

# Reaching independence: food supply, parent quality, and offspring phenotypic characters in kestrels

Pablo Vergara,<sup>a,b</sup> Juan A. Fargallo,<sup>a</sup> and Jesus Martínez-Padilla<sup>b</sup>

<sup>a</sup>Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, José Gutiérrez Abascal 2, 28006 Madrid, Spain and <sup>b</sup>Department of Ecology, Aberdeen Centre for Environmental Sustainability, School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

The duration of the postfledging dependence period (PFDP) is supposed to be modulated by the parent–offspring conflict: Offspring should extract the highest levels of parental investment, although parents may respond by setting fixed limits to the level of investment or by raising the costs of attempts to extract additional investment. In this context, longer PFDPs are expected in nests tended by higher quality parents and in dominant siblings. We explored these hypotheses with a combination of experimental and correlative results. First, we food supplemented offspring during the PFDP to study whether food supply during fledging, an indicator of parental quality, has an effect on the PFDP duration in the Eurasian kestrel. We found that the PFDP was longer in food-supplemented nests. Second, we measured the duration of the PFDP over 3 years under different environmental conditions to explore whether the quality of parents and nestling phenotype were correlated with the duration of PFDP. Correlative results suggest that fledglings raised by higher quality parents and in the year with poorer food conditions showed longer PFDP. Furthermore, male fledglings showing grayer coloration in the rump (an index of competitive capacity) have longer PFDPs than browner males. Overall, our results suggest that parent, rather than offspring characteristics, can modulate the PFDP duration mediated by food conditions, although more colored nestlings stay in the nest territory for longer periods. *Key words:* environment conditions, Eurasian kestrel, *Falco tinnunculus*, melanistic coloration, parent–offspring conflict, sibling competition. [*Behav Ecol* 21:507–512 (2010)]

According to the parent–offspring conflict theory (Trivers 1974), offspring will be selected to prolong the period of parental care, although parents will be selected to stop investing in their current offspring once the cost of parental care surpasses the benefits they obtain in terms of net lifetime reproductive success. In altricial bird species, the length of the postfledging dependence period (PFDP), defined as the period from the first flight until young birds gain independence from their parents (Mock and Parker 1997), is supposed to be modulated by the parent–offspring conflict (Ferrer 1992; Bustamante 1994b; Verhulst and Hut 1996). During this period, young develop foraging skills and complete their growth (Weathers and Sullivan 1989; Yoda et al. 2004; Kitowski 2005a; Schaubroth and Becker 2008), which may determine their future fitness (Sunde 2008; Gruebler and Naef-Daenzer 2008a). Several studies have examined different aspects of the parent–offspring conflict at nesting stage from theoretical and experimental perspectives. However, despite that has been postulated that parent–offspring conflict can be expected at postfledging period, the mechanisms acting during this period are unknown. This is due to the paucity of works focused on this topic, probably as a consequence of the difficulty in making observations of parent–offspring interactions once the chicks can fly. Studying the postfledging period is essential to have a complete view of the parent–offspring conflict.

According to Trivers (1974), a major factor affecting the duration of the PFDP might be the trend of parents to progressively decrease the feeding rate in order to promote their independence. Both correlative (Davies 1976; Moreno 1984; Bustamante and Hiraldo 1990; Ferrer 1992; Bustamante 1994b; Green and Cockburn 2001; Arroyo et al. 2002; Eldegard et al. 2003) and experimental studies (Davies 1978; Bustamante 1994b) support this idea. However, other authors have not found such a relationship between the duration of the PFDP and experimental food supply (Bustamante 1994b; Kennedy and Ward 2003), suggesting that parental investment might not be a main factor modulating the duration of the PFDP. In other words, the length of the PFDP is not only a parental decision (Bustamante and Hiraldo 1990; Bustamante 1995). This possibility has been proposed in species in which individuals are obligated to migrate, mainly those subsisting on highly seasonal food conditions (Bustamante and Hiraldo 1989, 1990, Bustamante 1994b) or those in which vacant territories are limited, and are acquired on a first-come first-served basis (Drent 1984, Ellsworth and Belthoff 1999). In such cases, selection could operate on young to disperse as soon as possible rather than increase parental care. However, these hypotheses, contrary to the trend predicted by Trivers (1974), cannot be taken as general rules because works on both migratory species (Gruebler and Naef-Daenzer 2008a, 2008b) and species defending territories (Sunde 2008) have found that offspring would rather extend dependency than disperse early.

Parent quality might determine the length of the PFDP (Balbontin and Ferrer 2005; Gruebler and Naef-Daenzer 2008b). Theory predicts that parents might invest according to the value of their brood (e.g., higher in earlier breeders) or that high-quality parents can afford the cost of investing more

Address correspondence to P. Vergara. E-mail: vergara@mncn.csic.es.

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in reproduction without compromising their own fitness (Clutton-Brock 1991). Therefore, it is expected that high-quality parents should invest more in parental care by feeding for longer periods, increasing the duration of the PFDP of their offspring. Previous studies have descriptively shown the positive relationship between the length of the PFDP and direct (territory quality: Balbontin and Ferrer 2005) or indirect (hatching date, Donazar and Ceballos 1990; McIntyre and Collopy 2006; Sunde 2008; brood size: Arroyo et al. 2002) indexes of parental quality. However, studies that include direct measurements of parent quality are needed to support the idea that the length of the PFDP mirrors parental quality.

The duration of the PFDP may also be influenced by offspring decisions, as deduced from Trivers (1974). Individual ability of siblings to compete for resources during the PFDP might itself influence how parent-offspring conflict is resolved. It has been described that dominant siblings during the PFDP try to monopolize the food delivered by parents (Arroyo et al. 2002; Kitowski 2005b; Vergara and Fargallo 2008). Therefore, the individual duration of the PFDP may be a result of competitive capacity, being longer in dominant siblings as they obligate subdominant siblings to leave the nest surroundings earlier (Bustamante and Hiraldo 1989; Nilsson and Gårdmark 2001; Arroyo et al. 2002). However, this pattern is far from consistent as suggested by different studies (Ferrer 1992; Bustamante 1994b, 1995; Ellsworth and Belthoff 1999; Amar et al. 2000; Balbontin and Ferrer 2005), showing that individual competitive ability is not a good predictor of PFDP duration.

In addition, previous studies showed shorter PFDPs in years of food abundance (Verhulst and Hut 1996; Arroyo et al. 2002). These results may be explained from the chick's point of view (Arroyo et al. 2002). Nestling body mass at the end of the PFDP may exert an important modulator effect because chicks are not able to leave the parental territory or colony before a critical threshold mass and/or size is reached (Schauroth and Becker 2008). In years of high food availability, chicks obtained this threshold body mass earlier than in years of poor food availability (Arroyo et al. 2002; Schauroth and Becker 2008), thus showing shorter PFDPs. Alternatively, this idea may also be explained from a parent's perspective: Parents decrease their feeding behavior under good conditions because fledglings are able to feed independently or because offspring reach the critical threshold mass and/or size earlier.

A little explored aspect that can involve variation in the duration of the PFDP is the expression of characters indicating offspring phenotypic quality. It is widely assumed that ornaments reflect phenotypic/genetic quality (Zahavi 1975; Hamilton and Zuk 1982). Thus, it would be expected that the degree of ornament expression mirrors the competitive capacity of individuals also in chicks. It has been recently described in the Eurasian kestrel *Falco tinnunculus* that the expression of a melanin-based trait indicating quality (gray rump coloration) also predicts the competitive capacity for prey delivered by parents during the PFDP (Vergara and Fargallo 2008). If we assumed that dominant siblings during the PFDP have longer postfledgling periods than subdominant nest mates, we should find a positive relationship between the expression of ornaments indicating quality and the length of this period. We cannot rule out, however, that high-quality individuals leave earlier the territory if that means an advantage in terms of fitness (e.g., Ellsworth and Belthoff 1999). However, to our knowledge, no previous work has studied the possible relationship between offspring ornaments and the duration of the PFDP.

We studied the PFDP in the Eurasian kestrel, a medium-sized raptor species that shows scramble sibling competition during both nestling and PFDPs (Fargallo et al. 2003; Vergara and

Fargallo 2008), typically breeding in open areas (Village 1990), which allows direct observations of fledgling behavior around the nest. Specifically, we performed a food supplementation experiment during the fledging period to test whether food supply by parents can modulate the duration of PFDP. If the degree of parental care defines the duration of the PFDP (e.g., Bustamante 1994b), we would expect longer PFDPs in food-supplemented broods. We also explored the duration of the PFDP over 3 years to assess its relationship with parental quality, measured as reproductive variables, age, and body condition. We expect a positive relationship between parental quality and the duration of the PFDP: High-quality parents may invest more in their offspring than low-quality pairs. To test the hypothesis that PFDP decreases in years of high food availability (Verhulst and Hut 1996; Arroyo et al. 2002), we studied the duration of PFDP during 3 years under different environmental conditions. Finally, at a correlative level, we explored the relationship between offspring competitive capacity (measured as coloration, sex, and body condition) and the duration of PFDP. Previous works showed that in the study species, the only nestling variable that explains sibling competition for prey during the PFDP was rump coloration (Vergara and Fargallo 2008). Thus, we predict that dominant siblings during the PFDP (grayer individuals, see Vergara and Fargallo 2008) will have longer PFDPs.

## METHODS

### Study species and general procedures

The Eurasian kestrel (hereafter kestrel) is a reversed sexually size dimorphic raptor, females being 20% heavier than males (Village 1990), in which male nestlings show reduced body and health condition with respect to females under food restrictions (Dijkstra et al. 1990; Wiehn and Korpimäki 1997; Fargallo et al. 2002), likely because of their lower competitive capacity (Fargallo et al. 2003). However, these disadvantages are later compensated during the PFDP, showing male fledgling's more competitive capacities than females to get the prey delivered by parents (Vergara and Fargallo 2008). In this species, fledglings of the same brood do not become independent on the same day, and the maximum within-brood difference in independence dates between the first and the last fledgling is on average 11.6 days (Bustamante 1994a). During the PFDP, fledglings stay in the nest (nest-box in our case, see below) or nest surroundings and parents transfer the prey to fledglings, promoting sibling competition (Bustamante 1994a; Vergara and Fargallo 2008). In this species, a high proportion of nestling males and a very low proportion of nestling females express gray instead of brown coloration on the rump and upper-tail coverts. This character increases its expression with better environmental conditions (Fargallo, Laaksonen, et al. 2007; Fargallo, Martínez-Padilla, et al. 2007; Vergara et al. 2009). As a result, it has been suggested that gray/brown rump coloration mirrors individual body condition and competitive capacity in male fledgling (Fargallo, Laaksonen, et al. 2007; Fargallo, Martínez-Padilla, et al. 2007; Vergara and Fargallo 2008) and breeder female (Vergara et al. 2009) kestrels.

The study was conducted during the breeding seasons of 2005, 2006, and 2007 in the Campo Azálvaro region (central Spain) where most kestrels breed in nest-boxes (Fargallo et al. 2009). The study area is an open, flat, and treeless grassland making kestrels easily detectable in nest surroundings from long distances (see Vergara and Fargallo 2007). The study area contains 62 nest-boxes in which about 30–45 kestrel pairs breed each year. The studied population of kestrels lays 5.0 eggs (range = 3–7) and produce 4.1 (range 1–7)

fledglings on average (Fargallo et al. 2001), and nestling kestrels fledge at 31.3 days (Vergara and Fargallo 2008). Nests were monitored every 1–2 days to detect laying date (day of the first egg laid in the nest) and hatching date. Hatchlings were marked with indelible ink and marked again every 5 days until banding (15 days after hatching). We used 3 categories for hatching order: first-hatched chick, last-hatched chick, and middle-hatched chicks (the remaining chicks between first and last hatched). At the age of 25 days, we measured the number of fledglings (2–6), took body measurements (tarsus length and body mass), and extracted 1 ml of blood from the brachial vein with a syringe for sexing chicks using molecular methods as described by Fridolfsson and Ellegren (1999) applied on kestrels (Fargallo et al. 2002). Moreover, the common assay of intradermal injection in the wing web of the T-cell mitogen phytohemagglutinin-P (0.3 mg of phytohemagglutinin-P dissolved in 0.1 ml of phosphate-buffered saline; see Fargallo et al. 2002, for procedures) was used as an index of health and condition (Tella et al. 2000; Alonso-Álvarez and Tella 2001). Chicks were injected at 25 days old and the reaction measured with a digital caliper the day after injection. We banded nestlings with an individual combination of 3 color rings. Adults were captured at the nest when nestlings were 10–13 days old, and body size measurements (tarsus length and body mass) were taken. Age of breeders (1 year old or adult) was determined by ring codes of individuals marked as nestlings or by plumage features (Village 1990; Vergara and Fargallo 2007).

### Rump coloration measurements

At day 26, we measured the percentage of gray with respect to brown covering the whole rump by digitally photographing the rump (see Vergara and Fargallo 2008, for procedures and repeatability). Rump coloration was grouped into 3 categories (Fargallo, Laaksonen, et al. 2007). In the category 1, we included all individuals with no gray coloration (brown individuals) and used the median (14.5%) to separate the other 2 categories such that category 2 < 14.5% of gray and category 3 > 14.5% of gray (Vergara and Fargallo 2008). However, because the main differences in sibling competition patterns occurred between category 3 and the other 2 categories (Vergara and Fargallo 2008), we grouped categories 1 and 2. In females, we only found individuals falling into categories 1 and 2, and thus, this categorization was maintained.

### Fledging observations

We began observations at the age of 32 days. We monitored nests and their surroundings every 2 days during the PFDP for 20-min periods to identify the individuals present in nest surroundings. We considered the “date of independence” as the last day the individual was observed and the duration of PFDP as the number of days passed from the day 32 until date of independence. We continued the observations 1 week after the last fledgling was seen in each nest to reliably assess PFDP of each fledgling and brood. Observations were performed with binoculars (8 × 30) and telescope (20 × 60–80) and were carried out between 5:00 AM and 11:00 AM and between 3:00 PM and 7:30 PM by a single observer in a car located more than 100 m away from the nest to avoid disturbances. We randomly modified the order in which nests were monitored each day to avoid daytime bias.

### Experimental treatment

During 2007, we performed an experiment to test whether food supplementation increases the duration of the PFDP.

We supplemented 9 nests (39 fledglings) every 2 days during the PFDP with commercial 1-day-old chickens. We began the experiment when the oldest chick of the nest was 34 days old. At that time, all chicks have fledged. In all cases, commercial 1-day-old chickens were consumed every 2 days. Food supplementation was adjusted to the number of fledglings remaining in the nest and their surroundings the last visit (1 commercial chicken per fledgling). Thirteen nests (53 fledglings) were considered as control nests, which were visited with the same frequency but without food supplementation.

Fieldwork and animal manipulation were carried out following ethical procedures as described in *Guidelines for the Use of Animals in Research* (The Association for the Study of Animal Behaviour). The permission to carry out the study was given by the Consejería de Medio Ambiente de la Junta de Castilla y León.

### Statistical procedures

We run models to describe the length of the PFDP. First, we used General Linear Mixed Models (GLMM) in SAS statistical software (SAS 1989–1996 Institute Inc., Cary, NC) to explore whether food supplementation during the PFDP (included as fixed factor) affected the duration of this stage (response variable). Second, we used GLMM to analyze whether the length of the PFDP was correlated with nestling and parent variables. Duration of the PFDP was included as a response variable, nestling and adult body size and condition variables, laying date and number of fledglings were included as covariates and year, nestling sex and parent age as fixed factors. Only control nests were included in this model. We repeated this model analyzing only fledgling males or fledgling females on different models and including rump coloration as a fixed factor. In all models, nest was included as a random factor to avoid pseudoreplication. In addition, 2-term interactions were also tested, except in the case of sex × rump coloration. The different categorization prevented us from analyzing this interaction, and for this reason, we analyzed the relationship between PFDP duration and rump coloration in each sex separately. Some of the explanatory variables could covary, so we fitted their effects to the observed data following a forward stepwise procedure, testing the significance of each variable, and adding only the variables that resulted in a better fit of the model. All tests are 2 tailed. Means ± standard error are given.

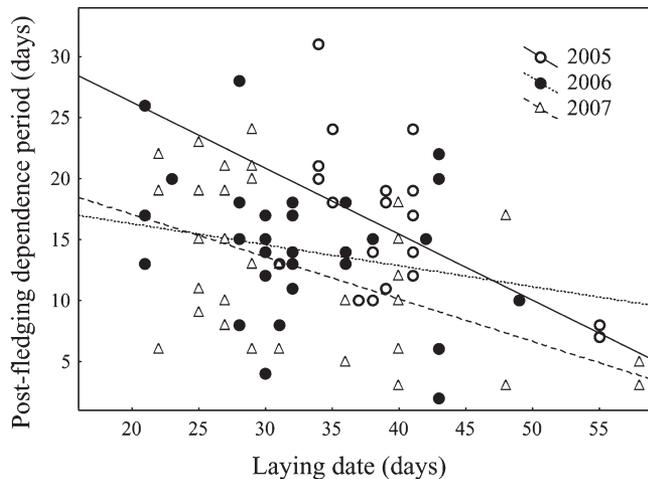
## RESULTS

### Food supplementation experiment

We found that food supplementation increased the length of PFDP (GLMM,  $F_{1,72} = 3.98$ ,  $P = 0.048$ ; laying date as covariate:  $F_{1,72} = 8.07$ ,  $P = 0.006$ , estimate =  $-0.23$ ; control nests  $12.7 \pm 1.1$  days,  $n = 55$  fledglings from 13 nests; food-supplied nests  $16.3 \pm 0.6$  days,  $n = 39$  fledglings from 9 nests). Fledglings from food-supplied nests became independent later. The rest of the adult and nestling variables, the number of fledglings, and all the 2-term interactions had no significant effects (all  $P > 0.1$ ).

### Duration of the PFDP, parent quality, and nestling variables

The length of PFDP in control nests was significantly explained by laying date (GLMM,  $F_{1,96} = 9.95$ ,  $P = 0.002$ , estimate =  $-0.23$ ; Figure 1), breeder female body mass (GLMM,  $F_{1,96} = 8.78$ ,  $P = 0.004$ , estimate = 0.13; Figure 2), and year (GLMM,  $F_{2,96} = 8.96$ ,  $P < 0.001$ ; 2005 =  $18.5 \pm 1.2$  days,  $n = 36$  fledglings from 9 nests; 2006 =  $14.2 \pm 1.0$  days,  $n = 52$  fledglings from 13 nests; 2007 =  $12.7 \pm 1.1$  days,  $n = 55$  fledglings



**Figure 1**  
Scatterplot between PFDP duration and laying date (1 = 1 April). Lines represent the best annual (2005, 2006, and 2007) fitted linear regression.

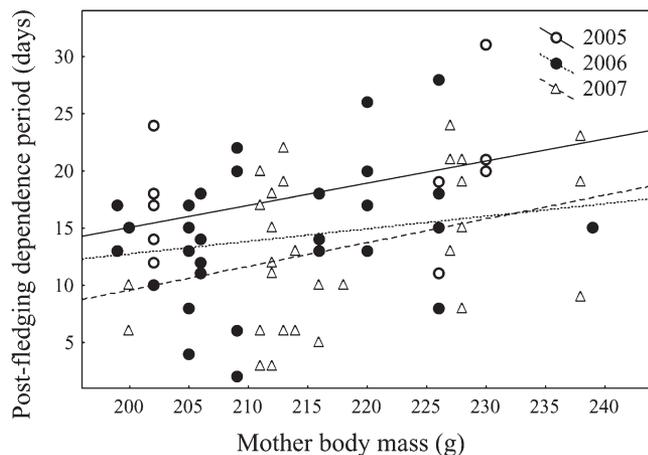
from 13 nests). Fledglings with heavier mothers laying earlier stayed in the nest surroundings for a greater number of days. Laying date  $\times$  year and female body mass  $\times$  year interactions had no significant effects (both  $P > 0.64$ ), suggesting that relationships between both variables and the duration of the PFDP were consistent between years (Figures 1 and 2). The rest of the adult and nestling variables (including the sex of nestlings), the number of fledglings, and the rest of 2-term interactions had no significant effects (all  $P > 0.1$ ).

Controlling for laying date (GLMM,  $F_{1,27} = 6.14$ ,  $P = 0.019$ , estimate =  $-0.20$ ) and year (GLMM,  $F_{2,27} = 4.89$ ,  $P = 0.015$ ), rump coloration of male fledglings ( $n = 53$  fledglings from 25 nests) significantly explained variation in the duration of PFDP (GLMM,  $F_{1,27} = 4.49$ ,  $P = 0.043$ ). Grayer males showing longer PFDP (Figure 3). In the case of females, rump coloration was not related to the duration of the PFDP ( $P = 0.75$ ).

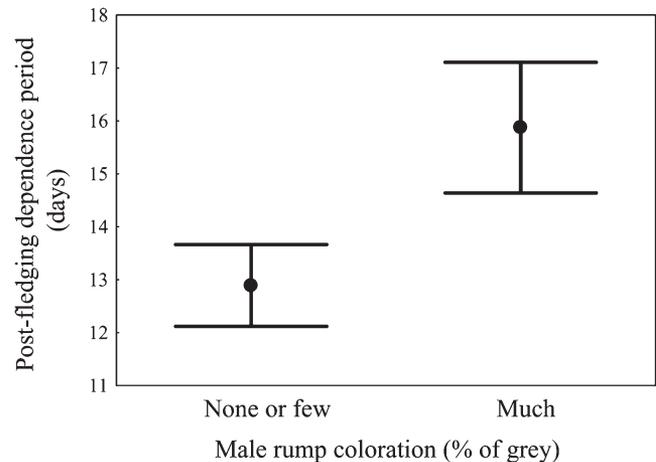
## DISCUSSION

### PFDP duration, food supply, and parental quality

In the present study, we showed that the duration of the kestrels' PFDP was negatively correlated with the advance of laying



**Figure 2**  
Scatterplot between PFDP duration and mother body mass. Lines represent the best annual (2005, 2006, and 2007) fitted linear regression.



**Figure 3**  
Differences in male fledgling PFDP duration in relation to rump coloration. Bars denote standard error.

date and positively correlated with mother's body mass, suggesting that parents of better quality tend to prolong the PFDP of their offspring. Our experiment showed that food supplementation during fledging also significantly increased the PFDP. This proposes that the positive correlation between parent quality and PFDP duration could be driven by food supply, with better parents increasing the duration of feeding period.

The resolution of factors modulating the length of PFDP has been tackled from different angles and with opposing results (e.g., Bustamante and Hiraldo 1990; Bustamante 1994b). The time at which offspring begin to reach independence is likely the stage at which natural selection is acting more strongly (Naef-Daenzer et al. 2001). Our results (both descriptive and experimental) indicate this and suggest that parental quality, at least in terms of food provisioning, may minimize this impact. Similar results have been found in other bird species (Davies 1978; Moreno 1984; Green and Cockburn 2001; Gruebler and Naef-Daenzer 2008b), especially in raptors (Bustamante 1993; Bustamante and Negro 1994; Arroyo et al. 2002, but see Bustamante and Hiraldo 1990; Bustamante 1995). Specifically in our study species, previous work has shown that the rate of prey delivery by parents was positively correlated with the number of fledglings and diminished at the end of the PFDP (Vergara and Fargallo 2008). These results suggest that the duration of PFDP in kestrels is mainly dependent on the adults.

In addition, we showed that parental quality (measured as laying date and mother's body mass) might influence the length of PFDP in agreement with previous works (e.g., Balbontin and Ferrer 2005). As mentioned above, we suggest that high-quality parents or those with better body condition may invest more in parental care by feeding for longer periods, thus increasing the duration of the PFDP of their offspring. Some ideas might explain why high-quality parents may invest more in parental care than low-quality pairs: High-quality individuals may invest more than low-quality pairs due to the higher reproductive value of their broods (Clutton-Brock 1991). Alternatively, high-quality parents may feed their offspring for more time if this investment does not increase their costs in terms of fitness. However, Gruebler and Naef-Daenzer (2008b) showed the inverse pattern between parent quality and the length of the PFDP: High-quality parents showed shorter PFDP than low-quality pairs. These authors suggested that high-quality parents might optimize their breeding strategy by reducing the duration of postfledging

care, potentially enhancing their future breeding attempts, or might provide more food to their chicks, thereby accelerating the postfledging development of juveniles and compensating for the negative effects of an early family breakup (Grüebler and Naef-Daenzer 2008b). The study by Grüebler and Naef-Daenzer (2008b), however, used a multibrood species (the barn swallow *Hirundo rustica*), what makes difficult to compare in terms of reproductive strategies with a species that only lay 1 clutch per breeding season (as the kestrel, present study). For example, individuals should invest less in a clutch when it is followed by another clutch in the same season (Verhulst et al. 1997), but single brood species are not subjected to this constraint, making it difficult to compare parental care between both groups of species. Nevertheless, both works suggest that PFDP duration is mainly an adult choice.

### Between-year differences in the duration of PFDP

Theory predicts that the length of the PFDP should be maximal in years of poor food conditions (Arroyo et al. 2002). Therefore, an effect of environmental conditions on the duration of PFDP should be expected. In our population, chicks at 25 days old were on average 10 and 7 g heavier in 2006 and 2007, respectively, than in 2005 (Fargallo JA, Vergara P, Martínez-Padilla J, unpublished data), suggesting that 2005 was a poorer year in terms of food availability compared with 2006 and 2007. In fact, the abundance of *Microtus arvalis*, one of the main kestrel prey in our study population (Fargallo 1999), was lower in 2005 than in 2006 and 2007 (see Fargallo et al. 2009). Accordingly, we found that the PFDP was longer in 2005 than in 2006 and 2007 (post hoc test  $P < 0.01$ ) but there was no difference between 2006 and 2007 ( $P > 0.05$ ). If we assumed that in the studied species the length of the PFDP is mainly an adult decision (as discussed previously), these results suggest that parents invest (duration of PFDP) less when food is abundant, possibly because offspring may reach an optimal condition for independence earlier than when food is scarce. This result is also in agreement with the hypothesis that PFDP duration is partly a fledgling decision: In poor food years, the length of the PFDP should be maximal to counteract the low supply by parents (Arroyo et al. 2002). Under low supply conditions, offspring may increase those behaviors addressed to receive higher parental investment, such as food solicitations to parents and thus increasing food deliver. It is necessary to study whether parents respond or not to chick's stimulus (begging) depending on environmental circumstances.

### Rump coloration, sibling competition, and the length of the PFDP

To our knowledge, no previous work has found a link between offspring coloration and the duration of the PFDP. We showed that the grayest males have longer PFDPs. The length of the PFDP is modulated by the ability to acquire food during this stage (Kitowski 2005b) and is dependent on its competitive ability and relative social status (Nilsson and Smith 1985, 1988). In agreement with this idea, Vergara and Fargallo (2008) showed that grayer male fledglings compete better than browner nest mates for prey during the PFDP. In addition, recent works have found that gray coloration in nestling male rumps was positively affected by body mass of mothers (Fargallo, Laaksonen, et al. 2007), and in stressful situations (increased levels of testosterone), this character was positively correlated with body mass (Fargallo, Martínez-Padilla, et al. 2007). This increasing evidence suggests that the expression of gray coloration in male nestlings can be used as an index of individual quality and supports the idea that nestling conditions can also delimit the length of this period (Arroyo et al. 2002). Browner male nestlings compete less effectively than

grayer males and could be obligated to abandon the nest territory earlier thus showing a shorter PFDP. Under the context that offspring may exert control on parental behavior (e.g., by increasing begging), we may expect that dominant siblings show the highest rate of solicitations to parents. Dominant siblings may obtain the highest benefit in terms of food intake as they are the most competitive when parents deliver their prey (e.g., Vergara and Fargallo 2008). But studies analyzing fledgling displays during the PFDP are essentials to corroborate such suggestions. Nevertheless, the present results suggest that rump coloration in male kestrel nestlings may act as an intrage class indicator of dominance (Senar 2006). A higher expression of gray coloration could provide benefits in competition for food or other resources in winter territories and thus in breeding performance in the following reproductive season (Fargallo, Laaksonen, et al. 2007; Fargallo, Martínez-Padilla, et al. 2007; Vergara and Fargallo 2007). This pattern was not found in the case of female fledglings. However, the fact that only a few females showed some gray in the rump may explain why no clear effects of gray coloration in females were found.

Finally, a lack of significant differences in the length of PFDP related to nestling variables is in agreement with previous works in the studied species (Bustamante 1994a) because these traits are not related to competitive capacity during that stage (Vergara and Fargallo 2008). In the specific case of sex, our previous study during the PFDP showed that male fledglings were more successful in obtaining prey that contribute higher biomass (large prey, e.g., voles, lizards), indicating a higher competitive capacity of males during this period with respect to their female brood mates (Vergara and Fargallo 2008). However, the total biomass received during the PFDP is not related to fledgling sex due to females capturing more small prey (e.g., insects) than males. Thus, both sexes could reach similar body conditions at the end of the PFDP (Vergara and Fargallo 2008), and this can be the cause for the lack of significant differences in the length of PFDP related to sex.

In conclusion, our study suggests that PFDP duration may be mainly determined by parental decisions and that the length of this period is modulated by the parent-offspring conflict theory. Higher quality parents may allow the prolonging of the PFDP due to their better condition or capacity to feed their offspring. On the other hand, more competitive individuals may force subdominant ones to leave the parental territory earlier. In our case, males showing the grayest coloration on their rumps showed longer PFDPs, supporting the idea that rump coloration may be considered as an index of quality (in terms of competitive capacity and dominance) in the study species. Our results also suggest that at least in the study population, delaying independence could be advantageous for fledglings (see Sunde 2008), but future works analyzing the fitness consequences of the length of PFDP (e.g., Grüebler and Naef-Daenzer 2008a) are needed to confirm this idea.

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