Mixed clutches in Montagu's harrier *Circus pygargus* nests: a maladaptive brood parasitism by galliform birds

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Capsule Cases of mixed clutches in raptor nests are very scarce in the literature. Among 279 harrier nests monitored between 1991–1996 and 2010–2011 in two different areas of central Spain, quail eggs were found in one harrier nest, and 13 others contained partridge eggs. Harrier eggs were smaller in nests which contained galliform eggs, and therefore more similar in size and appearance to the foreign eggs, which may suggest a maladaptative behaviour on the part of the galliforms.

Facultative interspecific nest parasitism has been reported in several bird species, including waterfowl, waders, galliforms and rallids (González-Kirchner & González-Kirchner 1989, Cuervo 1993, Amat 1998, David et al. 2005, Krakauer & Kimball 2009, Paul-Cervera 2010). In these cases, a species may lay their eggs in the nest of another species, but may also incubate its own eggs, thus increasing the opportunities to raise more offspring (Rodríguez-Teijeiro et al. 2003). However, there are few reported cases of interspecific clutches (hereafter 'mixed clutches') in raptor nests. There is a documented case of a Redhead, Aythya americana, laying eggs in a Northern Harrier Circus cyaneus nest (Fleskes 1992). This may be a maladaptive behaviour by the Redhead, because the ducklings would not be fed by the Harrier.

In this study, we describe the occurrence of mixed clutches in nests of Montagu's Harriers *Circus pygargus*, and also suggest some alternative explanations for the occurrence of such mixed clutches. The field work was conducted in Jarama-Henares (Madrid, Spain) and in the farmlands of La Mancha (Cuenca, Castilla-La Mancha, Spain), in 1991–1996 and 2010–2011, respectively. Both areas are currently dominated by non-irrigated farming of winter wheat, barley and rye,

alternating with sunflower fields (Cuenca) or small olive fields (Madrid). Although traditionally breeding in grassland, bushes or reeds, the Montagu's Harrier currently breeds primarily in cultivated areas in Western Europe (Arroyo et al. 2004). We visited nests during the laying period, and eggs were measured (maximum length and width to the nearest 0.05 mm) using vernier calipers. From these measurements, we calculated egg volume according to Hovt (1979) as $0.51 \times \text{length} \times \text{width}^2$. This measure was used to compare the sizes of eggs in mixed clutches versus eggs in harrier-only clutches, to test whether galliforms were choosing the nests which contained more similarly sized eggs. Eggs were identified using specialized guides (Harrinson & Castell 1998). In Madrid, we did not measure every egg in the monitored nests each year: in earlier years, we only measured unhatched eggs that remained in the nest at the end of the season, to minimize disturbance during incubation. However, unhatched eggs have not been shown to differ in size from hatched eggs (Arroyo, B. and Bretagnolle, V., pers. obs), so our measurements are likely a reliable estimator of the size of eggs in the whole clutch. We performed a linear mixed-model, with 'nest' as a random variable, 'egg volume' as the response variable (with a normal distribution), and 'nest type' as a categorical variable with two values ('mixed' or 'not mixed'). Due to limited data from the

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Cuenca population (only one nest containing galliform eggs), we did not perform statistical analyses and only compare average egg volume. Generalized liner mixed-model (GLMM) analysis was carried out with R version 2.15.1 (R Development Core Team 2012).

We monitored 279 nests (252 in Madrid, for which we had egg measurements in 61, and 27 in Cuenca). At the Madrid site, 13 harrier nests had mixed clutches (6 among the 61 with egg measurements), which contained two (n = 3) or one (n = 10) Redlegged Partridge Alectoris rufa eggs (5.1% of monitored nests). In Cuenca, we found one harrier nest (3.7% of monitored nests in this site) with two Common Quail Coturnix coturnix eggs. Both quail and partridge eggs were found while harrier females were incubating.

In Cuenca, the mixed-clutch nests had harrier eggs much smaller in volume (mean = 18.19 ± 0.83 cm³) than the other nests (24.54 ± 2.81 cm³). In Madrid, harrier nests with mixed clutches also had harrier eggs significantly smaller (20.44 ± 2.45 cm³) than those without mixed clutches (23.52 ± 2.18 cm³) ($F_{1, 57} = 21.2, P < 0.001$). The volume of the two quail eggs was 8.25 ± 0.6 cm³, close to other measurements found in the literature (Pizarro & Almeida 1956). The volume of two of the partridge eggs found in Madrid was 16.6 ± 1.8 cm³, also similar to those obtained in the literature (Cramp & Simmons 1980).

Cases of mixed clutches in nests of raptors are only scarcely mentioned in the literature (Fleskes 1992). Nevertheless, our data indicate that the presence of galliform eggs in Montagu's Harrier nests is more common than previously thought. These results are consistent with unpublished observations from other areas of the Iberian Peninsula. For example, in a sample of 62 Montagu's Harrier nests (central Spain), a case of odd eggs was reported (Hernández, M.A., pers. Comm.). The presence of quail eggs in several nests of Montagu's Harrier has also been recorded in northwestern Spain (Roman, J. and Ansola, L.M., pers. Comm.). Several hypotheses could explain these events, but we focus on the two most plausible ones. One may be that raptors take the eggs as a food resource and bring them to their nest, as eggs are an important part of the diet of Montagu's Harrier in Spain, at the beginning of the breeding season (Arroyo 1997, Terraube & Arroyo 2011). Eggs are also an important part of the diet in other populations of Montagu's Harrier; for example, in Netherlands (Koks et al. 2001), Poland (Wiącek & Niedźwiedź 2005) and Russia (Davygora 1995). However, during the incubation period, when foreign eggs appear, food is provided by the male to the female in an aerial foodpass. The female does not carry food to the nest, eating in specific feeding places away from it (Clarke 1996). In western France, a Grey Partridge *Perdix perdix* egg was found in a Montagu's Harrier nest (Arroyo, B., pers. obs.). In this region, the diet of Montagu's Harriers is based almost exclusively on voles (Millon *et al.* 2002), which is also inconsistent with the hypothesis that foreign eggs are transported to nests as potential food.

Instead, our data suggest that the most likely explanation of the occurrence of mixed clutches in Montagu's Harrier nests is a maladaptive brood parasitism attempt by the galliform species. Both Quail and Red-legged Partridge are common breeders in the farmland-dominated study areas. Quail females are known to lay eggs in nests of different species to increase the probability of a successful clutch (Madge & McGowan 2002) including Skylark Alauda arvensis (Prang et al. 1995, Suárez et al. 2009) and Red-legged Partridge nests (Casas et al. 2010). Egg coloration and egg size of Quail, Skylark and Partridge are relatively similar (Harrinson & Castell 1998); therefore, brood parasitism is likely between these species. The fact that harrier nests with mixed clutches had smaller eggs than nests without mixed clutches suggests a possible misidentification of harrier eggs by the galliforms, leading to this maladaptive strategy. Additionally, harrier clutches with smaller eggs are likely to belong to younger or poorly fed females (Salamolard 1998, Millon et al. 2008), which may have lower nest attendance, thus facilitating the likelihood of brood parasitism by the galliforms. Alternatively, adults of harrier nests with bigger eggs may be more efficient at removal of the smaller, foreign eggs coming from galliforms. However, no evidence of such removal was found. In conclusion, the occurrence of mixed clutches in Montagu's Harrier nests may be due to the ground-nesting habits of the predator, and its relatively similar egg size to the opportunistic brood parasites involved.

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