ($\chi^2 = 39.1$, $P < 0.001$; n = 332 eggs in the wild in 1996), but fledging success was similar ($\chi^2 = 0.04$, $P = 0.95$, n = 313 hatchlings in the wild in 1996).

Length of dependence period

In 1996, the 50 fledglings captive-reared at Deux Sèvres were individually marked with patagial tags (identified by colour codes and numbers). From 4 July to 31 August, daily observations were carried out at the hack site for one hour before and one hour after food placement (between 16:00 and 18:00 h). These observations were conducted from a car, parked no closer than 100 m from the hack site, using 8 × 42 binoculars and a 20–60× telescope. All birds in the vicinity of the hack site were identified by their individually numbered marks. No particular observational protocol or behavioural sampling method was used (either scan or focal individual), as the purpose of the observation was mainly to record whether individuals were still present at the hack site or not.

During these observations, hunting attempts or interactions with wild birds were also noted, but this was not systematic. We estimated the dependence period as the duration between the day of release and the last recorded sighting of the bird at the hack site. Two birds were found dead at or around the hack site, but causes of death could not be determined. Another was retrieved ill (and released again 20 days later). These three birds were removed from the analyses.

For comparison, data for the dependence period in wild birds were gathered from a large colony in 1996 at Rochefort, and several nests in Deux Sèvres in 1997. These nests were under no threat from harvesting. In order to determine the length of the dependence period for a sample of nestlings from these nests, we individually wing-tagged 37 nestlings from 14 focal nests and monitored them daily or every two days, during two hours each day. The duration of focal observations was set arbitrarily at two hours, as time intervals between two successive food passes at fledging exceptionally exceeds two hours (pers. obs.) and to coincide with the duration of observations at the hack site. As observations started some time after the first flight for some nests, the length of the dependence period was calculated as 30 days after hatching (which is the average age at first flight, pers. obs.) to the last day when the nestling was seen in the area still fed by its parents. Similarly to released birds, two fledglings found dead around the nest were removed from the analyses.

Sex, hatching date and condition

Sex of each chick was identified by differences in their iris colour (following the technique described by Picozzi 1981 for Hen Harrier *Circus cyaneus*), the males being greyish and the females chocolate brown. Sex identification is possible and accurate from age 10–15 days onwards (Leroux & Bretagnolle 1996). Ages of the young harriers were estimated from weight, wing-chord and tarsus-length, following Brignon (1997). Exact laying dates were known for some eggs from nest visits during the laying period; for the other eggs and for all chicks, laying dates were estimated using an average incubation period of 29 days (Cramp & Simmons 1980). Chick age (and thus hatching dates) was estimated from body measurements (Brignon 1997) on arrival at the rearing centre. Birds were weighed each day just before their first feed. Body condition was defined as the difference between fledgling mean weight at days 25–30 and the average asymptotic weight for each sex, and could be determined only for 44 of the 47 fledglings. Asymptotic weights were calculated from their growth curves using Richard's model (Brignon 1997).

Dispersal and return rate

In total, 129 captive-reared birds were marked on the day of release with patagial wing-tags, as well as 181 of the naturally fledged young in each of the study areas: thus, between 1995 and 1996, a total of 310 birds was marked (Table 1). Tags were coloured differently according to region, year of fledging, whether birds had fledged naturally or had been raised in captivity and, in 1996, whether they had been raised from an egg or chick stage. They were not, however, individually marked, except for the nestlings released at Deux Sèvres in 1996 and the naturally fledged young used for calculating the length of the post-fledging period (see above); these had individual numerical codes or symbols marked onto their coloured tags. For the fledglings that were not individually tagged, we cannot be certain that all resightings of marked birds corresponded to different individuals. Thus we considered a minimum number, based only on simultaneous sightings made at large surveys on particular days, and a maximum number, which considered that all birds seen at locations over 20 km apart were different individuals. Data obtained from the resighting of these marked birds were used to analyse dispersal and return rates of the different bird groups.

All means are expressed ± sd. Statistical analyses were conducted using the SPSS 6.1 and SAS 6.11 (SAS Institute 1988) packages. Non-parametric correlations (Spearman rank) were used to test the relationship between length of dependence period and other variables (age, date, condition), due to unequal variances among samples or according to hatching date. The differences in the length of dependence period according to sex or stage of entry were similarly tested with non-parametric tests (Mann–Whitney or Kruskal–Wallis). Differences in the proportion of wild and released birds that returned to the study area were tested with chi-squared tests, and the distribution of distances with Kolmogorov–Smirnov tests.

RESULTS

Length of dependence period in released and wild birds

Of the 47 birds successfully released at Deux Sèvres in

1996, 21 were taken as eggs and 26 as small chicks, 27 were male and 20 female. The average age at release was 33 ± 2 days (range 29–39) – similar to the estimated age of first flight in wild birds. The age at release was similar for birds reared from eggs (33 ± 2 days) and birds reared as chicks (34 ± 2 days). The average dependence period was 17.7 ± 12 days (range 0–47) and was longer in birds raised from egg stage (21.1 ± 12 days) than in birds taken as nestlings (14.9 ± 12 days), although not significantly (z = 1.84, P = 0.06). No significant difference was found between females (18.9 ± 13) and males (16.0 ± 12; z = 0.7, P = 0.4). No relationship was found between dependence period and the age at which a bird was released (r_s = 0.007, n = 47, P = 0.9) or between the age at which a bird became independent and the age at release (r_s = 0.105, n = 47, P = 0.5).

A significant relationship was found between length of the dependence period and date of release (r_s = –0.689, n = 47, P = 0.0001), with those birds released at later calendar dates having the shorter dependence periods. As birds were released approximately at the same age, this meant that birds hatched later had shorter dependence periods (r_s = –0.690, n = 47, P = 0.0001, eggs and chicks combined; see Fig. 1). The difference in the length of the dependence period between birds raised from egg or from nestling stage could be explained from their different hatching dates: birds raised from eggs hatched earlier on average than those taken as nestlings (Fig. 1).

The length of the dependence period varied greatly among fledglings of similar hatching dates, especially early in the season (Fig. 1). The residuals of the regression between the length of the dependence period and hatching date were negatively related to weight at fledging (r_s = –0.317, n = 44, P = 0.036) and to body condition (r_s = –0.326, n = 44, P = 0.031). Birds in better condition thus had shorter dependence periods for a given date than those in worse condition. No significant relationship was found between condition and hatching date (r_s = –0.207, n = 44, P = 0.2) but condition was found to increase with length of time spent in captivity (r_s = –0.461, n = 44, P = 0.002) and was therefore higher in birds raised from eggs than in birds taken as nestlings (z = 1.96, P = 0.05, Fig. 2). When analysing both types of birds separately, the relationship between the length of the dependence period and condition was still present in birds taken as nestlings (r_s = –0.432, n = 23, P = 0.04), but was not significant for birds raised from eggs (r_s = –0.156, n = 21, P = 0.5, Fig. 2).

The mean length of the dependence period in wild fledglings was 25.2 ± 8 days (range 1–37; n = 35). There was a significant difference in the length of the dependence period in wild birds between 1996 (27.2 ± 6 days, n = 29) and 1997 (15.8 ± 9 days, n = 6, z = 2.78, P = 0.005). More generally, the dependence period varied significantly among the four following groups: birds raised from eggs, taken as nestlings, naturally fledged in 1996, and in 1997 (χ^2_3 = 27.9, P = 0.0001). However, mean hatching dates also varied significantly among the four groups (χ^2_3 = 27.8, P = 0.0001), and the length of the dependence period was significantly related to hatching date (r_s = –1, n = 4 groups, P < 0.0001). Therefore, when differences in hatching dates were accounted for, no differences were

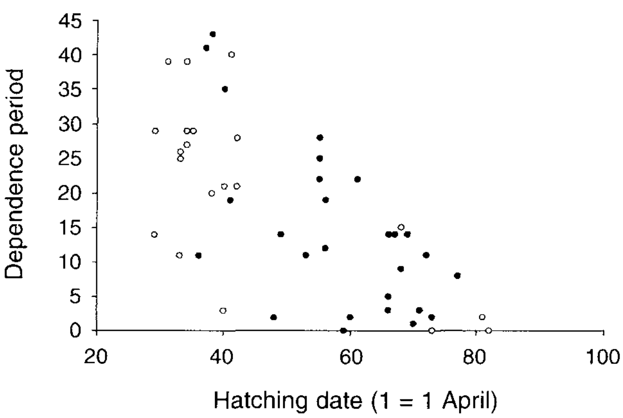

Figure 1. Relationship between dependence period and hatching date in male and female Montagu's Harrier fledglings released at Deux-Sèvres in 1996. ○, Birds raised from egg stage; ●, birds taken as nestlings.

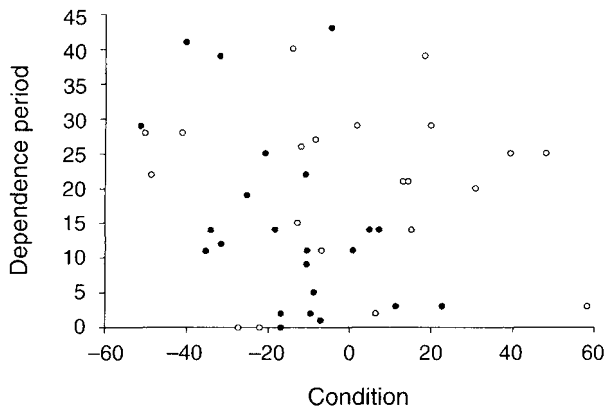

Figure 2. Relationship between dependence period and body condition (i.e. difference between weight at fledging and the asymptotic weight for each sex) in released Montagu's Harriers (Deux-Sèvres 1996). ○, Birds raised from egg stage; ●, birds taken as nestlings.

found for the length of the dependence period between captive-raised and naturally fledged young.

Resightings of marked birds

No significant differences in resighting rates were observed between birds that were marked and released at the two different captivity centres (χ^2_1 = 0.06, P = 0.8) or between birds that fledged naturally in different study areas (χ^2_2 = 4.89, P = 0.09), so data were pooled for analyses. At least 19 birds tagged in 1996 were resighted the same year after disappearance from the study areas. The directions of the sightings of marked birds during the migration period appeared to be similar for both released and naturally fledged birds (Fig. 3), although sample sizes were too small to allow statistical analyses.

Resighting rates were higher overall for captive-raised birds than for wild birds, although between-year differences were high (Table 1). There are at present insufficient data available to determine if there were any differences between the birds taken as eggs and those taken as chicks. The distribution of distances between resighting and birth/release locations indicated that released birds tended to be resighted closer to their releasing location than did the naturally fledged birds (D = 0.55, P = 0.009, Fig. 4). The frequency of resightings in relation to time after marking showed that there was a strong decline in recovery

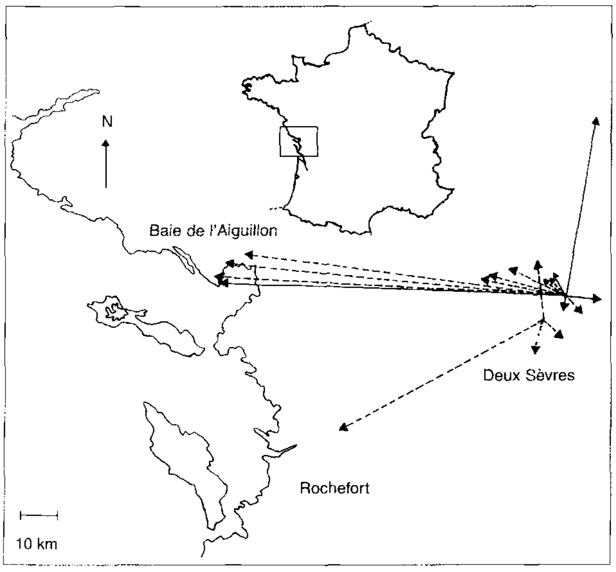

Figure 3. Location of observations of released (black arrows) and wild fledged (dashed arrows) juvenile Montagu's Harriers during the migratory period. The origin of each arrow indicates the release or birth site. The tip of the arrow indicates the location of the observation.

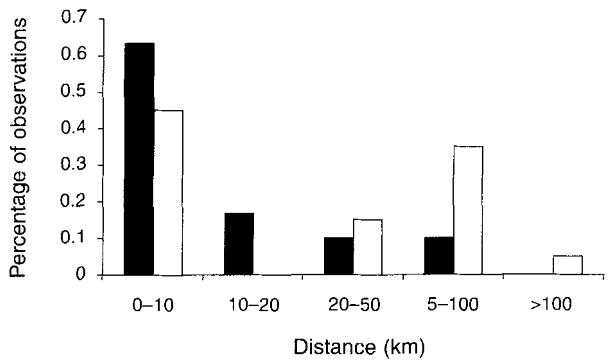

Figure 4. Proportion of distances between marking and resighting sites in years subsequent to marking for captive-raised (■) and wild (□) Montagu's Harriers.

rates after the first year for both groups of birds, but there appeared little difference between the two groups (Table 1).

DISCUSSION

The period between fledging and independence in raptors is the time when chicks can learn the essential skills for survival as an adult without the additional pressures of having to secure food to survive. The information available on the behaviour of young during this period suggests that raptors that take highly agile prey often play with objects in their feet (Kitowski 1994, Pandolfi 1996), whereas scavengers use this time to develop their gliding and kleptoparasitic skills (Bustamante & Hiraldo 1989) and soaring species develop their soaring capacities (Ferrer 1992). The length of this period may be influenced by the ability of the young to hunt for themselves (Brown 1966), the parental reduction in food provision or their aggression toward fledglings (Alonso *et al.* 1987, Bustamante 1993). Hacking provides a situation where parental influence is removed, therefore allowing other factors influencing the length of this period to be investigated more clearly.

Dependence period in released Montagu's Harrier

In our study, released Montagu's Harriers had an average dependence period of 17.4 days, far shorter than that of 33.7 days found by Pomarol (1994). A possible reason for this discrepancy may be that Pomarol excluded all data from birds which were not seen again at the hack site 10 days after their release. We retained those birds in our data set, as we had no

Table 1. Percentage of captively raised and naturally fledged wing-tagged Montagu's Harriers resighted in years subsequent to marking.

	Wild reared, marked in			Captive-reared, marked in		
	1995	1996	Total	1995	1996	Total
No. of fledglings wing-tagged	61	120	181	40	89	129
Seen 1 year later (%)	16.4 (10)	5.0 (6)	8.8	27.5–45.0 (11–18)	3.4 (3)	10.8–16.3
Seen 2 years later (%)	3.3 (2)	–	3.3	15.0–22.5 (6–9)	–	15.0–22.5
Total seen (%)	18.0–19.7 (11–12)	5.0 (6)	9.4–9.9	42.5–60.0 (17–24)	3.4 (3)	15.5–20.9

Sample size (number of birds) in brackets. Ranges refer to minimum and maximum number of different birds seen.

proof that these birds failed to reach independence. A few of the naturally fledged birds monitored also apparently left the nesting area on the first day of flight. Therefore, to allow direct comparisons, all birds were included in our analysis (except those birds that were found dead or ill after release). Even when we examined our data in the manner of Pomarol (1994), the average dependence period was 23.3 days, which still appears considerably shorter. Latitude may play a role in explaining the differences between the two studies, as the overall length of Montagu's Harriers' breeding season decreases with increasing northern latitude (Arroyo 1995).

We found no significant differences between sexes in relation to the length of their dependence period. This result appears to contradict the overall trend of increasing dependence length with size obtained by interspecific comparisons (Newton 1979), but could also be related to the relatively small sexual dimorphism in the Montagu's Harrier (Nieboer 1979). Pomarol (1994) found that the dependence period in released Montagu's Harriers was negatively correlated with both date and age at release. Similarly, we found that its length decreased as birds were released at later calendar dates; however, we found no relationship between its length and the age at which birds were released (possibly due to the narrower age ranges of release in our study), neither did we find that birds tended to become independent at the same age. Our data showed that the length of the dependence period in released Montagu's Harriers was mainly related to hatching date and body condition. The decrease in the length of this period with increasing hatching date has already been shown for this species (Pomarol 1994, Arroyo 1995) and for other species (Bustamante & Hiraldo 1990), and might be related to a migratory urge (Bustamante & Hiraldo 1990, Pomarol 1994). The relationship between body condition and the length of the dependence period is presumably linked to the fact that young require fat reserves to compensate for their poorer hunting skills; therefore birds in better condition can explore the surrounding area earlier, stay away longer and eventually disperse earlier (Frumkin 1994). Frumkin (1994) found that ultimate dispersal age in Sparrowhawks *Accipiter nisus* was negatively correlated with relative rate of body mass gain and Ferrer (1992) found that the first phase of the dependence period for the Spanish Imperial Eagle increased as physical condition of the young decreased. The lack of a relationship between body condition and the length of the dependence period in birds raised from the egg stage in this study may be related to their overall better body condition.

Comparison between released and wild Montagu's harriers

Released birds behaved like naturally fledged young and were often seen to interact with wild fledglings (pers. obs.). They were also seen to interact with the adults breeding around the hack site. On at least four occasions, birds taken at the egg stage (which therefore never saw adults during rearing) were seen begging for food from a female returning from a successful hunt (pers. obs.). Many released birds were also seen to spend the night with wild birds at a nearby roost. This suggests that the time spent in captivity did not adversely affect these birds' ability to recognize their own species. Similarly, some pellets collected from the birds at the hack site consisted not only of one-day-old chick feathers, but also of feathers from other young birds and also vole fur; actually, on at least six occasions, birds were seen successfully catching voles (pers. obs.). Overall, therefore, there is no evidence from this study that time in captivity had any effect on the behaviour of released birds. Similarly, Meyers and Miller (1992) could not detect differences in behaviour of captive-raised and wild-reared Bald Eagles *Haliaeetus leucocephalus*, and concluded that captive-reared birds were not imprinted on their environment. The remaining question is whether captive-reared birds were sexually imprinted, so that they will not reproduce. However, two one-year-old and one two-year-old captive-reared birds (two males and a female) were seen displaying with wild birds, and two nests of captive-reared birds were found in 1998.

In the only other detailed study on the post-fledging period for wild Montagu's Harriers, the average length of the dependence period was 24 days (Kitowski 1994), a comparable figure to that found in our study. Thus the dependence period seems to be slightly longer in wild birds than in captive-reared ones, despite a constant food supply throughout the dependence period. However, in our study, differences between captive-reared and wild birds arose mainly from differences in hatching date among groups. No proof exists, therefore, that captive-raised and naturally fledged birds differed in relation to the length of their dependence period (see also Meyers & Miller 1992). The two groups of birds appeared to have similar behaviour in terms of pre-migratory dispersion. Resightings of marked birds in years after marking suggested, in contrast, a slight difference of behaviour between released and wild birds, with the former showing stronger philopatric behaviour. The condition of released young was found to increase with the length of time spent in captivity, which suggests that birds in captivity were receiving more food than wild birds (as was also indicated by the overall better condition of birds raised from eggs than birds taken as nestlings). We therefore suggest that the higher resighting rates of captive-reared birds might be related to their better body condition, and result from a stronger philopatric behaviour and a better post-fledging survival.

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