Among passerines, aggression towards conspecific nests has been reported in two different scenarios, reflecting either a shortage of nesting places among cavity nesters, or as parental investment among polygynous species, but has been reported only rarely in monogamous, open ground-nesting species such as larks. We video-monitored ten Dupont’s Lark nests. This declining species has a patchy and restricted distribution in Iberia and northern Africa. We detected aggression toward one nest, during which a female deserted her clutch after being attacked by another Dupont’s Lark. This is the first record of nest abandonment resulting from intraspecific agonistic behaviour in the Alaudidae family. The high density and proximity of territories of Dupont’s Lark in the study area seems a likely explanation for such agonistic behaviour, which may be a neglected cause of nest failure in shrinking Dupont’s Lark populations living in small habitat patches.

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by more than 50% to only about 2,200 pairs; several populations have been completely extinguished in this period (Tellé et al. 2005; Pérez-Granados & López-Iborra 2013, 2014). The species mainly occurs in small and isolated habitat patches, in which it reaches greater densities than in continuous areas due to dispersal limitations (Vögeli et al. 2010; Pérez-Granados & López-Iborra 2013). Dupont’s Lark is a resident, territorial species, whose males respond quickly and aggressively towards intruders (De Juana et al. 2004; Garza et al. 2005). Inter-annual movements are very limited (mean dispersal movements are about 100 m) and most adult males retain their territories each year (Laiolo et al. 2007). There is very little published data on Dupont’s Lark breeding biology (but see Cañadas et al. 1988 and Herranz et al. 1994). Nest failure rate (46% to 84%) is high in this species, and avoiding nest predation is assumed to be the main driver of breeding success (Suárez et al. 2009). However, the effects of other environmental factors on breeding success seem not to have been considered. This study describes the first observation of nest failure in Dupont’s Lark resulting from intra-specific agonistic behaviour.

MATERIALS AND METHODS

We used continuous video surveillance to monitor ten Dupont’s Lark nests between 2011 and 2014, as part of an intensive study on the species in low scrub areas located in Rincón de Ademuz (40°05’N, 1°20’W, Valencia, Spain; see Study Area in Pérez-Granados & López-Iborra 2013). Nests were found by systematic searching and by observing the behaviour of adult larks, and were visited every two days once located. Nest activity was monitored by small video cameras (40×40×60 mm) provided with twelve infrared LEDs for night recording and a portable video recorder with motion detection, both powered by a 12V/44Ah automotive battery. Each camera was set 0.5 m from a nest and 1–3 cm above the ground. Cameras were connected to recorders by means of cables, and installed at distances of c20 m from a nest to minimize potential researcher effects. The recorders were housed in cryptic, weatherproof plastic boxes (80×170×230 mm) connected to a battery with a 2 m cable. Batteries were also protected in cryptic plastic bags, and cameras and cables were painted brown with spots.

If parents were not already ringed, they were captured and colour-ringed soon after locating a nest with chicks, or seven days later if it was found with eggs, to ensure that capture took place during the second half of the incubation period, during the time in which clutch desertion is unlikely (Herranz et al. 2000). Males were caught with a small spring-trap and females were captured with a passive trap located over the nest, which was only used for 15 min to minimize disturbance at the nest (Herranz et al. 2000).

We calculated the mean length of incubation bouts, measured as the elapsed time between two consecutive recordings during which the female entered and left the nest. We analysed possible alterations in female behaviour during the incubation period by comparing mean length of incubation bouts between days using one-way ANOVA.

RESULTS

Out of the ten nests monitored, six were successful (at least one chick fledged), three failed because of predation, and one nest (video-monitored in 2012) was attacked by an unmarked Dupont’s Lark during the incubation period. This nest was found partly built on 5 April. The first egg was laid in it on 13 April, and the camera was installed on 16 April, one day after completion of the clutch. After excluding videos in which bird behaviour could not be identified (e.g., a bird quickly crossing the recording frame), we analysed a total of 197 video recordings of this nest including 72 minutes of bird activity (mean duration of 21.4 ± 5.1 seconds per video). As the system only records images when it detects movement, it did not record the incubating female when she was motionless. A video recording made at 06:45 on 25 April, two days before the estimated hatching date, showed an unmarked Dupont’s Lark approaching the nest and attacking the incubating female from the front. The incubating female responded to the intruder and both individuals fought with their bills, not using their legs or claws. They continued fighting while walking and without flying, but almost immediately left the camera’s range (Fig. 1, Scenes A, B, and C). After the agonistic event, we continued video monitoring for four days and obtained six additional recordings, four on the same day that the aggression occurred and two on 27 April. All videos showed the female nest owner returning to her nest, looking at the clutch and promptly leaving the nest without incubating the eggs (Fig. 1, Scenes D, E, and F).

The unmarked lark did not return to the nest and no
other activities were recorded at the nest during the last two days of monitoring. The aggressor did not damage the eggs in any way. No agonistic behaviour was recorded during the nine days that the nest had been previously monitored. Furthermore, we found no evidence indicating that the female was disturbed on preceding days by aggression that could have occurred out of frame. The mean duration of incubation bouts was fairly homogeneous throughout the incubation period (ANOVA: $F_{7,75}=0.14; P=0.99$) and was very similar to that of successful nests (Cristian Pérez-Granados & Germán M. López-Iborra unpublished). No birds other than incubating parents were recorded at the other nests monitored during this study, and no nest was abandoned.

On the morning of 16 May, we found the breeding pair’s replacement nest, which contained three one-day-old chicks. Subsequent video monitoring revealed that all chicks successfully left the nest after eight days.

**DISCUSSION**

Dupont’s Lark is known to engage in territorial behaviour involving both sexes (Garza et al. 2005) and confrontations between males, fighting with their bills (De Juana et al. 2004; Suárez et al. 2009). Our results provide the first report of intraspecific aggression toward an incubating female in this species and the first evidence that this type of aggression can lead to nest failure, in this case by nest abandonment. There is no previous description of a similar behaviour in the family Alaudidae (De Juana et al. 2004; Suárez et al. 2009).

Intraspecific competition is expected to increase as density increases and as resource availability becomes limiting (Rosvall 2008; Yoon et al. 2012). During the year in which the agonistic behaviour was recorded, Dupont’s Lark density in the study area (1.12 males/10 ha; Cristian Pérez-Granados & Germán M. López-Iborra unpublished) was four times higher than the mean density estimated for Spanish populations (0.27 males/10 ha; Suárez 2010). Strict habitat selection of the species leads to the concentra-
tion of territorial males in areas where vegetation is more similar to the optimum resulting in even higher densities (Garza et al. 2005; Seoane et al. 2006) at a local scale. Mean distance between activity centres of neighbouring territorial males in our study area was only 95.45±35.41 metres (Cristian Pérez-Granados & Germán M. López-Iborra unpublished). This distance equals a radius of about half of that of a circle comprising the average territory core area estimated in one of the largest Spanish populations of the species (112.8 m in Layna moorland; Garza et al. 2005). Moreover, prior to the agonistic behaviour recorded, three male Dupont’s Larks had been ringed within a circle of 150 m around the attacked nest, and another two males were ringed within the same area after the incident. All of this evidence (small territories and high male densities) suggests strong intraspecific competition in our study area.

Proximity and overlap between territories is known to increase the frequency of aggressive behaviour (Rosvall 2008; Yoon et al. 2012), and is thought likely to have facilitated the attack on the incubating female. Some aggressive interactions have been observed between male Greater Short-toed Larks Calandrella brachydactyla with adjacent nests, but these agonistic acts were never directed towards incubating females (Jesús Herranz pers. com.). Unfortunately, it was not possible to identify the sex of the aggressor, which could shed more light on the causes of the aggression.

Population densities as high as the one estimated in our study area are not rare in Spain. Vögeli et al. (2010) and Pérez-Granados and López-Iborra (2013) found a negative relationship between Dupont’s Lark density and patch size, such that density was higher in habitat patches smaller than 200 ha. This pattern has been interpreted as an indicator of the existence of dispersal limitations, which promote an increase in density as the area of habitat patches shrinks (Vögeli et al. 2010; Pérez-Granados & López-Iborra, 2013). Thus, aggression at nests might be more frequent than previously presumed in isolated and fragmented habitats where populations reach high densities.

In contrast to intraspecific nest aggression observed in other species (Belles-Isles & Picman 1986; Hansson et al. 1997), in the event that we documented, the eggs were not punctured. If this is the norm for Dupont’s Lark, the outcome of such aggressive interactions would be indistinguishable from abandonment provoked by other causes and the percentage of deserted nests could set a maximum for the frequency of this behaviour. Unfortunately, only two studies have focussed on the breeding biology of Dupont’s Lark; one of them was based on a very small sample size (four nests, Cañadas et al. 1988) and the other did not report the causes of nest failure (Herranz et al. 1994). Therefore, no previous data relating to the frequency of nest abandonment exist for this lark. Considering studies of related species (Suárez et al. 2009), 5.2–10.8 % of failed nests of four lark species in the Mediterranean region were attributed to abandonment (Mean=7.5 %; N=559), after excluding obvious causes such as storms or cattle trampling. Abandonment occurred mainly during the incubation period, and thus there is room for the type of aggression we have described to occur in these species as well.

This study has revealed that intraspecific agonistic behaviour towards incubating females could be an overlooked cause of nest failure. Our data suggest that if these types of failures occurred more frequently than previously thought in dense but shrinking Dupont’s Lark populations, they could contribute to the decline of the species in some areas. However, this hypothesis is based on very few observations, thus a larger sample of nests should be video-monitored in different Dupont’s Lark populations to assess the frequency of this behaviour in different areas.

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REFERENCES

Nest failure owing to agonistic behaviour in Dupont’s Lark


