Ornis Fennica 93: 130–136. 2016

Brief report

Colour morph does not predict brood size in the Booted Eagle

José Enrique Martínez*, José Francisco Calvo, María Victoria Jiménez-Franco, Iñigo Zuberogoitia & Pascual López-López

*J.E. Martínez, Bonelli's Eagle Study and Conservation Group, Apdo. 4009, 30080 Murcia, Spain. * Corresponding author's e-mail: ecoljemt@um.es*
J.E. Martínez, J.F. Calvo, M.V. Jiménez-Franco, Departamento de Ecología e Hidrología. Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain
I. Zuberogoitia, Estudios Medioambientales Icarus, S.L. C/ San Vicente, 8. 6^a Planta. Dpto 8. Edificio Albia I, 48001 Bilbao, Spain
P. López-López, Terrestrial Vertebrates Group, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, C/ Catedrático José Beltrán 2, E-46980, Paterna, Valencia, Spain

Received 22 October 2015, accepted 19 February 2016

Mechanisms regulating colour polymorphism remain largely unknown and detailed investigation is required to explore the biological consequences on population dynamics. This paper presents the first study of the possible connection between colour polymorphism and productivity in a Booted Eagle (*Aquila pennata*) population breeding in south-eastern Spain. To that end we used 19 years of data of non-marked individuals. A total of 738 pale (91.6%) and 68 dark (8.4%) adult Booted Eagles were observed in our study area, including 57 territories. Our results suggest that colour morph of both sexes remained stable in the population over the study period. Although we found a higher number of offspring produced by parents exhibiting the dark morph than those of the pale morph, statistical differences were not significant. Hence, our models showed that colour polymorphism was not a good predictor of Booted Eagles' productivity, although further research by capture-recapture analysis would be needed to explore the influence of colour variation on fitness components at individual level and its consequences at population level of long-lived species.

1. Introduction

Polymorphism in colour is a widespread phenomenon in many animal taxa, and it is defined as the coexistence of two or more distinct and genetically determined colour morphs in one interbreeding population (Huxley 1955). Melanin-based colour variation within and between bird species normally has a strong genetic component (Hrubant 1955, Lank *et al*. 1995, Roulin *et al*. 1998, Krüger *et al*. 2001, Roulin & Dijkstra 2003), and such intraspecific colour variation is independent of sex, age and season (Butcher & Rohwer 1989), although it can occur in different frequency due to a geographical range (Burri *et al*. 2016). Despite the mechanisms responsible for the evolution and maintenance of colour polymorphisms in wild populations have been subject of intensive research (Sinervo & Lively 1996, Roulin 2004a, Gray & McKinnon 2007), this phenomenon still remains poorly understood (Galeotti *et al*. 2003, Roulin 2004a, Boerner & Krüger 2009).

One of the bird groups where colour polymorphism is most common are raptors (Chakarov *et al*. 2011). However, causal mechanisms regulating colour polymorphism remain largely unknown and more research is required to describe such patterns and the possible mechanisms that influence their occurrence (Johnson & Burnham 2013). In taxa exhibiting polymorphism, several hypotheses have been suggested about its biological consequences, including offspring production (Krüger *et al*. 2001, Johnson & Burnham 2013), predation risk (Roulin & Wink 2004), dispersal (Roulin 2013, Chakarov *et al*. 2013), differences in hatching date (Chakarov *et al*. 2011), bacterial infections (Saggese *et al*. 2008), ecto- and endoparasite burden (Galeotti & Sacchi 2003, Roulin 2004b, Chakarov *et al*. 2008), moult patterns (Brommer *et al*. 2003), behaviour (Korzan & Fernald 2007, Boerner & Krüger 2009, Bortolotti *et al*. 2011, Da Silva *et al*. 2013) and sexual selection (Roulin 2016). Nevertheless, to date, no information exist on the factors that may influence colour variation or its adaptive function in Booted Eagles *Aquila pennata*, a species for which the genetic basis of polymorphism still remains unknown (Galván *et al*. 2010).

The Booted Eagle is a long-lived trans-Saharan migrant which arrives in Europe in late March and leaves in late September (Cramp & Simmons 1980, Mellone *et al*. 2013, 2015). Although some individuals winter in the Mediterranean basin (Martínez & Sánchez-Zapata 1999), the majority of the population migrates to the Sahel region and tropical Africa (Cramp & Simmons 1980, Mellone *et al*. 2013). Booted Eagles use elaborated aerial displays to establish monogamous pair bond (Cramp & Simmons 1980), showing a high territory fidelity in the study area (Jiménez-Franco *et al*. 2013). In the breeding area, approximately one month after arrival (late April), females lay one to two eggs, rarely three, and breed normally 1–2 young per nest (Cramp & Simmons 1980). Booted Eagles exhibit one of two distinct colour morphs, pale or dark, which remain during their lifetime with some geographic variation (Cramp & Simmons 1980, Forsman 1999). Some authors have suggested that the ratio between the two colour morphs varies geographically across Europe with a higher percentage of the pale morph in the West (e.g. 80% in Spain, 70% in France and Austria) and a lower percentage in the East (e.g. 60% in Greece and Middle East, 50% in Caucasus, 20–30% in Russia, Ukraine and Turkmenistan; Glutz von Blotzheim *et al*. 1971, Cramp & Simmons 1980, Ferguson-Lees & Christie 2001, Karyakin 2007). In this paper we explore the link between productivity and a highly heritable phenotypic trait, plumage coloration, in a Booted Eagles population in south-eastern Spain.

2. Material and methods

This study was conducted in a semi-arid Mediterranean mountainous area located in the Special Protection Area for Birds "Sierras de Burete, Lavia y Cambrón" (code ES0000267) located in the centre of Murcia province, south-eastern Spain (coordinates: 38°00'N, 1°45'W). The study area covers about 10,000 ha, with elevations ranging from 550 to 1,234 m above sea-level. The climate is Mediterranean with a mean annual rainfall of c. 400 mm concentrated mostly during the spring and autumn. The landscape is characterized by mountain slopes covered by Aleppo pine forests (*Pinus halepensis*) interspersed with traditional agricultural ecosystems (cereals, vineyards, olive and almond groves). For more details of the study area, see Jiménez-Franco *et al*. (2014).

Between 1995 and 2013, an intensive monitoring of 57 territories was carried out during the breeding season. Territory occupation was assessed each year from late March to early May. Occupancy was determined when signs of territorial or mating behaviour were observed, including courtship and territorial flights and responses (e.g., elicited vocalizations, approaches), copulations, nest material transfers, the presence of at least one freshly refurbished nest or direct evidence of reproduction (details in Martínez *et al*. 2006a,b). We

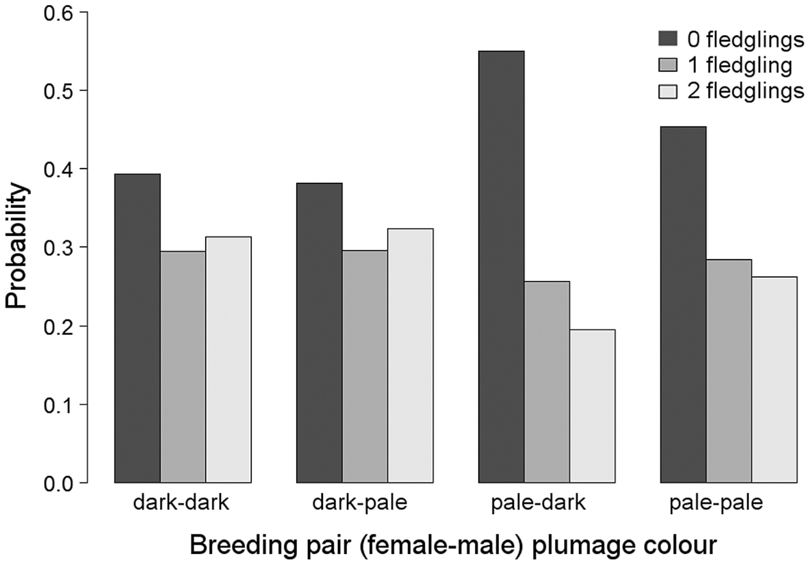

Fig. 1. Brood size probabilities fitted according to plumage colour of Booted Eagle pairs in south eastern Spain. Results are based on the mixed-effects ordinal regression model including an interaction term.

identified the plumage colouration in both pair members by direct observation (Galeotti & Sacchi 2003, Roulin *et al*. 2003, Brommer *et al*. 2005). Morph scoring followed the recognition scheme of Cramp & Simmons (1980), Del Hoyo *et al*. (1994) and Forsman (1999), where two morphs are recognized (dark and pale); with melanic individuals having a greater amount of eumelanic feathers. The sex of each individual was easily recognizable from its size and breeding behaviour (Jiménez-Franco *et al*. 2013). When a territory was occupied, at least three visits were made to record productivity (i.e., number of fledglings per monitored pair; Martínez *et al*. 2006a), considering those which survived to about 45 days old (Steenhof 1987).

Differences in the productivity in relation to plumage colour were tested using mixed-effects ordinal regression models. Following Otterbeck *et al*. (2015), we modelled productivity as an ordinal response variable (number of offspring: 0, 1, 2). We tested four different models using "male colour", "female colour", and their interaction were used as explanatory factors. To control for non-independence of breeding data, we included territory and year as random factors (affecting the intercept). Analyses were performed using the *clmm* function implemented in the *ordinal* package (Christensen 2015) for R-software version 3.2.2 (R Core Team 2015), which does maximum likelihood estimation using Laplace approximation of the likelihood. The level of significance for statistical analyses was set at $\alpha = 0.05$.

3. Results

The pale morph was widely predominant (91.6%) over the study period, with only 68 of 806 individuals (8.4%) exhibiting the dark morph. Most of dark morph individuals were females (62 of 68; i.e., 91.2%).

In Fig. 1 we showed brood size probabilities fitted according to plumage colour of Booted Eagles in our study area (female–male; dark–dark, dark–pale, pale–dark and pale–pale). However, the mixed-effects ordinal regression models showed no significant effects of colour morph on breeding productivity (Table 1).

4. Discussion

The ratio between pale and dark morphs in our study area was very similar to other Booted Eagles populations in the Western Palearctic region,

Table 1. Summary of mixed-effects ordinal regression models on the number of fledglings (R) in 403 breeding events recorded in 57 territories of Booted Eagles in south-eastern Spain. DF: dark female; DM: dark male; t_i: territory effects; y_i: year effects. Columns “Territory” and “Year” report the fitted random effect standard deviations of these factors.

Model	Coefficient	SE	z	P	Territory	Year
$R = \beta_1 \mathrm{DF} + \beta_2 \mathrm{DM} + t_i + y_i$	$\beta_1 = 0.305$	0.298	1.024	0.306	0.739	0.421
	$\beta_2 = –0.197$	0.895	–0.220	0.826	–	–
$R = \beta_1 \mathrm{DF} + \beta_2 \mathrm{DM} + \beta_3 \mathrm{DF}{\times}\mathrm{DM} + t_i + y_i$	$\beta_1 = 0.297$	0.301	0.986	0.324	0.739	0.421
	$\beta_2 = –0.389$	1.365	–0.285	0.776	–	–
	$\beta_3 = 0.339$	1.796	0.189	0.850	–	–

where the pale morph is largely dominant (Ferguson-Lees & Christie 2001). A recent research has revealed that dark morph nestlings of Booted Eagles exhibit lower levels of glutathione, a key intracellular antioxidant that inhibits the synthesis of eumelanin, than those of lighter morphs (Galván *et al.* 2010). These authors also found that dark female eaglets had higher levels of antioxidants other than glutathione and were in better body condition than light female eaglets. This result suggests an adaptive response of dark nestlings to compensate for reduced glutathione levels. According to these authors, dark individuals may pay a fitness cost (lower fecundity and survival as compared to pale eagles). Thus, it would be expected that pale Booted Eagles had higher productivity than dark individuals. However, our results showed similar values of productivity between different morph combinations in the breeding pairs (Fig. 1, Table 1).

Previous studies have shown that plumage morph in polychromatic species is one important predictor of productivity (Krüger *et al.* 2001, Johnson & Burnham 2013, Gangoso *et al.* 2015) and lifetime reproductive success (Krüger 2002, Brommer *et al.* 2005), along with others factors such as competition, weather, and territory quality (Krüger 2002). Our results are not consistent with these works since our models do not show significant relationship between plumage colouration and offspring production (Table 1). However, our results should be taken with caution because we did not have marked individuals in our population and their individual lifetime reproductive success could not be assessed in the long term. In this line, Brommer *et al.* (2005) found that grey tawny owls do not produce more offspring per breeding attempt, but have a longer breeding lifespan than brown individuals, and therefore manage to produce more fledglings and recruits during their lifetime. An additional hypothesis is needed to elucidate whether pale individuals have a longer breeding lifespan than dark individuals. In fact, lifespan is the main determinant of lifetime reproductive success in a variety of taxa (e.g., Clutton-Brock 1988). For this reason, pale Booted Eagles could not produce more offspring per breeding attempt, but could have a longer breeding lifespan than dark individuals, and therefore manage to produce more fledglings and recruits during their lifetime (Brommer *et al.* 2005). Previous studies in the same population of Booted Eagles suggested that nesting habitat quality, prey availability, predation, parasites and weather did not significantly influence productivity (Martínez *et al.* 2006a,b, Pagán *et al.* 2009, Jiménez-Franco *et al.* 2014, Bosch *et al.* 2015). These factors would be acting on natural selection in order to favour some phenotypic traits and the related effect on reproductive fitness (Price *et al.* 1984, Gibbs & Grant 1987, Galeotti *et al.* 2003, Roulin 2004a). Another possibility is that colour polymorphism is associated with offspring quality rather than offspring number (Roulin & Ducrest 2011). Considering the effect of habitat quality on productivity, high homogeneity in habitat quality, high prey availability and low precipitation, have scarce impact on individual fitness, and may explain the null effect of colour polymorphism on productivity (Karell *et al.* 2011). In fact, in the study area, reproductive output was related to individual quality instead of territory quality (Pagán *et al.* 2009, Jiménez-Franco *et al.* 2013, 2014). Therefore, future studies could include not only the effects of colour morph on Booted Eagle productivity, but also the interaction of colour polymorphism and habitat characteristics (Dreiss *et al*. 2012). Moreover, other individual attributes such as body condition or experience of individuals should be also considered in order to understand the natural mechanism behind these results.

Finally, further studies, by capture-recapture analysis, would be necessary to get insight into the adaptive value of colour polymorphism in raptors and the reason for its spread, maintenance, consequences in fitness and breeding output (Chakarov *et al*. 2011), and first-year survival (Roulin *et al*. 2010).

Acknowledgements. We would like to thank Andreas Lindén, Alexandre Roulin and an anonymous referee for their valuable suggestions. We thank Ramón Ruiz, Iluminada Pagán, Mario León, Ginés Gómez and Carlos González for field assistance in the study area. This work was funded by the Spanish Ministerio de Educación y Ciencia (project REN2002-324 01884/GLO, partially financed by FEDER funds) and the Consejería de Agua, Agricultura y Medio Ambiente of the Region of Murcia. M. V. Jiménez-Franco was supported by a FPU grant from the Spanish Ministerio de Educación y Ciencia (reference AP2009-2073). P. López-López was supported by a "Juan de la Cierva-incorporación" postdoctoral grant of the Spanish Ministry of Economy and Competitiveness (reference JCI-2014-19190). Authorization for the study was provided by the Consejería de Agua, Agricultura y Medio Ambiente of the Region of Murcia.

Värimuoto ei vaikuta pikkukotkan pesyekokoon

Lintujen väripolymorfia saattaa vaikuttaa populaatioiden demografiaan ja siten myös kantojen vaihteluihin. Tässä artikkelissa tutkimme ensimmäistä kertaa värimuodon ja poikastuoton mahdollista yhteyttä pikkukotkalla, tarkastelemalla tilannetta Espanjan kaakkoisosissa sijaitsevassa populaatiossa. Käytimme aineistoa 19 vuoden jaksolta ei-merkityillä yksilöillä. Kokonaisuudessaan tarkastelun kohteena oli 738 vaaleata (91,6 %) ja 68 tummaa (8,4 %) aikuista pikkukotkaa 57 reviirillä.

Tuloksemme mukaan värimuotojen osuudet populaatiossa pysyvät molemmilla sukupuolilla vakaina tutkimusjakson läpi. Vaikka tumman muodon vanhemmilla oli jokseenkin suurempi poikasmäärä vaaleaan muotoon verrattuna, ero ei ollut tilastollisesti merkitsevä. Siten, väripolymorfismi ei näytä oleva tärkeä selittäjä pikkukotkan lisääntymismenestykselle. Tosin, lisätutkimukset merkintä–takaisinpyyntianalyysin muodossa ovat tarpeen, jotta voisimme ymmärtää miten värimuoto vaikuttaa yksilöiden kelpoisuuteen ja demografiaan populaatiotasolla tällä pitkäikäisellä lajilla.

References

Boerner, M. & Krüger, O. 2009: Aggression and fitness differences between plumage morphs in the common buzzard (*Buteo buteo*). — Behavioral Ecology 20: 180–185.

Bortolotti, G.R., Stoffel, M.J. & Galván, I. 2011: Wintering Snowy Owls *Bubo scandiacus* integrate plumage colour, behaviour and their environment to maximize efficacy of visual displays. — Ibis 153: 134–142.

Bosch, J., Martínez, J.E., Calvo, J.F., Zuberogoitia, I. & Jiménez-Franco, M.V. 2015: Does rainfall affect the productivity of the Booted Eagle (*Aquila pennata*) during the breeding period in Mediterranean environments? — Journal of Ornithology 156: 1– 8.

Brommer, J.E., Pihlajamäki, O., Kolunen, H. & Pietiäinen, H. 2003: Life-history consequences of partial-moult asymmetry. — Journal of Animal Ecology 72: 1057–1063.

Brommer, J.E., Ahola, K. & Karstinen, T. 2005: The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. — Proceedings of the Royal Society B 272: 935–940.

Burri, R., Antoniazza, S., Gaigher, A., Ducrest, A.L., Simon, C., The European Barn Owl Network, Fumagalli, L., Goudet, J. & Roulin, A. 2016: The genetic basis of color-related local adaptation in a ring-like colonization around the Mediterranean. — Evolution 70: 140–153.

Butcher, G.S. & Rohwer, S. 1989: The evolution of conspicuous and distinctive coloration for communication in birds. — In Current Ornithology Vol. 6 (ed. Power, D.M.): 51–108. Plenum Press, New York.

Chakarov, N., Boerner, M. & Krüger, O. 2008: Fitness in common buzzards at the cross-point of opposite melanin–parasite interactions. — Functional Ecology 22: 1062–1069.

Chakarov, N., Boerner, M. & Krüger, O. 2011: Biological consequences of plumage polymorphism in common buzzard. — In Ecology and conservation of European forest-dwelling raptors (ed. Zuberogoitia, I. & Martínez, J.E.): 234–241. Diputación Foral de Bizkaia, Bilbao.

Chakarov, N., Jonker, R.M., Boerner, M., Hoffman, J.I. & Krüger, O. 2013: Variation at phenological candidate genes correlates with timing of dispersal and plumage morph in a sedentary bird of prey. — Molecular Ecology 22: 5430–5440.

Christensen, R. H. B. 2015: ordinal – Regression Models for Ordinal Data. — R package version 2015.6-28. http://www.cran.r-project.org/package=ordinal/.

Clutton-Brock, T.H. (ed.) 1988: Reproductive success. — University of Chicago Press, Chicago.

Cramp, S. & Simmons, K.E.L. 1980: Handbook of the birds of Europe, the Middle East and North Africa. Volume II. — Oxford University Press, Oxford.

Da Silva, A., van den Brink, V., Emaresi, G., Luzio, E., Bize, P., Dreiss, A.N. & Roulin, A. 2013: Melanin-based colour polymorphism signals aggressive personality in nest and territory defence in the tawny owl (*Strix aluco*). — Behavioral Ecology and Sociobiology 67: 1041–1052.

Del Hoyo, J., Elliot, A. & Sargatal, J. 1994: Handbook of the birds of the world, vol. 2. New world vultures to guineafowl. — Lynx Edicions, Barcelona.

Dreiss, A.N., Antoniazza, S., Burri, R., Fumagalli, L., Sonnay, C., Frey, C., Goudet, J. & Roulin, A. 2012: Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. — Journal of Evolutionary Biology 25: 103–114.

Ferguson-Lees, J. & Christie, D.A. 2001: Rapaces del mundo. — Editorial Omega, Barcelona. (In Spanish)

Forsman, D. 1999: The raptors of Europe and The Middle East. A handbook of field identification. — T & AD Poyser, London, UK.

Galeotti, P. & Sacchi, R. 2003: Differential parasitaemia in the tawny owl (*Strix aluco*): effects of colour morph and habitat. — Journal of Zoology 261: 91–99.

Galeotti, P., Rubolini, D., Dunn, P.O. & Fasola, M. 2003: Colour polymorphism in birds: causes and functions. — Journal of Evolutionary Biology 16: 635–646.

Galván, I., Gangoso, L., Grande, J.M., Negro, J.J., Rodríguez, A., Figuerola, J. & Alonso-Álvarez, C. 2010: Antioxidant machinery differs between melanic and light nestlings of two polymorphic raptors. — PLOS ONE 5: e13369.

Gangoso, L., Afán, I., Grande, J.M. & Figuerola, J. 2015: Sociospatial structuration of alternative breeding strategies in a color polymorphic raptor. — Behavioral Ecology 26: 1119–1130.

Gibbs, H.L. & Grant, P.R. 1987: Oscillating selection on Darwin`s finches. — Nature 237: 511–513.

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. 1971: Handbuch der Vögel Mitteleuropas. Band 4. Falconiformes. — Aula-Verlag, Wiesbaden.

Gray, S.M. & McKinnon, J.S. 2007: Linking color polymorphism maintenance and speciation. — Trends in Ecology & Evolution 22: 71–79.

Hrubant, H.E. 1955: An analysis of the color phases of the Eastern Screech Owl, *Otus asio*, by the gene frequency method. — American Naturalist 89: 223–230.

Huxley, J. 1955: Morphism in birds. — Acta Congressus Internationalis Ornithologicus XI: 309–328.

Jiménez-Franco, M.V., Martínez, J.E. & Calvo, J.F. 2014: Patterns of nest reuse in forest raptors and their effects on reproductive output. — Journal of Zoology 292: 64–70.

Jiménez-Franco, M.V., Martínez, J.E., Pagán, I. & Calvo, J.F. 2013: Factors determining territory fidelity in a migratory forest raptor, the Booted Eagle *Hieraaetus pennatus*. — Journal of Ornithology 154: 311–318.

Johnson, J.A. & Burnham, K.K. 2013: Timing of breeding and offspring number covary with plumage colour among Gyrfalcons *Falco rusticolus*. — Ibis 155: 177–188.

Karell, P., Ahola, K., Karstinen, T., Valkama, J. & Brommer, J.E. 2011: Climate change drives microevolution in a wild bird. — Nature Communications 2: 208. DOI: 10.1038./ncomm1213

Karyakin, I.V. 2007: The Booted Eagle in the Volga Region, Ural and Siberia, Russia. — Raptors Conservation 9: 27–62.

Korzan, W. J. & Fernald, R.D. 2007: Territorial male color predicts agonistic behavior of conspecifics in a color polymorphic species. — Behavioral Ecology 18: 318–323.

Krüger, O. 2002: Dissecting common buzzard lifespan and lifetime reproductive success: the relative importance of food, competition, weather, habitat and individual attributes. — Oecologia 133: 474–482.

Krüger, O., Lindström, J. & Amos, W. 2001: Maladaptive mate choice maintained by heterozygote advantage. — Evolution 55: 1207–1214.

Lank, D.B., Smith, C.M., Hanotte, O., Burke, T. & Cooke, F. 1995: Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. — Nature 378: 59–62.

Martínez, J.E. & Sánchez-Zapata, J.A. 1999: Invernada de aguililla calzada (*Hieraaetus pennatus*) y culebrera europea (*Circaetus gallicus*) en España. — Ardeola 46: 93–96. (In Spanish with English summary)

Martínez, J.E., Pagán, I. & Calvo, J.F. 2006a: Factors influencing territorial occupancy and reproductive output in the Booted Eagle *Hieraaetus pennatus*. — Ibis 148: 807–819.

Martínez, J.E., Pagán, I. & Calvo, J.F. 2006b: Interannual variations of reproductive parameters in a booted eagle (*Hieraaetus pennatus*) population: the influence of density and laying date. — Journal of Ornithology 147: 612–617.

Mellone, U., De La Puente, J., López-López, P., Limiñana, R., Bermejo, A. & Urios, V. 2013: Migration routes and wintering areas of Booted Eagles *Aquila pennata* breeding in Spain. — Bird Study 60: 409–413.

Mellone, U., De La Puente, J., López-López, P., Limiñana, R., Bermejo, A. & Urios, V. 2015: Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: a multi-scale approach. — Behavioral Ecology and Sociobiology 69: 75–82.

Otterbeck, A., Lindén, A. & Roualet, É. 2015: Advantage of specialism: reproductive output is related to prey choice in a small raptor. — Oecologia 179: 129–137.

Pagán, I., Martínez, J.E. & Calvo, J.F. 2009: Breeding performance and territorial occupancy in a migratory raptor do not follow ideal despotic distribution patterns. — Journal of Zoology 279: 36–43.

Price, T.D., Grant, P.R., Gibbs, H.L. & Bong, P.T. 1984: Recurrent patterns of natural selection in a population of Darwin's finches. — Nature 309: 787–789.

R Core Team 2015: R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org/

Roulin, A. 2004a: The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. — Biological Reviews 79: 815–848.

Roulin, A. 2004b: Proximate basis of the covariation between a melanin-based female ornament and offspring quality. — Oecologia 140: 668–675.

Roulin, A. 2013: Ring recoveries of dead birds confirm that darker pheomelanic Barn Owls disperse longer distances. — Journal of Ornithology 154: 871–874.

Roulin, A., Richner, H. & Ducrest, A.L. 1998: Genetic, environmental, and condition-dependent effects on female and male ornamentation in the barn owl *Tyto alba*. — Evolution 52: 1451–1460.

Roulin, A. & Dijkstra, C. 2003: Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. — Heredity 90: 359–364.

Roulin, A., Ducret, B., Ravussin, P.A. & Altwegg, R. 2003: Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. — Journal of Avian Biology 34: 393–401.

Roulin, A. & Ducrest, A.L. 2011: Association between melanism, physiology and behaviour: A role for the melanocortin system. — European Journal of Pharmacology 660: 226–233.

Roulin, A. & Wink, M. 2004: Predator–prey relationships and the evolution of genetic colour polymorphism: a phylogenetic analysis in diurnal raptors. — Biological Journal of the Linnean Society 81: 565–578.

Roulin, A., Altwegg, R., Jensen, H., Steinsland, I. & Schaub, M. 2010: Sex-dependent selection on an autosomal melanic female ornament promotes the evolution of sex ratio bias. — Ecology Letters 13: 616–626.

Roulin, A. 2016: Condition-dependence, pleiotropy and the handicap principle of sexual selection in melanin-based colouration. — Biological Reviews 91: 328–348.

Saggese, M.D., Tizard, I. & Phalen, D.N. 2008: Mycobacteriosis in naturally infected ring-neck doves (*Streptopelia risoria*): investigation of the association between feather colour and susceptibility to infection, disease and lesions type. — Avian Pathology 37: 443–450.

Sinervo, B. & Lively, C.M. 1996: The rock-paper-scissors game and the evolution of alternative male strategies. — Nature 380: 240–243.

Steenhof, K. 1987: Assessing raptor reproductive success and productivity. — In Raptor management techniques manual (ed. Giron Pendleton, B.A., Millsap, B.A., Cline, K.W. & Bird, D.M.): 157–170. National Wildlife Federation, Washington.