Medium-distance dispersal and stepping stones keep connectivity in Spanish metapopulation of Dupont's lark

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Background: We explore the metapopulation structure (populations and subpopulations) of the endangered Dupont's lark in Spain and identify critical nodes for the connectivity network. Also, we evaluate different connectivity scenarios according to potential dispersal capacity and presence of stepping stones in the network.

Methods: The study is carried out in peninsular Spain, using over 16,000 georeferenced observations from the period 2000-2017. We used GIS software to define populations and subpopulations based on the available scientific information, as well as potential stepping stones based on the MaxEnt probability of presence model. We defined a habitat attribute to quantify quality of each node and performed the connectivity model under different scenarios of dispersal capacity.

Results: Dupont's lark Iberian metapopulation comprises 24 populations and 100 subpopulations, plus 294 potential stepping stones. Potential dispersal distance and stepping stones play a crucial role in the network connectivity. Iberian Range – Ebro Valley population constitutes the core of the metapopulation and shows connectivity in the different indices and scenarios evaluated, but peripheral populations and subpopulations need the presence of stepping stones and/or potential long distance movements to join the network.

Discussion: Dupont's lark metapopulation is strongly fragmented with critical isolation of the peripheral subpopulations, specially in the Southern range. Metapopulation connectivity can be strengthened by preserving or improving adequate habitat in the most important stepping stones; thus, monitoring and protection of these areas are crucial for the conservation of the metapopulation. Current habitat loss due to intensification and rural abandonment urges to carry out management plans in critical nodes of the network. Research on juvenile dispersal could help to better understand the connectivity network and establish ecological corridors.

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Abstract

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Introduction

Connectivity of animal populations is of major importance for biodiversity conservation and plays a special role when managing threatened species (*Crooks & Sanjayan, 2006*; *Pascual-Hortal & Saura, 2006*). ~~When a landscape is fragmented~~, both ecosystem functionality and population persistence depend on the degree of connectivity between the habitat patches, which is associated to the dispersive processes of the focal species and to the landscape configuration (*Pascual-Hortal & Saura, 2007*). As habitat fragmentation occurs, ~~continuous areas are divided into smaller ones~~, whose isolation with the rest relies on factors such as patch size, distance to neighbours or the degree of permeability of the matrix between patches. As a consequence, small and isolated patches may have a lower probability of occupancy than large and connected ones (*Levins, 1970*; *Hanski, 1999a*), ~~though this finally depends~~ on the ecology of the studied species: minimum patch size required (*Vögeli et al., 2011*; *Shake et al., 2012*), dispersal capacity (*Rolstad, 2008*) or matrix composition (*Ricketts, 2002*; *Watling et al., 2010*). ~~As a general rule, an individual dispersing from a habitat patch will have a better access to other patches as they are closer and larger~~ (*Hanski, 1998*, *1999a*).

A fragmented group of patches can serve as one population if the connectivity between them is high enough to allow genetic flow, adopting a metapopulational structure (*Levins, 1969*; *Hanski, 1998*, *1999a*; *Hanski & Gaggiotti, 2004*). In this spatial configuration, the distribution, quality and connectivity among patches will determine the functionality of the whole group. In the traditional island biogeography theory, mainland areas ~~act as~~ source of individuals colonizing new areas (*MacArthur & Wilson, 2001*). Colonization probability depends mainly on size of the island and distance to the mainland (*MacArthur & Wilson, 2001*). In a metapopulational context, immigration may occur from different habitat patches and populations, each ~~of them~~ with its own ~~probability of connection~~ (*Hanski, 1998*). ~~When the degree of isolation of a patch of the metapopulation overtakes the threshold tolerated by the species, it will become unviable and heads toward an extinction process~~ (*Hanski, 1999a*). From the connectivity perspective, the loss of a part of the metapopulation can have consequences for the rest, being more or less severe depending on the importance of the lost patch in the whole network (*Hanski, 1999a*, *1999b*).

Graph ~~structures~~ ~~have shown to~~ be a useful tool for the analysis of the connectivity in fragmented populations (*Pascual-Hortal & Saura, 2006*; *Bodin & Saura, 2010*; *Saura & Rubio, 2010*)~~, and their use in landscape and conservation ecology is frequent~~ (*Baranyi et al., 2011*; *Foltête et al., 2020*). These models aim to describe the potential of movements in a fragmented population formed by disperse habitat nuclei ~~immersed in~~ a matrix of unsuitable or inhospitable territory for a particular species (*Pascual-Hortal & Saura, 2006*; *Bodin & Saura, 2010*; *Saura & Rubio, 2010*). ~~Moreover,~~ graph models offer quantitative information to identify critical patches for the maintenance of the functionality of the whole network (*Calabrese & Fagan, 2004*; *Visconti & Elkin, 2009*)~~. They~~ rely on network structures based on two elements: nodes and links between them (*Saura & Torné, 2009*). ~~The former~~ are patches of habitat ~~where the species occurs or might occur~~ (i.e., areas ~~with no presence~~ but adequate ~~to act~~ as *stepping stones*; *Loehle, 2007*). Links ~~represent~~ connections between nodes, ~~and are~~ frequently estimated as the distance between nodes. Each node is also given a numerical value a~~ccording to an attribute defining~~ its quality within the network; usually, habitat surface or other factor that describes focal species requirements (*Mazaris et al., 2013*; *Pereira et al., 2017*).

Dupont's ~~lark~~ (*Chersophilus duponti*; *Vieillot, 1824*) ~~constitutes~~ a paradigmatic case for the study of connectivity, given the high degree of both natural and human-induced fragmentation of its habitat in Spain (*García-Antón et al., 2019*), and its strong specialization (*Suárez, 2010*). It is a small passerine (17-18 cm; 32-47 g) ~~belonging to the Alaudidae family~~, extremely scarce and elusive, exclusive to Spain in the European context (*García-Antón et al., 2018*). Although it also occurs in North Africa (*de Juana & Suárez, 2020*), the Spanish population is completely isolated and shows own genetic (*García et al., 2008*) and morphological traits (*García-Antón et al., 2018*). It exclusively inhabits ~~plain~~ (~~below 10-15% slope~~) natural steppe lands that, in Iberia, are also linked to traditional anthropic uses (sheep extensive grazing), which maintains low (20-40 cm) vegetation and a high proportion of bare ground (*Garza & Suárez, 1990*; *Martín-Vivaldi et al., 1999*; *Garza et al., 2005*; *Garza et al., 2006*; *Nogués-Bravo & Agirre, 2006*; *Seoane et al., 2006*). ~~It is considered~~ sedentary, with ~~observations of~~ ~~adult~~ ~~individuals in~~ breeding sites all year long (*Cramp & Simons, 1980*; *Suárez et al., 2006*). ~~However, some evidences suggest the existence of juvenile dispersal (*García-Antón et al., 2015*), as well as sporadic long-distance movements, over 100 km, that might correspond to disoriented individuals mixed with other species flocks (*García & Requena, 2015*) or extreme weather conditions (*Dies et al., 2010*).~~

~~Population isolation has been identified as~~ one of the major concerns for ~~the species~~ in Spain (*Garza et al., 2004*; *Íñigo et al., 2008*; *Méndez et al., 2011*). Its ~~highly~~ fragmented distribution ~~could conform a~~ metapopulation~~al structure~~ (Gómez-Catasús *et al.,* 2018a; *García-Antón et al., 2019*; *Traba et al., 2019*), with different ~~units~~ ~~with~~ their own demographic parameters (*Pérez-Granados et al., 2017*), rare long dispersive movements connecting them (*García-Antón et al., 2015*) and rarer recolonization events of extinct patches (*Bota et al., 2016*). The sample bias toward adult males associated ~~to~~ the capture method (*Garza et al., 2003*; *Suárez, 2010*) provides ~~few~~ information regarding other age and sex classes, ~~though~~ the persistence of small and isolated nuclei suggests ~~the existence of~~ medium to longer distance movements~~,~~ ~~probably carried out by juveniles as supported by the few capture-recapture data available:~~ 4.5 km (*Pérez-Granados & López-Iborra, 2015*); 8 km (*V. Garza*, unpublished data); 33 km (*García-Antón et al., 2015*). Some recent records reveal the existence of longer movements: 37 km (recolonization of Timoneda de Alfés, Lleida; *Bota et al., 2016*), 80.40 km (Salinas de Marchamalo, Murcia; *García & Requena, 2015*) and 98.77 km (Albufera de Valencia; *Dies et al., 2010*), these being the minimum distance to the closest occupied locality. Historic observations reveal even longer distance events: 127 km (Barcelona), 241 km (Trebujena-

Sanlúcar, Cádiz), and up to 324 km (Marismas del Odiel, Huelva), among others (see Supplemental Table S1).

Dupont's lark ~~occupation distribution is restricted to~~ around 1,000 km^2 in Spain, while another 965 km^2 ~~shows unoccupied potential habitat~~ (*García-Antón et al., 2019*), which suggests that the ~~Iberian~~ metapopulation ~~could~~ be better connected than expected, if ~~such areas were playing the role of~~ stepping stones. ~~The last scientific information highlights~~ a generalized and pronounced decline in most ~~of the~~ Spanish populations (*Gómez-Catasús et al., 2018a*), ~~as well as a dramatic contraction in the distribution range~~ (*García-Antón et al., 2019*). As ~~the fragmentation process of natural steppe habitats currently continues~~, which is ~~considered a~~ main threat for Dupont's lark (*Íñigo et al., 2008*), identification of critical patches for the maintenance of the metapopulation connectivity is ~~basic~~ for the conservation of the species.

~~This work is addressed to~~ carry out a detailed analysis of Dupont's lark metapopulation ~~potential~~ connectivity in Spain, ~~which should be~~ a useful tool for the management and conservation of this threatened species. ~~The main objective is to evaluate the general connectivity of the metapopulation, using the most recent information for the species.~~ More specifically, ~~this work aims to~~: i) update the cartography of populations and subpopulations of the European Dupont's lark ~~range~~; ii) identify both vulnerable and critical nuclei from the connectivity point of view for the conservation of the metapopulation; iii) assess the role of unoccupied but adequate regions ~~in the functionality of~~ the ~~whole~~ metapopulation, testing the effect of different dispersal distances; iv) evaluate the degree of isolation of each nucleus; and v) propose adequate conservation measures for the maintenance of the metapopulation.

Materials & Methods

The ethics committee of Animal Experimentation of the Autonomous University of Madrid as an Organ Enabled by the Community of Madrid (Resolution 24th September 2013) for the evaluation of projects based on the provisions of Royal Decree 53/2013, 1st February, has provided full approval for this purely observational research (CEI 80-1468-A229).

Species observations

We used the database of georeferenced observations of Dupont's lark updated to 2017, including own unpublished data (TEG-UAM) and adding all available external records (*Traba et al., 2019*). We gathered a total of 17,755 Dupont's lark locations corresponding to the temporal series of 1985-2017, both years included. We considered as *recent* those observations belonging to the post-2000 period (n=17,282; 97.34%), when the II National Census was carried out (2004-2006; *Suárez, 2010*). This work allowed to standardize the field work using the territory mapping census method, which corrects the bias detected in previous works (*Garza et al., 2003*; *Pérez-Granados & López-Iborra, 2013*). Pre-2000 observations were considered *historic* and were not used in this work, as they do not represent the current distribution of the species (see *García-Antón et al., 2019*).

Among the *recent* locations, 14,203 (82.18%) came from own data (TEG-UAM), while the rest (3,079, 17.82%) was provided by administrations, ~~other~~ research entities and individual ornithologists. Finally, we discarded those observations out of the breeding period (from February to July, both included) and those considered rare due to their position in areas certainly unoccupied by the species, with the aim of avoiding those locations that could correspond to movements, and which would not represent settlement areas of the species. Finally, 16,676 observations were used to determine the current structure of populations and subpopulations of Dupont's lark in Spain.

Species habitat

Because of the lack of a detailed cartography of Dupont's lark habitat in ~~the whole national territory~~, we built a map of adequate habitat following the same rules as in the recent distribution model (*García-Antón et al., 2019*): by means of a GIS software (QGIS Development Team 2009), we intersected all the observations with the CORINE land use 2006 layer (maintaining the temporal correspondence with the period in which the majority of the observations belonged to, i.e.: II National Census, 2004-2006) and selected those land use categories that accounted for 95% of the observations (Supplemental Table S2). Then we extracted such categories from the most updated CORINE layer available (2012), in order to obtain the updated distribution of the land uses preferred by the species. From such surface, we discarded those areas with a slope over 15%, strongly rejected by the species (*Suárez, 2010*), obtained by means of a Digital Terrain Model with a 25 m resolution and achieving the final layer of adequate habitat of Dupont's lark in Spain.

Criteria for the definition of locality, subpopulation and population

We defined three sequentially ~~hierarchized~~ levels of actual occupancy by the species based on distance thresholds ~~substantiated in the scientific knowledge available to date~~ (*Laiolo, 2008*; *Suárez, 2010*; *Vögeli et al., 2010*; *Méndez et al., 2014*; *García-Antón et al., 2015*; *Bota et al., 2016*), as well as own unpublished data. Those were: locality, subpopulation and population. ~~We considered~~ all habitat patches separated by less than 1 km ~~as~~ belong~~ing~~ to the same *locality*, as this distance allows territorial males to be in close contact by singing or short-distance flights (*Suárez, 2010*; *Vögeli et al., 2010*). Data from capture-recapture of territorial adults indicate that they are ~~strongly~~ sedentary, with regular movements ~~below 2~~ 3 km (*Laiolo et al., 2007*; *Vögeli et al., 2008*; *Suárez, 2010*; *Vögeli et al., 2010*). Bioacoustic data suggest cultural similarity and adult males contact at a distance of 5 km (*Laiolo, 2008*), supported by the recovery of two marked adults at 5.4 and 5.8 km in Rincón de Ademuz, Valencia (*Pérez-Granados & López-Iborra, 2015*). There is only one record of an adult out of this range, recaptured at 13 km from its capture location (*V. Garza*, unpublished data). Thus, considering the strong sampling effort made on adults capture-recapture during the last 20 years (Suárez 2010; Traba *et al.* 2019), we established 5 km as the plausible threshold for resident movements. Therefore, a *subpopulation* was defined as the group of localities separated 5 km or less. Finally, a *population* was considered as the set of subpopulations separated by a maximum distance of 20 km, following a conservative criterion and accounting for the few available data on juvenile dispersal (up to 20 km in *Vögeli et al., 2010*, 33 km in *García-Antón et al., 2015*). This upper level represents those units that, despite being connected sporadically would maintain a high genetic similarity due to individuals exchange (*Méndez et al., 2011*; *Méndez et al., 2014*).

To define subpopulations, we generated a 2,5 km buffer on the observations layer to identify clusters or group of localities missing contact with neighbour ones (that is, being separated over 5 km). In the same way, we used a 10 km buffer to identify different populations (distance between observations above 20 km).

Dispersal scenarios

The compilation of historic and recent Dupont's lark observations out of the know breeding range (Supplemental Table S1) reveals the existence of longer displacements than the thresholds defined previously, considered as rare events corresponding to sporadic long-distance movements. Taking into account all together, we defined three potential dispersal distance scenarios (see below): short (5 km); medium (20 km) and long (100 km) distance dispersal.

Definition of stepping stones

We also identified those areas that, despite being unoccupied by the species, could be potentially used and relevant in the connectivity process due to their high probability of presence, as shown in the distribution model (*García-Antón et al., 2019*). To do so, we used the 1x1 km cells considered of potential distribution (n=5,575; those that accounted for a probability value higher than the mean of the 1,370 ones with confirmed presence, *García-Antón et al., 2019*). We discarded those cells intersecting with the observations buffer (included in the subpopulations layer), obtaining a total of 3,597 1x1 km cells of unoccupied potential habitat. Adjacent cells were grouped into clusters, resulting in 902 independent entities. Following a conservative criterion, we removed those formed by a single 1x1 km cell, reducing it to 294 clusters. Finally, we applied on them the same correction rule as in the habitat layer (selecting the preferred land use categories and the slope under 15%), and we removed the resulting patches with a surface under 20 ha (suggested threshold for the species occupancy; *Vögeli et al., 2010*), obtaining the final map of potential stepping stones for the connectivity network.

Nodes and habitat attribute

We built the connectivity model at a subpopulation level, to obtain a more detailed result and considering that subpopulations, better than populations, constitute the metapopulation functional units, each of them with its own extinction risk and probability of connection with the rest. This way, our network included one node for each subpopulation and stepping stone (in both cases, located in the centroid of the surface).

Each node was assigned a quantitative value that estimates its quality or importance in the network. We defined such attribute as Available Habitat Surface (AHS) and calculated it considering the surface of adequate habitat, its quality and its degree of fragmentation, according to the known ecology of the species, as following:

$$AHS = HS * HQ * 1/NP$$

Where HS (habitat surface) is the total surface of adequate habitat within the subpopulation (or stepping stone), calculated as the sum of all habitat patches within each one; HQ is habitat quality, estimated as the mean value of probability of presence of the intersecting

1x1 km cells, as estimated in the MaxEnt model (*García-Antón et al., 2019*); and NP is the number of patches of habitat inside its unit, as a measure of within subpopulation (or stepping stone) fragmentation. This way, each node obtained a value positively associated to its surface, quality and continuity of habitat.

To calculate the network links we used the linear distance between borders of each pair of subpopulations and stepping stones. We discarded the use of distances to the centroid due to the large size of some subpopulations, which could artificially increase the distance among neighbour patches.

Connectivity model

We used software Conefor (*Saura & Torné, 2009*) to generate the connectivity model, which is widely used to analyse network structures (*Saura et al., 2011*; *Vergara et al., 2013*; *Grafius et al., 2017*). It builds the model in a two-step process: First, it calculates a connectivity index for the whole network (PC, probability of connection). It is based on nodes quality (AHS attribute), the distance between nodes and the species' dispersal capacity. Then, it removes each node independently and calculates the loss of PC ~~according~~ to that removal (dPC), obtaining an estimation of the contribution of each node to the global structure.

Conefor also allows the comparison between different general scenarios by means of the *equivalent connectivity index* (EC, see *Saura & Torné, 2009*), a modification of PC provided in the same units than the node attribute (see *Saura et al., 2011*; *Saura & Torné, 2009*). Prior to subsequent analyses, we compared scenarios resulting from the different potential dispersal distances considered (see above): short (5 km), medium (20 km) and long distance (100 km) and the presence or absence of stepping stones in the network (building the network with two different node maps, one including exclusively subpopulations and another one with the addition of all the stepping stones).

To evaluate the importance of each node for the network, dPC is fractioned into three more specific metrics: dPC_{intra}, dPC_{flux} and $dPC_{connector}$ (*Pascual-Hortal & Saura, 2006*). The fraction dPC_{intra} refers to the internal quality of the node (intra-patch connectivity), as it had been defined through the attribute considered (in this case, AHS). Thus, it is independent of the distance to others nodes and its spatial position in the network. dPC_{flux} is a value of inter-patch connectivity, giving information about the degree of flow that each node generates within the network; this index considers all the connections in which each node is either the origin or the destination point, as well as the quality of such connections (based on the AHS of the nodes involved). So, dPC_{flux} depends on the spatial position of each node within the network, but also on the quality of those nodes it is connected to. Finally, $dPC_{connector}$ adds a second value of inter-patch connectivity, indicating the contribution of each node to the connectivity among the rest. This index provides information about the importance of each node for the maintenance of other nodes or group of nodes connectivity, that is, if it acts as a stepping stone whose absence would implicate that others increase their isolation or remain connected through a worse route (with a longer distance or passing through lower quality nodes). The total value of dPC is just the sum of these three fractions, so it gives a general value to each of the nodes in the network.

Finally, we calculated the matrix of probability of connection for each pair of nodes (subpopulations and stepping stones), what allows building connectivity maps for all different scenarios considered.

Results

Populations, subpopulations and stepping stones

Based on the map of post-2000 observations and after the application of considered criteria we obtained 123 subpopulations, 23 of which are currently extinct, considering the most recent field data, updated to 2019. After removing them, we defined a present network of 100 subpopulations, 24 populations, plus the already mentioned 294 potential stepping stones (Fig. 1, Supplemental Table S3, Supplemental Data S1).

The metapopulation structure (Fig. 1) is formed by a core region comprising the largest population: Iberian Range - Ebro Valley (considered two independent units to date, *Suárez, 2010*). West and northwards, the metapopulation shows a myriad of small populations dispersed through the Iberian Range (provinces of Soria, Zaragoza, Teruel, Navarra and Huesca), perhaps remnants of a historical more continued distribution. Further east and more isolated, the only Catalonian population: Alfés (Lleida province). Through the west (Zamora province) three small populations exist, with an apparent greater degree of isolation due to their distance with the central nucleus. Southwards, a group of 12 disperse populations and progressively more isolated from the core of the distribution are distributed along the provinces of Valencia, Cuenca, Toledo, Albacete, Murcia, Almería and Granada (Fig. 1, Supplemental Data S1).

Global connectivity under different scenarios

The EC index increased with the dispersal distance and with the presence of stepping stones (Table 1). Due to the marked effect of both factors on the network connectivity, all subsequent analyses were carried out considering all the different scenarios.

Classification of nodes ~~according to~~ internal importance index (dPC_{intra})

The subpopulations of *Monegros* (Z) and *Blancas* (TE) were highlighted as the most important areas regarding their internal quality (meaning the highest values of the AHS attribute), followed by *Torralba de los Frailes* (TE) (Table 2). These subpopulations showed the best relation between habitat surface, quality and continuity. No stepping stones were listed among the best nodes (a summary of the 10 most important nodes is shown in Table 2, the complete dataset is available in Supplemental Data S2 and S3).

Classification of nodes according to importance for flow generation (dPC_{flux})

The subpopulations of *Monegros* (Z) and *Blancas* (TE) were again the most important ones for this fraction, together with *Torralba de los Frailes* (TE), *Paramera de Molina* (GU) and *Gelsa* (Z) (Table 3). ~~According to~~ dPC_{flux} values, these subpopulations were those generating a larger number of connections as starting or ending point. No stepping stones were important when considering medium and long dispersal distances (20 or 100 km), but they appeared to be relevant in the scenario of short distance movements (5 km): *Monegrillo 2* (Z), *Alfajarín 1* (Z) and *Torralba de los Sisones* (TE) (top 10 ranking in Table 3, complete dataset is available in Supplemental Data S2 and S3).

Classification of nodes according to importance for connectivity maintenance ($dPC_{connector}$)

Three subpopulations, all included in the Iberian Range - Ebro Valley population, were the most important ~~according to~~ their function as connectivity nodes between others: *Paramera de Molina* (GU), *Layna* (SO) and *Altos de Barahona* (SO) (Table 4), followed by *Gelsa* (Z) and *Altiplano de Teruel* (TE), which were also present in all the scenarios. Four stepping stones were in top positions in the list: *Alba*, *Rubielos de la Cérida*, *Ojos Negros 1* and *Hoz de la Vieja*, all of them in Teruel province and within the Iberian Range - Ebro Valley population: (top 10 ranking in Table 4, complete dataset is available in Supplemental Data S2 and S3).

Classification of nodes according to general importance index (dPC)

Taking into account the sum of all previous fractions, *Monegros* (Z) and *Blancas* (TE) were highlighted as the most important subpopulations, followed by *Torralba de los Frailes* (TE) and *Paramera de Molina* (GU), all of them within the Iberian Range - Ebro Valley population (Table 5). When considering the presence of stepping stones, three important areas for the network connectivity were detected, also belonging to the same population: *Alba* (TE), *Rubielos de la Cérida* (TE) and *Cuerlas 1* (Z), which appear within the 10 most important nodes (Table 5). See Fig. 2 for a graphical view in an intermediate scenario (20 km dispersal and presence of stepping stones); the complete dataset is available in Supplemental Data S2 and S3.

Connectivity network

The degree of connectivity showed a strong variability under the different scenarios, highlighting the influence of potential dispersal distance and presence/absence of stepping stones in the metapopulation dynamics (Supplemental Data S3 contains the complete matrix, with the probability of connection for each pair of nodes under each scenario).

The most conservative possibility (5 km dispersal and absence of stepping stones) showed an extreme isolation, with connections among nearby subpopulations only in the central nucleus (Fig. 3). Moreover, these connections seemed to be weak (0.001-20% probability), and lacking inter-population connections. In this situation, all the subpopulations outside of the Iberian Range - Ebro Valley population would be completely isolated. For this dispersive distance, the presence of stepping stones would not be enough to connect the outermost subpopulations (Fig. 3).

When considering the increase of the dispersal capacity to 20 km, the situation changed notably. Despite the connections among nearby subpopulations continue being of low-to-medium probability, inter-subpopulation connectivity occurs within the Iberian Range - Ebro Valley population and in the western populations. With the presence of stepping stones, high probability connections (over 80%) were frequent in near all the subpopulations within and north to the Iberian Range - Ebro Valley population. The most western populations remain unconnected even under the stepping stones scenario. The situation of the southern part of the distribution remains dramatically unconnected, even considering the presence of stepping stones (Fig. 3).

When testing dispersive distances of 100 km, Dupont's lark Iberian metapopulation would be completely connected, including the extremely fragmented southern range (Fig. 3), and even without considering stepping stones.

Discussion

The criteria applied in this work led to 24 populations and 100 subpopulations currently occupied and conforming the Dupont's lark Spanish metapopulation. This structure is dynamic and should be periodically updated ~~according to~~ continuous monitoring. 23 additional subpopulations became extinct in the last 2 decades and should be regularly monitored to verify possible recolonizations. Population turnover is an extremely rare event and Dupont's lark seems not to fit a classic Levins model of colonization-extinction balance. On the contrary, extinctions seem to be permanent, in a source-sink pattern that reveals a contraction process from the peripheral subpopulations to the core of the distribution. 294 habitat patches spread out between the distribution range could be working as stepping stones and increasing metapopulation connectivity, although they are heterogeneously distributed. The center of the metapopulation shows the higher values of connectivity. The distant western populations could be better connected than expected ~~to date~~, but the southern range is critically isolated and ~~accounts for~~ the majority of recent subpopulation extinctions. This work has allowed to ~~point~~ those subpopulations and stepping stones critical for the connectivity network and should constitute a useful tool for management, particularly avoiding habitat loss and fragmentation in such areas. Dispersal mechanisms remain poorly known, but a medium-distance dispersal (20-30 km), probably by juveniles, seems to fit to actual configuration, and could help to explain the persistence of isolated populations.

Populations, subpopulations and stepping stones

~~According to the~~ metapopulation structure and our definition of populations (n=24) and subpopulations (n=100), the two main nuclei considered to date (Iberian Range and Ebro Valley) turn into one single, large population. The map of subpopulations presents continuity in the central nucleus and a strong degree of fragmentation and isolation southwards and in the western range, which is in accordance with previous consideration (*Suárez, 2010*). This highlights the vulnerability of those most peripheral nuclei of the metapopulation, as genetic analysis has previously showed (*Méndez et al., 2011*), which also present a higher extinction risk (*Méndez et al., 2014*; *Gómez-Catasús et al., 2018a*).

Potential stepping stones are numerous (n=294), ~~though unevenly distributed,~~ but their importance in metapopulation dynamics seems to be high. ~~The majority of them~~ are ~~located~~ in the easternmost distribution (Teruel and Zaragoza provinces) while ~~the southern range presents an almost complete lack of these elements~~, which could help to explain the dramatic trends of the southernmost subpopulations (*Gómez-Catasús et al., 2018a*). ~~On the contrary,~~ the apparently ~~strong~~ isolation of the western range (Zamora province) ~~could be better connected than expected thanks to the higher abundance of stepping stones~~ (Fig. 1). It has been previously reported the absence of the species in apparently optimal areas (*García-Antón et al., 2019*), much of them considered as stepping stones in this work. Whether these areas could correspond to empty patches in a classic colonization-extinction balance (Levins 1969) remains unknown. However, population turnover in Dupont's lark seems to be extremely rare in Dupont's lark at both metapopulation (*García Antón et al.*, in prep.) and local scales (*Gómez-Catasús et al., 2018b*). To our knowledge, just one known subpopulation has been recolonized after being extinct (*Bota et al., 2016*). ~~Own~~ intensive field work in the Iberian Range along the study period has recorded one single patch (not locality nor subpopulation) reoccupied (own data). Rather than a classical Levins model, Dupont's lark metapopulation could adopt a source-sink structure (*Hanski, 1998*, *1999a*), in which the smaller and more isolated subpopulations would be in more risk of extinction due to its lower connectivity with the core of the distribution, besides other risks associated to its lower size. More than 50% of the Iberian subpopulations have less than 5 individuals (*Traba et al., 2019*), which from a genetic and demographic point of view suggests low medium-term viability, if there is no connection with other nuclei (*Méndez et al., 2011*, *2014*).

In relation to extinction process, those subpopulations extinct during the post-2000 period (n=23, which means ~~18.7~~% of the extant subpopulations at the beginning of the century) could correspond, following metapopulation dynamics, to stochastic factors or to changes in habitat quality (*Hanski, 1999a*). In the first case, such patches would be immediately available for recolonization, as the one recorded by *Bota et al.* (2016) in Alfés (Lleida) in 2015. In the latter, that subpopulation would not be available for recolonization until habitat is restored. As plant succession may cause major habitat changes in steppe-lands, especially after extensive grazing abandonment (*Peco et al., 2006, Íñigo et al., 2008; Gómez-Catasús et al., 2019*), it would be necessary to promote active management to guarantee its long-term persistence. Recent initiatives addressed to improve Dupont's lark habitat through habitat management have shown positive results (LIFE Ricotí in Soria, local projects in Valencia region; see a revision in *Traba et al., 2019*), and could be a useful tool for key areas (such as critically isolated subpopulations or important areas for the connectivity network). Anyway, long-term effective measures for habitat and species conservation should include the promotion of traditional sheep grazing, in order to avoid dramatic plant structure changes and maintain habitat functionality. Short-term management in the most critical areas to avoid changes in land uses that threaten the species' habitat, mainly wind farms (*Gómez-Catasús et al., 2018b*) and ploughing (*Garza et al., 2004*; *Íñigo et al., 2008*) should be implemented urgently.

In Supplemental Data S1 we offer detailed and updated cartography of the metapopulation, with numbered and named populations and subpopulations that can constitute a useful guide for the different regional administrations to work with a common structure. Management coordination is of vital importance in the case of Dupont's lark, as several regional administrations are affected by its distribution and share populations or subpopulations.

Global connectivity under different scenarios

Despite the apparent strong fragmentation and high degree of isolation of Dupont's lark metapopulation, our results suggest two elements that seem to be relevant for the connectivity of the whole network and contributing to explain the prevalence of the smallest and most isolated subpopulations, which were expected to be extinct according to the population viability models (*Laiolo et al., 2008*; *Suárez, 2010*), genetic structure (*Méndez et al., 2011*, *2014*), and data on the general situation of the species (*Suárez, 2010*; *Traba et al., 2019*). First, the large surface of vacant adequate habitat (*García-Antón et al., 2019*), that should be interpreted as a network of stepping stones unnoticed to date. There is, approximately, the same surface of potential habitat than that of confirmed presence (around 1,000 km^2; *García-Antón et al., 2019*). The evaluation of the Equivalent Connectivity index (EC) showed that the role of these unoccupied potential areas seems crucial for the functionality of the network, even with a stronger influence than the increase of potential dispersal distance of the species (Table 1). The relative low values of stepping stones in dPC_{intra} (Table 2) but higher ones in dPC_{flux} and $dPC_{connector}$ (Tables 3 and 4) suggest that these patches may have lower habitat quality than occupied subpopulations (~~according to~~ the AHS attribute), thus being unsuitable for occupancy, but a high importance in the metapopulation connectivity process.

On the other hand, results of the simulation of different dispersive distances (Fig. 3) suggest that 2-5 km maximum dispersal distance assumed previously (*Laiolo et al., 2007*; *Vögeli et al., 2008*; *Vögeli et al., 2010*; *Suárez, 2010*) could have undervalued actual dispersal ability of the species. Recent records of longer dispersal movements, that could correspond to juvenile dispersal (*García-Antón, 2015*), recolonization (*Bota et al., 2016*) or sporadic long-distance movements (*García and Requena, 2015*, *Dies et al., 2010*), as well as historical records summarized in Supplemental Table S1, point to medium to large dispersal events that could be contributing to slow down local extinction as fast as predicted by the viability models (*Laiolo et al., 2007*; *Suárez, 2010*).

Node~~s~~ importance

~~Indices~~ dPC_{intra}, dPC_{flux} and dPC all ~~pointed to~~ the same most important nodes: *Monegros* (Z), *Blancas* (TE), *Torralba de los Frailes* (TE) and *Paramera de Molina* (GU), all of them located in the Iberian Range – Ebro Valley population. The conservation of these top ranked subpopulations is imperative to ensure the conservation of the metapopulation, as it is also crucial to focus on the third fraction of dPC ($dPC_{connector}$). In the case of Dupont's lark, in which isolation may constitute a critical factor for the species conservation, those subpopulations with a higher value in $dPC_{connector}$ should receive special attention, as their loss could implicate the subsequent extinction of other subpopulations or groups of subpopulations. Several nodes of the Iberian Range close to the geographical centroid of the metapopulation are included in this set, mainly *Layna* (SO), *Paramera de Molina* (GU) and *Altos de Barahona* (SO), as well several stepping stones that are also among the top ranked nodes: *Alba*, *Rubielos de la Cérida*, *Ojos Negros 1* and *Hoz de la Vieja*, among others (Table 4). All nodes (subpopulations and stepping stones) mentioned above should be considered of high priority and concern, and included in national and/or regional species conservation plans, as their protection and management seem to be crucial for the maintenance of the species. Supplemental Data S3 includes the complete lists of nodes importance by province in all the scenarios considered and should constitute a useful management tool for regional administrations.

Connectivity network

In the most restrictive scenario (dispersal of 5 km and absence of stepping stones), the metapopulation showed practically total isolation among subpopulations, excepting low probability connections within the Iberian Range – Ebro Valley. Assuming a medium dispersal distance of 20 km, a significant increase of connections appears within the central distribution, though their probability continued being low. Thus, the uttermost western populations kept isolated, and their maintenance seems to depend on the presence of stepping stones to avoid their isolation. The most unfavourable situation is shown by the southern subpopulations, which remain completely isolated unless there are movements of 100 km.

The strong general population decline of the species described recently (*Gómez-Catasús et al., 2018a*) and its current and future distribution (*García-Antón et al., 2019*), together with the existing genetic analyses (*Méndez et al., 2011*; *Méndez et al., 2014*) point to a high degree of isolation but, at the same time, to the prevalence of small and isolated peripheral subpopulations. As a consequence, we consider as the most probable situation the coexistence of several of the scenarios evaluated here. ~~According to movements of the different age classes,~~ adult ~~displacements below~~ 1 km are ~~considered events of high probability~~, and intra and inter-sexual communication at this distance must be ~~a~~ common ~~phenomenon~~. Adult movements between 1 and 5 km are considered mid-to-low probability events; those between 5 and 20 km, of low probability; and those over 20 km must be considered highly improbable events. Juveniles are presumable the dispersive fraction of the population, as it is widespread in bird species (they are prone to leave their natal site, to move long distances across non-habitat areas and to settle new populations with few initial individuals, *Rojas et al., 2016*). We consider juvenile movements of 5 km of very high probability; those comprising 5-20 km, of high probability; 20-100 km movements, of low probability; and over 100 km, of very low probability. This last distance would represent rare events corresponding to sporadic long-distance movements (Supplemental Table S1).

The situation of the species, with dramatic declines and ongoing habitat fragmentation and contraction (*Gómez-Catasús et al., 2018a*; *García-Antón et al., 2019*) urges to act on the species and habitat management. In the current context of land intensification and rural abandonment, Dupont’s lark habitat has a finite lifetime. As smaller patches disappear, the larger ones, which presently hold the majority of the population, will become more vulnerable due to the loss of linked habitat and the decrease of connectivity. Besides, several aspects of this species remain partially unknown and are crucial for its conservation, as dispersal mechanisms, reproductive biology or genetics, which are needed for a detailed evaluation of the connectivity and population viability of Dupont’s lark.

Conclusions

This work offers to the regional administrations with presence of Dupont's lark in its territory the list of the most important areas to protect. Most urgently, actions implying habitat loss and fragmentation must be avoided in such critical areas (such as ploughing, windfarms or reforestations). Additionally, the increase of habitat quality both in short (restoration measures) and long terms (extensive grazing) is desirable for matapopulation conservation. We also offer an updated structure of populations and subpopulations (and potential stepping stones) that should help coordinating management among administrations. Isolation of the southern range is extreme and, according to the recent subpopulation extinctions, we speculate a near-future distribution restricted to the current metapopulation core. Research on dispersal, specially on juvenile monitoring, would help clarifying movement patterns in the metapopulation and establishing ecological corridors to increase connectivity.

Acknowledgements

We wish to acknowledge to Francisco Quico Suárez, who led the Dupont's lark research group until his early death in 2010. Many people collected data in the field; we especially wish to thank: A. Agirre, R. Aymí, M. Calero, E. Carriles, J. T. García, I. Hervás, J. H. Justribó, E. G. de la Morena, J. J. Oñate and J. Viñuela. Data used in this paper come from different projects, in particular the II National Census (2004–2006), granted by the Spanish Ministry of Environment; the Dupont's lark Monitoring Program in Medinaceli Region, funded by Fundación Patrimonio Natural de Castilla y León, and the projects "Criteria for the management and conservation of the Spanish population of Dupont's lark, supported by Fundación Biodiversidad, of the Ministry of Agriculture, Food and Environment; LIFE Ricotí (LIFE15-NAT-ES-000802), supported by the European Commission; and BBVA-Dron Ricotí, funded by the BBVA Foundation. All birds were captured and processed following the Wild Birds Ringing Manual and under the correspondent official licenses. This is a contribution to the Excellence Network Remedinal 3CM (S2013/MAE-2719), supported by Comunidad de Madrid.

References

Baranyi G, Saura S, Jordán, F (2011) Contribution of Habitat Patches to Network Connectivity: Redundancy and Uniqueness of Topological Indices. Ecological Indicators - ECOL INDIC. 11. 1301-1310. 10.1016/j.ecolind.2011.02.003.

Bodin Ö, Saura S (2010) Ranking Individual Habitat Patches as Connectivity Providers: Integrating Network Analysis and Patch Removal Experiments. Ecological Modelling. 221:2393-2405

Bota G, Giralt D, Guixé D (2016) La Alondra Ricotí en Cataluña: evolución histórica de una población en el límite del área de distribución. II Meeting of the Dupont's lark Experts Group, Madrid

Calabrese J, Fagan W (2004) A Comparison-Shopper's Guide to Connectivity Metrics. Frontiers in Ecology and The Environment 2(10):529-536

Cramp S, Simmons KEL (1980) The Birds of the Western Palearctic. Vol. II, Oxford University Press, Oxford

Crooks KR, Sanjayan M (2006) Connectivity Conservation. Cambridge University Press

De Juana E, Suárez F (2020) Dupont's lark (*Chersophilus duponti*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona (retrieved from https://www.hbw.com/node/57638)

Dies B, Alcocer T, Llorens V, Piera M, Marín P, Ruiz P (2010) Alondra Ricotí: una primera cita para l'Albufera. http://www.birdingalbufera.es/?q = es/node/496

Foltête J, Savary P, Clauzel C, Bourgeois M, Girardet X, Saharoui Y, Vuidel G, Garnier S (2020) Coupling landscape graph modeling and biological data: a review. Landscape Ecol. https://doi.org/10.1007/s10980-020-00998-7

García-Antón A, Garza V, Traba J (2015) Dispersión de más de 30 Km en un macho de primer año de Alondra Ricotí (Chersophilus duponti) en el Sistema Ibérico. I Meeting of the Dupont's lark Experts Group, Granada, Spain

García-Antón A, Garza V, Traba J (2018) Climate, isolation and intraspecific competition affect morphological traits in an endangered steppe bird, the Dupont's lark *Chersophilus duponti*. Bird Study 65(3):373-384

García-Antón A, Garza V, Hernández Justribó J, Traba J (2019) Factors affecting Dupont´s lark distribution and range regression in Spain. PLOS ONE. 14. e0211549. 10.1371/journal.pone.0211549.

García JT, Suárez F, Garza V, Calero-Riestra M, Hernández J, Pérez-Tris J (2008) Genetic and phenotypic variation among geographically isolated populations of the globally threatened Dupont's lark *Chersophilus duponti*. Mol. Phylogenet. Evol. 46:237–251

García T, Requena C (2015) Alondra Ricotí en las Salinas de Marchamalo. https://pachequerobirder.blogspot.com/2015/08/alondra-ricoti-en-las-salinas-de.html

Garza V, Suárez F (1990) Distribución, población y selección de hábitat de la Alondra de Dupont (Chersophilus duponti) en la península ibérica. Ardeola 37:3–12

Garza V, Traba J, Suárez F (2003) Is the European population of Dupont's lark Chersophilus duponti adequately estimated? Bird Study 50:309-311

Garza V, Suárez F, Tella JL (2004) Alondra de Dupont, Chersophilus duponti. In: Madroño A, González C, Atienza JC (eds). Libro Rojo de las Aves de España. Madrid: Dirección General para la Biodiversidad-SEO/BirdLife pp 309–312

Garza V, Suárez F, Herranz J, Traba J, García de la Morena EL, Morales MB, González R, Castañeda M (2005) Home range, territoriality and habitat selection by the Dupont's lark Chersophilus duponti during the breeding and postbreeding periods. Ardeola 52:133–146

Garza V, García JT, Calero M, Suárez F (2006) Tendencias y situación actual de las poblaciones de la Alondra Ricotí Chersophilus duponti en Andalucía, España. Ecología 20:85–96

Gómez-Catasús J, Pérez-Granados C, Diego A, Bota G, Giralt D, López-Iborra G, Serrano D, Traba J (2018a). European population trends and current conservation status of an endangered steppe-bird species: The Dupont's lark *Chersophilus duponti*. PeerJ 6:e5627 https://doi.org/10.7717/peerj.5627

Gómez-Catasús J, Garza V, Traba J (2018b) Effect of wind farms on small passerine birds: occurrence, abundance and population trends of a threatened species, the Dupont's lark

Chersophilus duponti. Journal of Applied Ecology 55(4):2033-2042. https://doi.org/10.1111/1365-2664.13107

Gómez-Catasús, J., Garza, V., Morales, M.B. *et al.* Hierarchical habitat-use by an endangered steppe bird in fragmented landscapes is associated with large connected patches and high food availability. *Sci Rep* **9,** 19010 (2019). https://doi.org/10.1038/s41598-019-55467-2

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I (1999a) Metapopulation ecology. Oxford University Press

Hanski I (1999b) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209-219

Hanski I, Gaggiotti O (2004) Ecology, Genetics and Evolution of Metapopulations. Academic Press

Íñigo A, Garza V, Tella JL, Laiolo P, Suárez F, Barov B (2008) Action Plan for the Dupont´s Lark Chersophilus duponti in the European Union. SEO/Birdlife – BirdLife International – Comisión Europea

Laiolo P, Vögeli M, Serrano D, Tella JL (2008) Song Diversity Predicts the Viability of Fragmented Bird Populations. PLoS One. https://doi.org/10.1371/journal.pone.0001822

Laiolo P, Vögeli M, Serrano D, Tella JL (2007) Testing acoustic versus physical marking: two complementary methods for individual-based monitoring of elusive species. Journal of Avian Biology. https://doi.org/10.1111/j.2007.0908-8857.04006.x

Laiolo P (2008) Characterizing the spatial structure of songbird cultures. Ecological Applications. https://doi.org/10.1890/07-1433.1

Laiolo P, Vögeli M, Serrano D, Tella JL (2008) Song Diversity Predicts the Viability of Fragmented Bird Populations. PLoS One. https://doi.org/10.1371/journal.pone.0001822

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America. https://doi.org/10.1093/besa/15.3.237

Levins R (1970) Extinction. In: Gerstenhaber M (ed) Lecture notes on mathematics in the life sciences. Annals of New York Academy of Sciences Vol. 231, pp 75-107

Loehle C (2007) Effect of ephemeral stepping stones on metapopulations on fragmented landscapes. Ecological Complexity. https://doi.org/10.1016/j.ecocom.2007.02.015

MacArthur RH, Wilson EO (2001) The Theory of Island Biogeography. Princeton University Press

Martín-Vivaldi M, Martín JM, Archila F, López E, de Manuel LC (1999) Caracterización de una nueva población reproductora de Alondra de Dupont (Chersophilus duponti) (Passeriformes, Alaudidae) en el Sureste ibérico. Zoologica Baetica 10:185–192.

Mazaris AD, Papanikolaou AD, Barbet-Massin M, Kallimanis AS, Jiguet F, Schmeller DS, Pantis JD (2013) Evaluating the Connectivity of a Protected Areas' Network under the Prism of Global Change: The Efficiency of the European Natura 2000 Network for Four Birds of Prey. PLoS One. https://doi.org/10.1371/journal.pone.0059640

Méndez M, Tella JL, Godoy JA (2011) Restricted gene flow and genetic drift in recently fragmented populations of an endangered steppe bird. Biological Conservation. https://doi.org/10.1016/j.biocon.2011.07.011

Méndez M, Vögeli M, Tella JL, Godoy JA (2014) Joint effects of population size and isolation on genetic erosion in fragmented populations: finding fragmentation thresholds for management. Evol Appl 7(4):506-18

Nogués-Bravo D, Agirre A (2006) Patrón y modelos de distribución espacial de la alondra ricotí Chersophilus duponti durante el periodo reproductor en el LIC de Ablitas (Navarra). Ardeola 53:55–68

Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21:959–967

Pascual-Hortal L, Saura S (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. Landscape and Urban Planning. https://doi.org/10.1016/j.landurbplan.2007.03.005

Pereira J, Saura S, Jordán F (2017) Single-node vs. multi-node centrality in landscape graph analysis: key habitat patches and their protection for 20 bird species in NE Spain. Methods in Ecology and Evolution. https://doi.org/10.1111/2041-210X.12783

Pérez-Granados C, López-Iborra GM (2013) Census of breeding birds and population trends of the Dupont's lark Chersophilus duponti in Eastern Spain. Ardeola 60(1):143-150

Pérez-Granados C, López-Iborra GM (2015) Baja dispersión adulta y baja tasa de recaptura juvenil de la alondra ricotí (Chersophilus duponti) en el Rincón de Ademuz (Valencia). XX Iberian Ringing Congress

Pérez-Granados C, López-Iborra GM, Garza V (2017) Breeding biology of the endangered Dupont's lark Chersophilus duponti in two separate Spanish shrub-steppes Bird Study 64(3):328-338

Ricketts TH, Gretchen CD, Ehrlich PR, Fay JP (2002) Countryside Biogeography of Moths in a Fragmented Landscape: Biodiversity in Native and Agricultural Habitats. Conservation Biology. https://doi.org/10.1046/j.1523-1739.2001.015002378.x

Rolstad J (2008). Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biological Journal of the Linnean Society 42:149-163

Saura S, Torne J (2009) Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software. 24(1)135-139

Saura S, Rubio L (2010) A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography. https://doi.org/10.1111/j.1600-0587.2009.05760.x

Saura S, Estreguilb C, Mouton C, Rodríguez-Freireb M (2011) Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). Ecological Indicators. https://doi.org/10.1016/j.ecolind.2010.06.011

Seoane J, Justribó JH, García F, Retamar J, Rabadan C, Atienza JC. Habitat-suitability modelling to assess the effects of land-use changes on Dupont's lark Chersophilus duponti: a case study in the Layna Important Bird Area. Biological Conservation 8:241–252

Suárez F, Garza (1989) La invernada de la Alondra de Dupont, Chersophilus duponti, en la Península Ibérica. Ardeola 36:107-110

Suárez F, Garcia JT, Sampietro FJ, Garza V (2006) The non-breeding distribution of Dupont's lark Chersophilus duponti in Spain. Bird Conservation International 16:317-323.

Suárez F (2010) La Alondra Ricotí (Chersophilus duponti). Dirección General Para La Biodiversidad. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid

Shake CS, Moorman CE, Riddle JD, Burchell MR (2012) Influence of Patch Size and Shape on Occupancy by Shrubland Birds. The Condor 114(2):268-278

Suárez F (2010) La Alondra Ricotí (Chersophilus duponti). Dirección General Para La Biodiversidad. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid

Traba J, Garza V, García-Antón A, Gómez-Catasús J, Zurdo J, Pérez-Granados C, Morales MB, Oñate JJ, Herranz J, Malo J (2019) Criterios para la gestión y conservación de la población española de alondra ricotí Chersophilus duponti. Fundación Biodiversidad, Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid

Vergara PM, Pérez-Hernández CG, Hahn IJ, Soto GE (2013) Deforestation in central Chile causes a rapid decline in landscape connectivity for a forest specialist bird species. *Ecol Res* 28:481–492

Visconti P, Elkin C (2009). Using connectivity metrics in conservation planning - When does habitat quality matter? Diversity and Distributions. https://doi.org/10.1111/j.1472-4642.2009.00564.x

Vögeli M, Laiolo P, Serrano D, Tella JL (2008) Who are we sampling? Apparent survival differs between methods in a secretive species. Oikos. https://doi.org/10.1111/j.1600-0706.2008.17225.x

Vögeli M, Serrano D, Pacios S, Tella JL (2010) The relative importance of patch habitat quality and landscape attributes on a declining steppe-bird metapopulation. Biological Conservation. https://doi.org/10.1016/j.biocon.2009.12.040

Vögeli M, Laiolo P, Serrano D, Tella JL (2011) Predation of experimental nests is linked to local population dynamics in a fragmented bird population. Biology Letters 7:954–957

Watling J, Nowakowski A, Donnelly M, Orrock J (2011) Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. Global Ecology and Biogeography 20(2):209-217

Figure 1

Map of current populations, subpopulations and stepping stones of the Iberian metapopulation of Dupont's lark.

Black contours represent populations (n=24), green polygons are subpopulations (n=100) and black dots indicate stepping stones (n=294). Red crosses represent the 23 subpopulations of recent extinction (post-2000). See detailed cartography in Supplemental File S1.

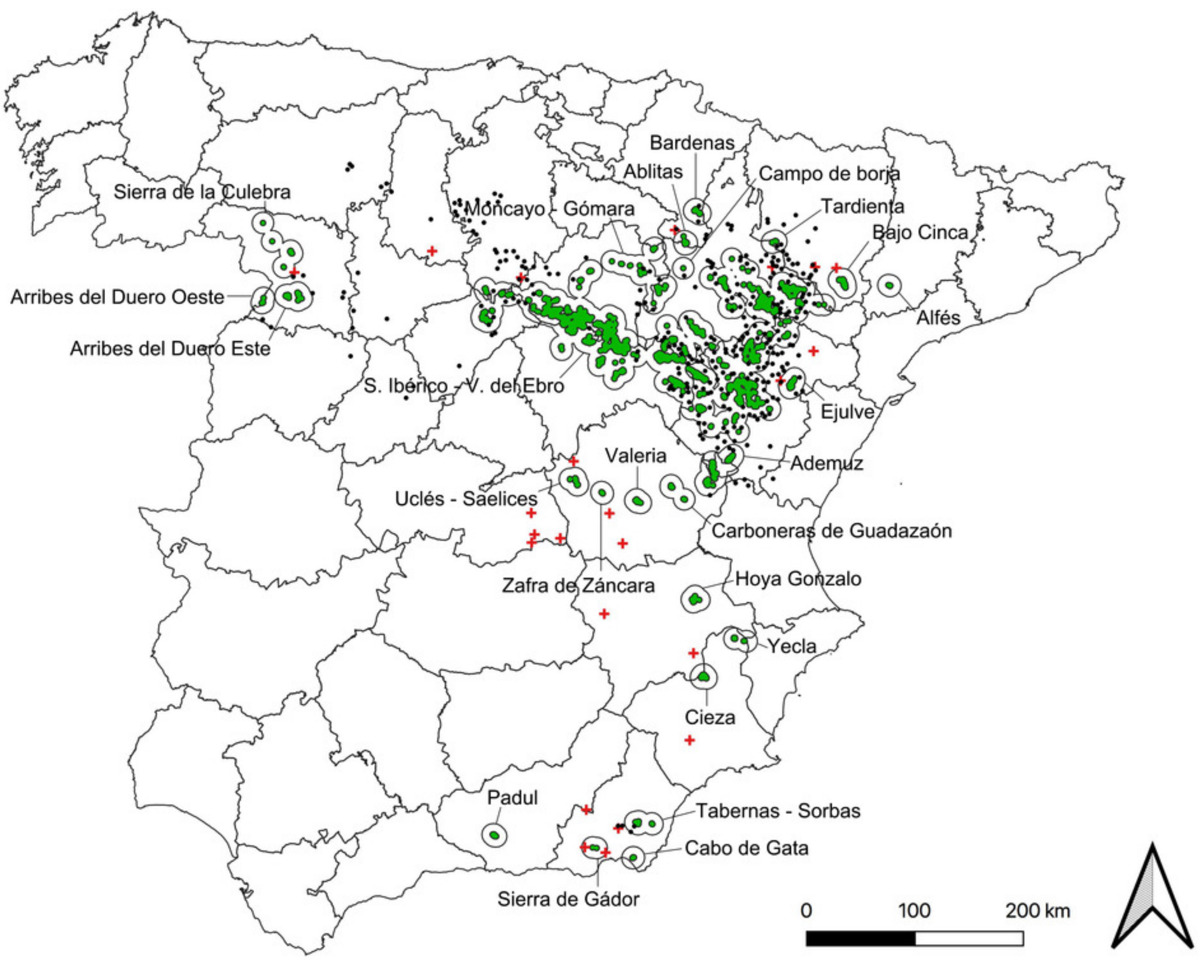

Figure 2

Map of nodes importance in the Iberian metapopulation of Dupont’s lark.

Nodes classified according to general importance index (dPC). The core of the distribution, focused in the Iberian Range - Ebro Valley population, gathers the most important nodes. Here we show an intermediate scenario, with a dispersal distance of 20 km and presence of stepping stones. Maps for all possible scenarios are included in Supplemental File S2.

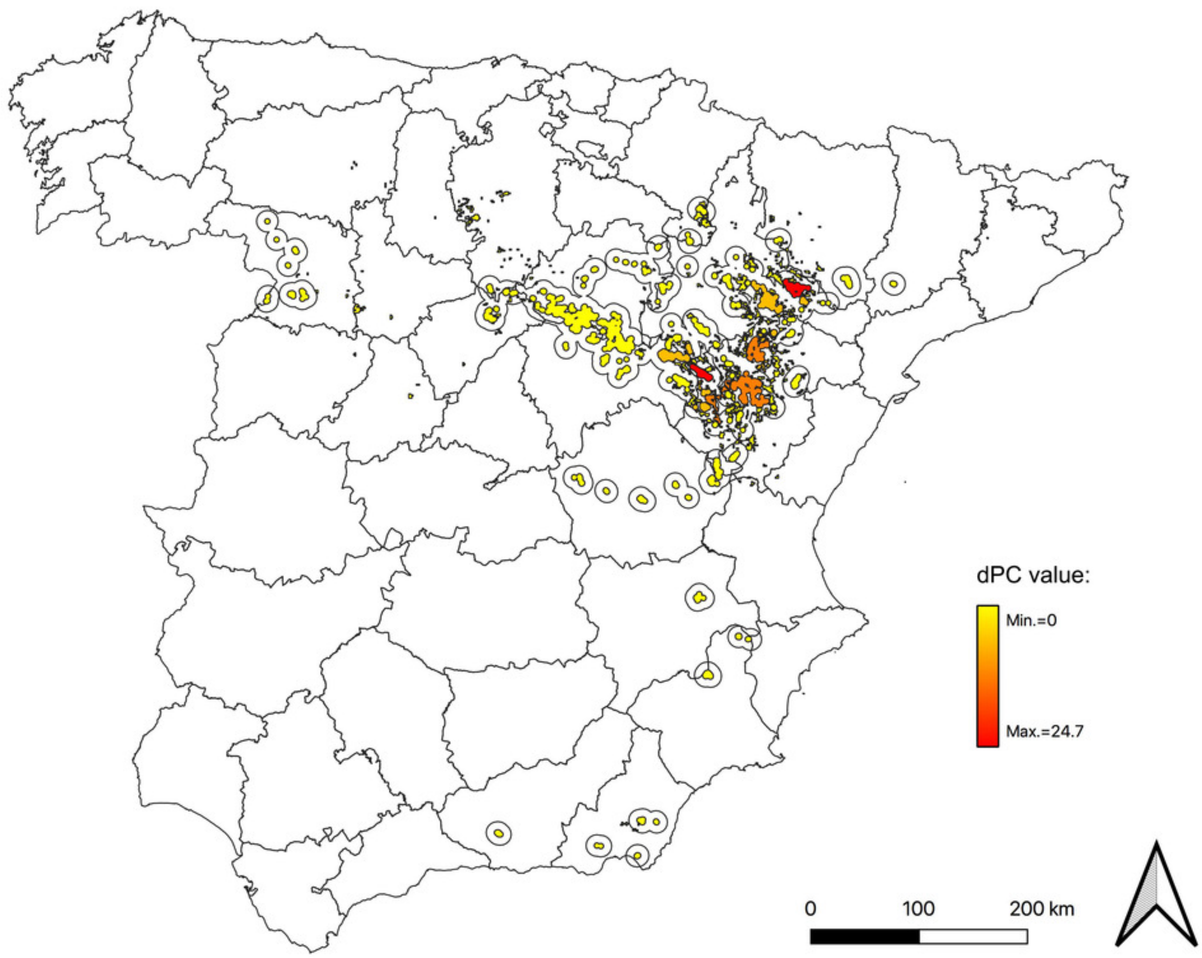

Figure 3

Probability of connection of Dupont's lark metapopulation under the different scenarios evaluated.

Effect of the dispersal distance (5, 20 and 100 km) and the presence/absence of stepping stones in the probability of connection among Dupont's lark subpopulations. See Supplemental File S3 for the complete matrix of probability of connection for node pairs.

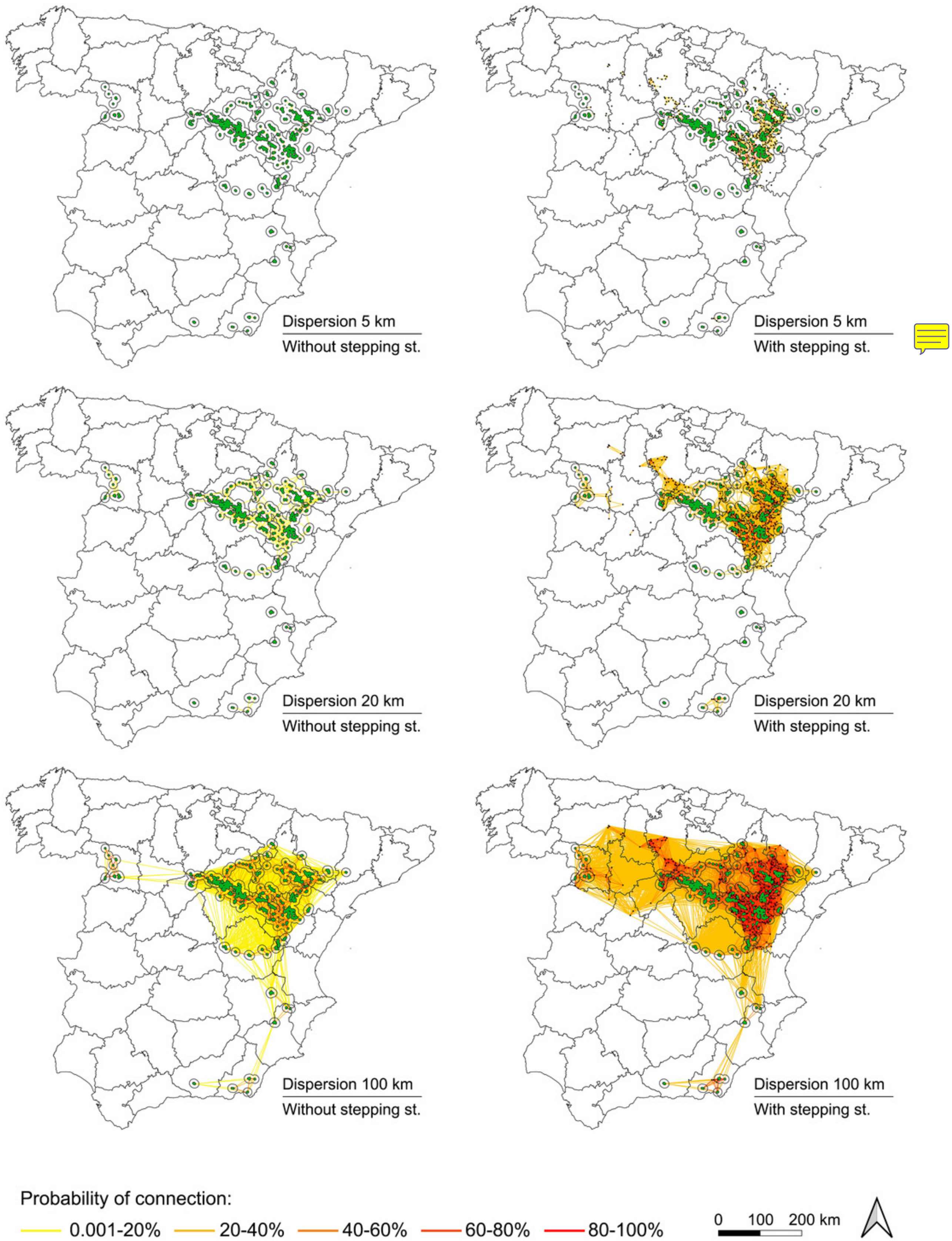
Dispersion 5 km
Without stepping st.
Dispersion 5 km
With stepping st.
Dispersion 20 km
Without stepping st.
Dispersion 20 km
With stepping st.
Dispersion 100 km
Without stepping st.
Dispersion 100 km
With stepping st.
Probability of connection:
0.001-20%
20-40%
40-60%
60-80%
80-100%
0
100
200 km

Table 1(on next page)

Equivalent Connectivity Index (EC) comparison among different scenarios of dispersal and presence/absence of stepping stones.

The Equivalent Connectivity Index represents the global connectivity of the metapopulation. Both dispersal and stepping stones generate increments in connectivity, with a stronger effect of the latter.

Dispersal distance	EC without s. stones	EC with s. stones
Short distance dispersal (5 km)	8935.65	14560.55
Medium distance dispersal (20 km)	11529.18	24340.81
Long distance dispersal (100 km)	21956.86	46319.15

Table 2 (on next page)

Summary of the 10 most important nodes for intra-patch connectivity (dPC_{intra}).

dPC_{intra} makes reference to the internal importance of each node (habitat surface, quality and continuity) and doesn’t depend on spatial position or proximity to other nodes. Thus, results are the same for all scenarios of dispersal and here we only show presence/absence of stepping stones. See the complete list in Supplemental File S3.

Without stepping stones			**With stepping stones**		
Name	Prov.	dPC_{intra}	Name	Prov.	dPC_{intra}
Monegros	Z	33.34	Monegros	Z	4.49
Blancas	TE	17.77	Blancas	TE	2.39
Torralba de los Frailes	TE	4.16	Torralba de los Frailes	TE	0.56
Bardenas	NA	2.64	Bardenas	NA	0.36
Lécera	Z	2.10	Lécera	Z	0.28
Pinilla del Campo	SO	1.49	Pinilla del Campo	SO	0.20
Campo Romanos	Z	1.47	Campo Romanos	Z	0.20
Paramera de Molina	GU	1.39	Paramera de Molina	GU	0.19
Orihuela del Tremedal	TE	1.25	Orihuela del Tremedal	TE	0.17
Gelsa	Z	1.16	Gelsa	Z	0.16

Table 3(on next page)

Summary of the 10 most important nodes for flow generation in the network (dPC_{flux}).

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental File S3.

Short distance dispersal (5 km)			Medium distance dispersal (20 km)			Long distance dispersal (100 km)		
Without stepping stones								
Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}
Monegros	Z	7,64	Blancas	TE	15,14	Blancas	TE	20,86
Gelsa	Z	7,06	Monegros	Z	13,48	Monegros	Z	19,70
Torralba de los Frailes	TE	5,82	Torralba de los Frailes	TE	11,07	Torralba de los Frailes	TE	11,30
Paramera de Molina	GU	5,33	Paramera de Molina	GU	7,89	Lécera	Z	7,22
Blancas	TE	3,52	Gelsa	Z	7,81	Paramera de Molina	GU	6,94
Alforque	Z	1,05	Belchite	Z	3,34	Campo Romanos	Z	5,49
Pinilla del Campo	SO	1,02	La Torresaviñán	GU	2,82	Gelsa	Z	5,35
Milmarcos-Llumes	GU	1,02	Lécera	Z	2,81	Orihuela del Tremedal	TE	5,21
Pozalmuro	SO	0,89	Cenegro	SO	2,61	Belchite	Z	5,09
Cenegro	SO	0,82	Alforque	Z	2,54	La Torresaviñán	GU	4,85
With stepping stones								
Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}
Blancas	TE	14,77	Blancas	TE	16,33	Monegros	Z	15,01
Monegros	Z	14,03	Monegros	Z	13,50	Blancas	TE	12,94
Torralba de los Frailes	TE	7,64	Torralba de los Frailes	TE	8,08	Torralba de los Frailes	TE	6,42
Paramera de Molina	GU	6,11	Paramera de Molina	GU	5,25	Lécera	Z	4,74
Gelsa	Z	4,79	Orihuela del Tremedal	TE	5,07	Paramera de Molina	GU	3,84
Orihuela del Tremedal	TE	4,23	Lécera	Z	5,00	Orihuela del Tremedal	TE	3,70
(SS) Monegrillo 2	Z	3,62	Gelsa	Z	3,74	Belchite	Z	3,44
Pozondón	TE	3,11	Belchite	Z	3,48	Campo Romanos	Z	3,43
(SS) Alfajarín 1	Z	2,69	Pozondón	TE	3,38	Gelsa	Z	3,19
(SS) Torralba de los Sisones	TE	2,58	Celadas Este	TE	2,51	La Torresaviñán	GU	2,48

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Table 4 (on next page)

Summary of the 10 most important nodes for connectivity maintenance ($dPC_{connector}$).

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental File S3.

Short distance dispersal (5 km)			**Medium distance dispersal (20 km)**			**Long distance dispersal (100 km)**		
Without stepping stones								
Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}
Paramera de Molina	GU	2.38	Paramera de Molina	GU	6.65	Layna	SO	8.28
Layna	SO	0.87	Layna	SO	4.58	Segura de los Baños	TE	8.22
Altos de Barahona	SO	0.83	Altos de Barahona	SO	3.57	Paramera de Molina	GU	7.89
Gelsa	Z	0.78	Gelsa	Z	2.60	Altos de Barahona	SO	7.08
Pozalmuro	SO	0.11	Maranchón	GU	1.55	Altiplano de Teruel	TE	3.78
Aldealpozo	SO	0.06	Villar del Salz	TE	1.30	Blancas	TE	3.60
Cueva de la Hoz	GU	0.04	Azaila	TE	1.28	Maranchón	GU	2.86
Altiplano de Teruel	TE	0.02	Alforque	Z	1.25	Azaila	TE	2.52
Alforque	Z	0.02	Blancas	TE	1.03	Lécera	Z	2.50
Conquezuela	SO	0.01	Altiplano de Teruel	TE	0.91	Gelsa	Z	2.16
With stepping stones								
Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}
(SS) Alba	TE	9.30	(SS) Alba	TE	12.12	Segura de los Baños	TE	7.91
Villar del Salz	TE	6.89	Segura de los Baños	TE	10.24	Layna	SO	4.90
(SS) Rubielos de la Cérida	TE	6.70	(SS) Rubielos de la Cérida	TE	10.20	(SS) Rubielos de la Cérida	TE	4.09
Paramera de Molina	GU	5.70	Villar del Salz	TE	8.32	(SS) Alba	TE	4.07
(SS) Ojos Negros 1	TE	4.85	Altiplano de Teruel	TE	8.26	Altiplano de Teruel	TE	4.03
(SS) Cuerlas 1	Z	4.68	Blancas	TE	5.97	Altos de Barahona	SO	3.97
Blancas	TE	3.84	(SS) Ojos Negros 1	TE	5.25	Paramera de Molina	GU	3.80
Pozondón	TE	3.54	(SS) Hoz de la Vieja	TE	5.08	(SS) Pinilla Trasmonte	BU	3.48
(SS) Celadas	TE	2.98	(SS) Moneva	Z	4.75	(SS) Hoz de la Vieja	TE	3.06
Monegros	Z	2.37	Paramera de Molina	GU	4.41	Villar del Salz	TE	2.76

Table 5(on next page)

Summary of the 10 most important nodes for the connectivity according to the global index dPC.

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental File S3.

Short distance dispersal (5 km)			Medium distance dispersal (20 km)			Long distance dispersal (100 km)		
Without stepping stones								
Name	Prov.	dPC	Name	Prov.	dPC	Name	Prov.	dPC
Monegros	Z	40.99	Monegros	Z	33.79	Blancas	TE	27.40
Blancas	TE	21.29	Blancas	TE	26.85	Monegros	Z	25.50
Torralba de los Frailes	TE	9.98	Paramera de Molina	GU	15.37	Paramera de Molina	GU	15.06
Paramera de Molina	GU	9.10	Torralba de los Frailes	TE	13.62	Torralba de los Frailes	TE	12.05
Gelsa	Z	8.99	Gelsa	Z	11.10	Segura de los Baños	TE	10.18
Bardenas	NA	2.64	Layna	SO	5.77	Lécera	Z	10.06
Pinilla del Campo	SO	2.51	Altos de Barahona	SO	4.89	Layna	SO	9.67
Lécera	Z	2.27	Belchite	Z	4.73	Altos de Barahona	SO	8.67
Orihuela del Tremedal	TE	1.90	Lécera	Z	4.42	Gelsa	Z	7.70
La Torresaviñán	GU	1.77	Alforque	Z	3.89	Belchite	Z	7.08
With stepping stones								
Name	Prov.	dPC	Name	Prov.	dPC	Name	Prov.	dPC
Monegros	Z	28.96	Blancas	TE	24.70	Monegros	Z	17.19
Blancas	TE	25.30	Monegros	Z	20.46	Blancas	TE	16.28
Paramera de Molina	GU	12.33	(SS) Alba	TE	14.04	Segura de los Baños	TE	9.14
(SS) Alba	TE	11.22	Segura de los Baños	TE	11.67	Paramera de Molina	GU	7.69
Torralba de los Frailes	TE	9.49	(SS) Rubielos de la Cérida	TE	10.93	Torralba de los Frailes	TE	6.60
Villar del Salz	TE	7.96	Altiplano de Teruel	TE	10.31	Belchite	Z	6.20
Gelsa	Z	7.37	Paramera de Molina	GU	9.84	Layna	SO	5.59
(SS) Rubielos de la Cérida	TE	7.35	Villar del Salz	TE	9.40	Altiplano de Teruel	TE	5.46
Pozondón	TE	6.83	Torralba de los Frailes	TE	8.76	(SS) Alba	TE	5.36
(SS) Cuerlas 1	Z	6.43	Belchite	Z	6.74	Lécera	Z	5.17