Misdirected incubation in Common Kestrels *Falco tinnunculus*: a case of visual stimulus?

José Carrillo-Hidalgo

Carrillo-Hidalgo J 2022. Misdirected incubation in Common Kestrels *Falco tinnunculus*: a case of visual stimulus? Biodiversity Observations 12: 46-53
27 May 2022
DOI: 10.15641/bo.1225
Introduction

Nesting sites are a resource that has ecological effects on individual fitness, population density, and community structure (Newton 2013). The availability of suitable nesting sites may lead to interspecific competition resulting in usurpation of these resources, bringing about, occasionally, mixed interspecific clutches. With the exception of brood parasitism cases in birds, it is rare to observe misdirected incubation within cavity-nesters and there seems to have been an involvement, in most cases, of secondary cavity-nesters (Wiebe 2000). Among raptors, secondary cavity-nesters rely on cliff ledges, burrows, tree cavities or artificial structures such as buildings.

Several nest usurpation behaviours have been documented in species of raptors that compete with other non-raptor species (Newton 2013). Some species of raptors have been found to incubate waterfowl (Anatidae) eggs. For instance, Osprey Pandion haliaetus and Canada Goose Branta canadensis laying in the same nest (Fannin 1894); American Kestrel Falco sparverius incubating and hatching a Bufflehead Bucephala albeola egg and their own clutch (Dawson & Bortolotti 1997); Eastern Screech-Owl Megascops asio incubating and hatching a Wood Duck Aix sponsa eggs (Artuso 2007). Regarding the Common Kestrel Falco tinnunculus, Shrub (1993) mentioned a mixed interspecific clutch of this falcon species and Jackdaws Corvus monedula in the same nest.

In 2020, I filmed a wild Common Kestrel pair incubating a clutch of two feral pigeon Columba livia eggs (plus two more fertile feral pigeon eggs added at a later date by the author) in a rocky cavity used alternately by both species. This misdirected incubation by kestrels was observed during ongoing long-term research studying the influence of climatic variability on the reproductive ecology of the Common Kestrel Falco t. canariensis, the subspecies occurring in the western Canary Islands and Madeira (Kangas et al. 2018).

The study area comprises a southern xerophytic scrub in Granadilla de Abona (0–275 m a.s.l.) on Tenerife Island (27°55′ and 28°40′N, 16–17°W; Canary Islands archipelago), 292 km (at the closest point) off the coast of Morocco. The vegetation is predominantly composed of Euphorbia balsamifera, E. canariensis, Plocama pendula, Schizogyne sericea, Ceropogia fusca, Launaea arborescens and Argyranthemum...
spp. The climate is characterised by arid and semiarid conditions with frequent strong winds (del Arco et al. 2006).

The kestrels on Tenerife Island are single brooded, breed as solitary pairs and generally nest in rocky cavities or ledges on cliffs in areas characterised by weathered pyroclastic and basaltic deposits. They do not construct a nest per se, but instead lay eggs directly on the rocky, earthy or sandy surface, sometimes in a shallow scrape. The mean laying date of the population is 15 March (SD = 13.0, range: 5 March–7 April, N = 162 clutches) and the mean clutch size is 4.50 (SD = 0.74, range: 3–6, N = 162 clutches; Carrillo-Hidalgo et al. 2020). Interspecific nest-competition with other syntopic species such as Long-eared Owl Asio otus and, especially, feral pigeons Columba livia is common in the study area (Carrillo-Hidalgo unpubl. data). Because the population of pigeons has increased in the study area over the last nine years (2012–2020), this species usually takes over the suitable nesting sites for kestrels (Carrillo-Hidalgo unpubl. data).

Methods and Materials

From 2007–2020 (except 2017), we monitored 58 nesting sites in which kestrels have been known to lay eggs. Every year, each potential nesting site was monitored from the start of the breeding season in February until June, when the last fledglings leave their nests. Regular visits to the 58 nesting sites were made to determine laying date, clutch size, brood size, age of nestlings (at each visit) and number of fledglings.

The observations of the Common Kestrels’ misdirected incubation behaviour were made near to agricultural greenhouses and a goat enclosure (distance < 400 m). The nesting site was located in an old disused reservoir, excavated in a pyroclastic deposit (259 m a.s.l.), in which four cavities are currently used by feral pigeons as roosting and breeding-sites. Records show that kestrels bred in the most suitable cavity (the habitual cavity), oriented towards the east, for eight years from 2007. In 2018, pigeons bred in the habitual cavity and kestrels bred in a rocky cavity (the secondary cavity) 6.33 m away from the same wall of the habitual nesting site and 3.90 m above the ground.

To confirm this unusual incubation behaviour in the kestrels, I set up a GoPro HERO 3+ camera (GoPro, Inc., San Mateo, CA, USA) and hid it on a ledge at the entrance of the nesting site. I filmed the incubation behaviour of the kestrel pair for a total duration of 3 hours 20.2 minutes, in separate sessions on three days (6, 14 and 22 April 2020). Filming started at 11h35, 10h15 and 14h10 solar time on these three days. We checked the focal kestrel territory from 18 March to 20 May weekly.

Results

On 18 March 2020 (the first day of observation in this kestrel territory), the habitual cavity was unoccupied and the secondary cavity contained a clutch of two feral pigeon eggs (Figure 1). We did not observe the kestrels on this date.

When we checked the habitual cavity on 31 March, we observed a non-ringed female kestrel leave the secondary cavity. Closer inspection of this secondary cavity revealed a nesting site containing a clutch of two feral pigeon eggs.

On 6 April I observed a female kestrel leave the secondary cavity again and I verified that the two pigeon eggs were warm (Figure 2). In addition, the habitual cavity contained a pigeon nest with two eggs. Both cavities that had been used by kestrels to nest in the reservoir (the habitual cavity and the secondary cavity) were now occupied by pigeons in 2020. Therefore, the kestrels were not able to lay any eggs. On viewing the camera footage filmed on this day, I was able to confirm that the female was the first of the pair to return to the nest, 19 min 03 s after my departure. The footage also showed how she turned over the pigeon eggs, and she is only replaced by the male for 2 min 44 s (Figure 3). At 18h00 solar time on 6 April, to probe the intensity of the instinct of the kestrel’s incubation, I transferred two fertile eggs from the pigeons’ nesting site in the habitual cavity to the secondary cavity.

On 14 April the female kestrel was observed incubating all four warm pigeon eggs, and she hid in the deepest part of the cavity when she was aware of my presence.
Figure 1: Nesting rocky cavity with the feral pigeon’s *Columba livia* usual clutch of two eggs which was incubated by kestrels *Falco tinnunculus*. Credit: José Carrillo-Hidalgo
Figure 2: Female kestrel incubating the feral pigeon’s *Columbia livia* eggs. Credit: José Carrillo-Hidalgo.
Figure 3: Male kestrel incubating the feral pigeon’s *Columbia livia* eggs. Credit: José Carrillo-Hidalgo.
On this date, the camera footage showed that only the female incubated the four pigeon eggs, and she returned to the nest 17.4 minutes after my departure.

However, on 22 April there was only one cold pigeon egg left in the nest and the kestrels were no longer present in the area. No kestrels were sighted in the area from that day onwards.

The camera footage allowed me to monitor the incubation by both the female (2 hours 3.5 minutes) and the male kestrel (2.7 minutes). It also enabled me to determine that the appropriate EURING age code for both birds was code 8 (hatched three or more years ago) (Forsman 1999, EURING 2020).

**Discussion**

To our knowledge, this misdirected incubation represents the first record of a Common Kestrel incubating eggs in a non-raptor species’ nest in the wild. Interspecific competition for nesting sites is common in birds, including several cliff-nesting raptor species (Newton 2013). Nest usurpation may result from an increase in the population size of the usurping species and the limited availability of suitable nesting sites (i.e. nest holes). Indeed, feral pigeons find abundant food daily in the goat enclosure 391 m away from the reservoir and this has led to an increase in the feral pigeon population which competes with the kestrels for nesting sites. This suggests that there is competition for this particular site in the reservoir because there are alternative nesting sites (rocky cavities in the weathered volcanic relief) in the neighbouring ravine in which the kestrels can breed.

This unusual incubation behaviour may have biological disadvantages for kestrels. For instance, it can lead to an increase in daily energy expenditure especially for the male, to tend to reproductive activities (Masman et al. 1986). The male is responsible for hunting and provisioning food for the female and the family, at least, until the chicks are 15 days old (Masman et al. 1989). In fact, any reproductive effort reduces the parent’s residual reproductive value (Clutton-Brock 1991), and increased parental effort in kestrels is associated with an increased risk of death next year (Daan et al. 1996). Also, incubating eggs in a pigeon’s nest implies some potential parasitism costs because this columbiform is known to be associated with a larger parasitic load and a greater diversity of ectoparasites (Møller 1990, Haag-Wackernagel & Bircher 2010). Increased energy demands of incubation due to high ectoparasitic load can influence a bird’s health and physical condition (Potti & Merino 1995, Valera et al. 2004) and, consequently, it could affect future fecundity or survival (Williams 2012). In addition, in the case of the pigeon clutch not being abandoned by them, the kestrel pair could run a risk of fighting against nest-owner pigeons.

Some external stimuli visually detected by birds (e.g. nest, clutch) can trigger physiological and behavioural reactions which fit the conditions for incubation (Hall 1987). However, certain foreign objects such as pebbles and other stones, pieces of guano, snails, pine cones, mammalian bones or golf balls also may act as an incubation stimulus in birds (Knight & Erickson 1977, Coulter 1980, Mellink 2002, Langlois et al. 2015, Power et al. 2018). The female kestrel attracted by the visual stimulus of pigeon eggs, and without any suitable nesting-sites in which to lay her own eggs, was apparently stimulated enough to incubate them. I interpreted the misdirected incubation behaviour in this pair of kestrels as a process mediated by the external stimulus of pigeon eggs (Steen & Parker 1981, Beukeboom et al. 1988).

Falcon breeders take advantage of this kind of behaviour. For instance, to translocate a pair of nesting Peregrine Falcons *Falco peregrinus* from one building to another nearby, falcon breeders remove their fertile eggs and place a fake clutch of chicken eggs in another nest tray on the chosen building. Within several hours, the female Peregrine Falcon incubates the fake clutch. Later, falcon breeders replace the fake eggs for the original ones (DM Bird, McGill University, 2021, unpubl. data).

Because I also filmed the incubation of pigeon eggs by the male kestrel, it is plausible that female-male auditory interactions were enough to stimulate the male to join her (Village 1990). Because this kestrel pair was attracted to incubating pigeon eggs, which are very different in colour, shape and size to those of kestrels (Harrison 1977), one might consider this to be a characteristic behaviour of an “accepter-species” (i.e. those that lack recognition of their own eggs, even non-mimetic eggs; Rothstein 1975).
Acknowledgements

Field work was performed with the permission of the Canary Government (Cabildo de Tenerife). I am especially grateful to DM Bird for suggesting certain references and for his meticulous review of an earlier version of this manuscript. In addition, an earlier version of this manuscript was improved by the comments of JM Aparicio and T Birkhead. D Calzadilla-Uttley helped with the English. Suggestions from the editors improved the manuscript.

References

Artuso C 2007. Eastern Screech-owl hatches Wood Duck eggs. Wilson Journal of Ornithology 19: 110–112.

Beukeboom L, Dijkstra C, Daan S, Meijer T 1988. Seasonality of clutch size determination in the Kestrel Falco tinnunculus: An experimental approach. Ornis Scandinavica 19: 41–48.

Carrillo-Hidalgo J, González-Dávila E, Molina-Borja M, Fernández-Lugo S 2020. Lizard provisioning and breeding success of kestrels inhabiting an island xeric environment. Journal of Arid Environments 181: 104224. https://doi.org/10.1016/j.jaridenv.2020.104224

Clutton-Brock TH 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey (USA).

Coulter MC 1980. Stones: an important incubation stimulus for gulls and terns. Auk 97: 898–899.

Dawson RD, Bortolotti GR 1997. Misdirected incubation in American Kestrels: a case of competition for nest sites? Wilson Bulletin 109 (4): 732–734.

del Arco M, Pérez de Paz PL, Acebes JR, González-Mancebo JM, Reyes-Betancort JA, Bermejo JA, de Armas S, González-González R 2006. Bioclimatology and climatophilous vegetation of Tenerife (Canary Islands). Annales Botanici Fennici 43: 167–192.

EURING – The European Union for Bird Ringing 2020. The EURING Exchange Code 2020. Helsinki, Finland. ISBN 978-952-94-4399-4

Fannin J 1894. The Canada Goose and Osprey laying in the same nest. Auk 11: 322.

Forsman D 1999. The raptors of Europe and the Middle East. A handbook of field identification. T & A D Poyser, London (UK).

Haag-Wackernagel D, Bircher AJ 2010. Ectoparasites from feral pigeons affecting humans. Dermatology 220: 82–92 DOI: 10.1159/000266039

Hall MR 1987. External stimuli affecting incubation behaviour and prolactin secretion in the duck (Anas platyrhynchos). Hormones and Behavior 21: 269–287.

Harrison C 1977. Guía de campo de los nidos, huevos y polluelos de España y de Europa, Norte de África y Próximo Oriente. Ediciones Omega, Barcelona (Spain).

Kangas VM, Carrillo J, Debray P, Kvist L 2018. Bottlenecks, remoteness and admixture shape genetic variation in island populations of Atlantic and Mediterranean Common Kestrels Falco tinnunculus. Journal of Avian Biology e01768.

Knight RL, Erickson AW 1977. Objects incorporated within clutches of the Canada Goose. Western Birds 8: 108.

Langlois LA, Murböck K, Bulla B, Kempenaers B 2015. Unusual incubation: Long-billed Dowitcher incubates mammalian bones. Ardea 100: 206–210.

Masman D, Gordijn M, Daan S, Dijkstra C 1986. Ecological energetics of the European Kestrel: Field estimates of energy intake throughout the year. Ardea 74: 24–39.

Møller AP 1990. Effects of parasitism by a haematophagous mite on reproduction in the Barn Swallow. Ecology 71: 2345–2357.

Newton I 2013. Bird populations. HarperCollins Publishers, London (UK).
Potti J, Merino S 1995. Louse loads of Pied Flycatchers: Effects of host’s sex, age, condition and relatedness. Journal of Avian Biology 26: 203–208.

Power A, Newton S, O’Connor I 2018. Common Terns Sterna hirundo incubating Common Garden Snail shells Helix aspersa on Rockabill Island. Seabird 31: 88–91.

Rothstein SI 1975. Mechanisms of avian egg-recognition: do birds know their own eggs? Animal Behaviour 23: 268–278.

Shrubbs M 1993. The Kestrel. The Hamlyn Publishing, London.

Steen JB, Parker H 1981. The egg-“numerosat”. A new concept in the regulation of clutch-size. Ornis Scandinavica 12: 109–110.

Valera P, Hoi H, Darolová A, Kristofik J 2004. Size versus health as a cue for host choice: A test of the tasty chick hypothesis. Parasitology 129: 59–68.

Village A 1990. The Kestrel. T & A D Poyser, London.

Wiebe K 2000. Northern Flicker incubates Hooded Merganser egg. British Columbia Birds 10: 13–15.

Williams TD 2012. Physiological adaptations for breeding in birds. Princeton University Press, Princeton.