First documented case of Tawny Pipit *Anthus campestris* nest parasitism by Common Cuckoo *Cuculus canorus* in Spanish steppes

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Abstract - Interspecific brood or nest parasitism is a relatively common breeding behavior in birds. Through this reproductive tactic, brood-parasites avoid the costs associated with raising and maintaining chicks by laying their eggs in the nests of the host species in which they are specialized. The common cuckoo (*Cuculus canorus*) follows this brood parasite strategy. Female cuckoos lay their eggs in the nests of other bird species, mimicking egg shape, size, and color of the host species. In this paper we report the first documented case of parasitism of tawny pipit nests by the common cuckoo in Spanish steppe habitats, where no record of parasitism on this species has been reported to date.

Key words: Breeding behavior, breeding strategy, brood-parasites, interspecific interactions, nest host species.

Riassunto - Primo caso documentato di parassitismo di un nido di calandro *Anthus campestris* da parte del cuculo *Cuculus canorus* nelle steppe spagnole.

Il parassitismo interspecifico della covata o del nido è un comportamento riproduttivo relativamente comune negli uccelli. Attraverso questa tattica riproduttiva, i parassiti di cova evitano i costi associati all'allevamento e al mantenimento dei pulcini deponendo le uova nei nidi della specie ospite nella quale sono specializzati. Il cuculo (Cuculus canorus) segue questa strategia di parassitismo di cova. Le femmine di cuculo depongono le uova nei nidi di altre specie di uccelli, imitando la forma, le dimensioni e il colore delle uova della specie ospite. In questo lavoro riportiamo il primo caso documentato di parassitismo di nidi di calandro da parte del cuculo in habitat steppici spagnoli, dove finora non sono stati registrati casi di parassitismo su questa specie.

Parole chiave: comportamento riproduttivo, parassitismo di cova, cuculo, calandro, Spagna.

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INTRODUCTION

To avoid the costs of raising their offspring, brood-parasites lay their eggs in the nests of host species, which will take over the subsequent parental care of the parasitized chicks (Davies, 2000; Payne, 2020). This behavior is known as interspecific brood- or nest-parasitism (Payne, 2020). This breeding strategy carries a high reproductive cost for the hosts, as the parasitic brood usually monopolizes parental care, preventing its nestmates from feeding properly, and may even lead to the elimination of the rest of the clutch, both in the egg and hatching stages (Davies, 2000; Avilés & Parejo, 2011).

The common cuckoo *Cuculus canorus* is an example of an obligate-nest parasite (Honza *et al*., 2001; Cramp & Simmons, 2004), known to potentially parasitise multiple host species (Lowther, 2015). Females do not construct their own nests, but lay an egg in a different species nest, which is incubated and subsequently fed by the parental hosts, with a nestling period of 17-18 days (Payne *et al*., 2020).

To avoid or reduce the risk of rejection of parasitic eggs by hosts, cuckoo females generate replicas of the host species eggs in shape, size, and coloration (Avilés & Møller, 2004). These patterns of parasitism avoidance and host response are typically evolutionary arms races in which a greater degree of specialization on the part of the parasite should result in greater success. However, hosts also evolve to detect and reject parasitic eggs. Given the enormous variety of host species (more than 125 passerines species are parasitized by the common cuckoo in Europe; Lowther, 2015; Campobello & Sealy, 2020), the generation of egg replicates by common cuckoo females represents an interesting adaptation, where groups of females prefer the nest of a particular host species to lay their eggs. Several alternatives have been proposed to explain the maintenance of egg mimicry. The 'host preference' hypothesis suggests that cuckoos parasitize a single

species with which it matches in color and spotting pattern (Baker, 1942; Lack, 1968). Some studies provide strong evidence endorsing this hypothesis as the most plausible (Moksnes & Røskaft, 1987; Marchetti *et al*., 1998, Davies, 2000, Gibbs *et al*., 2000; Campobello & Sealy, 2009; but see Honza *et al*., 2001), as well as other alternatives which are not mutually exclusive. For example, the 'nest site' hypothesis (Wyllie, 1981; Moksnes & Røskaft, 1987) predicts that each female cuckoo parasitizes a group of host species with similar eggs or nesting sites. The 'habitat imprinting' hypothesis (Teuschl *et al*., 1998) predicts that common cuckoos will establish their home ranges in areas consisting primarily of habitat similar to their natal habitat. Lastly, the 'natal philopatry' hypothesis (Brooke & Davies, 1991) predicts that one-year-old birds tend to return to the place where they were born.

The tawny pipit *Anthus campestris* is a small passerine (16.5-17 cm, Cramp, 2004; Tyler & Christie, 2020) typical of steppe habitats, and for which little information is available about its breeding biology and ecology, particularly in Spain (see review in Calero-Riestra, 2015). The species arrives in Spain in March and reaches its peak densities in May (Tyler & Christie, 2020). Nest construction, which is primarily built by the female, is on the ground, in a small cavity filled with dry green material. Construction lasts between 3 and 4 days in Spanish populations (Calero-Riestra, 2015). Eggs are sub-elliptical, white, or gray with brown, reddish, ochre, or black spots. Average egg size is 21.9 mm long (23.8 mm maximum) and 15.7 mm wide (16.6 mm maximum) (Calero-Riestra, 2015). One egg is laid each day until the full clutch is laid, with incubation beginning between the penultimate and last egg (Calero-Riestra, 2015). Incubation usually lasts 14 (13-15) days in Spain (Calero-Riestra, 2015). Modal clutch size is 4 eggs (1-5) (Calero-Riestra, 2015). Nestlings are semiprecocial (Cramp & Simmons, 2004), leave the nest after 14 days, and still take another 7 days to fledge (Calero-Riestra, 2015).

Tawny pipit nest parasitism by the common cuckoo has been generically mentioned in Europe (Cramp & Simmons, 2004), but has not been documented for Spain to date (Calero-Riestra, 2015). In this paper we report the first case of tawny pipit nest parasitism by the common cuckoo in Spanish steppe habitats.

METHODS

The work has been carried out in Altos de Barahona and Paramo de Layna Special Protection Areas (SPAs). These are two relevant areas for the conservation of steppe birds such as Dupont's lark *Chersophilus duponti*, the greater short-toed lark *Calandrella brachydactyla*, Thekla's lark *Galerida thecklae* or the tawny pipit. The SPAs are located in south Soria (central Spain), and are plain plateaus around 1150 m above sea level, dominated by short shrubs such as *Genista pumila*, *G. scorpius*, *Thymus spp*. and *Satureja intricata*. The climate is continental Mediterranean, with a mean temperature of 10.6 °C and a mean annual rainfall of 500 mm.

During four consecutive breeding seasons (2016-2019), we conducted a steppe bird census and monitored nests. All nests found came both from fortuitous findings or from actively searching through parental tracking after finding a breeding adult, usually carrying bait in its beak. Nests were geo-referenced, and the status in which they were found was noted (under construction, with eggs, with nestlings, abandoned). Afterwards, nests were monitored every 2-8 days (mean ± SD= 4.14 ± 2.19 days), avoiding interfering with adults, and manipulating the eggs only to check if the nest had been abandoned. Phenological phase (eggs incubation, hatching, fledging) was noted in each visit. When possible, prior to fledging, chicks were metal banded, and biometric, blood and feces samples were taken for subsequent analysis.

RESULTS

Over the four breeding seasons studied, nine tawny pipit nests were found and monitored (2016: 3; 2017: 1; 2018: 1; 2019: 4), of which only one (11.1%) found in 2019 was parasitized. Monitoring dates are presented in Table 1.

As indicated in Table 1, the deposition of the parasitic egg could have occurred between May 23 to May 26. Up to 4 different observers (AB, JGC, MR, DB), all with long experience in detecting and monitoring steppe passerine

Tab. 1 - Parasitized nest monitoring. For each phenological phase the date (ascertained or estimated) is indicated. Ascertained dates coincide with monitoring days, whereas probable dates refer to the estimate made based on what was observed on monitoring days. / Monitoraggio dei nidi parassitati. Per ogni fase fenologica è indicata la data (accertata o stimata). Le date accertate coincidono con i giorni di monitoraggio, mentre quelle probabili si riferiscono alla stima effettuata sulla base di quanto osservato nei giorni di monitoraggio.

Phenological phase	Ascertained date	Estimated date
Nest construction (Fig. 1A)	May 16	
Nest construction	May 20	
1st egg	May 22	
2nd egg		May 23
3rd egg		May 24
4th egg		May 25
Parasitic egg		May 23- 26
Start of incubation		May 26
Incubation with 5 eggs	May 28	
Incubation with 5 eggs	May 31	
Incubation with 5 eggs	June 4	
End of incubation (hatching)		June 6
Eggs hatched with cuckoo chicken (Fig. 1B)	June 12	
Predated (Fig. 1C)	June 14	June 13

nests, monitored the nest between May 26 to June 4. None of them detected differences between eggs, so parasitism was not described until hatching (June 12). The parasitic chick expelled all eggs from the nest and remained in the nest being fed by the adults until the nest was predated (Fig. 1).

DISCUSSION

While Old World cuckoos use more than 125 species as hosts (Lowther, 2015; Campobello & Sealy, 2020; Payne *et al*., 2020), this is the first record of common cuckoo parasitism on a tawny pipit nests in Spain. Despite the wide host diversity, female cuckoos show medium-high specificity, aiming to lay eggs that mimic those of their hosts (Baker, 1942; Lack, 1968; Moksnes & Røskaft, 1995; Avilés & Møller, 2004). This suggests a high capacity for egg size and color modification within the species. In fact, this nest parasitism was indistinguishable from tawny pipit eggs, despite the long experience of observers.

There are some unknowns about the common cuckoo's ability to lay nearly identical mimic eggs resembling those of the host. While this ability has been neglected by some authors (Moksnes & Røskaft, 1995), others have investigated it (Avilés & Møller, 2004). Interestingly, a high degree of mimicry is to be expected in host-parasite systems that have coexisted for a long time in their evolutionary history, so despite this being the first documented case of egg-laying parasitism of a tawny pipit nest in Spain, it cannot be ruled out that this is a more frequent phenomenon that has gone unnoticed until now.

The highly skilled egg mimicry, given the large number of species parasitized by common cuckoos (Lowther, 2015; Payne, 2020), could be explained by several hypotheses. According to the 'habitat imprinting' hypothesis, the search for nests to parasitize could be guided by habitat structure and/or nest selection (Honza *et al*., 2001). That is, there would be groups of cuckoos that parasitize nests with similar characteristics (on the ground, small) in similar habitats (open shrub steppe), for which they would generate eggs with similar shapes and colors. Honza *et al*. (2001) described a pattern of shape and coloration of common cuckoo eggs that they called the *pipit pattern* due to the high similarity found in eggs deposited in the nests of ground-nesting species. Eggs of different coexisting ground-nesting steppe bird species (skylark, Dupont's lark, Thekla lark, greater short-toed lark) share shape, size and coloration, which is consistent with the habitat and nest selection hypotheses (Honza *et al*., 2001). In addition, the parasitized nest in this case was relatively close to a tree, which could have increased the risk of parasitism (Tyler & Christie, 2020). Even though ground-nesting host species have lower rejection rates than species that breed in trees or shrubs (Martín-Vivaldi *et al*., 2013), parasitism of nests located on the ground should be an unsuccessful strategy, due to the high risk of predation (Yanes & Suárez, 1995). To avoid this, when chicks are threatened, they expel dark, foul-smelling liquid from their cloaca. This repellent is especially effective for mammalian predators (Payne, 2020). Notwithstanding, nest parasites should optimize their nest selection strategy to reduce other risks in addition to egg detection and expulsion by hosts.

The parasitic chick expelled all other eggs from the nest, causing their deaths, which is a common behavior (Davies, 2000). The tawny pipit is a migratory bird with a relatively late arrival to the breeding areas. Thus, there is a narrow temporal margin for the tawny pipit to lay second clutches, for which there is anecdotal evidence (Calero-Riestra, 2015). The individual effect of losing the entire clutch may represent a very high reproductive cost for the parents, since predation rates in steppe ground-nesting birds are exceedingly high, sometimes exceeding 80% of the eggs (Yanes & Suárez, 1995; Calero-Riesta, 2015).

In this work we provide data describing the first record of common cuckoo parasitism on a tawny pipit nest in Spain. These are data to expand the list of birds parasitized by the common cuckoo, though much work is still needed to define the selection pattern of parasitized nesting behavior in the common cuckoo.

Fig.1 - A) Tawny pipit nest building. B) Tawny pipit nest with cuckoo chick and C) predated nest with one of the tawny pipit eggs out of the nest. / A) Costruzione del nido di calandro. B) Nido di calandro con pulcino di cuculo e C) nido predato con una delle uova di calandro fuori dal nido. (Photos / Foto: TEG-UAM team).

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