Ornis Fennica 88:217–225. 2011

The quality of chicks and breeding output do not differ between first and replacement clutches in the Eagle Owl *Bubo bubo*

Chiara Bettega, María del Mar Delgado, Letizia Campioni, Paolo Pedrini & Vincenzo Penteriani*

C. Bettega, M.M. Delgado, L. Campioni, Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/ Americo Vespucio s/n, 41092 Seville, Spain
M.M. Delgado, Metapopulation Research Group, Department of Biosciences, FI-00014, University of Helsinki, Finland
P. Pedrini, Trento Natural History Museum, via Calepina 14, 38122, Trento, Italy
*V. Penteriani, Finnish Museum of Natural History, Zoological Museum, University of Helsinki, FI-00014 Helsinki, Finland; Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/ Americo Vespucio s/n, 41092 Seville, Spain. * Corresponding author's e-mail: penteriani@ebd.csic.es*

Received 9 January 2011, accepted 16 May 2011

Replacement clutches can be crucial to the breeding success of avian species, although several factors may influence their outcome and the quality of chicks. Here we compare first and replacement clutches of Eagle Owls in terms of chick quality, timing of breeding, and number of eggs and fledglings. We hypothesize that the propensity to abandon nests and start a new clutch could have evolved because females are able to produce chicks that are as good as the ones of the first clutch. We found that nestlings in replacement clutches were not significantly different from nestlings in first clutches, in terms of immune system and body condition; nor were there significant differences in clutch and brood size. Our findings may be explained by the fact that clutches were laid early in the season, perhaps by high-quality parents, and that food resources are plentiful in the study area. In order to maximize fitness, individuals have to adjust optimally the investment of resources in different life-history traits. Thus, the re-nesting behaviour of Eagle Owls may be seen as a way to solve the trade-off between one trait (survival) favoured over another (reproduction), when one of them has a disproportionate effect on fitness.

1. Introduction

The costs of reproduction, that is, the division of reproductive effort between current and future breeding attempts (Williams 1966), represent an important aspect of life-history theory, i.e., how organisms allocate time and energy to different traits, facing a series of trade-offs, in order to maximize their fitness (Gadgil & Bossert 1970, Stearns 1989). Egg production can be demanding for birds, and thus parental decisions may be crucial to balance the benefit from the current brood in relation to the cost to the adult in terms of survival (Visser & Lessells 2001) and somatic maintenance

(Kirkwood 1987), parental care (Wendeln *et al.* 2000), future fitness (Nager *et al.* 2001) and the quality of the offspring (Sorci *et al.* 1997, De Neve *et al.* 2004).

If the cost of attending the nest results in a reduction of parental fitness e.g. through predation or disturbance, parents may decide to desert the nest (Bauchau & Seinen 1997, Fernández & Reboreda 2000, Verboven & Tinbergen 2002, Bourgeon *et al.* 2006) and lay a replacement clutch. Several bird species re-nest after a failure of a previous attempt (e.g., Martin 1995, Amat *et al.* 1999, Hipfner *et al.* 2004, Antczak *et al.* 2009), and thus replacement clutches provide an important contribution to an individual's lifetime reproductive success. Nevertheless, the choice between whether to re-lay or not might be constrained by seasonal factors, timing of breeding losses and female condition. In fact, first clutches are usually larger than the following replacement clutches (Parker 1981, Brown & Morris 1996, Rooneem & Robertson 1997, Amat *et al.* 1999, Gasparini *et al.* 2006b), and females are more prone to re-nest if the loss occurs during brood raising (Antczak *et al.* 2009). The probability of re-nesting is also higher in females that lay their first clutches earlier in the season, which seems to be correlated with their quality (Hipfner *et al.* 1999).

Moreover, early breeding and high quality of the female may positively influence the reproductive success of a replacement clutch, as well as the quality and the probability of recruitment of the chicks, at least in comparison with late-season first broods. De Neve *et al.* (2004) and Sorci *et al.* (1997) found that the quality of Magpie *Pica pica* chicks from replacement clutches is poorer compared to first clutches, suggesting less favourable environmental conditions late in the season: the amount and value of food influence nestling quality and immunocompetence.

Up to now re-laying ecology has been widely studied – mostly experimentally – in terms of nestling quality (Sorci *et al.* 1997, De Neve *et al.* 2004, Hipfner *et al.* 2004, Gasparini *et al.* 2006a), chick survival (Hipfner 2001) and costs of re-laying and parental investment (Gasparini *et al.* 2006b, Antczak *et al.* 2009). While the majority of the studies concern seabirds, waterfowl and passerines, information on replacement clutches in birds of prey appears scarce in terms of comparisons between breeding attempts i.e., first-clutch *vs.* replacement-clutch chicks. Falconiforms and strigiforms are able to lay replacement clutches (Morrison & Walton 1980, Simmons 1984, Forsman *et al.* 1995, Catlin & Rosenberg 2008), although this behaviour is relatively more common among smaller species and at lower latitudes (Newton 1979). Among medium-sized and large raptors, successful replacement clutches have been occasionally recorded, examples including European Bonelli's Eagle *Aquila fasciata* (Moleón *et al.* 2009), most vulture species (Mundy *et al.* 1992, Martínez & Blanco 2002), Spanish Imperial Eagle *Aquila adalberti* (Margalida *et al.* 2007), Peregrine Falcon *Falco peregrinus* and Gyrfalcon *Falco rusticolus* (Cade & Temple 1977).

The eagle owl *Bubo bubo* is a large, long-lived nocturnal species, with slow growth and a long nestling period (minimum 30–40 days; Penteriani *et al.* 2005). Normally each pair has more than one nest within its territory, a nest usually being a small depression scraped in the ground where the female can lay 1–5 eggs. Breeders show both fidelity to the nesting place and the mate, at least during the same reproductive season, i.e. if females abandon the first clutch, males do not choose another mate. Replacement clutches after failure of early first clutches have been frequently reported (Penteriani 1996, Olsson 1997, Balluet & Faure 2006). As a general rule, if discovered in their nest during incubation, female Eagle Owls prefer to abandon the nest and start a new (replacement) clutch. During a long-term study on this species, we could record a number of cases where the females, after being disturbed during egg laying (generally by hunters or people collecting wild asparagus), deserted the first clutch and laid a replacement clutch in another nest. Such information allowed us to compare first and replacement clutches of Eagle Owls in terms of (a) multiple morphological and physiological parameters of chicks, (b) timing of breeding, (c) number of eggs, and (d) number of fledglings.

When discovered, incubating Eagle Owl females are faced with a "dilemma" on whether to return to the nest (and, consequently, avoiding the cost of producing new eggs by incubating the first clutch) or whether to restart the breeding cycle from the beginning by laying a replacement clutch in a different (potentially safer) place. According to the life-history theory, individuals should maximise their fitness by investing in the most successful clutch (Gadgil & Bossert 1970, Stearns 1989). If there is a low risk of first-clutch failure, individuals should invest more in the first clutch than in a possible replacement clutch. Inversely, if there is a high risk of first-clutch failure, individuals should invest more (or at least equally much) in a replacement clutch. Beside strategic adjustments, there are also environmental constraints that can directly affect differential investment made in first and replacement clutches.

The original aspect of Eagle Owls is that they have (a) very few natural enemies (other predators), and (b) no a priori first-clutch failure except when they have to abandon the first clutch. Nevertheless, replacement clutches seem frequent in this species (Penteriani 1996). Because the investment made in first *versus* replacement clutches is also driven by the risk of clutch loss, the widely-distributed and extremely eclectic Eagle Owl may have evolved an ability to re-nest, to allow the species better chances to breed successfully in each of the extremely different habitats which it occupies (Penteriani 1996).

Nest sites with high risk of predation, such as active quarries and towns, and nests on the ground (most of our study nests, and those in desert, tundra and taiga regions), are common for this species. The vulnerability of nests to predators might mediate the balance of investment between first and replacement clutches (Milonoff 1991, Martin 1995), variation in numbers of broods being frequently explained by nest-site features and nest predation (Martin 1995). Thus, we hypothesize that one of the proximate factors determining the propensity to abandon nests and start a new clutch could be due to the female's capacity to produce chicks that are as good as the ones of the first clutch, i.e., offspring quality between first and replacement clutch should be similar. As a consequence, we expect that the chicks of both clutches have similar physical characteristics.

2. Material and methods

2.1. Study site and nest locations

The present study was conducted during 2003–2007 in the Sierra Norte, SW Spain (Sierra Morena massif; 37°30' N, 06°03' W), a hilly area ranging between 60 and 200 m a.s.l. For more details, see Penteriani *et al.* (2005). In this area, breeding densities of Eagle Owls can reach about 40 breeding territories per 100 km², egg laying starting from the end of December to March and clutch size varying between one and five eggs. We sought for nests using a combination of methods, including (a) passive auditory surveys of call displays at sunrise and sunset, when the vocal activity of breeding adults is most intense (Delgado & Penteriani 2007); (b) passive auditory surveys of calling young during the entire night, mainly from when chicks were ca. 100 days old until the end of July, i.e., before juveniles begin dispersal in our study area or stay far from the nest (Delgado *et al.* 2009); and (c) searching rocky areas to detect nests, pellets and feeding perches. See Penteriani *et al.* (2004) and Mora *et al.* (2010) for more details.

2.2. First and replacement clutches: measurements of chick quality

Chick measurements and blood samples were collected when nestlings were about 30–35 days old (for both first and replacement cluthes). Blood samples (2 mL) were collected from the brachial vein and they were stored in tubes with heparin at 4°C until the arrival at the laboratory, where they were centrifuged for 10 min at 4,000 rpm; plasma was separated and stored at –78°C. Blood samples were used to measure nestlings' biochemical parameters (i.e., cholesterol, triglycerides and free glycerol, uric acid, urea and total protein concentrations) and immune measures of stress and health, i.e., red cells, total leukocyte count (TLC), heterophile, lymphocyte, monocyte, eosinophile and basophile ratios, as well as intensity of *Leucocytozoon* parasites; more details in Penteriani *et al.* (2007) and Delgado *et al.* (2010). We measured body mass with 1 kg Pesola scales to the nearest 10 g, and took morphometric measurements of forearm length, bill, tarsus and wing using a digital caliper to the nearest 0.1 mm, following Delgado and Penteriani (2004). Logarithm of body mass and forearm length were summarized into a biometrical index, the Body Condition Index (BCI), estimated by a reduced major axis (RMA) regression (Green 2001).

Table 1. Biochemical and morphological parameters of nestlings belonging to a first or a replacement clutch. a = bill including cere, b = body-condition index. For details, see text.

	First clutch			Replacement clutch		
Variable	Mean (n)	SD	Min–Max	Mean (n)	SD	Min–Max
Colesterol mg/dl	216.2 (91)	39.2	144.0–302.0	229.4 (12)	42.3	183.9–277.6
Triglycerides mg/dl	112.5 (91)	67.4	20.3–344.3	143.1 (12)	68.6	51.6–211.5
Glycerol mg/dl	3.2 (68)	2.4	0.1–10.4	7.1 (10)	5.8	2.4–18.4
Uric acid mg/dl	12.4 (90)	4.8	3.8–23.2	11.5 (12)	4.0	6.1–17.4
Total proteins	3.9 (91)	0.9	2.1–6.0	4.4 (12)	0.7	3.6–5.3
% Red cells	44.7 (92)	8.1	28.2–70.2	44.6 (11)	4.3	39.9–52.0
TLC (leukocytes/µl)	30,040.6 (85)	21,459.2	35.0–96,700.0	31,428.6 (9)	29,503.4	8,800.0–82,000.0
% Heterophile	38.4 (81)	17.4	10.0–80.0	43.7 (9)	17.3	24.0–68.0
% Lymphocyte	33.2 (81)	13.6	0.0–71.0	32.7 (9)	18.0	8.0–57.0
% Monocyte	8.5 (80)	6.0	0.0–28.0	9.8 (9)	6.4	2.0–23.0
% Eosinophile	19.4 (81)	11.6	1.0–52.0	15.7 (9)	9.3	5.0–34.0
Leucocytozoon/100fields	6.0 (84)	9.3	0.0–39.2	8.9 (9)	18.4	0.0–49.7
Left wing length	400.2 (86)	91.5	220.0–600.0	379.6 (9)	82.6	288.0–515.0
Forearm length	156.7 (87)	21.0	120.0–200.0	144.1 (9)	27.7	122.0–193.0
BCER[a]	43.5 (90)	5.0	33.4–56.0	40.4 (12)	2.4	37.3–43.6
Bill depth	18.5 (86)	4.1	10.6–26.4	20.6 (9)	2.9	17.3–25.6
Tarsus length	83.1 (91)	10.7	66.2–109.1	77.9 (12)	6.7	68.6–86.9
Weight	1,265.6 (91)	239.1	770.0–1,800.0	1,121.4 (12)	138.0	920.0–1,300.0
BCI[b]	0.0 (66)	0.01	–0.1–0.1	0.0 (8)	0.1	–0.1–0.1

2.3. Statistical analyses

The dependent variable "nesting attempt" (first *vs.* replacement clutch) was subjected to a generalized linear mixed model (GLMM) analysis assuming binomial error structure. Because we had repeated measures for the same nest over different years, we considered the variable "nest" nested in year as a random effect. Before running each model, we checked for collinearity, i.e., high correlation between the explanatory variables (Zuur *et al.* 2009), which allowed us to remove correlated variables (Table 1). The explanatory variables were initially separated in three groups, successively analysed using three models: (1) the morphological group, with chick sex, age, and bill and tarsus length as dependent variables; (2) the physiological group, including cholesterol, triglycerides, and uric acid and total protein concentration; and (3) the immune measure group, which included red cells, TLC, heterophiles, lymphocytes, monocytes, eosinophiles and *Leucocytozoon* as dependent variables. Parameters were analysed separately because (a) some variables in these three groups were available for just a sub-sample of individuals (i.e., representing those individuals for which it was possible to collect the specific information sought); and (b) covariate effects were likely to differ between groups. As suggested by Crawley (2007), (i) model simplification was performed by backward selection of variables from the full model, and (ii) models were compared using likelihood ratio tests to find a minimal adequate model. All statistical analyses were performed in R 2.10.1 statistical software (R Development Core Team 2009) with lme4 package (Bates & Maechler 2009). Statistical significance was set at $a < 0.05$.

3. Results

From 133 nesting attempts recorded during the study period, we were able to determine 20 replacement clutches following 25 failed clutches. Thus, replacement took place in 80% of the clutches. General information on replacement clutches was generally recorded for the whole sample, whereas it was possible to collect data on chick quality for only 12 nestlings from five replacement clutches (*versus* 78 nestlings from 46 successful first clutches). Females generally changed nest site to lay the replacement clutch, but the female used the same nest for re-nesting in one case. A replacement clutch was never laid when the female deserted the nest following disturbance during or immediately after hatching. Failures in a replacement clutch were not followed by a third attempt to re-lay.

The number of first-clutch fledglings (2.4 ± 0.8 chicks, $n = 31$) was slightly smaller than that of replacement clutches (2.6 ± 0.8 chicks, $n = 7$ replacement clutches). First clutches ($n = 7$) were laid between the 28th of December and the 23rd of February (average laying date 19th of January). Replacement clutches ($n = 7$) were laid between the 20th of January and the 15th of March (average laying date 10th of February). The interval between first and replacement clutches ranged from 6 to 41 days (mean interval = 20.7 days, SD = 14.0, $n = 7$). The longest interval (41 days) refers to the earliest first clutch that failed (28th of December).

The GLMM showed that the characteristics of chicks did not significantly differ between first and replacement clutches regarding all the variables considered here ($P > 0.1$ in all cases). Thus, the chicks of first and replacement clutches had similar morphological, physiological and immune characteristics (Table 1).

4. Discussion

Eagle Owl nestlings in the replacement clutches were not significantly different from nestlings in the first clutches in terms of immune system and body condition. This result could be explained by several factors. The first breeding attempts followed by a replacement clutch happened early in the breeding season, allowing the laying of a replacement clutch within the normal variation in phenology in our study area. Some studies have indeed found evidence on the importance of breeding early in terms of nestling quality. Sorci *et al.* (1997) found that Magpie *Pica pica* nestlings in replacement clutches were less immunocompetent than nestlings of first clutches, suggesting reduced food availability late in the season. This has been confirmed by De Neve *et al.* (2004), although they pointed out that also the earlier the first clutch is laid, the higher the breeding success of a possible replacement clutch. A similar outcome has been found in the Kittiwake *Rissa tridactyla* (Gasparini *et al.* 2006a). Thus, in the case of a failure in the first breeding attempt, high-quality parents breeding early in the season can re-nest and produce a similar number of good-quality nestlings, compared to early first broods (Hipfner 2001), at least assuming that food availability is high. As a consequence, the pairs that produced a replacement clutch may have been of higher quality, because they were early breeders. However, it is important to stress that the breeding season of Eagle Owl in Spain usually starts earlier than at higher latitudes, and trophic resources are greater, which might facilitate the laying of replacement clutches also among lower-quality pairs. Early first clutches influence the probability of re-laying in other large raptors as well, such as the European Bonelli's Eagle (Moleón *et al.* 2009) and the Griffon Vulture *Gyps fulvus* (Martínez *et al.* 1998).

Although Eagle Owls showed a high re-laying rate (80%), re-laying never occurred when the female was disturbed within a week from hatching, but the female sometimes delayed her return to the nest and consequently small chicks may have died because they were not yet able to thermoregulate. When disturbance occurs at the beginning of the nestling period, we suggest that the investment in the first clutch is too high to be compensated by a replacement one, both because of the physiological condition of the female and/or the lower quality of new chicks (Hansson *et al.* 2000, Antczak *et al.* 2009). This is a general pattern in larger birds of prey, as a failure at an early stage of the first clutch appears to be crucial for initiating a new one (Newton 1979). Moreover, in many species the increasing length of the previous breeding attempt negatively influences the hatching success of the subsequent replacement clutches (Hansson *et al.* 2000), as well as their clutch size (Antczak *et al.* 2009).

First and replacement clutches contained a similar number of eggs, the latter being slightly larger than the former. For most species of raptors clutch size usually slightly decreases between subsequent nesting attempts (Morrison & Walton 1980). In other species, the size of the replacement clutch can be considerably smaller, although the female can compensate for this by producing bigger eggs (De Neve *et al.* 2004). Again, prey abundance and early clutches may also be important factors, as females would have sufficient time and food to build up new energy resources. Other studies have actually confirmed the importance of female quality (the quality hypothesis; Brinkhof *et al.* 1993, Verhulst *et al.* 1995) in affecting clutch size, producing an equal number of eggs in both first and replacement attempts (Christians *et al.* 2001) or even larger replacement clutches (Wheelwright & Schultz 1994). First and replacement clutches did not significantly differ from each other in terms of number of fledglings, perhaps because replacement clutches were laid when rabbits *Oryctolagus cuniculus*, the main prey of Eagle Owls (Delibes & Hiraldo 1981) in our study area, were still abundant, allowing Eagle Owl parents to successfully raise an equal number of chicks. Although the interval between clutches was longer than the one documented in other large raptors (e.g., 19–30 days for the European Bonellis' Eagle; Cabeza & de la Cruz 2001, 19–29 days for the White-tailed Eagle *Haliaeetus albicilla*; Fentzloff 1975), three replacement clutches were laid within less than two weeks from the loss of the first one.

Although we only tested for the possibility that the chick quality in replacement clutches could be one factor determining the high frequencies of egg desertion and high rates of replacement cluthces in the Eagle Owl, it is important to mention that such a trait may generally only represent one of the proximate factors determining the observed pattern of re-laying. In fact, the main evolutionary force influencing the capacity to re-lay is the risk of first-clutch loss or abandonment – which explains the occurrence of re-nesting – although the replacement clutch may be of lower quality or contain fewer eggs than the first one (e.g., Coulson & Thomas 1985, Milonoff 1989, Sandercock & Pedersen 1994, Moreno 1998, Hipfner *et al*. 1999, Gasparini *et al*. 2006b).

Eclecticism in the choice of nest sites, eager renesting and high-quality broods represent an undeniable advantage for the species (Resetarits 1996, Madsen & Shine 1999). It is also intriguing that Eagle Owls seem to adopt a strategy that is "half way" towards the expectation of the re-nesting hypothesis (Milonoff 1991). Under this hypothesis (a) in species that are unlikely to suffer breeding failure (because they breed in safe sites), individuals maximize their fitness by laying large first clutches early in the season and preserve few resources for re-nesting attempts; whereas (b) individuals from species breeding in vulnerable nest sites lay smaller first clutches, allowing them to produce more eggs if the first attempt fails (Cody 1966, Slagsvold 1982, 1984). Eagle Owls frequently nest in relatively unsafe places (such as on the ground), but seem to put similar effort on both clutches. This is an unexpected result: under natural conditions only a minority of pairs lose their eggs during the first breeding attempt (and hence do not have to produce a replacement clutch), so natural selection should favour a strategy that allow individuals to invest most of their resources in the first breeding attempt, retaining only a limited amount of resources for an unlikely event to produce a replacement clutch (Milonoff 1991, Martin 1995, Hipfner *et al*. 2001).

In the present case study, the temporal stability in the quality of the environment (high and constant food availability; Penteriani *et al*. 2008) is probably an important factor to be considered when evaluating reproductive output. Due to the fact that reproductive output can be an outcome of constant food availability, parents may provide roughly equal care for all offspring in both first and replacement clutches. Actually, the number of broods generally increases with food availability (Bromssen & Jansson 1980, Simons & Martin 1990, Rodenhouse & Holmes 1992). Because individuals have to adjust energy use among different life-history traits optimally in order to maximize their fitness, allocation of resources in one trait is often made at the expense of other traits that usually have less of an impact on fitness (Stearns 1992). Under this perspective, the re-nesting behaviour of Eagle Owls may be seen as a way to solve the trade-off between one trait (survival) favoured over another (reproduction), when one of them has a disproportionate effect on fitness.

To conclude, our study highlights the importance of replacement clutches on the fecundity of large, long-lived species such as the Eagle Owl, stressing the need to pay special attention to this life-history trait in ecological and evolutionary research. In the specific case of Eagle Owls, females tend to abandon the nest to restart incubation in a different nest if disturbed during incubation. The ability to produce a replacement brood of a quality equal to the first one may represent a crucial safety strategy for this species that nests on the ground in a large part of its distribution range (Penteriani 1996). Several questions on the breeding ecology of the Eagle Owl remain open. For example, does the eclecticism in nesting habits lead to an evolutionary flexibility in the investment on both first and replacement broods or, vice versa, could some traits of the life history of this species determine an innate ability to re-nest, consequently allowing this species to breed everywhere?

Acknowledgements. Comments and suggestions by Dr. Patrik Byholm and an anonymous referee greatly improved the first draft of the manuscript. The work was funded by a research project of the Spanish Ministry of Science and Innovation (CGL2008-02871/BOS; with FEDER co-financing). V.P. was granted by the Spanish Secretaría General de Universidades, Ministry of Education (Salvador de Madariaga Program) and M.M.D by a post-doctoral fellowship of the Spanish Ministry of Science and Innovation.

Huuhkajan poikasten laatu ja pesimätulos eivät eroa ensimmäisen ja uusintapesyeen välillä

Uusintapesyeet voivat olla merkittäviä lintujen pesimämenestykselle, mutta niiden tulokseen ja poikasten laatuun vaikuttavat monet tekijät. Vertaamme huuhkajan (*Bubo bubo*) ensimmäisiä ja uusintapesyeitä suhteessa poikasten laatuun, pesinnän ajoittumiseen sekä muna- ja poikasmäärään. Oletamme, että taipumus herkästi hylätä pesä ja yrittää uudelleen ovat kehittyneet, koska naaraat kykenevät tuottamaan yhtä laadukkaita poikasia ensi- ja uusintapesinnässä. Havaitsimme, että pesäpoikaset olivat immuunisysteemiltään ja ruumiinkunnoltaan samanlaisia ensi- ja uusintapesyeissä, eivätkä myöskään muna- ja poikasmäärät eronneet merkitsevästi.

Havaintojamme voivat selittää, että pesyeet munittiin pesimäkauden alussa, kenties hyvälaatuisten vanhempien toimesta, ja että ravintoa oli runsaasti tarjolla. Kelpoisuuden optimoimiseksi yksilöiden täytyy tasapainottaa resurssien käyttönsä eri elinkiertotekijöiden välillä. Huuhkajan tapa yrittää uutta pesintää voidaan siten nähdä yhden tekijän (oma selviytyminen) asettamisena toisen tekijän (jälkeläistuotto) edelle silloin, kun toinen tekijä vaikuttaa kelpoisuuteen suhteettoman voimakkaasti.

References

Amat, J.A., Fraga, R.M. & Arroyo, G.M. 1999: Replacement clutches by Kentish plovers. — Condor 101: 746–751.

Antczak, M., Goławski, A., Kuźniak, S. & Tryjanowski, P. 2009: Costly replacement: how do different stages of nest failure affect clutch replacement in the red-backed shrikes *Lanius collurio*? — Ethology Ecology & Evolution 21: 127–136.

Balluet, P. & Faure, R. 2006: Le Grand-duc d'Europe *Bubo bubo* dans le département de la Loire. Eléments de biologie. — Nois Oiseaux 53: 195–208. (In French)

Bates, D. & Maechler, M. 2009: lme4 – Linear mixed-effects models using S4 classes. — Version 0.999375-31. URL http://lme4.r-forge.r-project.org/

Bauchau, V. & Seinen, I. 1997: Clutch desertion and renesting in pied flycatchers: an experiment with progressive clutch removal. — Animal Behaviour 54: 153–161.

Bourgeon, S., Criscuolo, F., Bertile, F., Raclot, T., Gabrielsen, G.W. & Massemin, S. 2006: Effects of clutch sizes and incubation stage on nest desertion in the female common eider *Somateria mollissima* nesting in the high Arctic. — Polar Biology 29: 358–363.

Brinkhof, M.W.G., Cavé, A.J., Hage, F.J. & Verhulst, S. 1993: Timing of reproduction and fledging success in the coot *Fulica atra*: evidence for a causal relationship. – Journal of Animal Ecology 62: 577–587.

von Bromssen, A. & Jansson, C. 1980: Effects of food addition to willow tit *Parus montanus* and Crested Tit *P. cristatus* at the time of breeding. — Ornis Scandinavica 11: 173–178.

Brown, K.M. & Morris, R.D. 1996: From tragedy to triumph: renesting in ring-billed gulls. – The Auk 113: 23–31.

Cabeza Arroyo, A. & de la Cruz Solís, C. 2001: Puesta de reposición con éxito de Águila-azor Perdicera *Hieraaetus fasciatus* en Extremadura (SW España). — Ardeola 48: 233–236. (In Spanish)

Cade, T.J. & Temple, S.A. 1977: The Cornell University falcon programme. — In World Conference on Birds of Prey, Vienna 1975, Report of Proceedings (ed. Chancellor, R.D.): 353–369. International Council for Bird Preservation.

Catlin, D.H. & Rosenberg, D.K. 2008: Breeding dispersal and nesting behavior of burrowing owls following experimental nest predation. — American Midland Naturalist 159: 1–7.

Christians, J.K., Evanson, M. & Aiken, J.J. 2001: Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. — Journal of Animal Ecology 70: 1080–1087.

Cody, M.L. 1966: A general theory of clutch size. — Evolution 20:174–194.

Coulson, J.C. & Thomas, C. 1985: Differences in the breeding performance of individual kittiwake gulls, *Rissa tridactyla* (L.). — In Behavioural ecology: ecological consequences of adaptive behavior (ed. Sibly, R.M. & Smith, R.H.): 489–503. Blackwell Scientific Publications.

Crawley, M.J. 2007: The R book. — John Wiley & Sons, Ltd., Chichester.

De Neve, L., Soler, J.J., Soler, M. & Pérez-Contreras, T. 2004: Differential maternal investment counteracts for late breeding in magpies *Pica pica*: an experimental study. – Journal of Avian Biology 35: 237–245.

Delgado M.M. & Penteriani V. 2004: Gender determination of Eurasian eagle owls (*Bubo bubo*) by morphology. – Journal of Raptor Research 38: 375–377.

Delgado M.M. & Penteriani V. 2007: Vocal behaviour and neighbour spatial arrangement during vocal displays in eagle owls (*Bubo bubo*). – Journal of Zoology 271: 3–10.

Delgado M.M., Penteriani V. & Nams, V.O. 2009: How fledglings explore surroundings from fledging to dispersal. A case study with eagle owls *Bubo bubo*. — Ardea 97: 7–15.

Delgado M.M., Penteriani V., Revilla, E. & Nams, V.O. 2010: The effect of phenotypic traits and external cues on natal dispersal movements. – Journal of Animal Ecology 79: 620–632.

Delibes, M. & Hiraldo, F. 1981: The rabbit as prey in the Iberian Mediterranean ecosystem. — In Proceedings of the World Lagomorph Conference (ed. Myers, K. & MacInnes, C. D.): 614–622. Guelph University Press.

Fentzloff, C. 1975: Erfolgreiche zucht und adoption von Seeadlern (*Haliaeetus albicilla*). — Deutscher Falkenorden 1975: 28–40. (In German)

Fernández, G.J. & Reboreda, J.C. 2000: Egg losses and nest desertion in greater rheas *Rhea Americana*. — Ibis 142: 29–34.

Forsman, E.D., Giese, A., Manson, D. & Sovern, S. 1995: Renesting by spotted owls. — Condor 97: 1078–1080.

Gadgil, M. & Bossert, W.H. 1970: Life historical consequences of natural selection. – American Naturalist 104: 1–24.

Gasparini, J., Roulin, A., Gill, V.A., Hatch, S.A. & Boulinier, T. 2006a: In kittiwakes food availability partially explains the seasonal decline in humoral immunocompetence. — Functional Ecology 20: 457–463.

Gasparini, J., Roulin, A., Gill, V.A., Hatch, S.A. and Boulinier, T. 2006b: Kittiwakes strategically reduce investment in replacement clutches. — Proceedings of the Royal Society of London B 273: 1551–1554.

Green, A. 2001: Mass/length residuals: measures of body condition or generators of spurious results? — Ecology 82: 1473–1483.

Hansson, B., Bensch, S. & Hasselquist, D. 2000: The quality and the timing hypotheses evaluated using data on great reed warblers. — Oikos 90: 575–581.

Hipfner, J.M. 2001: Fitness-related consequences of relaying in an Arctic seabird: survival of offspring to recruitment age. — The Auk 118: 1076–1080.

Hipfner, J.M., Gaston, A.J., Martin, D.L. & Jones, I.L. 1999: Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? — Journal of Animal Ecology 68: 988–998.

Hipfner, J.M., Charleton, K. & Davies, W.E. 2004: Rates and consequences of relaying in cassin's auklets *Ptychoramphus aleuticus* and rhinoceros auklets *Cerorhinca monocerata* breeding in a seasonal environment. — Journal of Avian Biology 35: 224–236.

Kirkwood, T.B.L. 1987 Immortality of the germ-line versus disposability of the soma. — In Evolution of longevity in animals (eds. Woodhead, A.D. & Thompson, K.H.): 209–218. Plenum Press.

Madsen, T. & Shine, R. 1999: Life-history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). — Ecology 80: 989–997.

Margalida, A., González, L.M., Sánchez, R., Oria, J., Prada, L., Caldera, J., Aranda, A. & Molina, J.I. 2007: A long-term large-scale study of the breeding biology of the Spanish imperial eagle (*Aquila adalberti*). — Journal of Ornithology 148: 309–322.

Martin, T.E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. — Ecological Monographs 65: 101–127.

Martínez, F., Blanco, G. & Rodríguez, R. 1998: Rate, timing and success of clutch replacement by colonial griffon vultures (*Gyps fulvus*). — Ornis Fennica 75: 145–148.

Martínez, F. & Blanco, G. 2002: Use of alternative nests for clutch replacement in the Egyptian vulture *Neophron percnopterus*. — Ardeola 49: 297–299.

Milonoff, M. 1989: Can nest predation limit clutch size in precocial birds? — Oikos 55: 424–427.

Milonoff, M. 1991: Renesting ability and clutch size in precocial birds. — Oikos 62:189–194.

Moleón, M., Martín-Jaramillo, J., Nieto, J., Benítez, J.R. & Bautista, J. 2009: Successful replacement clutches in European bonelli's eagles (*Hieraaetus fasciatus*). — Journal of Raptor Research 43: 164–165.

Mora, O., Delgado, M.M. & Penteriani, V. 2010: Secondary sex-ratio in Eurasian eagle-owls: early-breeding females produce more daughters. — Journal of Raptor Research 44: 62–65.

Moreno, J. 1998: The determination of seasonal declines in breeding success in seabirds. — Etología 6: 17–31.

Morrison, M.L. & Walton, B.J. 1980: The laying of replacement clutches by Falconiforms and Strigiforms in North America. — Journal of Raptor Research 14: 79–85.

Mundy, P., Butchart, D., Ledger, J. & Piper, S. 1992: The vultures of Africa. — Academic Press, London, UK.

Nager, R.G., Monaghan, P. & Houston, D.C. 2001: The cost of egg production: increased egg production reduces future fitness in gulls. — Journal of Avian Biology 32: 159–166.

Newton, I. 1979: Population ecology of raptors. — T & AD Poyser, Berkhamsted, U.K.

Olsson, V. 1997: Breeding success, dispersal, and long-term changes in a population of eagle owl *Bubo bubo* in southeastern Sweden 1952–1996. — Ornis Svecica 7: 49–60.

Parker, H. 1981: Renesting biology of Norwegian willow ptarmigan. — Journal of Wildlife Management 45: 858–864.

Penteriani, V. 1996: The eagle owl. — Edagricole, Bologna, Italy. (In Italian)

Penteriani, V., Delgado, M.M., Gallardo, M. & Ferrer, M. 2004: Spatial heterogeneity and structure of bird populations: a case example with the eagle owl. — Population Ecology 46: 185–192.

Penteriani, V., Delgado, M.M., Maggio, C., Aradis, A. & Sergio, F. 2005: Development of chicks and pre-dispersal behaviour of young in the eagle owl *Bubo bubo*. — Ibis 147: 155–168.

Penteriani, V., Delgado, M.M., Alonso-Alvarez, C., Viqueira, N., Sergio, F., Bartolommei, P. & Thompson, L. 2007: The importance of visual cues for nocturnal species: eagle owl fledglings signal with white mouth feathers. — Ethology 113: 934–943.

Penteriani, V., Delgado, M.M., Bartolommei, P., Maggio, C., Alonso-Alvarez, C. & Holloway, G.J. 2008: Owls and rabbits: predation against substandard individuals of an easy prey. — Journal of Avian Biology 39: 215–221.

R Development Core Team. 2009: R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Resetarits, W.J. 1996: Oviposition site choice and life-history evolution. — American Zoologist 36: 205–215.

Rodenhouse, N.L. & Holmes, R.T. 1992: Results of ex- perimental and natural food reductions for breeding black-throated blue warblers. — Ecology 73: 357–372.

Rooneem, T.M. & Robertson, R.J. 1997: The potential to lay replacement clutches by tree swallows. — Condor 99: 228–231.

Sandercock, B.K. & Pedersen, H.C. 1994: The effect of renesting ability and nesting attempt on egg-size variation in willow ptarmigan. — Canadian Journal of Zoology 72: 2252–2255.

Simmons, R.E. 1984: Do northern harriers lay replacement clutches? — Journal of Raptor Research 18: 103–106.

Simons, L.S. & Martin, T.E. 1990: Food limitation of avian reproduction: an experiment with the cactus wren. — Ecology 71: 869–876.

Slagsvold, T. 1982: Clutch size variation in passerine birds: the nest predation hypothesis. — Oecologia 54:159–169.

Slagsvold, T. 1984: Clutch size variation of birds in relation to nest predation: on the cost of reproduction. — Journal of Animal Ecology 53: 945–953.

Sorci, G., Soler, J.J. & Møller, A.P. 1997: Reduced immunocompetence of nestlings in replacement clutches of the European magpie (*Pica pica*). — Proceedings of the Royal Society of London B 264: 1593–1598.

Stearns, S.C. 1989: Trade-offs in life-history evolution. — Functional Ecology 3: 259–268.

Stearns, S.C. 1992: The evolution of life histories. — Oxford University Press, Oxford, UK.

Verboven, N. & Tinbergen J.M. 2002: Nest desertion: a trade-off between current and future reproduction. — Animal Behaviour 63: 951–958.

Verhulst., S., van Balen, J.H. & Tinbergen, J.M. 1995: Seasonal decline in reproductive success of the great tit: variation in time or quality? — Ecology 76: 2392–2403.

Visser, M.E. & Lessells, C.M. 2001: The costs of egg production and incubation in great tits (*Parus major*). — Proceedings of the Royal Society of London B 268: 1271–1277.

Wendeln, H., Becker, P.H. & Gonzáles-Solís, J. 2000: Parental care of replacement clutches in common terns (*Sterna hirundo*). — Behavioral Ecology and Sociobiology 47: 382–392.

Wheelwright, N.T. & Schultz, C.B. 1994: Age and reproduction in savannah sparrows and tree swallows. — Journal of Animal Ecology 63: 686–702.

Williams, G.C. 1966: Natural selection, the costs of reproduction, and a refinement of Lack's principle. — The American Naturalist 100: 687–690.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009: mixed effects models and extensions in ecology with R. — Springer, UK.