



Original Article

# Disentangling the effect of parental care, food supply, and offspring decisions on the duration of the postfledging period

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The postfledging dependence period (PFDP) is a crucial stage in the development of altricial birds. This period is regulated by parental investment, in terms of food provisioning and protection, and the demands of young associated with their development and physical condition. We examine the relative role of parental investment, food provisioning, and offspring decisions on the PFDP regulation in the Spanish imperial eagle (*Aquila adalberti*) by comparing the PFDP timing among young from non-manipulated territories, food supplemented territories, and birds translocated by hacking methods in the absence of adults and with ad libitum food supply. We found that extra food homogenized the nutritional condition of young and reduced the length of the first stage of PFDP, which is related to flight development and thus dependent on body condition. However, hacked birds did not reduce this stage despite ad libitum food, likely due to the lack of parental stimulus to develop advanced flights. Although the presence of adults might accelerate young becoming independent, hacked birds did not extend significantly the whole PFDP and all birds eventually started dispersal. Thereby, the PFDP regulation was primarily under offspring control, and modulated secondarily by parental effects independently of food provisioning and laying date. The length of this period seems to be constrained mainly by the inherent benefits of early dispersal on ultimate fitness in accordance with ontogenic hypotheses. In addition, hacking was shown to be an effective translocation method when properly used, without negative drawbacks for young development during the PFDP.

**Key words:** *Aquila adalberti*, food supplementation, parent–offspring conflict, postfledging dependence period, Spanish imperial eagle, translocation.

## INTRODUCTION

After fledging, young of altricial bird species are still dependent for some time on parental care. This period, from first flight out of the nest until birds attain independence from their parents, is known as the postfledging dependence period (hereafter: PFDP) and represents a vital stage for young birds (Mock and Parker 1997; Cox et al. 2014). The development during this stage may affect subsequent survival probabilities and performance of young birds after the break up of family ties (Ferrer 1993b; Newton 1998; Green and Cockburn 2001; Naef-Daenzer et al. 2001; Cox et al. 2014). This period is modulated by the parent–offspring conflict, according to

which young are expected to prolong the length of this period in order to maximize their probability of surviving to reproductive age, while adults will tend to reduce their investment in their current offspring when the associated costs exceed the benefits they gain in terms of net lifetime reproductive success (Trivers 1974; Clutton-Brock 1991; Verhulst and Hut 1996).

Different studies have focused on the proximal factors influencing the length of the PFDP across different avian taxa. These factors are not only related to both parental and offspring traits (e.g., Naef-Daenzer et al. 2001; Arroyo et al. 2002; Tarwater and Brawn 2010) but also related to environmental conditions (e.g., Lens and Dhondt 1994; Russell 2000). Food availability has proven to be one of the main factors that determine the duration of the PFDP as well as young decisions related to the independence onset (Bustamante 1994; Yoerg 1998; Eldegard and Sonerud 2010; Vergara et al.

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2010). According to the resource competition hypothesis, dominant siblings will tend to monopolize resources and extend their stay in the parental territory, whereas subordinates will be forced to leave the territory earlier (Murray 1967). However, ontogenic hypotheses state that dominant siblings can reach a better body condition that permits them to attain independence earlier than subordinates in a worse condition (Holekamp 1986; Ferrer 1992). In this respect, additional food supply has resulted in variation of the length of the PFDP in some species (Bustamante 1994; Vergara et al. 2010) but not in others (Kennedy and Ward 2003). Therefore, the role of food availability is not completely clear and seems to vary in relation to other constraining factors such as postdependence spatial strategies of young (migratory vs. dispersal; e.g., Bustamante 1994).

In addition, adults can also promote the independence of juveniles by direct interactions, as described for some species which increase aggressive behaviors toward the juveniles (e.g., Sherrod 1983; Alonso et al. 1987). Although the role of food availability on the PFDP regulation has been relatively well studied, no further investigation has examined the influence of parental care beyond food provisioning, probably due to the intrinsic difficulty of performing experiments with parental exclusion. This is especially true for large-size long-lived species with prolonged parental care (Kenward et al. 1993). In this sense, reintroductions using young birds in the absence of adults provide a valuable alternative approach to test the relevance of such parental effect on the regulation of the PFDP (Meyers and Millar 1992; Amar et al. 2000).

In reintroduction programs of phylopatric bird species, such as raptors, hacking techniques are usually applied as a soft release method with proven effective results (for a review see Cade 2000). This technique implies that young birds are translocated to the hacking facilities, in the reintroduction area, where they spend a period of time until attaining flight capability and being released to the wild. Once released, they stay in the area during the PFDP until independence, in the absence of parents and with a regular food supply. Therefore, reintroduction projects offer an exceptional framework to explore the dependence regulation under proximate quasi-experimental conditions otherwise hardly reproducible (Sarrazin and Barbault 1996).

In this study, we examine the relative role of parental care and offspring decisions on the regulation of the length of the PFDP of juvenile Spanish imperial eagles (*Aquila adalberti*) by testing the influence of food availability and parental behavior. This is a long-lived non-migratory bird of prey with a relatively prolonged PFDP (Alonso et al. 1987; Ferrer 1992). The length of the PFDP in this species is related to parental quality, which determines the start of the reproductive season (i.e., laying date), and thus the relative amount and temporal extension of parental investment. However, the regulation of this period seems to depend also on offspring development. Ferrer (1992) described 2 different stages within the dependence period: a first half (i.e., from the first flight out of the nest to the first soaring flight) controlled by flight development of young, which in turn depends on their physical condition, and a second half (i.e., from the first soaring flight to independence) in which adults tend to reduce their investment by decreasing food provisioning and their presence. Furthermore, parents show aggressive behaviors toward the young to check their flight capacity (Ferrer 1992). The parent-offspring conflict seems to take place in the second stage of the PFDP, resulting in a trade-off between parental and young decisions, which shapes the postfledging duration of this species.

We compare young from territories with and without artificial food supplementation, as well as hacked birds released under

regular food supply and absence of parents. Under the ontogenic hypothesis, we predict that supplemented and hacked young would present a shorter first stage of the PFDP compared with non-manipulated birds due to a general improvement of nutritional condition as a result of higher food availability. A better condition would speed up the physical development of young and the acquisition of essential flight skills, such as soaring flights, which eventually determine the length of this stage. On the other hand, under the resources competition hypothesis, we predict that hacked birds would have noticeably longer second stage of the PFDP than non-manipulated young since they are not constrained either by parental decisions or food competition, whereas supplemented young can prolong this stage at a certain degree because they are not limited by food availability but still dependent on parental decisions.

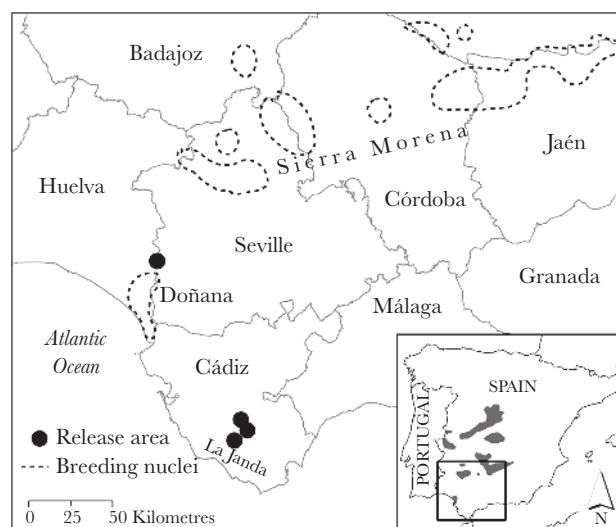
## METHODS

### Study area

The study was conducted in the region of Andalusia, southern Spain. Data were collected from breeding territories in the subpopulation of Doñana National Park (1049.7 km<sup>2</sup>; 36°56'N, 6°30'W) and the subpopulation of Sierra Morena (≈11 000 km<sup>2</sup>), as well as a reintroduction project in the province of Cadiz (≈36°20'N, 5°48'W) and a reinforcement program in the area of Doñana using hacking techniques (Figure 1). Altitudes range from 0 to 1200 m a.s.l., and the climate corresponds to dry-humid Mediterranean (Rivas-Martínez 1986). Sierra Morena and the hacking area in Cadiz are characterized by low-medium-altitude hilly landscapes with Mediterranean forests, scrublands, grasslands, and crops, whereas Doñana area is represented by fresh water marshlands and a mixture of Mediterranean scrubland and pinewoods surrounded by crops.

### Study species

The Spanish imperial eagle is a long-lived large-size endemic species from the Iberian Peninsula (Ferrer and Negro 2004). It is the



**Figure 1**

Map of the study area in Andalusia (southwestern Spain). Release areas corresponding to reintroduction and reinforcement programs in Cadiz and Doñana are shown, as well as the breeding areas in the subpopulations of Doñana and Sierra Morena.

most threatened bird of prey in the European continent and one of the rarest in the world (VU category in the IUCN Red List, *BirdLife International* 2008). After a population decline throughout the first half of the 20th century, the species has experienced a gradual recovery in the last 30 years (*Ortega et al.* 2009), reaching 407 pairs in 2013 (National Working Group, unpublished data). The species is monogamous, territorial, and resident, with an age of first breeding of 4–5 years and a low productivity rate of 0.75 chicks per pair and year on average (*Ferrer and Calderón* 1990). Reproduction usually lasts 8 months from February, when laying starts, until October, when last juveniles left the natal area. Incubation period takes on average 44 days and nestling period around 75 days (*González* 1991). As already noted, this species presents a long PFDP (51 days on average, range: 35–67 days; *Ferrer* 1992). Once juveniles become independent, they show dispersal behavior (*González et al.* 1989; *Ferrer* 1993a), which involves exploratory movements, use of temporary settlement areas, visits to breeding areas, and returns to their natal population, until recruiting to the breeding population.

### Data collection, food supplementation, and hacking

A data set of 142 young Spanish imperial eagles monitored in 18 nonconsecutive years (1986–2009) was used. The final sample comprised 47 young from nonsupplemented territories in Doñana and Sierra Morena subpopulations, 47 from territories with food supplementation in the same breeding areas, and 48 from hacking (76 females and 66 males; 24 eaglets from single broods, 65 from 2-chick broods, 51 from 3-chick broods, and only 2 from 4-chick broods).

Supplemented territories were provided with additional food since some weeks before egg laying and until all young achieved independence and left the parental territory. Additional food provided consisted of a minimum of 2 dead and eviscerated domestic rabbits ( $\approx 1000$  g/rabbit) every 2 days per territory. Rabbits were placed on perches close to the nest without disturbing the birds, and subsequent visits were made to ensure that food was taken by adults.

In 2002, a reintroduction program of the Spanish imperial eagle started in the province of Cadiz, in southern Andalusia (*Muriel et al.* 2011), where the species became extinct as breeder at the end of 1950s (*González et al.* 1989). Likewise, in 2005 a reinforcement program was also started in the area of Doñana as part of a wider conservation plan (*Ferrer et al.* 2013). Between 2002 and 2010, 58 young Spanish imperial eagles were released by means of hacking techniques in 3 nearby locations in La Janda area in the province of Cadiz ( $6.44 \pm 2.3$  young/year, range = 4–12) and 15 in the Doñana area ( $3 \pm 1.23$  young/year, range = 2–5). Wild-hatched nestlings were translocated when  $47.8 \pm 6.1$  days old to the hacking facilities where they spent  $28.8 \pm 6.2$  days before fledging. They were fed twice a day with 1 dead and eviscerated wild rabbit ( $\approx 500$  g/rabbit) per young and day throughout the hacking stage. During the PFDP, they were provided with an average of 1 eviscerated wild rabbit per young and day on artificial feeders close to the hacking facilities, and a minimum of 2 live domestic pigeons ( $\approx 350$  g/pigeon) per young and week to encourage hunting behavior. Therefore, food supply throughout hacking and PFDP can be considered to be ad libitum since mean daily food requirements estimated per young Spanish imperial eagle in captivity are around 200–300 g (*Delibes* 1978). Artificial feeding was provided avoiding physical contact with eaglets and was continued at least 2–3 days after the last young definitely left the release area.

### Offspring body condition and sex determination

Plasma urea value was used as a reliable indicator of the nutritional condition of young at late nestling stage (*Ferrer* 1994). As for many other raptors and birds with poor fat reserves, urea levels increase as a response to starvation and decrease after refeeding because it is produced as a nitrogenous residual when tissue proteins are actively mobilized as energy source (*García-Rodríguez, Ferrer, Carrillo, et al.* 1987). Given that urea levels were determined before fledging, they reflected the initial body condition of individuals prior to the application of treatments during the PFDP.

At least 2 mL of blood was extracted from the brachial vein of each nestling when 40–70 days old. Extractions were made between 11:00 and 16:00 h to minimize daily variation of biochemical parameters (*García-Rodríguez, Ferrer, Recio, et al.* 1987). Blood was kept in heparin tubes and subsequently centrifuged (4000 revolutions per minute [rpm] during 10 min). Plasma was separated and immediately frozen ( $-40$  °C) until subsequent analysis. Biochemical analyses were carried out with a Hitachi 705 multichannel automatic analyzer, with the reagents recommended by Boehringer-Mannheim Diagnostics (Darmstadt, Germany), and a TARGA BT10000 automatic analyzer (Biotechnica Instruments SpA, Rome, Italy) with the reagents from Quimica Clínica Aplicada, S.A. (Spain). Urea values were measured by means of the same urease method with both analyzers.

Sex of young was determined by means of the forearm measurement (*Ferrer and De le Court* 1992). Forearm length, from the front of the folded wrist to the proximal extremity of the ulna, was measured using a metal ruler with stop ( $\pm 1$  mm). Weight and tarsus length were also measured with a 5-kg spring scale ( $\pm 50$  g; Pesola AG, Switzerland) and a digital caliper ( $\pm 0.1$  mm, Mitutoyo Corp.), respectively. In addition, 48 nestlings from 2006 to 2009 were also sexed by molecular methods. For these analyses, some few drops were kept in ethylenediaminetetraacetic acid and ethanol 70% and then centrifuged (3000 rpm, 10 min) to separate the cellular fraction. Primers E6 (2550F) and E7 (2718R) were used for polymerase chain reaction amplification following *Fridolfsson and Ellegren* (1999).

### Radio-tagging and postfledging monitoring

At the time of marking, 134 nestlings were equipped with backpack radio-transmitters (TW-3, Biotrack Ltd., UK; HSPB 14003, Wildlife Materials Inc.; and solar-powered 5/XOB 17-04, Wagener Telemetrieanlagen, Germany). Eight more nestlings were tagged with satellite transmitters: 5 with Doppler-PTTs plus 10-g radio-tag (Microwave Telemetry Inc.), 1 with a battery-supplied Doppler-PTT (North Star Science and Technology), and 2 with solar GPS-PTTs (Microwave Telemetry Inc.). Transmitters were fixed using a Teflon harness (*Kenward* 1987) and did not exceed a maximum of 2.5% of their body weight at fledging. Nestlings were also marked with a metal ring from the Spanish Environmental Department and a colored coded ring to be read from distance.

Observations started when young left the nest, which is defined as the time when the young was observed flying or perched on a place inaccessible from the nest, and concluded when young reached independence. Independence date was considered the first day that the young did not spend the night in the “natal” territory (*Ferrer* 1992). “Natal” territory was considered to be the area within a radius of 3.25 km from the nest or the hacking facilities respectively, in accordance to the mean internest distance estimated by *González* (1991) for the species (6.5 km). During the PFDP, each

young was located at least every 2 days by visual contact or radio-telemetry, using a portable receiver (models Stabo, GFT, Germany and R1000, Communication Specialist Inc.) and a 3-element Yagi directional antenna.

### Statistical analysis

We fitted linear mixed models (LMMs) in R v3.1.2 environment (R Development Core Team 2014) to explore the effects of food supplementation and parent absence on the regulation of the PFDP. In this sense, we considered the factor treatment with 3 levels: 1) non-manipulated, composed by young birds from nonsupplemented territories; 2) supplemented, young from territories with artificial food supply; and 3) hacked, for translocated juveniles released by hacking method and thus with artificial feeding and without adults during their PFDP.

Initially, we looked for differences in hatching date and body condition of young among treatments. We ran a simple model with hatching date as response variable and treatment as fixed factor. Then, we tested the effect of treatment, brood size, sex, and hatching date on young body condition measured as urea levels at late nestling stage. In this model, we also included the first order interactions of each fixed predictor with treatment. For this and subsequent analyses, body condition was log-transformed before entering in the models in order to obtain a better distribution of residuals. Brood size factor was also recategorized into 3 levels: 1 chick, 2 chicks, and broods of 3 or more chicks.

Finally, we ran 5 different models with fledging age, independence age, first PFDP phase length (i.e., from fledging to first soaring flight), second PFDP phase length (i.e., from first soaring flight to independence), and duration of total PFDP (i.e., from fledging to independence), as response variables, respectively. We first fitted a saturated model that included treatment, brood size, and sex as fixed factors and hatching date and body condition (i.e., plasma urea levels) as covariates. One-way interactions between the factor treatment and the other fixed factors were also considered since our purpose was to look for differences among treatments in the regulation of the PFDP, and whether these differences depended on number of chicks, gender, offspring condition, or hatching date. We centered covariates hatching date and body condition prior to analysis by subtracting values by the mean so that main effects of factors would remain biologically interpretable when involved in interactions with covariates (Schielzeth 2010; Grueber et al. 2011). Brood identity and year were included in all the models as random factors to avoid pseudoreplication within nests and to account for interannual variation respectively. Normality of residuals distribution was checked in all initial saturated models.

We used an information-theoretic approach to select the best models and perform multimodel inference (Burnham and Anderson 2002). First, we build a set of nested models from each saturated LMM with all possible combinations of fixed effects and the same random effects structure (year, brood identity) using the *MumIn* package (Bartón 2015). Models were fitted by maximum likelihood to allow the comparison of different fixed-effects structures and were ranked according to the Akaike information criterion corrected for small sample sizes (AICc) and the difference in AICc value between each model and the top model with the lowest AICc ( $\Delta$ AICc; see Supplementary Material). Models with a  $\Delta$ AICc less than 2 receive strong support and are considered to be equivalent (Burnham and Anderson 2002). Therefore, natural model-averaging (without shrinkage) based on the relative model weight ( $W_i$ ) was performed on the subset of top models with  $\Delta$ AICc < 2 to account

for model selection uncertainty and to derive robust parameter estimates for fixed effects (Grueber et al. 2011). The model-averaging analysis also provided the unconditional standard error and the 95% confidence intervals (CI) of parameter estimates. Parameters with CI that do not include 0 are interpreted as having a relevant effect on the response variable.  $\zeta$  values and corresponding tests for these effects are also shown. The statistical significance was set to  $P < 0.05$ . Values reported refer to mean  $\pm$  1 standard deviation.

## RESULTS

### General results

Hatching took place on average on 23 April  $\pm$  8.9 days (range 3 April–14 May,  $n = 142$ ). Mean urea plasma level in nestlings was  $19.3 \pm 12.6$  mg/dL (range 4–87 mg/dL,  $n = 142$ ). Young left the nest with a mean age of  $75.8 \pm 4.8$  days (range 64–94 days,  $n = 142$ ) and reached independence on average on 30 August  $\pm$  10.8 days (range 8 August–27 September,  $n = 126$ ), when  $129.2 \pm 11.9$  days old (range 104–155 days,  $n = 126$ ). The mean length of the whole PFDP, from fledging to independence, was  $53.6 \pm 11.5$  days (range 29–76 days,  $n = 126$ ). The first phase of the PFDP lasted on average  $23.2 \pm 8.4$  days (range 6–43 days,  $n = 142$ ), whereas the duration of the second phase was  $29.6 \pm 11.5$  days on average (range 6–61 days,  $n = 124$ ). Observed mean raw values for each timing variable of the PFDP in non-manipulated, supplemented, and hacked birds are shown in Table 1.

### Hatching date and body condition

Hatching date did not vary significantly among treatments ( $F_{2,116.78} = 0.34$ ,  $P = 0.714$ ) after accounting for the effects of brood identity and year, which discards a relevant bias in the selection of broods according to the timing of reproduction.

We found that body condition of nestlings was affected by the timing of breeding, with individuals hatched later in the season having higher urea levels and thus worse body condition (Table 2). Although supplemented and hacked birds tended to have initial higher urea levels (non-manipulated:  $15.7 \pm 5.6$  mg/dL; supplemented:  $20 \pm 15.0$  mg/dL; hacked:  $22.1 \pm 14.3$  mg/dL), our analysis showed that after accounting for hatching date and random effects those differences among treatments were not supported (Table 2; Supplementary Material). In addition, nestling body condition presented an important interannual variation, whereas brood identity effect was not relevant (Table 2). This shows the importance of temporal variability of feeding conditions, and that most of

**Table 1**  
Observed mean raw values ( $\pm$  1 standard deviation) of timing variables in days by treatment (non-manipulated, supplemented, and hacked) during the PFDP in young Spanish imperial eagles in southern Spain

Variable	Non-manipulated	Supplemented	Hacked
Fledging age	75.4 $\pm$ 4.3	74.9 $\pm$ 4.8	77.2 $\pm$ 4.9
Independence age	129.2 $\pm$ 9.6	126.4 $\pm$ 13.8	131.3 $\pm$ 12.8
Length of first phase of PFDP	24.9 $\pm$ 8.0	18.7 $\pm$ 7.0	25.8 $\pm$ 8.3
Length of second phase of PFDP	28.9 $\pm$ 8.0	31.5 $\pm$ 13.6	28.9 $\pm$ 13.0
Total length of PFDP	53.8 $\pm$ 9.5	52.3 $\pm$ 12.7	54.3 $\pm$ 12.6

**Table 2**

**Summary of multimodel-averaged coefficients for the effect of predictors on nestling body condition (i.e., plasma urea values), fledging age, and independence age in young Spanish imperial eagles in southern Spain**

Parameter	Estimate	SE	CI	VI	$\zeta$ value	<i>P</i>
Body condition						
<b>(Intercept)</b>	<b>2.830</b>	<b>0.066</b>	<b>(2.702, 2.958)</b>		<b>43.189</b>	<b>&lt;0.001</b>
<b>Hatching date</b>	<b>0.016</b>	<b>0.005</b>	<b>(0.007, 0.025)</b>	<b>1.00</b>	<b>3.493</b>	<b>&lt;0.001</b>
Sex (male)	-0.061	0.077	(-0.212, 0.090)	0.31	0.788	0.431
Random effects						
Year	0.040	0.023			1.700	0.044
Brood identity	0.008	0.030			0.260	0.398
Residual	0.188	0.036			5.240	<0.001
Fledging age						
<b>(Intercept)</b>	<b>75.564</b>	<b>0.696</b>	<b>(74.199, 76.928)</b>		<b>108.530</b>	<b>&lt;0.001</b>
Treatment (supplemented)	-0.729	1.060	(-2.807, 1.349)	0.58	0.688	0.492
Treatment (hacked)	1.450	1.001	(-0.513, 3.412)	0.58	1.448	0.148
Hatching date	-0.033	0.048	(-0.127, 0.060)	0.25	0.696	0.486
Condition	-0.382	0.779	(-1.909, 1.146)	0.12	0.490	0.624
Random effects						
Year	—	—			—	—
Brood identity	6.006	3.235			1.860	0.032
Residual	16.113	3.176			5.070	<0.001
Independence age						
<b>(Intercept)</b>	<b>128.747</b>	<b>1.694</b>	<b>(125.428, 132.066)</b>		<b>76.024</b>	<b>&lt;0.001</b>
Treatment (supplemented)	-0.465	2.454	(-5.274, 4.345)	1.00	0.189	0.850
<b>Treatment (hacked)</b>	<b>4.504</b>	<b>2.160</b>	<b>(0.271, 8.737)</b>	<b>1.00</b>	<b>2.085</b>	<b>0.037</b>
Hatching date	-0.398	0.223	(-0.835, 0.039)	1.00	1.785	0.074
<b>Treatment (supplemented) × hatching date</b>	<b>-0.574</b>	<b>0.243</b>	<b>(-1.051, -0.098)</b>	<b>0.82</b>	<b>2.362</b>	<b>0.018</b>
<b>Treatment (hacked) × hatching date</b>	<b>-0.658</b>	<b>0.288</b>	<b>(-1.222, -0.095)</b>	<b>0.82</b>	<b>2.288</b>	<b>0.022</b>
<b>Condition</b>	<b>9.657</b>	<b>4.653</b>	<b>(0.538, 18.776)</b>	<b>0.36</b>	<b>2.076</b>	<b>0.038</b>
Treatment (supplemented) × condition	-10.520	5.695	(-21.682, 0.642)	0.36	1.847	0.065
<b>Treatment (hacked) × condition</b>	<b>-13.614</b>	<b>5.216</b>	<b>(-23.837, -3.392)</b>	<b>0.36</b>	<b>2.610</b>	<b>0.009</b>
Sex (male)	-2.249	1.704	(-5.588, 1.090)	0.27	1.320	0.187
Random effects						
Year	—	—			—	—
Brood identity	24.609	15.618			1.580	0.058
Residual	72.915	15.596			4.680	<0.001

Natural model-averaging on the subset of LMMs with  $\Delta AICc < 2$  was applied. Estimates, unconditional SE, 95% CI, VI of parameters, and  $\zeta$  and *P* values for statistical effects are shown. Fixed effects are shown in a decreasing order of VI, and those with CI which do not span 0 (i.e., significant effect at  $P < 0.05$ ) are shown in bold. Variance components of random effects were computed by reassessing the top model (lowest AICc) by REML. Estimates for random effects correspond to variances. VI, relative importance; SE, standard error.

the expected internest variation disappeared when accounting for hatching date.

### Timing of the PFDP

The age at which young fledged from their nest was not significantly affected by treatment (Table 2; Supplementary Material) despite the observed tendency of individuals from hacking to fledge slightly later than supplemented and non-manipulated birds (Figure 2a).

We found that although reintroduced birds tended to become independent and leave the “natal” territory at slightly older average ages (Tables 1 and 2), these difference among treatments were strongly dependent on hatching date and body condition (Table 2; Supplementary Material). In general, birds hatched later tended to become independent at younger ages (Table 2). This negative correlation was significantly stronger in supplemented and hacked birds than in non-manipulated birds. Consequently, supplemented and, in particular, hacked birds became independent at older ages when hatched early in the season, but at younger ages if hatched later, in relation to non-manipulated birds (Figure 4a). On the other hand, differences among treatments in the age at which young left the “natal” territory were also dependent on body condition. Specifically, the age at independence was not correlated with body condition in supplemented and hacked birds, whereas

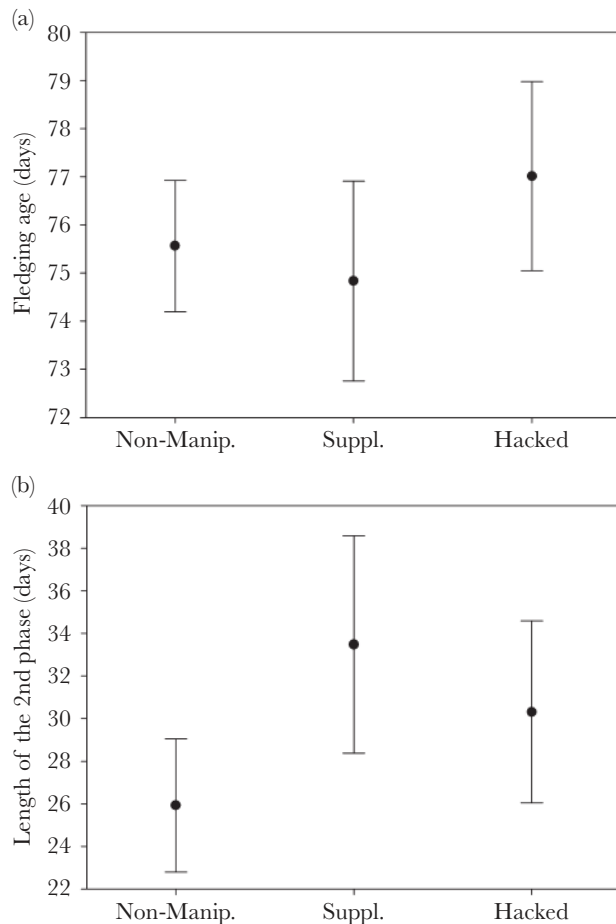
in non-manipulated birds those individuals in worse physical condition reached independence at older ages (Figure 3a).

### Length of the first phase of the PFDP

We observed that on average the duration of the first phase of the PFDP was shorter in supplemented birds than in non-manipulated and hacked birds (Tables 1 and 3). However, the analyses showed that those differences among treatments were strongly dependent on body condition (Table 3; Supplementary Material). Although non-manipulated young showed a positive relationship between the duration of this stage and urea values measured at the nestling stage, that is, birds in poorer condition extended the first phase, supplemented and hacked birds did not show any relevant correlation (Figure 3b). These results were consistent even when forcing hatching date into the averaged model to account for the influence of hatching date on body condition.

### Length of the second phase of the PFDP

We found a strong effect of treatment on the duration of the second phase of the PFDP (Table 3), which was clearly longer in supplemented birds and slightly longer in hacked birds in relation to non-manipulated ones (Figure 2b). In addition, the duration of this period was negatively correlated with hatching date independently

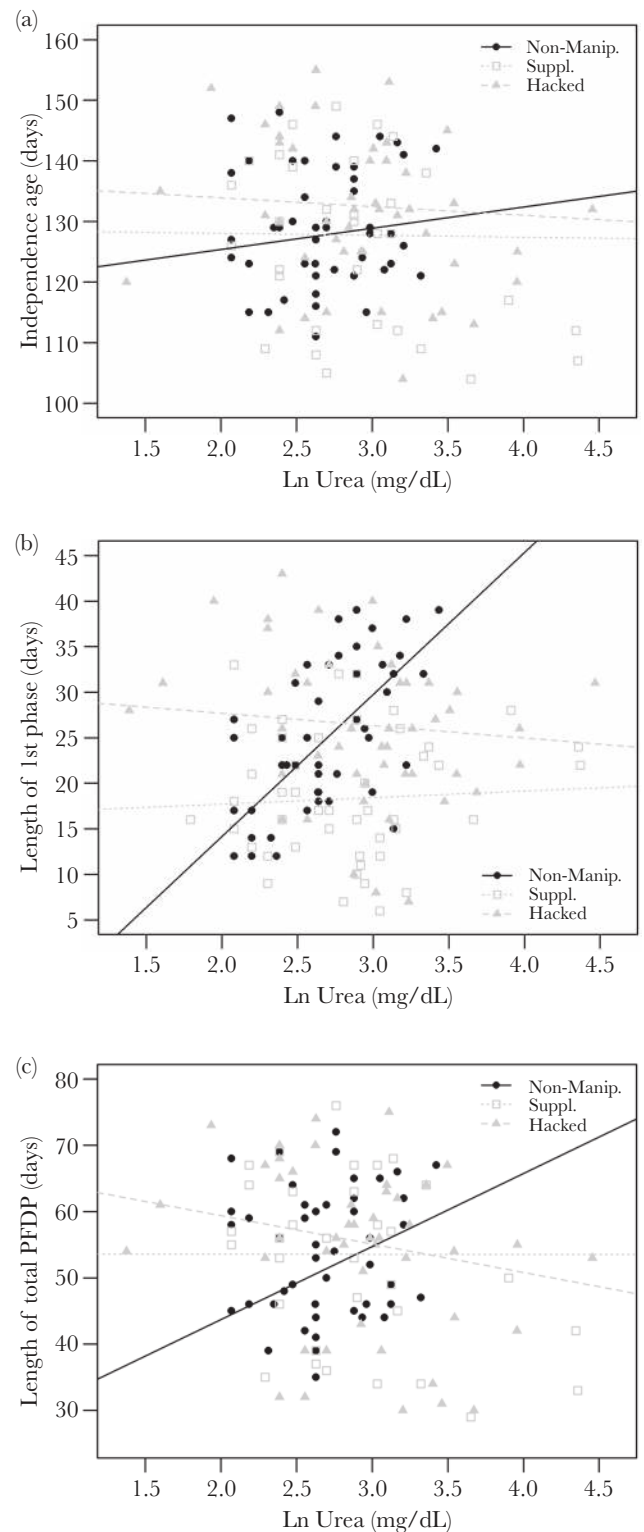


**Figure 2** Differences in fledging age (a) and length of the second phase of the PFDP (b) among non-manipulated, supplemented, and hacked young Spanish imperial eagles. Symbols and error bars show estimated coefficients and 95% CIs from the averaged model (Tables 2 and 3). Differences in fledging age among treatments are represented despite showing little support in the analysis (Table 2). Hacked and, in particular, supplemented birds extended notably the length of the second phase of the PFDP in relation to non-manipulated birds (Table 3).

of treatment, that is, birds hatched later in the season showed a shorter second period (Table 3; Figure 4b).

### Total length of the PFDP

Despite the observed average length of the total PFDP was slightly longer in reintroduced birds than in supplemented ones (Table 1), the analysis did not show evidence for a significant effect of treatment on its own (Table 3; Supplementary Material). However, the interaction of treatment with body condition received a strong support in explaining the variation observed in the total length of the PFDP (Table 3). Specifically, there was no relevant correlation between body condition and the duration of this period in supplemented and hacked birds, whereas in non-manipulated birds those individuals in poorer nourishment conditions prolonged the duration of the PFDP (Figure 3c). In addition, hatching date showed also a strong negative correlation with the duration of the PFDP independent of treatment (Table 3; Figure 4c). Consequently, individuals hatched later in the season had shorter total PFDP.



**Figure 3** Relationship between independence age (a), length of first phase (b), and total PFDP (c) with body condition (log-transformed plasma urea values) for non-manipulated, supplemented, and hacked young Spanish imperial eagles. Points represent the raw observed values, and lines the best-fitted linear regression on predicted values for each treatment derived from the averaged model (Tables 2 and 3). The interaction between treatment and body condition was supported for all 3 variables. Log-urea values were back transformed to the original scale after centering for analyses.

**Table 3**

**Summary of multimodel-averaged coefficients for the effect of predictors on the length of the different phases and the total duration of the PFDP in young Spanish imperial eagles in southern Spain**

Parameter	Estimate	SE	CI	VI	$\zeta$ value	<i>P</i>
Length of first phase of PFDP						
<b>(Intercept)</b>	<b>26.687</b>	<b>1.591</b>	<b>(23.568, 29.805)</b>		<b>16.772</b>	<b>&lt;0.001</b>
<b>Treatment (supplemented)</b>	<b>-8.571</b>	<b>1.805</b>	<b>(-12.108, -5.033)</b>	<b>1.00</b>	<b>4.749</b>	<b>&lt;0.001</b>
Treatment (hacked)	-0.290	1.850	(-3.916, 3.335)	1.00	0.157	0.875
<b>Condition</b>	<b>15.454</b>	<b>2.991</b>	<b>(9.591, 21.317)</b>	<b>1.00</b>	<b>5.166</b>	<b>&lt;0.001</b>
<b>Treatment (supplemented) × condition</b>	<b>-14.871</b>	<b>3.512</b>	<b>(-21.754, -7.988)</b>	<b>1.00</b>	<b>4.235</b>	<b>&lt;0.001</b>
<b>Treatment (hacked) × condition</b>	<b>-16.948</b>	<b>3.399</b>	<b>(-23.610, -10.286)</b>	<b>1.00</b>	<b>4.986</b>	<b>&lt;0.001</b>
Brood size (2)	2.638	1.815	(-0.919, 6.195)	0.25	1.454	0.146
Brood size (3)	0.463	2.060	(-3.575, 4.501)	0.25	0.225	0.822
Sex (male)	-0.926	1.106	(-3.093, 1.242)	0.23	0.837	0.403
Random effects						
Year	10.380	6.226			1.670	0.048
Brood identity	12.730	6.845			1.860	0.032
Residual	31.010	6.133			5.060	<0.001
Length of second phase of PFDP						
<b>(Intercept)</b>	<b>25.924</b>	<b>1.593</b>	<b>(22.801, 29.047)</b>		<b>16.270</b>	<b>&lt;0.001</b>
<b>Treatment (supplemented)</b>	<b>7.550</b>	<b>2.604</b>	<b>(2.446, 12.654)</b>	<b>1.00</b>	<b>2.899</b>	<b>0.004</b>
<b>Treatment (hacked)</b>	<b>4.387</b>	<b>2.178</b>	<b>(0.119, 8.655)</b>	<b>1.00</b>	<b>2.015</b>	<b>0.044</b>
<b>Hatching date</b>	<b>-0.711</b>	<b>0.108</b>	<b>(-0.923, -0.498)</b>	<b>1.00</b>	<b>6.557</b>	<b>&lt;0.001</b>
Condition	-1.825	1.641	(-5.041, 1.390)	0.37	1.113	0.266
Random effects						
Year	3.983	8.009			0.500	0.310
Brood identity	47.081	16.125			2.920	0.002
Residual	43.840	10.085			4.350	<0.001
Total length of PFDP						
<b>(Intercept)</b>	<b>53.284</b>	<b>1.668</b>	<b>(50.015, 56.553)</b>		<b>31.946</b>	<b>&lt;0.001</b>
Treatment (supplemented)	0.846	2.456	(-3.967, 5.659)	1.00	0.344	0.731
Treatment (hacked)	3.177	2.125	(-0.988, 7.343)	1.00	1.495	0.135
<b>Hatching date</b>	<b>-0.667</b>	<b>0.153</b>	<b>(-0.966, -0.367)</b>	<b>1.00</b>	<b>4.357</b>	<b>0.000</b>
<b>Condition</b>	<b>10.939</b>	<b>4.281</b>	<b>(2.547, 19.330)</b>	<b>1.00</b>	<b>2.555</b>	<b>0.011</b>
<b>Treatment (supplemented) × condition</b>	<b>-11.017</b>	<b>5.072</b>	<b>(-20.958, -1.076)</b>	<b>1.00</b>	<b>2.172</b>	<b>0.030</b>
<b>Treatment (hacked) × condition</b>	<b>-15.303</b>	<b>4.815</b>	<b>(-24.739, -5.866)</b>	<b>1.00</b>	<b>3.178</b>	<b>0.001</b>
Sex (male)	-1.853	1.651	(-5.089, 1.383)	0.29	1.122	0.262
Treatment (supplemented) × hatching date	-0.366	0.254	(-0.864, 0.132)	0.20	1.442	0.149
Treatment (hacked) × hatching date	-0.405	0.280	(-0.953, 0.144)	0.20	1.446	0.148
Random effects						
Year	4.217	8.908			0.470	0.318
Brood identity	28.578	17.869			1.600	0.055
Residual	61.408	14.512			4.230	<0.001

Natural model-averaging on the subset of LMMs with  $\Delta AIC_c < 2$  was applied. Estimates, unconditional SE, 95% CI, VI of parameters, and  $\zeta$  and *P* values for statistical effects are shown. Fixed effects are shown in a decreasing order of VI, and those with CI which do not span 0 (i.e., significant effect at  $P < 0.05$ ) are shown in bold. Variance components of random effects were computed by reassessing the top model (lowest AIC<sub>c</sub>) by REML. Estimates for random effects correspond to variances. VI, relative importance; SE, standard error.

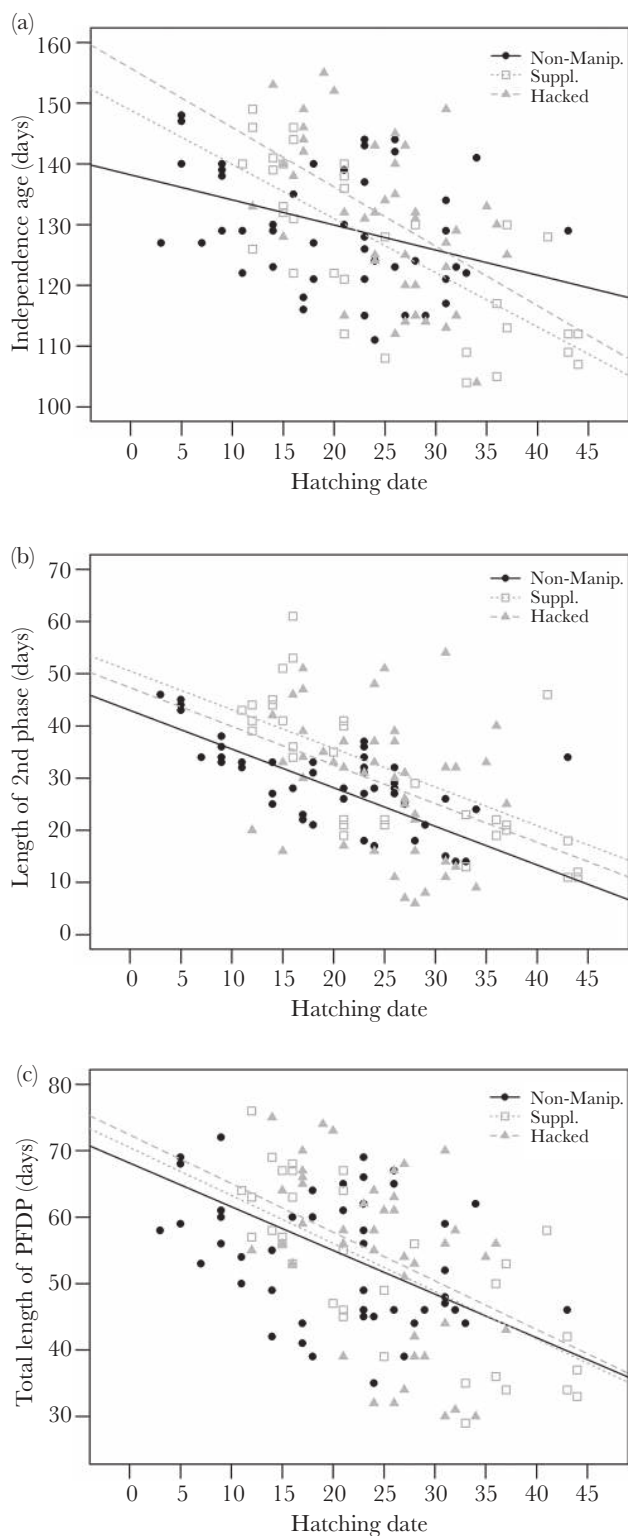
In general, the covariance components of the random effects showed a similar pattern for all the timing response variables evaluated. Brood identity accounted for an important proportion of variance in models for fledging age, independence age, length of first and second phase of PFDP, and, to a lesser extent, for total PFDP (Tables 2 and 3), suggesting that variation of such variables is nest-dependent and hence greater among than within broods. On the other hand, year effect, or interannual variability, was only relevant for the length of first phase of PFDP, which is actually dependent on young body condition and thus on feeding conditions.

## DISCUSSION

Our approach using food supplementation and hacking techniques allowed us to study the effect of parental care independently of food supply and test the relative role of both components in the regulation of the PFDP in a long-lived species with relatively prolonged postfledging care such as the Spanish imperial eagle. We showed

that although the PFDP followed the general scheme described by Ferrer (1992), the control exerted by offspring decisions on the post-fledging timing was greater than expected. Interestingly, we found that young barely extended the total length of the dependence period and attained independence despite the absence of parental pressure and the ad libitum food supply. This is in accordance with an adaptive value of selection for early dispersal due to potential benefits that may provide in terms of ultimate fitness (Nilsson and Smith 1988; Ellsworth and Belthoff 1999; Clobert et al. 2001). We also found that parental care may modulate to some extent post-fledging timing beyond the effect of timing of reproduction (i.e., hatching date) and food provisioning, as for instance encouraging flight development. Likewise, we corroborated the role of food supply on young body condition and the regulation of the PFDP, particularly during the first stage of the PFDP.

Body condition of nesting imperial eagles was closely related to hatching date as already showed by Ferrer (1994). As in many birds, the timing of reproduction seems to be controlled as a great extent



**Figure 4**

Relationship between independence age (a), length of second phase (b), and total PFDP (c) with hatching date (1 = 1 April) for non-manipulated, supplemented, and hacked young Spanish imperial eagles. Points represent the raw observed values, and lines the best-fitted linear regression on predicted values for each treatment derived from the averaged model (Tables 2 and 3). The interaction between treatment and hatching date was strongly supported for independence age but not for the length of the second and total PFDP. Hatching date values were back transformed to the original scale after centering for analyses.

by the female physical condition during the prelaying stage, which in turn is related to territory quality (Newton and Marquiss 1984; Ferrer 1994; Verhulst and Nilsson 2008; Vergara et al. 2010).

The age at which young leave the nest depends on their physical development and the acquisition of flight capabilities (Starck and Ricklefs 1998). However, we did not find any relevant relationship with nestling body condition nor with additional food supplementation. In addition, only a slight nonrelevant increase in average fledging age was observed in hacked individuals, likely caused by the intentional delay of their release in order to encourage a better flying performance at fledging.

The length of the first stage of the PFDP, from the first flight out of the nest to the first soaring flight, was mainly related to fledgling body condition and the treatment effects. We found that under natural conditions (i.e., non-manipulated territories) the duration of this first stage was dependent on young body condition, with birds in poorer condition showing longer periods, as already described by Ferrer (1992). Conversely, in supplemented and hacked birds the duration of the first phase of PFDP was not related to their body condition. This suggests that food supplementation during the PFDP would have probably improved the physical condition of managed young eagles, at least of those worse nourished individuals at nestling stage, which in turn would enable young to make earlier soaring flights and reduce the extension of this first phase. In this respect, young from supplemented territories shortened this period on average in comparison to those from nonsupplemented nests. Once fledglings in supplemented territories leave the nest they can access directly to extra food in addition to parental provision, which would accelerate their physical improvement during the PFDP. However, the duration of this stage in hacked individuals was longer than in supplemented birds and did not differ on average from non-manipulated eagles despite the ad libitum food supply. Alonso et al. (1987) and Ferrer (1992) observed in the Spanish imperial eagle that, soon after fledging, adults tend to increase the distance of food deliveries, which gradually forces young to increase the frequency and distance of directional flights toward the adults. This parental behavior appears to encourage the development of flight skills, especially soaring flight necessary for longer movements. Under hacking conditions, without parental care and with regular and predictable food availability inside or nearby the hacking facilities, the absence of such motivation may lead to later acquisition of soaring capability. Thus, hacked birds appear to be subjected to a trade-off between the reduction of this first phase due to a better food provisioning and nutritional condition, and its extension given the lack of parental stimulus to develop advanced flight skills, which finally conducts to a length of this first phase comparable to that observed in non-manipulated birds at average body condition.

The second stage of the PFDP (i.e., from first soaring flight to independence) is supposed to be under parental control in the Spanish imperial eagle (Ferrer 1992). The extension of this stage would depend theoretically on the timing of breeding (i.e., hatching date), and thus on prelaying adult condition, because early breeders could prolong their current investment in reproduction without jeopardizing future reproduction (Ferrer 1992). Adults would also exert a direct regulation on this stage by shortening the time they spent near fledglings, reducing food provisioning, and increasing aggressive-like displays toward the young during this second phase of the PFDP (Alonso et al. 1987; Ferrer 1992). Our results are congruent with the limiting effect of the reproductive timing on the time window that young have before becoming independent.



But, interestingly, we found that this is ultimately determined by fledglings as shown by hacked birds, which extended on average their stay in the release area only slightly, and finally became independent despite the constant food supply and the absence of adult pressure. In fact, the observed negative correlation between hatching date and the duration of the second stage, the total PFDP and the age at which they leave their “natal” territory cannot be explained solely by adult control because also hacked birds showed also this relationship. Therefore, this behavioral pattern reveals an endogenous motivation for independence and dispersal beyond other external factors.

The adjustment of the 2 phases that conform the PFDP, determined the overall length of this period and the final achievement of independence. An average shorter first stage in supplemented birds allowed them to prolong their stay in the natal area without extending the total period, whereas hacked birds attained independence at a later age owing to the combination of a slightly delayed release and somewhat longer PFDP. Likewise, the PFDP length reflected the treatment-dependent influence of body condition on the duration of the first phase and the general effect of timing of reproduction (i.e., hatching date) on the second one. As already pointed out, whereas non-manipulated birds in worse physical condition extended their total stay in the natal area due to the prolongation of the first stage of the PFDP, supplemented and hacked birds were not apparently conditioned by their physical condition measured before fledging. Probably, the dilution of the expected relationship between condition and length of the PFDP for “managed” birds was a consequence of the improvement of their nutritional condition throughout the PFDP. Additionally, timing of reproduction seems to constrain the time window required to accomplish the necessary development before independence and the onset of dispersal. This temporal limitation has been noted in other bird species, especially in those migratory species where departure exerts a stronger pressure in family break up (e.g., Bustamante and Hiraldo 1990; Berthold 1996; Arroyo et al. 2002), even in captive-reared individuals with no parental control (e.g., hacked Montagu’s harrier *Circus pygargus*; Amar et al. 2000).

In the present study, we show that the control exerted by offspring on the PFDP regulation seems to be broader and more relevant than expected, not only during the first phase of the PFDP but also on the final decision of leaving the natal area. The observed pattern suggests that young independence is subjected primary to evolutionary pressures related to subsequent performance during dispersal and further fitness consequences (Lidicker and Stenseth 1992; Clobert et al. 2001). The end of the PFDP would be then motivated at last by the dispersal onset, which should not be excessively postponed. This idea is consistent with the ontogenic dispersal hypothesis proposed by Ferrer (1993b) for this species according to which earlier hatched and better nourished young tend to disperse longer. This behavioral pattern has been already shown in other avian taxa, with advanced dispersal of higher competitive individuals (e.g., Nilsson and Smith 1988; Ellsworth and Belthoff 1999), but not in other species in which dominant individuals disperse later, in accordance to the resource competition hypothesis (e.g., Langen 2000; Ekman et al. 2002; Middleton and Green 2008). The selection for a philopatric or dispersive strategy would therefore be the result of a trade-off between the immediate benefits provided by prolonged parental cares and long-term advantages of early dispersal. For juvenile imperial eagles there should be inherent benefits in early dispersal, such as the occupation of better settlement areas or breeding vacancies, that finally may led to higher survival, earlier

recruitment, and greater net lifetime reproductive output (Nilsson 1989, 1990; Walls et al. 1999; Clobert et al. 2001).

Finally, we also confirm that hacked individuals in the absence of parents behaved naturally and similarly to non-manipulated birds and that food supply under hacking conditions may even improve the overall body condition of young in the same way than birds from supplemented territories. In this respect, the observed juvenile survival during the PFDP and early dispersal of translocated young eagles in the reintroduction project in Andalusia was comparable to that of non-manipulated individuals (Muriel et al. 2011). Previous studies have also recorded similar or even higher survival rates of hacked birds in comparison to wild-reared ones (e.g., Amar et al. 2000, but see Tavecchia et al. 2009). Therefore, when properly implemented hacking techniques do not seem to compromise the natural development of young eagles and might even improve the subsequent performance of release individual, at least of those undernourished and from low-quality territories. Management actions and scientific studies should ideally be associated with a positive feedback connection. Researchers may benefit from using those actions as opportunities for large-scale field experiments, whereas practitioners may obtain valuable information for adaptive management essential to optimize methods and outcomes (Sarrazin and Barbault 1996). This is particularly interesting in endangered species that are usually protected under strict conservation measures but subjected to multiple management actions.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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