

Conspecific density and habitat quality drive the defence and vocal behaviour of a territorial passerine

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Territorial defence depends on highly interrelated factors such as food abundance and conspecific density. We used Dupont's Lark *Chersophilus duponti* as a model species to evaluate the response of a territorial bird to a foreign male playback, examining how conspecific density, habitat quality and male body condition impact responses. The study was conducted in central Spain with variable male density. Response (yes/no), latency time, distance to the playback speaker, and the number of songs and other vocalizations were monitored for 5 min. Habitat quality was estimated using BlueNDVI vegetation index extracted from high-resolution drone imagery, which is a proxy for arthropod prey biomass. Conspecific density (Kernel Density Estimator) and male body condition were calculated to assess their effect on response and intensity. We applied generalized linear mixed models (GLMMs) to determine which factors predicted the response and its intensity. There was a greater response probability in areas with a higher density of conspecifics and in areas of poorer habitat quality (i.e. lower BlueNDVI values). In contrast, latency time was longer in areas with lower conspecific density. Intrasexual communication (singing and calling rates) increased with habitat quality. Intraspecific communication (other vocalizations) increased in poorer quality habitats and at a higher density of conspecifics. Body condition was not related to any variables. Our results suggest that male density, sometimes used as an indicator of an area being well conserved for the species, may reflect areas of poorer habitat quality occupied by unpaired floater males, whereas paired territorial males would occupy and defend higher quality areas, leading to lower density.

Keywords: breeding season, food availability, intraspecific competition, male density, territory defence.

Territorial defence is described in a wide variety of taxa and occurs when one individual continuously defends an area against the presence or the intrusion of conspecifics (Christensen & Radford 2018) or heterospecifics (Garcia & Arroyo 2002, Peiman & Robinson 2010, Barrero *et al.* 2023b). The 'active territorial defence' hypothesis predicts that individuals, pairs or groups of territorial animals defend a fixed area to obtain preferential access to resources such as food, mates and optimal

breeding sites (Brown 1964, Golabek *et al.* 2012). When these resources are essential, primarily during the breeding season, the territory can be characterized as an exclusive use space (Barg *et al.* 2005) that is defended against intruders, especially individuals of the same sex and species (Barg *et al.* 2005, Begon *et al.* 2006).

In general, intraspecific aggression depends on a wide range of interrelated factors, such as food availability, timing within the breeding cycle and conspecific density (Garcia & Arroyo 2002, Yoon *et al.* 2012, Niederhauser *et al.* 2021). Territorial behaviour can therefore have important effects on population structure and dynamics by reducing

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intraspecific competition through a cost–benefit relationship that regulates population density (López-Sepulcre & Kokko 2005). Territorial behaviour may ensure the necessary resources for survival and breeding (López-Sepulcre & Kokko 2005, Botero & Vehrencamp 2007), which makes it critical to the understanding of animal ecology (Adams 2001).

Variation in the intensity of territorial defence and the sex targeted for exclusion may indicate the resource being competed for (i.e. food or a mate; Carrillo & González-Dávila 2013). Territorial defensive behaviours may be expressed by one or a combination of aggressive or visual displays and acoustic signals (Darwin 2008, Kodric-Brown & Brown 2015). The ‘dominance hypothesis’ predicts that large body size should be associated with a high fitness, high dominance and high feeding rank, and that this association between morphology and behaviour should become more intense under conditions of intense intraspecific competition (e.g. Persson 1985, Craig & Douglas 1986). Therefore, territorial behaviour, together with other traits driven by sexual selection, such as body size (Price 1984), plumage colouration (White 2020) or body condition (Peig & Green 2009), may accurately reflect the relative quality of the individuals (Kodric-Brown & Brown 2015), their hierarchical position and the quality of the territory they hold (i.e. honest signals; Kipper *et al.* 2006, Golab *et al.* 2013, Moreno 2016, Beltrão *et al.* 2021).

The expression of honest signals may be critical for female mate choice but may also reduce the risk or intensity of intrasexual competition (Kipper *et al.* 2006, Bradbury & Vehrencamp 2011), a costly behaviour for individuals. In the case of songbirds, territorial defence is typically performed by males (Catchpole & Slater 2008) and is often regulated by acoustic communication (Brumm & Todt 2004). Acoustic communication is defined as the active transmission from a sender to a receiver and, as predicted by the ‘dual function’ hypothesis, has generally been associated with critical aspects of the avian life cycle, such as mate attraction and territory defence (Catchpole & Slater 2008, Bradbury & Vehrencamp 2011, Hill *et al.* 2018). In addition, the intensity and quality of acoustic signals may also be determined by the abundance of conspecifics, leading to changes in signal redundancy, as well as in the typology, spectral and temporal characteristics of vocalizations (Hamao *et al.* 2011, Barrero *et al.* 2020).

Acoustic communication in birds has great variability and can generally be expressed in the form of songs or calls (Araya-Ajoy & Dingemanse 2014). Songs are long and elaborate signals whose primary function is related to attracting a potential mate and intrasexual competition (Slagsvold *et al.* 1994, Catchpole & Slater 2008), whereas calls are innate, structurally simpler and usually produced to maintain contact within a group, alarm to danger, signal food or during confrontations with other individuals (Marler 2004, Catchpole & Slater 2008). Other simpler and low-amplitude vocalization types are also known, for which both intra- and intersexual communication functions are assumed: these are clucks and alarms (Todt & Naguib 2000, Wright & Dahlin 2007). It has been suggested that the complexity of acoustic emissions can be an honest indicator of male quality (Catchpole & Slater 2008, Cramer 2013).

In birds, population structure and territorial systems are dominated by breeding adults, whereas juveniles and immatures are subordinate, with lower survival rates and less success in territory acquisition and mating (Newton 1998, Campioni *et al.* 2010). As a result, immatures may show differences in habitat preference, selection and use compared with adults (e.g. Campioni *et al.* 2010, 2012). Floater males (Moreno 2016) are individuals with no territory to defend (Penteriani *et al.* 2011) but they still exert pressure on breeding adults by competing for territory or mates (López-Sepulcre & Kokko 2005, van de Pol *et al.* 2007). Thus, a floater male may occupy the vicinity of good-quality territories to gain knowledge of the area and conspecifics (Smith 2015), learning from territorial male singing (‘acoustic mimicry’ hypothesis; see Craig & Jenkins 1982), make extra-pair copulation attempts (Moreno 2016) or wait for such a territory to become available (Golab *et al.* 2013). This interference competition from floater males may result in intense territorial mate guarding behaviour in territorial males, which can lead to a density-dependent decrease in reproductive success (Moreno 2016).

Here, we performed a playback test aiming to assess whether there are differences in the behavioural response probability of a highly territorial passerine with high vocal activity as a function of (1a) conspecific density and (1b) habitat quality. We also aim to evaluate whether the intensity of the response varies with (2) habitat quality, conspecific density and close intrasexual competition. Finally, we assessed whether (3) the intensity of the

response depends on the physical condition of the males. The sequential order of the objectives reflects an increase in complexity and a parallel decrease in sample size (i.e. in the third objective only those males that responded to the test, which were ringed and for which we had biometric information, were considered in the analyses). We performed a single experiment in several localities with different population densities, where we measured habitat quality (in terms of food availability), intra-sexual competition and the physical condition of individuals. We measured different movement and presence parameters (response probability, latency time and minimum distance to the playback) and different song performance parameters (vocal activity rate, singing rate, calling rate, alarm rate and clucking rate) which could be honest signals of individual quality in many songbird species, as they have a direct energetic cost (Cramer 2013, Searcy *et al.* 2014). Therefore, according to the 'active territorial defence' hypothesis, we expect a higher probability of territorial response, with a shorter latency time and more intense response (greater number of vocalizations) in areas with higher conspecific density due to higher competition for food or mates. In agreement with the 'dominance' hypothesis, we expect that better quality territories will be defended with a greater number and intensity of territorial responses and to be occupied by males with better physical condition (Ardia 2005, Kipper *et al.* 2006). These males will show more immediate response and a higher vocal intensity (mainly through complex vocalizations, such as songs and calls; Deoniziak & Osiejuk 2020), whereas males in poorer physical condition will show greater wariness of confrontation (mainly through simple vocalizations, such as alarms and clucks). We expect this contrast will be more pronounced in areas of higher male density, where intrasexual competition is also greater (Yoon *et al.* 2012).

METHODS

Study species

Dupont's Lark *Chersophilus duponti* is a shy and elusive species, and is very difficult to detect visually. It is a threatened steppe passerine (IUCN 2022) whose territorial behaviour has never been studied previously. The species' breeding season in the study area (see below) runs from the end of February to late June (Pérez-Granados *et al.* 2017,

Barrero *et al.* 2023a). It is a species described as socially monogamous, although extra-pair copulations may occur (Gómez-Catasús *et al.* 2016). It is distributed in territorial aggregations even on a small scale, mainly due to the reduction and fragmentation of the available habitat (Laiolo & Tella 2005, Tella *et al.* 2005), where males maintain a territory throughout the year, increasing the intensity of territorial behaviour during the breeding season (Garza *et al.* 2005, Pérez-Granados & López-Iborra 2015), encouraged by a male-biased sex ratio (0.79; Vögeli *et al.* 2007). Their vocal activity is mainly composed of territorial calls, songs and alarm calls emitted by males only (Laiolo *et al.* 2007, Pérez-Granados *et al.* 2018). Territorial calls (calls hereafter) consist of short whistles that have the function of announcing a male's identity within territories (Laiolo *et al.* 2007), whereas the song is a complex acoustic vocalization consisting of four or five sequences that are repeated in the same order and used in a sexual context during reproduction (Laiolo *et al.* 2008, Laiolo & Tella 2008). Pérez-Granados *et al.* (2018) suggested that the song is not a target for sexual selection by female choice based on seasonal changes of vocal activity but may instead be directed at nearby males. Therefore, singing activity would be determined by sexual selection by male competition, whereas calls may be mainly related to mate attraction, as evidenced by the relaxation of calling activity after the first months of the breeding season (Pérez-Granados *et al.* 2018). Alarms, on the other hand, consist of two to four repeated units and are presumably emitted by males to repel conspecific or predator intruders from their territories (Laiolo *et al.* 2005). Although the clucking call in Dupont's Lark has not been previously described, it is a common low-intensity vocalization uttered during the breeding season in all surveyed populations (A. Barrero pers. obs). Its function is unclear but field observations suggest that it is an intraspecific warning signal unique to the species (other similar alarm calls are mimicked by other larks; see Laiolo *et al.* 2005).

Study area

The study area is in the Iberian System (Soria and Guadalajara provinces, central Spain; Fig. 1). It spreads over shrub-steppe habitats, partially within the Special Protection Areas for Birds (SPAs) of 'Altos de Barahona' and 'Paramos de Layna'

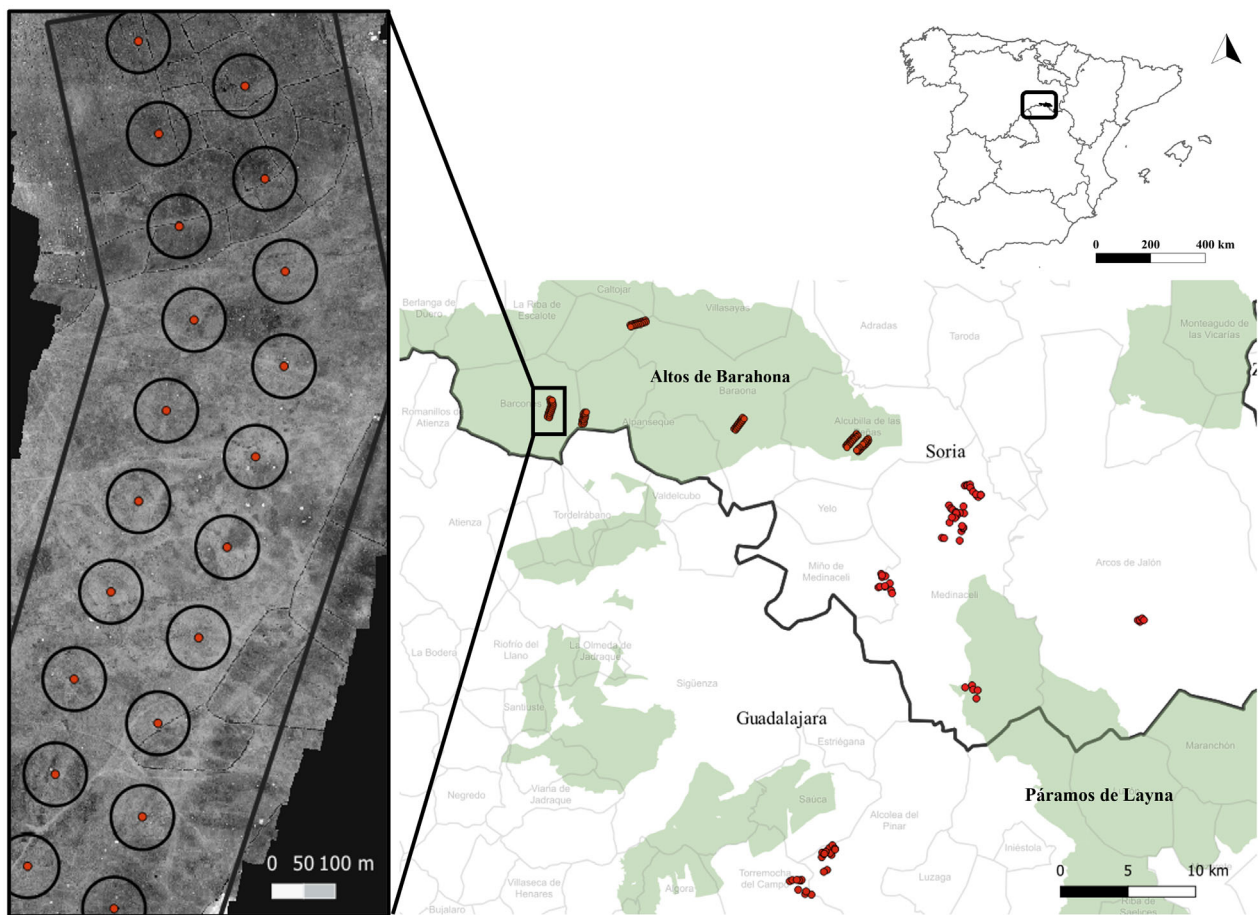


Figure 1. Location of the study area. Inset is of the study area in southern Soria and northern Guadalajara. The centres of the sampling stations (red dots) are represented. The name and area of the Special Areas of Conservation (SAC) and Special Protection Areas for Birds (SPA) of the European Union's Natura 2000 Network (ES4170148 and ES4170120, respectively) are shown in green. The sampling plots in the inset are shown with a sampling buffer of 50×50 m (black line). The sampling plots are overlaid with the high-resolution UAV imagery from which the BNDVI values were extracted.

(ES4170148 and ES4170120, respectively; Fig. 1). The landscape is characterized by flat areas dominated by short shrubs (< 50 cm), such as *Thymus* spp., *Genista pumila*, *Genista scorpius* and *Lavandula latifolia*, a high proportion of bare soil, and a smaller area of cultivated fields and scattered trees (see Gómez-Catasús *et al.* 2019, Zurdo *et al.* 2021). The density of Dupont's Lark males per locality ranges from 0 to 2.15 males/10 ha, one of the highest densities in the Iberian Peninsula (Traba *et al.* 2019; Table 1).

Study localities and plots

Between 2016 and 2017, we sampled 15 localities separated by 1–20 km (mean \pm sd 8.03 ± 6.77 ;

Fig. 1) where the area of shrub-steppe habitat ranged from 5 to 318 ha. A locality is defined as a set of habitat patches separated by < 1 km (García-Antón *et al.* 2021). To address objective 1a, we sampled the 15 localities (Table 1) that made up the study area. To address objectives 1b, 2 and 3, six specific plots were delimited in five of the sampled localities (see Barrero *et al.* 2023b for a more detailed description), all of them within the SPA 'Altos de Barahona'. The surface area of the plots ranged from 53 to 72.3 ha (61.0 ± 9.19 ; Table 1). All localities had similar characteristics: an elevation of approximately 1150 m. a.s.l., a slope $< 10\%$ and similar plant communities (see Zurdo *et al.* 2021 for a complete description of the plant community).

Table 1. The total area, number of sampling points and male density of Dupont's Lark per sampled plot. The locality name and sampling year is also given.

Locality	Plot	Area (ha)	Sampling stations	Density (males/10 ha)	Year
Blocona	–	318	21	0.389	2016
Yuba	–	21	13	0.633	2016
Ambrona	–	220	11	0.515	2016
Sierra Ministra	–	287	1	0.083	2016
Sagides	–	118	5	0.203	2016
Esteras	–	5	5	0.250	2016
Las Morras	–	300	6	0.156	2016
La Raída	–	25	6	0.255	2016
Las Huesas	–	12	6	0.554	2016
San Lorenzo	–	44	7	0.164	2016
Barcones	Barcones	72	20	2.153	2017
Marazovel	Marazovel	53	14	0.213	2017
Barahona	Barahona	70	16	1.433	2017
Rello	Rello	70	18	0	2017
Alcubilla de las Peñas	Alcubilla de las Peñas 1	55	17	0.170	2017
	Alcubilla de las Peñas 2	55	18	0.044	2017

Dupont's Lark censuses

Dupont's Lark territories were mapped between March and June of both sampling years (2016 and 2017) using the territory mapping method, the recommended census method for monitoring this species (Pérez-Granados & López-Iborra 2017). A transect of approximately 2 km long crossed the centre of each patch of potential habitat, and all vocalizing males within a bandwidth of 500 m on either side of the transect were georeferenced (GPS error ± 5 m), assuming full detectability within the bandwidth (see Pérez-Granados & López-Iborra 2017). Surveys started approximately 1 h before sunrise, the peak vocal activity for Dupont's Lark, and lasted about 40 min. Transects were repeated three times during the spring, alternating the starting point on each visit. One of the visits was always carried out in the week before performing the behavioural tests (see below). Dupont's Lark territories were defined by gathering observations over multiple visits and considering all birds heard simultaneously. Density estimates were obtained by dividing the total number of territories by the amount of available habitat (ha) at each plot.

Capture, ringing and individual marking of males

Captures and ringing of individuals were carried out using spring-traps baited with mealworms

Tenebrio molitor and using a species-specific recording to attract them. In total, 79.7% of males censused in the week before the behavioural tests were captured. We captured and ringed the individuals 1 week in advance of the behavioural test to reduce any post-capture stress. Trapped birds were ringed using metal and coloured rings to allow individual recognition during behavioural testing. The following morphological measurements were taken: wing length, length of the 8th primary (P8) and tail length to the nearest 1 mm using a ruler; tarsus length (bent toes) using a digital calliper (accuracy 0.01 mm); and body mass using a digital balance to the nearest 0.1 g. All trapped birds were assigned to sex using biometric discriminatory functions in hand (see Vögeli *et al.* 2007). The age of birds could not be resolved beyond them being adults, due to the moulting pattern of the species (Svensson 1992).

Behavioural tests

In April/May 2016 and 2017, between one and 21 sampling stations were placed in each locality (Table 1) depending on the surface area of the locality. Stations were regularly spaced 250 m apart to reduce the risk of overlap with adjacent male territories (Garza *et al.* 2005) and the risk that playback would be heard by neighbouring males. Consecutive playback experiments were separated by a minimum of 20 min. We opted for such a procedure as we aimed to cover whole

habitat patches and not just the locations with known presence of territorial males, especially due to the high presence of floater males in the species (Suárez *et al.* 2009). To prevent different stimuli from eliciting different responses (de Kort *et al.* 2009), at every station we played the same male playback stimulus, consisting of a sequence of different vocalization types (songs, calls and alarms) recorded in high quality from three Dupont's Lark males from different areas of the distribution range, excluding the study area. The stimulus was always played in the same order and at the same volume from a stationary vehicle after waiting for 5 min after arrival to reduce the potential effect of car intrusion into the territory. The playback was then activated for up to 15 min (maximum). If during this time the presence of a male was detected, the behavioural test began without disabling the playback. For 5 min we recorded the behavioural response of males (see below; Table 2). Individual recognition was based on the colour ring code. If the male left the

sampling station before the test ended, response rates were adjusted to the experimental time elapsed. If no individual responded to the call within 15 min, the test was recorded as 'no response' and observers moved to the next sampling station. Sampling was carried out from sunrise to approximately 3 h after sunrise and only during days with suitable weather conditions (no rain or wind). Only sampling stations within the plots (where we measured habitat quality, Table 1) were sampled a second time, 3 weeks after the end of the first round, thus covering most of the breeding period of the species.

Behavioural variables

Eight variables were considered characteristic of the territory defence behaviour of male Dupont's Larks. We measured three variables related to bird movement and presence (Bollen 2003, Montesana *et al.* 2020): response (yes/no); latency or time to test response (seen or heard), defined as the time

Table 2. Behavioural variables used to measure playback response intensity.

	Variable	Description	Objective(s)	Measure
Response	Response (yes/no)	Response or non-response to playback at the sampling stations	1a, 1b	-
	Minimum distance	Minimum distance of the individual to sampling station	2, 3	m
	Latency time	Time elapsed since the playback is activated until an individual responds	2, 3	s
	Vocal activity rate	Sum of all vocalizations/time	2, 3	c/s
	Singing rate	Songs/time	2, 3	cc/s
	Calling rate	Calls/time	2, 3	r/s
	Alarm rate	Alarms/time	2, 3	r/s
	Clucking rate	Clucks/times	2, 3	ca/s
Explanatory	Phenology	Day on which the test was carried out. The first recording date (16 March 2016) was set as the baseline date (0), and the remaining dates were defined as the number of days to the baseline date	1, 2, 3	Day
	Hour	Time at which each behavioural test was conducted	1, 2, 3	h
	KDE	Probability of finding a male within the subpopulation, calculated from a kernel density map	1, 2, 3	kernel
	BlueNDVI	Indicator of habitat quality, as a proxy for arthropod biomass (food availability)	2, 3	num
	Nearest-neighbour distance	Shortest distance to the nearest territory centre	1, 2, 3	M
	Physical condition	Male quality as measured by body weight and tarsus	3	num
	Ringed bird	Difference between males ringed before or after behavioural tests	2	

A description and the objectives of the study in which they are used are included. Abbreviations: c/s, total rate of vocalizations, number of vocalizations divided by recording time in seconds; ca/s, clucking rate, number of clucks divided by recording time in seconds; cc/s, singing rate, number of complete songs divided by recording time in seconds; h, hour; m, metres; m/10 h, males per 10 ha; num, numeric; r/s, alarm rate, number of alarms divided by recording time in seconds; r/s, calling rate, number of calls divided by recording time in seconds; s, seconds.

elapsed (in seconds) since the test started until the male appeared; and minimum distance (in metres) of approach to the sampling station (Table 2). In addition, we measured five variables related to the acoustic response of males to the playback: vocal activity rate, singing rate, calling rate, alarm rate and clucking rate (Table 2). These different acoustic variables reflect song complexity in terms of duration, abundance and diversity (Boogert *et al.* 2008, Hill *et al.* 2015) and have been related to aggressiveness (Searcy *et al.* 2014, Kareklas *et al.* 2019).

Explanatory variables

To evaluate the intensity of intrasexual competition, we calculated two variables related to male density in each locality. First, we calculated a Kernel Density Estimator (KDE) function for each year using the male territory mapped in each year and locality (10 000 pixels). The KDE provides higher probability values to those areas with a larger number of territories, adjusting the assigned values according to the smoothing parameter (Worton 1989). Thus, the KDE of each plot and year can be interpreted as a surrogate of intrasexual competition at a landscape scale (Ryder *et al.* 2012, Yoon *et al.* 2012, Martínez-Padilla *et al.* 2014). We estimated KDEs using the SAGA Kernel Density Estimation function in QGIS v.2.18 (QGIS Development Team 2017) with a smoothing factor of 500 m, as this is the maximum home-range described for Dupont's Lark (37.3 ha; Garza *et al.* 2005, Gómez-Catasús *et al.* 2019). We then used a 50-m-radius buffer around each sampling station to calculate the average KDE value per sampling station. Secondly, we calculated the Euclidean distance from each sampling station to the nearest territory using territory locations recorded during territory mapping (nearest-neighbour distance hereafter).

In the case of covariates, to estimate the habitat quality per plot, the Blue Normalized Difference Vegetation Index (BNDVI) was used as a proxy of arthropod biomass (i.e. food availability for insectivorous birds; Table 2). The BNDVI was calculated exclusively on the six delimited and sampled plots (Table 1), extracting the information from high-resolution unmanned aerial vehicle (UAV) imagery. UAV images were collected in June 2017 using a fixed-wing drone (SRPAS model A2) flying 120 m above the ground (equivalent to a focal

length of 5.2 mm), which provided a ground resolution (GSD) of 4 cm/pixel. Strong correlations between arthropod biomass and BNDVI have already been shown for the study area (see complete methods and results in Traba *et al.* 2022). As with the KDE, we used a 50-m-radius buffer around each sampling station to average the BNDVI value per sampling station.

Next, to assess the effect of the physical condition of males on their response activity, a physical condition index (CI; Table 2) was estimated for every individual captured. We used the residuals of the regression between body mass and structural size as an index of individual body condition, following the procedure described by Peig and Green (2009). In our case, the body mass variable was weight (g) and the morphometric variable related to individual size was tarsus length (mm).

To control for the potential effect of previous capture on the behavioural response of males (Oñate-Casado *et al.* 2021), we included a fixed factor to differentiate ringed from unringed males. We also recorded the phenology (calendar date) and the sampling hour in which the behavioural tests were carried out to control for seasonal and diurnal variation of behavioural responses (Table 2).

Statistical analysis

Fixed covariates were z-standardized (mean = 0 and sd = 1), and log ($x + 1$) transformed to achieve linearity.

To determine whether the male response probability varied as a function of intrasexual competition (male density; objective 1a, Table 2) we built a generalized linear mixed model (GLMM) with a binomial adjustment ($n = 287$ sampling stations: year = 2016 and 2017). The response (yes/no) to playback was used as the response variable. The KDE value at each sampling station and the nearest-neighbour distances were used as predictors, in addition to date and time as covariates. Year was introduced as a fixed factor, and locality and sampling station as random factors.

Secondly, to determine whether the response (yes/no) varied as a function of habitat quality (objective 1b, Table 2), a second GLMM with a binomial adjustment was used, which included only the 2017 data ($n = 206$ sampling stations), the period for which drone flights were available. The response (yes/no) was again used as the response variable, and habitat quality (i.e. BNDVI)

values were used as a proxy of habitat quality, and KDE and nearest-neighbour distances were included as predictors. Date and time were included as covariates, and plot and sampling station as random factors.

The intensity of the male response to playback and its relationship with the predictor variables (objective 2, Table 2) was analysed only for the stations where a positive response occurred and information on habitat quality was available ($n = 69$ sampling stations; year = 2017). A separate GLMM (Gaussian error structure) was fitted for each behavioural and acoustic variable, including KDE, habitat quality (i.e. BNDVI), nearest-neighbour distance, ringed bird, date and time as covariates, and plot and sampling station as random factors.

Finally, to determine whether male body condition was associated with male response intensity (objective 3, Table 2), we used the subset of data for which biometric values were available ($n = 55$). A separate (Gaussian error structure) was constructed for each behavioural and acoustic response variable, incorporating the physical condition index, habitat quality (i.e. BNDVI), KDE and nearest-neighbour distance as predictors, date and time as covariates, and the plot and sampling stations as random factors.

All candidate models were ranked according to Akaike's information criterion corrected for small samples (AICc, Burnham & Anderson 2002). For each candidate model we calculated its Akaike weight (w_i), which represents the relative probability of a model being better than other candidate models, as well as the AICc differences (Δ_i). In cases where only one model was obtained in the interval $\Delta_i \leq 4$, this was considered to be the only plausible model. If more than one model was obtained within the interval $\Delta_i \leq 4$, they were all considered to be equally plausible (Burnham & Anderson 2002) and thus models were averaged using the formula revised by Burnham and Anderson (2004) to calculate the average coefficients and the unconditional standard errors (USEs). The relative importance of each variable in the final model was also calculated. Following Burnham and Anderson (2002), the effect of variables was considered significant when the 95% confidence interval of their estimator did not contain the zero value. All analyses were performed using R software (v.3.5.2; R Core Team 2017) and the packages 'lme4' (Bates *et al.* 2014), 'MuMin' (Barton 2010) and 'car' (Fox *et al.* 2012).

RESULTS

Of the 287 sampling stations visited over the two sampling years, birds responded at 109 stations, of which 69 were recorded within plots where habitat variables were measured and from which we had biometric data for 55 different males.

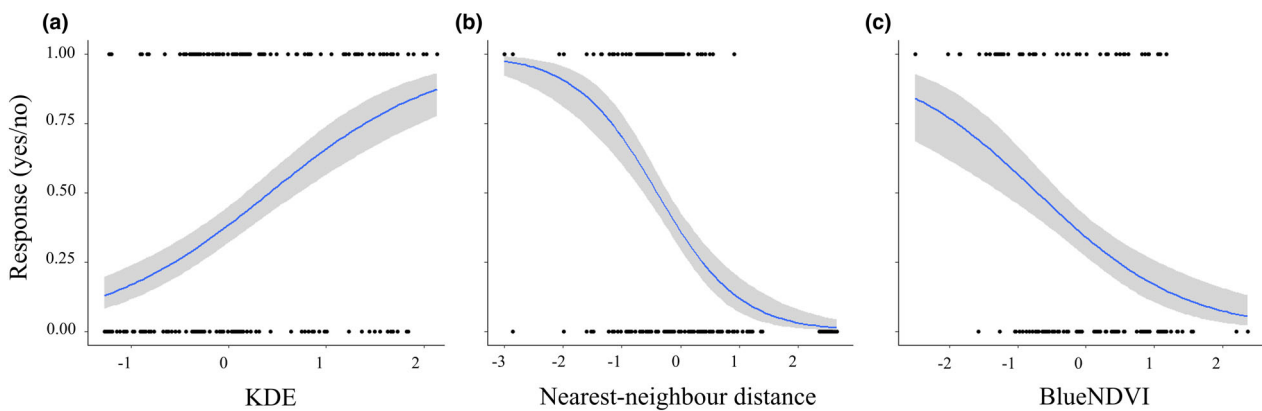
The probability of response of male Dupont's Larks increased significantly in areas with a higher density of males, both at the landscape scale (KDE: $P < 0.05$) and at the local scale (nearest-neighbour distance: $P < 0.05$), both effects with similar but opposite magnitudes (Table 3; Fig. 2a,b). When habitat quality was incorporated in the model, male response probability increased significantly in plots with higher male density at the landscape scale (KDE: $P < 0.01$) but significantly less so in areas of higher habitat quality (BlueNDVI: $P < 0.05$), with male density exerting twice the effect of habitat quality (Table 4; Fig. 2c).

When testing whether the response intensity of male Dupont's Larks varied as a function of habitat quality, male density, competition and phenology variables (date and time), we observed that male physical condition was not incorporated in the averaged model (within $\Delta_i \leq 4$) for any of the response variables analysed (SOM Appendix S1: Table S1). We therefore refitted all models without this variable to obtain more robust results by using a larger sample size ($n = 287$ vs. 55 behavioural tests with information on male physical condition), because main results remained unaltered. The following results (Table 5) showed:

- 1 latency time was significantly higher in areas with lower male density (KDE: $P < 0.05$; Fig. 3a) and at the end of the survey period ($P < 0.01$), with KDE having twice as strong an effect as phenology;
- 2 the vocal activity rate (Fig. 3b) and the calling rate (Fig. 3c) were higher in areas with higher habitat quality (in both cases $P < 0.05$);
- 3 the singing rate was significantly higher in areas with lower male density at the landscape scale (KDE: $P < 0.01$; Fig. 3d) but with higher male density at the local scale (shorter nearest-neighbour distances: $P < 0.05$; Fig. 3e), although the effect at the landscape scale was three times higher;
- 4 the alarm rate was higher in areas with poorer habitat quality ($P < 0.05$; Fig. 3f), in areas with higher male density at the landscape scale

Table 3. Regression coefficients and confidence intervals from GLMMs of the response probability of male Dupont's Larks ($n = 271$).

Response variable	Predictor variables	Estimate	se	Confidence interval		P-value
				2.5%	97.5%	
Response (yes/no)	Intercept	-0.448	0.54	-1.499	0.605	0.404
	KDE	0.878	0.42	0.105	1.650	0.025
	Nearest-neighbour distance	-0.784	0.48	-1.502	-0.065	0.032
	Date	0.202	0.20	-0.173	0.578	0.291
	Hour	0.162	0.28	-0.283	0.608	0.476
	Year 2017	-1.056	0.66	-2.359	0.246	0.112

Significant P -values are highlighted in bold.**Figure 2.** Effect of 'Kernel Density Estimator' (KDE) (a), 'Nearest-neighbour distance' (b) and 'BlueNDVI' (c) on the response probability of male Dupont's Larks in the study area. Variables on the x-axis are log-transformed. Mean (blue lines) and 95% Bayesian credible interval (BCI) (grey surfaces) are depicted.**Table 4.** Regression coefficients and confidence intervals from GLMMs of the response probability of male Dupont's Larks, also incorporating the effect of habitat quality.

Response variable	Predictor variables	Estimate	se	Confidence interval		P-value
				2.5%	97.5%	
Response (yes/no)	Intercept	-1.079	0.469	-2.006	-0.151	0.022
	KDE	1.665	0.508	0.511	2.819	0.004
	Nearest-neighbour distance	-0.582	0.046	-1.500	0.334	0.213
	Date	0.065	0.022	-0.371	0.503	0.767
	Hour	-0.103	0.023	-0.560	0.353	0.656
	BNDVI	-0.822	0.036	-1.549	-0.094	0.026

Significant P -values are highlighted in bold.

(KDE: $P < 0.05$) and at the beginning of the survey period ($P < 0.05$), with BNDVI having twice the effect of phenology and KDE in this model;

- 5 the clucking rate increased in areas of poorer habitat quality ($P < 0.05$; Fig. 3g);
- 6 the proximity of approach to the playback was lower in males ringed the week before the

Averaged model	Parameter	Estimate	se	Adjusted se	Z	P-value
Latency time	(Intercept)	-0.007	0.25	0.25	0.03	0.975
	Phenology	-0.26	0.13	0.13	2.07	0.038
	KDE	-0.46	0.17	0.18	2.57	0.010
	Ringed bird	-0.28	0.32	0.33	0.88	0.376
	Hour	0.12	0.12	0.12	0.98	0.328
Vocal activity rate	(Intercept)	0.07	0.26	0.27	0.27	0.786
	BNDVI	0.29	0.12	0.13	2.26	0.023
	Ringed bird	0.27	0.29	0.30	0.91	0.359
Calling rate	KDE	-0.18	0.15	0.16	1.11	0.266
	(Intercept)	0.09	0.35	0.35	0.27	0.783
	BNDVI	0.41	0.18	0.19	2.20	0.027
	Ringed bird	0.34	0.26	0.27	1.26	0.206
Singing rate	KDE	0.15	0.19	0.19	0.77	0.437
	(Intercept)	0.25	0.62	0.63	0.40	0.683
	KDE	-0.63	0.23	0.24	2.65	0.007
	Nearest-neighbour distance	-0.26	0.13	0.13	2.03	0.042
	BNDVI	0.31	0.19	0.20	1.57	0.115
Alarm rate	Phenology	0.18	0.09	0.10	1.79	0.072
	Ringed bird	-0.04	0.25	0.26	0.18	0.853
	(Intercept)	-0.16	0.31	0.31	0.52	0.603
	BNDVI	-0.41	0.18	0.18	2.24	0.024
	Ringed bird	0.42	0.29	0.30	1.40	0.161
	Phenology	-0.26	0.13	0.13	2.03	0.042
	Hour	-0.19	0.12	0.12	1.55	0.121
Clucking rate	KDE	0.24	0.12	0.12	1.97	0.048
	(Intercept)	0.05	0.23	0.23	0.23	0.821
	BNDVI	-0.38	0.17	0.18	2.14	0.032
	Ringed bird	0.35	0.30	0.31	1.13	0.260
	KDE	0.20	0.12	0.13	1.59	0.111
	Hour	-0.20	0.12	0.12	1.67	0.095
Minimum distance	Nearest-neighbour distance	-0.16	0.12	0.12	1.32	0.189
	(Intercept)	-0.73	0.35	0.36	2.05	0.041
	Ringed bird	-0.99	0.24	0.24	4.10	<0.0001
	Nearest-neighbour distance	-0.13	0.10	0.10	1.31	0.191
	KDE	0.09	0.16	0.17	0.56	0.576

Averaged coefficient of the selected mixed models ($\Delta AICc < 4$; Estimate), standard error (se), adjusted se, Z-statistic (Z), and P-values are shown. Significant P-values are highlighted in bold.

behavioural tests than for unringed males ($P < 0.01$).

DISCUSSION

This is the first experimental work providing evidence of territorial behaviour of this highly elusive and threatened species and, more specifically, of its defence and territorial and social organization during the breeding season. We found that male Dupont's Larks varied their territorial defence as a function of two main factors: male density (as a

proxy for intrasexual competition) and BNDVI (as a proxy for food availability and hence habitat quality). This study has shown that male Dupont's Larks were more likely to respond in areas with a high male density at a landscape scale (KDE; an increase of 1 KDE in male density multiplies the odds of response by $e^{1.665} = 5.286$), which also corresponded to areas of poor habitat quality (SOM Appendix S2: Fig. S1). Responses in areas of poor habitat quality were mostly in the form of alarms and clucks. Conversely, the intensity of territorial response (more songs and calls) was greater in areas

Table 5. Model averaging results for each behavioural response variable for male Dupont's Larks.

with low male density at the landscape scale but with high habitat quality and great intrasexual competition at a local scale (distance to the nearest territory), even though males also took longer to respond to the acoustic intrusion. Our results suggest that males located in territories with higher habitat quality (i.e. higher BNDVI, higher arthropod biomass) inhabit areas with a lower density of conspecifics and defend their territory more intensely, emitting more complex songs and at a higher vocal rate. In contrast, males located in poorer quality areas behave like floaters, and responded quickly but cautiously to the simulated intrusion of a foreign male, emitting alarms (with lower statistical power) and clucks, but not showing intensive territory defence. These results should, however, be considered cautiously as our predictors of habitat quality and intrasexual competition were based on a single proxy. Further research should aim to consider a larger number of surrogates to provide a more complete measurement of habitat quality and intrasexual competition.

As we predicted, and in agreement with the 'active territorial defence' hypothesis, we found a strong positive relationship between the behavioural response of male Dupont's Larks and conspecific density, with a strong effect at both landscape and local scales. The positive influence of landscape-scale male density (KDE) and negative effect of the distance to the nearest territory on the number of male responses indicate that male Dupont's Larks responded more in areas with a high density of conspecifics and high local intraspecific competition, respectively. Similar results have been found in populations of Orange-crowned Warblers *Oreothlypis celata*, where levels of aggression in response to simulated territorial intrusions were higher in areas with higher densities of conspecifics (Yoon *et al.* 2012). When habitat quality was incorporated into the model, male Dupont's Larks responded more in areas with higher landscape-scale male density (KDE), but poorer-quality areas (lower BNDVI values), with the effect shown by KDE being twice that of BNDVI. More competitive breeding environments may lead to greater territorial response (Pérez-Granados & López-Iborra 2015), though this may carry associated additional costs when resource exchange is a priority. In general, in birds, higher quality territories are occupied by adult males of better individual quality (Moreno 2016) whereas young satellite males are more likely to be relegated to suboptimal areas in

lower quality habitats (Laiolo *et al.* 2008, Penteriani *et al.* 2011, Gołab *et al.* 2013) where there are sufficient resources for survival but not for nesting (Penteriani *et al.* 2011).

As we hypothesized, the latency time of the male response was shorter as competition increased (higher KDE values), especially at the end of the survey period. Kareklas *et al.* (2019) found that male European Robins *Erithacus rubecula* that emitted more complex songs had a shorter response latency and sang more often, which was positively related to individual display intensity. In contrast, here we found that males with a shorter response latency were those with the lowest singing rate. Accumulation of floater males in suboptimal areas (Laiolo *et al.* 2008, Penteriani *et al.* 2011, Gołab *et al.* 2013) could explain why males occupying these areas responded faster to playback than those inhabiting areas with a lower male density (low KDE values). Faster responses occurred at a lower singing intensity (as total vocalizations increased with BNDVI) than from males that already occupy an optimal territory. This assumption agrees with prior studies, such as that by Garamszegi *et al.* (2006), where young and inexperienced male Collared Flycatchers *Ficedula albicollis* showed shorter latency periods than older males, which have a selective advantage in finding breeding partners more quickly. In our case, although it has half the effect of KDE, response latency increased as the breeding season advanced, which suggests a more active search for an optimal and available breeding territory during the first half of the breeding period (Gołab *et al.* 2013). Our results suggest that territorial adult Dupont's Lark males may occupy higher quality territories earlier than younger, less aggressive individuals, as seen in other species (Rosvall 2011, Scales *et al.* 2013), with the latter relegated to lower habitat quality locations, though in Collared Flycatchers such males do show an earlier willingness to fight (Garamszegi *et al.* 2006).

Higher vocalization and calling rates also occurred in areas of better habitat quality, and the singing rate was higher in areas with a lower male density at the landscape scale (KDE values), but with higher intrasexual competition at the local scale (the effect of nearest-neighbour distance being three times lower than the KDE). These findings suggest that more aggressive males defending better quality territories, which coincide with areas of lower density of conspecifics (see the

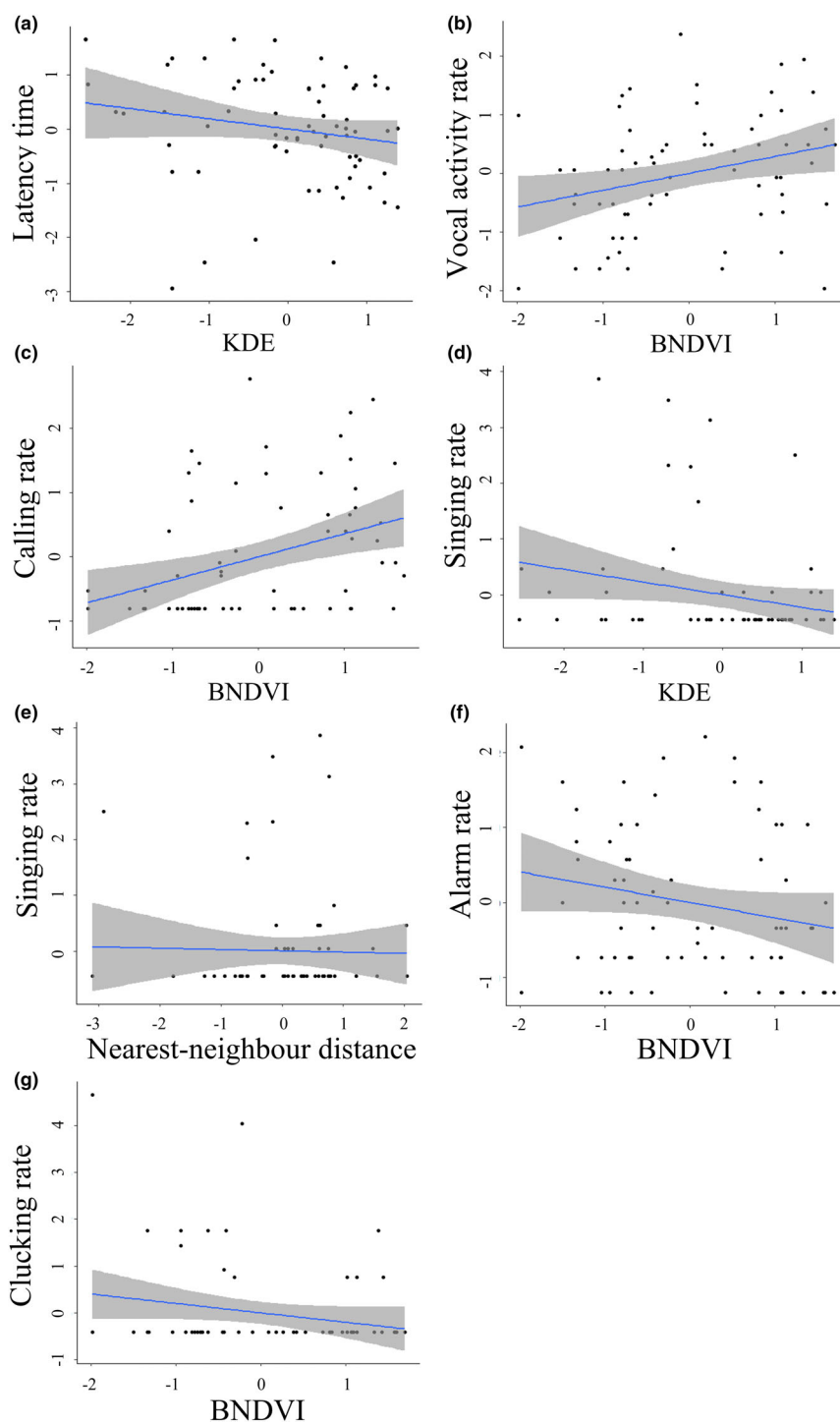


Figure 3. Effect of ‘Kernel Density Estimator’ (KDE), ‘BlueNDVI’ and ‘Nearest-neighbour distance’ on the acoustic response variables of male Dupont’s Larks in the study area. Variables are log-transformed and standardized. Mean (blue lines) and 95% BCI (grey surfaces) are depicted.

significant and negative linear relationship between the two variables in SOM Fig. S1), did so more actively through a greater number of vocalizations, mostly calls and songs (see also García *et al.* 2023). Male Dupont's Larks in this situation may emit vocalizations and territorial calls at a higher rate as a signal of a high willingness to defend an optimal breeding territory (Vögeli *et al.* 2007) or a mate, given the male-biased sex ratio in the species (Vögeli *et al.* 2007, Suárez *et al.* 2009). Male vocalization rate has been associated with motivation, arousal and level of aggression in several songbirds (Catchpole & Slater 2008), which may play an important role in mate choice and male-male competition (Szymkowiak & Kuczyński 2017, Opaev *et al.* 2019). Previous studies found that male Blackcaps *Sylvia atricapilla* settled in higher-quality territories with a lower density of conspecifics may display more intense territorial defence (Hoi-Leitner *et al.* 1995), which has been shown to correlate positively with reproductive success both with intra-pair copulations (Song Sparrows *Melospiza melodia*, see Reid *et al.* 2004, Potvin *et al.* 2015) and with extra-pair copulations (Great Reed Warbler *Acrocephalus arundinaceus*, see Leisler *et al.* 2000). These results suggest that male Dupont's Larks that respond most strongly to simulated intrusion may be paired, while nearby satellite or floater males in poorer quality territories would be waiting for their opportunity. Thus, dawn songs in this species would accomplish both territorial defence and attract potential mates or extra-pair copulations, as pointed out by Pérez-Granados *et al.* (2018), although definitive data to support this assumption are still needed (Laiolo *et al.* 2008).

Males relegated to poorer quality territories, which coincide with areas with higher male density, mainly used alarms and clucks when responding to playback, especially at the beginning of the survey period. This finding concurs with previous studies that observed male Dupont's Larks producing warning calls to repel intruders from their territories (Laiolo *et al.* 2005). As an intraspecific short and simple warning signal, unique to the species, the clucking call could be emitted for deterrence, threat or alarm purposes (Marler 2004, Catchpole & Slater 2008). Several studies support the hypothesis that alarm vocalizations may be adopted to defend resources as a less energetically demanding alternative to full song (Araya-Ajoy & Dingemanse 2014, Jurisevic *et al.* 2015), precisely

during a time (typically the beginning of the breeding season) when energy investment in breeding and foraging is particularly critical. A higher alarm rate during the first half of the breeding season is also in agreement with previous descriptive studies of Dupont's Larks (Pérez-Granados *et al.* 2018). Araya-Ajoy *et al.* (2016) showed that Great Tits *Parus major* that mostly used alarms as a response to intrusions achieved relatively low extra-pair breeding success. If these results are considered in the context of the low density of females in Dupont's Lark populations (Vögeli *et al.* 2007), areas of poorer habitat quality would be more likely to be occupied by unpaired satellite males.

Some work has shown that birds can learn from previous experiences and make future decisions accordingly (e.g. Bradbury & Vehrencamp 2011), which could make them more challenging to recapture (Oñate-Casado *et al.* 2021) or even alter their behavioural response (Budka *et al.* 2019). However, our findings suggest that territorial responses of male Dupont's Larks were not affected by previous experience. Behavioural responses were unaffected by earlier capture, but previously trapped males approached playback more closely than unringed birds. The given personality or description of the reactive-proactive (or shy-bold) continuum suggests that 'proactive' individuals are bolder, more aggressive and more risk-prone compared with individuals at the 'reactive' end of the continuum (Groothuis & Carere 2005), which may have ecological consequences. For instance, Wolf *et al.* (2007) stated that bold individuals tend to maintain a higher productivity associated with a potential cost to their survival, compared with shy individuals, which may explain why male Dupont's Larks that were previously captured also showed bold behaviour during later testing.

Finally, despite evidence from other studies correlating behaviour with body condition (Ardia 2005, Kipper *et al.* 2006), and contrary to our hypothesis based on the 'dominance hypothesis', response intensity did not vary with individual body condition. A positive relationship between vocal intensity in territorial defence and body condition has been described in many bird species (Cramer 2013, Searcy *et al.* 2014), though several authors have noted that body condition indices estimated using measures of mass and size do not sufficiently explain the individual's instantaneous energy reserves (Brown 1996, Green 2001, Searcy *et al.* 2004). The absence of sexual dimorphism

and of conspicuous ornamental traits in Dupont's Lark and the small variation in body size among adult males (García-Antón *et al.* 2018) suggests that songs might be considered a better honest signal than biometric traits (Murphy *et al.* 2008). Ultimately, our results suggest that physical condition, as we measured it, does not function as an honest signal of response intensity in males of this species. However, it is also possible that the index considered may not be an adequate measurement of the condition of the birds or that it might be impacted by external factors not considered in this study (e.g. breeding status or blood parasites, see Bustillo-de la Rosa *et al.* 2022).

CONCLUSIONS

Our study provides new experimental evidence of the territorial behaviour and social organization of the Dupont's Lark, a strict insectivore and habitat-specialist of high conservation concern. Territorial males, inhabiting better quality territories, had a delayed but more intense defence response, emitting a greater number of vocalizations, calls and songs compared with those males located in poorer quality areas. Despite its difficulty, future work should incorporate information on the reproductive status of individuals to examine whether the intensity of territorial defence and physical condition are related to breeding status of the monitored birds. In addition, it would be interesting to determine the settlement status of non-breeding males. Future work on improving habitat quality for this species could help to resolve this question. The possibility that the density of individuals is not reflective of habitat quality (Vögeli *et al.* 2010, Pérez-Granados & López-Iborra 2013) is critical when working with endangered species and should be explored further. Management aimed at favouring areas with a high density of individuals could represent an ecological trap for the species if these individuals fail to disperse or had a lower fitness, so gaining insights into the optimal conditions for the species must be a priority to ensure the persistence of the Dupont's Lark.

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AUTHOR CONTRIBUTIONS

Adrián Barrero: Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing; formal analysis; data curation; supervision. **Julia Gómez-Catasús:** Writing – review and editing; investigation; methodology; formal analysis. **Cristian Pérez-Granados:** Writing – review and editing; investigation. **Daniel Bustillo-de la Rosa:** Investigation; writing – review and editing. **Juan Traba:** Conceptualization; validation; supervision; funding acquisition; project administration; resources; writing – review and editing; methodology.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest. No financial benefits will result from publication.

ETHICAL NOTE

This article does not contain any studies with human participants or animals performed by any of the authors.

INFORMED CONSENT

All authors agree with the contents of the article.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available in the ZENODO repository, <https://doi.org/10.5281/zenodo.7071089>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Results of models in which physical condition has been incorporated.

Appendix S2. Distribution of Dupont's Lark males according to habitat quality.