

Wind farms affect the occurrence, abundance and population trends of small passerine birds: The case of the Dupont's lark

Julia Gómez-Catasús¹  | Vicente Garza^{1,2} | Juan Traba¹

¹Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain

²C/ Vía Límite, 29 E-28029 Madrid, Spain

Correspondence

Julia Gómez-Catasús

Email: julia.gomez@uam.es

Funding information

European Commission, Grant/Award Number: Life Ricotí (LIFE15-NAT-ES-000802); Excellence Network Remedial 3CM (S2013/MAE-2719); Fundación Patrimonio Natural de Castilla y León; Biodiversity Foundation - Ministry of Agriculture, Food and Environment; Fundación BBVA, BBVA-Ricotí-project; European Social Fund for the Youth Employment Initiative

Handling Editor: Ailsa McKenzie

Abstract

1. The assessment of the effects of wind farms on bird populations is commonly based on collision fatality records. This could undervalue the effect of wind farms on small-sized birds. We evaluate the effect of wind turbines on occurrence, abundance and population trends of a threatened small passerine species, the Dupont's lark *Chersophilus duponti*. To our knowledge, this is one of the first studies addressing the effect of wind farms on population trends using time-series data from multiple wind farms.
2. We estimated population trends by fitting a switching linear trend model with the software TRIM (Trend & Indices for Monitoring data). We used multiannual data surveys of five populations in the presence of wind farms and nine in their absence (2008–2016 period). Furthermore, we fitted a logistic and a negative binomial regression model to test the effect of wind farm proximity on species occurrence and abundance in 2016, respectively. We incorporated local connectivity and habitat availability estimates in both models as predictors.
3. Results showed a negative trend overall, but that was significantly more regressive in the presence of wind farms: 21.0% vs. 5.8% average annual decline in the absence of wind farms.
4. Dupont's lark occurrence and abundance in 2016 were negatively affected by measures of population isolation and positively affected by the distance to wind farms.
5. These results highlight the negative effect of isolation and wind farm proximity on Dupont's lark population parameters. Taking into account the metapopulation structure exhibited by the species in the study area, this work established a 4.5-km threshold distance from wind farms, beyond which Dupont's lark populations should be unaffected.
6. *Synthesis and applications.* This work highlights the negative impact of wind farms on small-sized birds and provides a 4.5-km threshold distance that should be taken into account in the design of future wind energy projects. Moreover, we suggest an analytical approach based on population trends, species abundance and occurrence variation in relation to wind farms, useful for the assessment of wind farm impacts on small-sized birds.

KEYWORDS

abundance, connectivity, Dupont's lark, habitat loss, metapopulation, *Passeriformes*, population trends, wind farms

1 | INTRODUCTION

The effects of wind farms on birds have received considerable attention (see e.g. Atienza, Martín Fierro, Infante, Valls, & Domínguez, 2011; Erickson, Wolfe, Bay, Johnson, & Gehring, 2014; Kuvlesky et al., 2007; Northrup & Wittemyer, 2013; Powlesland, 2009). However, these effects are not well understood for specific sites and species. Potential impacts can be categorized into two main types: (1) direct mortality through collision with wind turbines and associated power lines (Barrios & Rodríguez, 2004; De Lucas, Ferrer, Bechard, & Muñoz, 2012; Drewitt & Langston, 2008; Erickson et al., 2014); and (2) spatial displacement due to habitat loss, disturbance (visual, noise and vibration impacts) or barrier effects to movements (De Lucas, Janss, & Ferrer, 2004; Larsen & Guillemette, 2007; Pearce-Higgins, Stephen, Langston, Bainbridge, & Bullman, 2009; Pruett, Patten, & Wolfe, 2009; Winder et al., 2014; Zwart, Dunn, McGowan, & Whittingham, 2015). These impacts can have immediate effects on species abundance or density. Moreover, long-term displacement effects can impact population viability through diminishing body conditions, survival, breeding success and fecundity (Campedelli, Londi, Cutini, Sorace, & Tellini-Florenzano, 2013; Carrete, Sánchez-Zapata, Benítez, Lobón, & Donázar, 2009; Dahl, Bevanger, Nygård, Røskoft, & Stokke, 2012; De Lucas et al., 2004; Leddy, Higgins, & Naugle, 1999; Martínez-Abraín et al., 2012; Winder, Gregory, McNew, & Sandercock, 2015) and can eventually affect species abundance or density more insidiously.

Available information on the effects of wind farms on small passerine birds is scarce. The commonly used methods based on collision fatality records may underestimate the direct effect of wind farms on mortality rates of small-sized birds (Atienza et al., 2011), due to their low detectability and high rate of carcass disappearance (Erickson et al., 2014; Morrison, 2002). Moreover, the likelihood of direct mortality depends on factors such as the species' susceptibility to collision, weather conditions, season, wind farm location or structural attributes of turbines (Barrios & Rodríguez, 2004; De Lucas et al., 2012; Drewitt & Langston, 2008). Given this scenario, the direct effect of wind farms on small-sized birds cannot be adequately assessed through collision events. To address this problem, other analytical approaches based on species occurrence, bird density or abundance, or productivity variation in relation to wind farm presence, must be used to estimate the effect in a metapopulation context (De Lucas et al., 2004; Devereux, Denny, & Whittingham, 2008; Leddy et al., 1999; Stevens, Hale, Karsten, & Bennett, 2013).

In this study, we evaluated the effect of wind farms on small-sized birds using the Dupont's lark *Chersophilus duponti* (Vieillot, 1820) as a model species. The Dupont's lark is one of the scarcest passerine birds in Europe, classified as "near threatened" by IUCN (BirdLife International, 2017), as "Endangered" in the Red Book of the Birds of Spain (Garza, Suárez, & Tella, 2004) and as "Vulnerable" in the Spanish National Catalogue of Threatened Species (Real Decreto 139/2011, 4th February). Its distribution is restricted to the Iberian Peninsula and North Africa, with the Iberian System

plateau and the Ebro Valley steppes (central and NE Spain, respectively) hosting the two core European populations (Suárez, 2010). At a landscape scale, the distribution of the species is determined by patch size, connectivity between patches and characteristics of the landscape matrix (Vögeli, Serrano, Pacios, & Tella, 2010). At a micro-habitat scale, the species occupies flat (less than a 10%–15% slope) steppes with pillow-shaped and short (c. 20–40 cm) shrubs, avoiding dry pastures and cereal fields (Garza et al., 2005). The plateau landscapes selected by the Dupont's lark are flat, open and windy areas, with a clear overlap existing between the optimal habitat for the species and suitable areas for wind farm implementation (Laiolo & Tella, 2006; Suárez, 2010).

Wind farms have been broadly described as one of the major threats to Dupont's lark populations (Garza & Traba, 2016; Íñigo et al., 2008), though their impact has never been quantified. Paradoxically, since 2008, the monitoring of Dupont's lark populations has been linked to environmental impact statements for wind farms, providing us with a relatively large serial dataset suitable to evaluate their long-term impact. In this work, we assessed the effect of wind farms on the population trends of 14 Dupont's lark populations (five in the presence and nine in the absence of wind farms) using serial data for the years 2008–2016. In addition, we evaluated wind farm proximity effect on species' occurrence and abundance in 2016, controlling for differences in local connectivity estimates and habitat availability measures according to the metapopulation framework (Hanski, 1999; Moilanen & Hanski, 1998). We predicted that wind farms would have a negative impact on the species associated with the risk of collision during their aerial courtship display (Erickson et al., 2014), with behavioural and fitness alterations due to visual and noise disturbance (Rodríguez et al., 2017; Zwart et al., 2015) or with increases in nest predation rates due to changes in the predator community (Lekuona, 2001). These impacts should be reflected through the negative effect of wind farms on population trends, occurrence and abundance.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is the "Tierra de Medinaceli" region located in the south of Soria (central Spain; 02°26'35.1"W, 41°11'28.9"N; c. 1200 m a.s.l.; Figure 1) and covers around 200 km². The climate is Continental Mediterranean, with a mean temperature of 10.6°C and a mean annual rainfall of 500 mm. The study area is located between the "Altos de Barahona" and "Páramo de Layna" Special Protection Areas (SPAs), constituting a key zone to ensure the connectivity between these two protected areas, which host about 13% of the Dupont's lark European populations (Garza et al., 2010). The landscape is a flat, short shrub steppe dominated by *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Linum suffruticosum* (Garza et al., 2005). Cereal fields, ploughings and conifer afforestations, subsidized by the Common Agricultural Policy (CAP) of the European Union, are interspersed in the territory. The habitat is fragmented at different

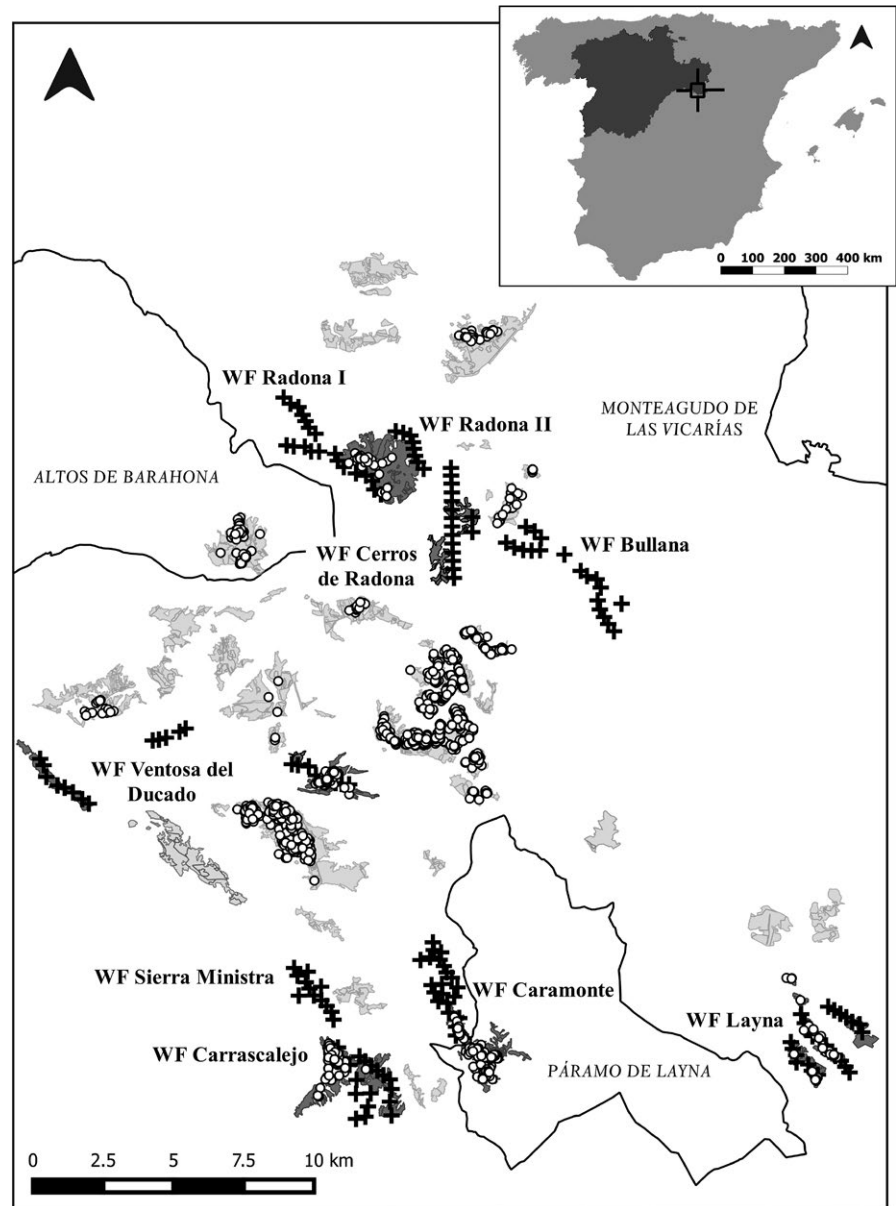


FIGURE 1 “La Tierra de Medinaceli” region (Soria, central Spain). The map illustrates the potential habitat patches for the Dupont’s lark with (dark grey) and without (pale grey) wind farms; it also shows Dupont’s lark territories in the study period 2008–2016 (white dots) and the location of wind turbines (crosses). Wind farms (WF) and SPA names (capital letters) are indicated

spatial scales as a result of natural (geological) processes and human activities, resulting in a metapopulation scenario comprising 25 patches of optimal habitat for the species (i.e. short shrub with slopes lower than 15%; Garza et al., 2005) (Figure 1). The species was present in 14 of 25 patches during the 2008–2016 period (hereafter, Dupont’s lark populations) (Figure 1).

The Medinaceli Wind Resource Area is located in this same region (Figure 1). It is composed of nine wind farms, six of them located in the vicinity of five of the 14 Dupont’s lark populations (Figure 1; Table 1). Wind farm construction began between 2007 and 2008. Eight of nine wind farms became operational in 2009 (Bullana, Caramonte, Carrascalejo, Cerros de Radona, Radona I, Radona II, Sierra Ministra and Ventosa del Ducado) and one in 2011 (Layna). Each wind farm consists of 10–32 turbines of 2000–2300 kW per turbine. The hub height of turbines ranges from 67 to 80 m and the rotor diameter from 77 to 90 m (Sources: www.aeeolica.org and www.thewindpower.net). Patches with and without wind farms

do not differ in habitat availability ($M \pm SD$; 166.35 ± 119.78 ha vs. 141.76 ± 85.72 ha; F -value = 0.20; $p = .66$), altitude (1164 ± 86 m vs. 1113 ± 58 m; F -value = 1.75; $p = .21$) or slope ($2.42 \pm 0.87\%$ vs. $2.48 \pm 1.83\%$; F -value = 0.11; $p = .75$).

2.2 | Dupont’s lark surveys

In this study, we followed the census methodology commonly employed in other works (Garza, Traba, & Suárez, 2003; Pérez-Granados & López-Iborra, 2013; Tella, Vögeli, Serrano, & Carrete, 2005). Areas with potential habitat for the species were identified using aerial photogrammetry and visual inspection (see also Garza et al., 2005). Transects were placed through the centre of potential habitat patches and were walked during the nine study seasons by only one observer (2008–2016). The number of transects per habitat patch was between 1 and 19 and was proportional to patch size. Each itinerary was repeated at least twice per season in those

TABLE 1 Dupont's lark populations in the study area

Dupont's lark populations ^a	Change rate (%)	Δ Number of territories ^b	n 2016 ^c	Available habitat (ha) ^d	Wind farm
Aguaviva de la Vega	-100	-10	0	201.47	No
Alcubilla de las Peñas	50	2	6	101.81	No
Ambrona-Miño	-14	-8	49	202.48	No
Beltejar	-50	-1	1	69.78	No
Blocona	-32.8	-21	43	239.10	No
Conquezuela	-50	-5	5	0.79	No
Esteras de Medinaceli	-79.2	-19	5	130.11	Caramonte
Layna-Obetago	-100	-12	0	148.92	Layna
Miño-Medinaceli	-86.7	-13	2	78.75	Ventosa del Ducado
Miño-Yelo	-100	-2	0	55.66	No
Radona	-100	-13	0	375.05	Radona I and Radona II
Sierra Ministra	-66.7	-10	5	98.90	Carrascalejo
Taroda	-42.8	-3	4	220.40	No
Yuba	75	3	7	184.38	No

^aName of Dupont's lark populations refers to the municipality where it is located.

^bChange in number of territories per population from 2008 to 2016.

^cPopulation size in 2016 (number of males).

^dPatch size.

Change rates of -100% correspond to local extinctions.

populations where the species was extinct for more than 3 years and between four and six times in the remaining populations. This number of survey visits produces reliable Dupont's lark population estimates (Pérez-Granados & López-Iborra, 2017). The starting point was alternated with the aim of surveying each patch when the highest singing activity of the species is recorded. Surveys were carried out during the breeding period (from the end of March until the middle of June) at dawn, moving the starting hour forward as the season progressed (from c. 5:00 to c. 3:00 solar hour) and with duration depending on the singing activity of individuals, but never lasting more than 1.5 hr.

The position of singing males was recorded using a GPS. We used the territory mapping method to locate male territories, since it provides more accurate results when studying territorial passerine species (Bibby, Burgess, Hill, & Mustoe, 2000). Territories were delimited by gathering accumulated observations from different surveys and interpreting simultaneously contacted neighbouring males (Tellería, 1986). Population size was expressed as the minimum number of territories, considering different populations when Dupont's lark territories in the study period (2008–2016) were separated by more than 1 km, since more than 95% of within-territory movements occur within this distance (Vögeli, Laiolo, Serrano, & Tella, 2008).

2.3 | Connectivity, habitat availability and proximity to wind farms

Connectivity between populations was estimated using two indices. Total connectivity index (C_1) provides information about the position of each population in relation to the metapopulation

context (core or satellite population). This was calculated as the distance from the centroid (average coordinates) of each population (estimated from Dupont's lark territories during the study period in each population) to the centroid of all territories in 2016. The relative connectivity index (C_2) provides information about the proximity to other populations that could be a source of individuals. This was measured as the distance from the centroid of each population to the centroid of the territories of the nearest occupied population in 2016 (Vögeli et al., 2010). Both connectivity indexes were estimated using all Dupont's lark territories in the study period (2008–2016) to avoid the problem of data absence in 2016 for extinct populations.

Habitat availability was measured as the optimal habitat surface per patch (i.e. short shrub with slopes lower than 15%; Garza et al., 2005). Habitat patches separated by less than 1 km were considered within the same population (Vögeli et al., 2008). Proximity to wind farms was calculated as the distance from the centroid of each population to the nearest wind turbine. All these variables were calculated with the software QGIS 2.14.0 (Quantum GIS Development Team, 2009) to be incorporated in the probability of occurrence and the abundance models (see below).

2.4 | Statistical analysis

We evaluated Dupont's lark population trends between 2008 and 2016 using the software TRIM (*Trend & Indices for Monitoring data*, TRIM 3.54; Pannekoek & Van Strien, 2006). TRIM estimates annual indices and evaluates trends in these indices implementing log-linear models, an approach commonly employed in temporal series analysis (e.g. Delgado, Morales, Traba, & De la Morena,

2009; Wretenberg, Lindström, Svensson, & Pärt, 2007). This software was used because it: (1) allows the analysis of time series with an absence of data; (2) takes into account overdispersion and serial correlation in data; (3) incorporates significant change points in trends; and (4) assesses the effects of covariates in indices and trends (Pannekoek & Van Strien, 2005). TRIM calculates indices that represent the effect of change between years, which indicates relative variation in the total population. At the first time point, the index value is 1 and is taken as a point reference for quantifying the relative temporal trends in subsequent years. We fitted a switching linear trend model by a stepwise selection of change points in trends and incorporated the covariate “wind farms” (presence/absence of wind farms). TRIM uses Wald tests for the significance of change points and for the significance of the effect of the covariate on population trends. When the difference between parameters before and after a change point is not different from zero (default significance threshold: 0.2), the corresponding change point is removed from the model attending to the parsimony principle (Pannekoek & Van Strien, 2005). Since our data presented light overdispersion and serial correlation (1.189 and 0.364 respectively), we employed a generalized estimating equation (GEE) approach for the estimation procedure. The best-fit model was selected attending to three criteria: (1) goodness-of-fit tests (likelihood ratio test and Chi-squared); (2) Akaike information criterion (AIC); and (3) Wald tests for the significance of the slope parameter, changes in slope and effect of the covariate, since the two previous criteria are not fully reliable when data present either overdispersion or serial correlation (Pannekoek & Van Strien, 2005).

To evaluate the effect of wind farms and other explanatory variables on the occurrence and abundance of Dupont’s lark in 2016, we used a logistic (1 presence, 0 absence; logit link function) and a negative binomial regression (log-link function), respectively. Connectivity (C_1 , C_2), habitat availability and proximity to wind farms were incorporated as predictors in both models. In our case, the logistic regression model is equivalent to the probability of extinction since absences are local extinctions that took place during the study period. The best models were selected according to two criteria: (1) the deviance statistic for model comparison (drop1 function in R); and (2) the log-likelihood ratio Chi-squared statistic for the global significance of the model. The explained variance of the models was calculated as the deviance explained (D^2). We employed the packages stats (R Core Team, 2002) and lmer (Hothorn et al., 2017) in the free R software (v. 1.0.143; R Development Core Team, 2009) for model selection.

3 | RESULTS

Twelve of the 14 studied populations experienced a dramatic decline while two slightly increased in population size during the study period (Table 1). Populations with wind farms showed an overall decline during the study period (between 66% and 100%), including

two local extinctions (Radona and Layna-Obetago). Two of nine populations with no wind farms also suffered local extinctions, but with a slighter decrease in bird numbers (Table 1).

The final model included five change points in slope and wind farm covariate and fitted to a log-linear distribution ($\chi^2 = 99.70$, $df = 89$, $p = .21$; likelihood ratio = 109.62, $df = 89$, $p = .07$; AIC = -68.38). The stepwise procedure revealed five significant change points, specifically years 2008 (Wald test = 4.00; $df = 2$; $p < .2$), 2009 (Wald test = 39.75; $df = 2$; $p < .001$), 2010 (Wald test = 22.02; $df = 2$; $p < .001$), 2011 (Wald test = 5.29; $df = 2$; $p < .2$) and 2013 (Wald test = 4.11; $df = 2$; $p < .2$). Wald tests revealed that both the slope parameter (Wald test = 28.48; $df = 1$; $p < .001$) and the effect of the wind farm covariate (Wald test = 34.29; $df = 5$; $p < .001$) were significant, supporting the results of the goodness-of-fit tests.

All of the 14 Dupont’s lark populations in “La Tierra de Medinaceli” region experienced an average annual decline of 9% (95% confidence interval, 95% CI [-11.6, -6.5%]; $p < .01$). Interannual variability was considerable, showing a generalized decline of 47.8% in the period 2009–2010, and an average annual decline of 18.1% in the period 2011–2013 (Table 2). Interpopulation variability hinders stable population trend values for other time periods and was classified as “uncertain” by the TRIM criteria due to large 95% CIs including a 0% change rate (Table 2; Pannekoek & Van Strien, 2006). A source of interpopulation variability was the presence of wind farms. Populations in the presence of wind facilities experienced a 21.0% average annual decline (95% CI [-25.8, -17.0]; $p < .01$), four times higher than populations in the absence of these infrastructures (5.8% average annual decline; 95% CI [-8.3, -3.4%]; $p < .01$; Figure 2).

The logistic model analysing the probability of occurrence of Dupont’s lark in 2016 incorporated the distance to the centroid of all territories in 2016 (total connectivity index C_1 ; likelihood ratio test, LRT = 3.66; $p = .055$) and the distance to wind farms (LRT = 5.59; $p = .017$), explaining 42.2% of total deviance (LogLik = -4.84; $\chi^2 = 7.06$; $p = .029$). Probability of occurrence decreased with the distance to the centroid of all territories in 2016 (total connectivity index C_1), though this was non-significant (i.e. core populations presented a higher probability of occurrence than satellite populations) (Table 3). Distance from wind farms had a positive marginal effect, reflecting an increase in the probability of occurrence as distance to wind facilities increased, reaching its maximum at 4.5 km (Figure 3).

Dupont’s lark abundance in 2016 significantly increased with the distance to wind farms (LRT = 10.03; $p < .01$) and decreased with the distance to the centroid of all territories in 2016 (total connectivity index C_1 ; LRT = 12.39; $p < .001$). This model explained 56.6% of total deviance (LogLik = -42.47; $\chi^2 = 11.91$; $p < .01$) (Table 4).

4 | DISCUSSION

Our results suggest that wind infrastructures have a significant and deleterious impact on populations of a small and seriously threatened

	Annual change rate (%)	95% CI ^a	TRIM trend ^b
2008–2009 period			
Overall trend	13.9%	[-12.2; 39.9]	Uncertain
Populations without WF	21%	[-1.7; 41.9]	Uncertain
Populations with WF	4.5%	[-23.6; 31.1]	Uncertain
2009–2010 period			
Overall trend	-47.8%	[-61.2; -33.9]	Drastic decline
Populations without WF	-42.6%	[-54.3; -30.9]	Drastic decline
Populations with WF	-60%	[-88.2; -31.7]	Drastic decline
2010–2011 period			
Overall trend	16.1%	[-21.5; 53.9]	Uncertain
Populations without WF	29%	[-4.9; 63.1]	Uncertain
Populations with WF	-13%	[-46.5; 20.2]	Uncertain
2011–2013 period			
Overall trend	-18.1%	[-33.1; -3.2]	Moderate decline
Populations without WF	-16.5%	[-30.2; -2.9]	Moderate decline
Populations with WF	-21%	[-52.1; 9.8]	Uncertain
2013–2016 period			
Overall trend	4.4%	[-7.1; 15.8]	Uncertain
Populations without WF	5%	[-5.1; 15.5]	Uncertain
Populations with WF	-11%	[-32.9; 11.2]	Uncertain

^a95% confidence interval.

^bTrend classification attending to TRIM criteria (Pannekoek & Van Strien, 2006).

Overall trends for the 14 Dupont's lark populations in each period are indicated in bold.

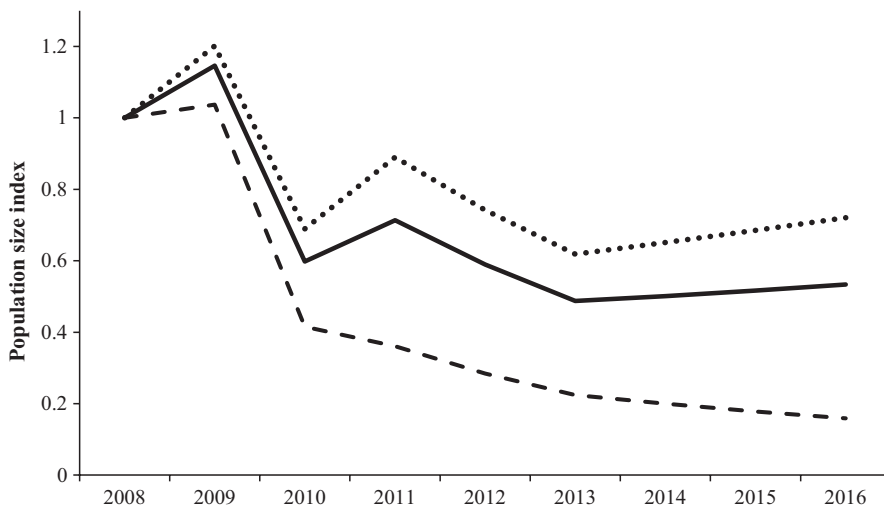


FIGURE 2 Switching linear trend model indexes for five Dupont's lark populations in the presence of wind farms (striped line), nine populations with no wind farms (dotted line) and overall trend for the 14 populations in "La Tierra de Medinaceli" region (continuous line)

passerine bird, the Dupont's lark. To our knowledge, this is the first study specifically addressing the effect of wind farms on Dupont's lark populations, despite that many authors have drawn attention to the subject (Garza & Traba, 2016; Íñigo et al., 2008; Laiolo & Tella, 2006; Pérez-Granados & López-Iborra, 2013; Suárez, 2010). In addition, it is the first study to evaluate the effects of wind farms on small passerine birds, in general (De Lucas et al., 2004; Leddy et al., 1999; Stevens et al., 2013).

Wind farms can have a negative effect on birds (Atienza et al., 2011; Drewitt & Langston, 2006). Consequently, it is expected that population trends and both the occurrence and abundance of some species coexisting with wind farms will be affected in the long term by the implementation of these facilities. Our results highlight the negative effect of wind farms on Dupont's lark population trends. Populations in the presence of wind farms experienced a 21% average annual decline, about four times higher than similar populations

TABLE 3 Regression coefficients of logistic regression analysing the effects on the probability of occurrence of Dupont's lark in 2016 at 14 populations

	β^a	SE ^b	Z value ^c	p ^d
Intercept	3.3405	2.5062	1.333	.1826
Total connectivity index C ₁	-0.4139	0.2632	-1.573	.1158
Distance to wind farms (km)	1.419	0.8151	1.741	.0817

^aRegression coefficients.

^bStandard error of regression coefficients.

^cZ-statistic for regression coefficients.

^dp-value.

Marginally statistically significant p-values are indicated in bold.

in the absence of these facilities (5.8% average annual decline). In addition, both the occurrence and the abundance of Dupont's lark in 2016 were negatively affected by the proximity to wind farms. To our knowledge, this is the first evidence of the impact that wind farms have on passerine population trends, as this has been scarcely addressed (Meek, Ribbands, Christer, Davy, & Higginson, 1993) even for other groups of birds (Campedelli et al., 2013; Meek et al., 1993). Our results agree with the effects of wind farms described on the abundance (De Lucas et al., 2004; Stewart, Pullin, & Coles, 2005) and probability of occurrence (Pearce-Higgins et al., 2009; Stevens et al., 2013) of other passerine species (see however Devereux et al., 2008).

The effects of wind farms on birds have been described as site, season and species specific (Barrios & Rodriguez, 2004; De Lucas et al., 2012). The Dupont's lark is a ground-nesting species with crepuscular activity, terrestrial habits and secretive and territorial behaviour, relying on acoustic signals for communication (Gómez-Catasús, Barrero, Garza, & Traba, 2016). Its typical aerial courtship displays at heights of 100–150 m during dawn (Gómez-Catasús et al., 2016) make the birds prone to collision

TABLE 4 Regression coefficients of negative binomial regression analysing the effects on Dupont's lark abundance in 2016 at 14 populations

	β^a	SE ^b	Z value ^c	p ^d
Intercept	2.802	0.839	3.340	<.001
Total connectivity index C ₁	-0.269	0.079	-3.380	<.001
Distance to wind farms (km)	0.764	0.225	3.387	<.001

^aRegression coefficients.

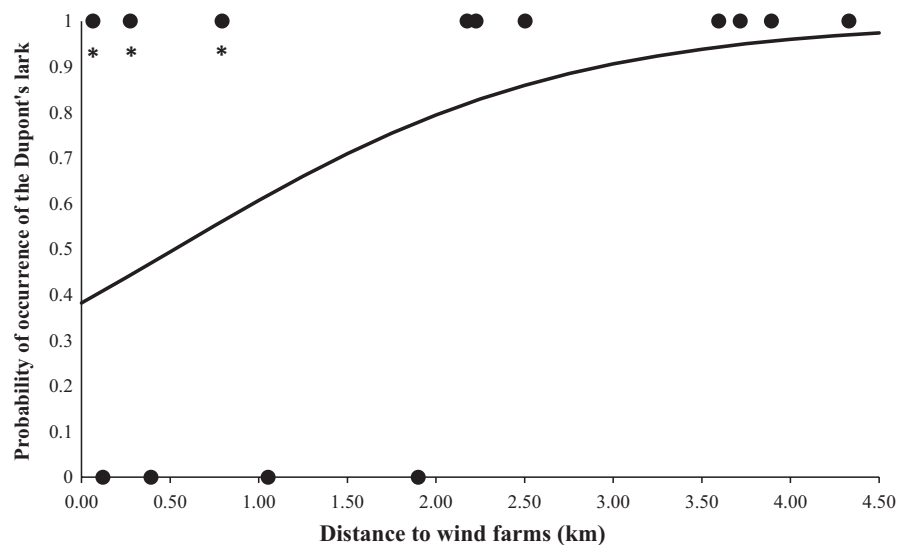
^bStandard error of regression coefficients.

^cZ-statistic for regression coefficients.

^dp-value.

Statistically significant p-values are indicated in bold.

with wind turbines (mean hub height in the study area is 76.6 m) (Powlesland, 2009). Nighttime lighting systems associated with turbines may have negative impacts on the species' behaviour or may increase exhaustion and the likelihood of collision at night (Gehring, Kerlinger, & Manville, 2009; Rodríguez et al., 2017). On the other hand, turbines could be perceived as a predation risk for this species adopting a cryptic evasion strategy, increasing the probability of displacement (Stevens et al., 2013). Moreover, changes in predator communities associated with wind farms and roads (Frey & Conover, 2006; Lekuona, 2001) may increase the frequency of nest predation (Hethcoat & Chalfoun, 2015) or affects on nest-site selection (Wallander, Isaksson, & Lenberg, 2006). Finally, the auditory impact of turbines could drive an acoustic masking effect decreasing the ability of birds to communicate vocally (Bayne, Habib, & Boutin, 2008; Francis, Ortega, & Cruz, 2009; Goodwin & Shriver, 2011). This could have an impact on territory defence (Zwart et al., 2015), pairing (Habib, Bayne, & Boutin, 2007) or calls for survival (e.g. begging or alarm calls; Leavesley & Magrath, 2005; Leonard & Horn, 2005), with direct consequences on breeding densities and reproductive success

FIGURE 3 Effect of the distance to wind farms on the probability of occurrence of Dupont's lark in 2016. Observed values for the 14 populations (black dots) and predicted values by the model (black line) are shown. The three remaining populations in the presence of wind farms are marked with asterisk (*): "Esteras de Medinaceli," "Sierra Ministra" and "Miño-Medinaceli" (see Table 1 for population changes in 2008–2016)

(Bayne et al., 2008; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011).

The analytical approach employed allowed us to identify a threshold distance to wind farms of 4.5 km, which should be taken into account when designing new wind facilities within the Dupont's lark distribution. The naturally fragmented distribution of optimum habitat in the study area could be an important driver explaining this threshold, due to the presence of a non-optimal habitat matrix around each subpopulation (Figure 1). However, this threshold distance suggests that wind farms drive the extinction of Dupont's lark populations, since displacement seems unlikely for this species, which is described as a short-distance disperser (dispersal distance of adults is lower than 2 km; Laiolo, Vögeli, Serrano, & Tella, 2007; Vögeli et al., 2008). In addition, overall declining population trends (Table 2; Figure 2) and local extinction events support this hypothesis.

Dupont's lark occurrence and abundance was also analysed controlling for differences in local connectivity estimates and habitat availability measures, key factors in a metapopulation context (Hanski, 1999). Habitat availability did not have an effect on Dupont's lark populations in our study. However, abundance and the probability of Dupont's lark occurrence (i.e. probability of non-extinction) were higher in core populations than in peripheral populations (total connectivity index C_1). These results are coherent with a higher probability of recolonization in connected populations (Hanski, 1999; Moilanen & Hanski, 1998) and with the centripetal extinction pattern described for the species (Garza & Traba, 2016; Suárez, 2010; Tella et al., 2005; Vögeli et al., 2010). In addition, connectivity has genetic consequences on Dupont's lark populations (Méndez, Tella, & Godoy, 2011; Méndez, Vögeli, Tella, & Godoy, 2014), which could partially explain the effects observed on Dupont's lark abundance and occurrence.

The results presented in this work highlight the effect of wind farms on small-sized birds and their role as an accelerator of declining population trends in endangered species. The particular case study of the Dupont's lark suggests that other important concomitant factors could be underlying the overall declining trends (9% average decline). Land-use changes, agriculture intensification and habitat quality loss due to abandonment of traditional extensive livestock systems (Garza & Traba, 2016; Íñigo et al., 2008; Suárez, 2010) seem to be the main drivers of a generalized decline in population trends (Garza & Traba, 2016; Pérez-Granados & López-Iborra, 2014; Tella et al., 2005), aggravated by genetic processes (Méndez et al., 2011, 2014). Future research should focus on disentangling the mechanisms underlying the detected turbine impacts in order to correctly design wind energy projects. The analytical approach employed based on population trends, species abundance and occurrence variation in relation to wind farms could be useful to assess the effect of wind farms on small-sized birds. This allowed us to identify a 4.5-km threshold distance that should be taken into account in the design of future wind energy projects within the distribution areas of endangered passerine birds in a metapopulation context.

ACKNOWLEDGEMENTS

We thank Manuel B. Morales and Adrián Barrero for interesting discussions on this research. This work was supported by the Education, Youth and Sport Bureau (Madrid Regional Government) and the European Social Fund for the Youth Employment Initiative (PEJ15/AMB/AI-0059). The data used came from the Dupont's Lark Monitoring Program in Medinaceli Region, funded by Fundación Patrimonio Natural de Castilla y León. This is a contribution to the Excellence Network Remedial 3CM (S2013/MAE-2719), supported by Comunidad de Madrid; the project "Scientific basis for the National Conservation for Dupont's Lark in Spain," supported by Fundación Biodiversidad, of the Ministry of Agriculture, Food and Environment; the Life-Ricotí-project (LIFE15-NAT-ES-000802), granted by the European Commission; the BBVA-Ricotí-project, granted by the BBVA Foundation.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; V.G. collected the data; J.G-C. analysed the data and wrote the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.pn2k8> (Gómez-Catasús, Garza, & Traba, 2018).

ORCID

Julia Gómez-Catasús  <http://orcid.org/0000-0001-8949-5318>

REFERENCES

- Atienza, J. C., Martín Fierro, I., Infante, O., Valls, J., & Domínguez, J. (2011). *Directrices para la evaluación del impacto de los parques eólicos en aves y murciélagos (versión 3.0)*. Madrid: SEO/BirdLife.
- Barrios, L., & Rodríguez, A. (2004). Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *Journal of Applied Ecology*, 41, 72–81. <https://doi.org/10.1111/j.1365-2664.2004.00876.x>
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22, 1186–1193. <https://doi.org/10.1111/j.1523-1739.2008.00973.x>
- Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. (2000). *Birds census techniques* (2nd ed.). London, U.K.: Academic Press.
- BirdLife International. (2017). *Chersophilus duponti* (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2017: e.T22717380A117697133. Retrieved from <http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22717380A117697133.en>.
- Campedelli, T., Londi, G., Cutini, S., Sorace, A., & Tellini-Florenzano, G. (2013). Raptor displacement due to the construction of a wind farm: Preliminary results after the first 2 years since the construction. *Ethology Ecology & Evolution*, 26, 376–391. <https://doi.org/10.1080/03949370.2013.862305>

- Carrete, M., Sánchez-Zapata, J. A., Benítez, J. R., Lobón, M., & Donazar, J. A. (2009). Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biological Conservation*, 142, 2954–2961. <https://doi.org/10.1016/j.biocon.2009.07.027>
- Dahl, E. L., Bevanger, K., Nygård, T., Røskoft, E., & Stokke, B. G. (2012). Reduced breeding success in white-tailed eagles at Smøla wind-farm, western Norway, is caused by mortality and displacement. *Biological Conservation*, 145, 79–85. <https://doi.org/10.1016/j.biocon.2011.10.012>
- De Lucas, M., Ferrer, M., Bechard, M. J., & Muñoz, A. R. (2012). Griffon vulture mortality at wind farms in southern Spain: Distribution of fatalities and active mitigation measures. *Biological Conservation*, 147, 184–189. <https://doi.org/10.1016/j.biocon.2011.12.029>
- De Lucas, M., Janss, G. F., & Ferrer, M. (2004). The effects of a wind farm on birds in a migration point: The Strait of Gibraltar. *Biodiversity & Conservation*, 13, 395–407. <https://doi.org/10.1023/B:BIOC.0000006507.22024.93>
- Delgado, M. P., Morales, M. B., Traba, J., & De la Morena, E. L. G. (2009). Determining the effects of habitat management and climate on the population trends of a declining steppe bird. *Ibis*, 151, 440–451. <https://doi.org/10.1111/j.1474-919X.2009.00927.x>
- Devereux, C. L., Denny, M. J., & Whittingham, M. J. (2008). Minimal effects of wind turbines on the distribution of wintering farmland birds. *Journal of Applied Ecology*, 45, 1689–1694. <https://doi.org/10.1111/j.1365-2664.2008.01560.x>
- Drewitt, A. L., & Langston, R. H. W. (2006). Assessing the impacts of wind farms on birds. *Ibis*, 148, 29–42. <https://doi.org/10.1111/j.1474-919X.2006.00516.x>
- Drewitt, A. L., & Langston, R. H. W. (2008). Collision effects of wind-power generators and other obstacles on birds. *Annals of the New York Academy of Sciences*, 1134, 233–266. <https://doi.org/10.1196/annals.1439.015>
- Erickson, W. P., Wolfe, M. M., Bay, K. J., Johnson, D. H., & Gehring, J. L. (2014). A comprehensive analysis of small-passerine fatalities from collision with turbines at wind energy facilities. *PLoS ONE*, 9, e107491. <https://doi.org/10.1371/journal.pone.0107491>
- Francis, C. D., Ortega, C. P., & Cruz, A. (2009). Noise pollution changes avian communities and species interactions. *Current Biology*, 19, 1415–1419. <https://doi.org/10.1016/j.cub.2009.06.052>
- Frey, S. N., & Conover, M. R. (2006). Habitat use by meso-predators in a corridor environment. *Journal of Wildlife Management*, 70, 1111–1118. [https://doi.org/10.2193/0022-541X\(2006\)70\[1111:HUBMIA\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1111:HUBMIA]2.0.CO;2)
- Garza, V., Justribó, J. H., Carriles, E., del Pozo, R., Hernández, J. L., & Suárez, F. (2010). El censo actual: Distribución, poblaciones y conservación. I. Castilla y León: Soria. In F. Suárez (Ed.), *La Alondra ricotí Chersophilus duponti* (pp. 207–214). Madrid: Dirección General para la Biodiversidad. Ministerio de Medio Ambiente y Medio Rural y Marino.
- Garza, V., Suárez, F., Herranz, J., Traba, J., García de la Morena, E. L., Morales, M. B., ... Castañeda, M. (2005). Home range, territoriality and habitat selection by the Dupont's Lark *Chersophilus duponti* during the breeding and postbreeding periods. *Ardeola*, 53, 133–146.
- Garza, V., Suárez, F., & Tella, J. L. (2004). Alondra de Dupont. In A. Madroño, C. González & J. C. Atienza (eds.), *Chersophilus duponti. Libro Rojo de las Aves de España* (pp. 309–312). Madrid: Dirección General para la Biodiversidad-SEO/BirdLife.
- Garza, V., & Traba, J. (2016). Retos para la conservación de una especie amenazada. Alondra ricotí, el fantasma del páramo. *Quercus*, 359, 24–33.
- Garza, V., Traba, J., & Suárez, F. (2003). Is the European population of Dupont's Lark *Chersophilus duponti* adequately estimated? *Bird Study*, 50, 309–311. <https://doi.org/10.1080/00063650309461325>
- Gehring, J., Kerlinger, P., & Manville, A. M. (2009). Communication towers, lights, and birds: Successful methods of reducing the frequency of avian collisions. *Ecological Applications*, 19, 505–514. <https://doi.org/10.1890/07-1708.1>
- Gómez-Catasús, J., Barrero, A., Garza, V., & Traba, J. (2016). Alondra ricotí – *Chersophilus duponti*. In A. Salvador & M. B. Morales (eds.), *Enciclopedia virtual de los vertebrados Españoles*. Madrid: Museo Nacional de Ciencias Naturales. Retrieved from: <http://www.vertebradosibericos.org>
- Gómez-Catasús, J., Garza, V., & Traba, J. (2018). Data from: Wind farms affect the occurrence, abundance and population trends of small passerine birds: The case of the Dupont's lark. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.pn2k8>
- Goodwin, S. E., & Shriver, W. G. (2011). Effects of traffic noise on occupancy patterns of forest birds. *Conservation Biology*, 25, 406–411. <https://doi.org/10.1111/j.1523-1739.2010.01602.x>
- Habib, L., Bayne, E. M., & Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, 44, 176–184. <https://doi.org/10.1111/j.1365-2664.2006.01234.x>
- Halfwerk, W., Holleman, L. J., Lessells, C. K., & Slabbekoorn, H. (2011). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48, 210–219. <https://doi.org/10.1111/j.1365-2664.2010.01914.x>
- Hanski, I. (1999). *Metapopulation ecology*. Oxford, U.K.: Oxford University Press.
- Hethcoat, M. G., & Chalfoun, A. D. (2015). Towards a mechanistic understanding of human-induced rapid environmental change: A case study linking energy development, nest predation and predators. *Journal of Applied Ecology*, 52, 1492–1499. <https://doi.org/10.1111/1365-2664.12513>
- Hothorn, T., Zeileis, A., Farebrother, R. W., Cummins, C., Millo, G., & Mitchell, D. (2017). *Package 'lmtree': Testing linear regression models. Version 0.9-35*. Retrieved from: <https://cran.r-project.org/web/packages/lmtree/lmtree.pdf>
- Íñigo, A., Garza, V., Tella, J. L., Laiolo, P., Suárez, F., & Barov, B. (2008). *Action plan for the Dupont's lark Chersophilus duponti in the European Union*. Madrid: SEO/BirdLife/BirdLife International.
- Kuvlesky, W. P., Brennan, L. A., Morrison, M. L., Boydston, K. K., Ballard, B. M., & Bryant, F. C. (2007). Wind energy development and wildlife conservation: Challenges and opportunities. *Journal of Wildlife Management*, 71, 2487–2498. <https://doi.org/10.2193/2007-248>
- Laiolo, P., & Tella, J. L. (2006). Fate of unproductive and unattractive habitats: Recent changes in Iberian steppes and their effects on endangered avifauna. *Environmental Conservation*, 33, 223–232. <https://doi.org/10.1017/S0376892906003146>
- Laiolo, P., Vögeli, M., Serrano, D., & Tella, J. L. (2007). Testing acoustic versus physical marking: Two complementary methods for individual-based monitoring of elusive species. *Journal of Avian Biology*, 38, 672–681. <https://doi.org/10.1111/j.2007.0908-8857.04006.x>
- Larsen, J. K., & Guillemette, M. (2007). Effects of wind turbines on flight behaviour of wintering common eiders: Implications for habitat use and collision risk. *Journal of Applied Ecology*, 44, 516–522. <https://doi.org/10.1111/j.1365-2664.2007.01303.x>
- Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, 70, 365–373. <https://doi.org/10.1016/j.anbehav.2004.10.017>
- Leddy, K. L., Higgins, K. F., & Naugle, D. E. (1999). Effects of wind turbines on upland nesting birds in conservation reserve program grasslands. *The Wilson Bulletin*, 111, 100–104.
- Lekuona, J. M. (2001). *Uso del espacio por la avifauna y control de la mortalidad de aves en los parques eólicos de Navarra durante un ciclo anual*. Report. Dirección General de Medio Ambiente. Departamento de

- Medio Ambiente, Ordenación del Territorio y Vivienda. Gobierno de Navarra, Spain.
- Leonard, M. L., & Horn, A. G. (2005). Ambient noise and the design of begging signals. *Proceedings of the Royal Society of London B: Biological Sciences*, 272, 651–656. <https://doi.org/10.1098/rspb.2004.3021>
- Martínez-Abraín, A., Tavecchia, G., Regan, H. M., Jimenez, J., Surroca, M., & Oro, D. (2012). Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy. *Journal of Applied Ecology*, 49, 109–117. <https://doi.org/10.1111/j.1365-2664.2011.02080.x>
- Meek, E. R., Ribbands, J. B., Christer, W. G., Davy, P. R., & Higginson, I. (1993). The effects of aero-generators on moorland bird populations in the Orkney Islands, Scotland. *Bird Study*, 40, 140–143. <https://doi.org/10.1080/00063659309477139>
- Méndez, M., Tella, J. L., & Godoy, J. A. (2011). Restricted gene flow and genetic drift in recently fragmented populations of an endangered steppe bird. *Biological Conservation*, 144, 2615–2622. <https://doi.org/10.1016/j.biocon.2011.07.011>
- Méndez, M., Vögeli, M., Tella, J. L., & Godoy, J. A. (2014). Joint effects of population size and isolation on genetic erosion in fragmented populations: Finding fragmentation thresholds for management. *Evolutionary Applications*, 7, 506–518. <https://doi.org/10.1111/eva.12154>
- Moilanen, A., & Hanski, I. (1998). Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology*, 79, 2503–2515. [https://doi.org/10.1890/0012-9658\(1998\)079\[2503:MDEOHQ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2503:MDEOHQ]2.0.CO;2)
- Morrison, M. L. (2002). *Searcher bias and scavenging rates in bird/wind energy studies*. National Renewable Laboratory Report, NREL/SR-500-30876, Golden, Colorado, USA.
- Northrup, J. M., & Wittemyer, G. (2013). Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, 16, 112–125. <https://doi.org/10.1111/ele.12009>
- Pannekoek, J., & Van Strien, A. (2005). *TRIM 3 manual (Trends & indices for monitoring data)*. Voorburg: Statistics Netherlands.
- Pannekoek, J., & Van Strien, A. (2006). *TRIM version 3.54 (Trends & Indices for Monitoring data)*. Voorburg: Statistics Netherlands.
- Pearce-Higgins, J. W., Stephen, L., Langston, R. H., Bainbridge, I. P., & Bullman, R. (2009). The distribution of breeding birds around upland wind farms. *Journal of Applied Ecology*, 46, 1323–1331. <https://doi.org/10.1111/j.1365-2664.2009.01715.x>
- Pérez-Granados, C., & López-Iborra, G. M. (2013). Census of breeding birds and population trends of the Dupont's lark *Chersophilus duponti* in Eastern Spain. *Ardeola*, 60, 143–150. <https://doi.org/10.13157/arla.60.1.2012.143>
- Pérez-Granados, C., & López-Iborra, G. M. (2014). ¿Por qué la alondra ricotí debe catalogarse como 'En peligro de extinción'? *Quercus*, 337, 18–25.
- Pérez-Granados, C., & López-Iborra, G. M. (2017). Assessment of counting methods used for estimating the number of territorial males in the endangered Dupont's Lark. *Ardeola*, 64, 75–84. <https://doi.org/10.13157/arla.64.1.2017.sc2>
- Powlesland, R. (2009). *Impact of wind farms on birds: A review*. Wellington: Publishing Team, Department of Conservation.
- Pruett, C. L., Patten, M. A., & Wolfe, D. H. (2009). Avoidance behavior by prairie grouse: Implications for development of wind energy. *Conservation Biology*, 23, 1253–1259. <https://doi.org/10.1111/j.1523-1739.2009.01254.x>
- Quantum GIS Development Team. (2009). *Quantum GIS geographic information system*. Open Source Geospatial Foundation Project. Retrieved from <https://www.qgis.org/es/site/>
- R Core Team. (2002). *The R stats package*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from: <http://www.r-project.org>
- R Development Core Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Rodríguez, A., Holmes, N. D., Ryan, P. G., Wilson, K., Faulquier, L., Murillo, Y., ... Le Corre, M. (2017). Seabird mortality induced by land-based artificial lights. *Conservation Biology*, 31, 986–1001. <https://doi.org/10.1111/cobi.12900>
- Stevens, T. K., Hale, A. M., Karsten, K. B., & Bennett, V. J. (2013). An analysis of displacement from wind turbines in a wintering grassland bird community. *Biodiversity and Conservation*, 22, 1755–1767. <https://doi.org/10.1007/s10531-013-0510-8>
- Stewart, G. B., Pullin, A. S., & Coles, C. F. (2005). *Effects of wind turbines on bird abundance. Systematic review no. 4*. Birmingham: Centre for Evidence-Based Conservation.
- Suárez, F. (2010). *La alondra ricotí (Chersophilus duponti)*. Madrid: Dirección General para la Biodiversidad, Ministerio de Medio Ambiente y Medio Rural y Marino.
- Tella, J. L., Vögeli, M., Serrano, D. Y., & Carrete, M. (2005). Current status of the threatened Dupont's lark in Spain: Overestimation, decline and extinction of local populations. *Oryx*, 39, 1–5. <https://doi.org/10.1017/S0030605305000165>
- Tellería, J. L. (1986). *Manual para el censo de los vertebrados terrestres*. Madrid: Raíces.
- Vögeli, M., Laiolo, P., Serrano, D., & Tella, J. L. (2008). Who are we sampling? Apparent survival differs between methods in a secretive species. *Oikos*, 117, 1816–1823. <https://doi.org/10.1111/j.1600-0706.2008.17225.x>
- Vögeli, M., Serrano, D., Pacios, F., & Tella, J. L. (2010). The relative importance of patch habitat quality and landscape attributes on a declining steppe-bird metapopulation. *Biological Conservation*, 143, 1057–1067. <https://doi.org/10.1016/j.biocon.2009.12.040>
- Wallander, J., Isaksson, D., & Lenberg, T. (2006). Wader nest distribution and predation in relation to man-made structures on coastal pastures. *Biological Conservation*, 132, 343–350. <https://doi.org/10.1016/j.biocon.2006.04.026>
- Winder, V. L., Gregory, A. J., McNew, L. B., & Sandercock, B. K. (2015). Responses of male Greater Prairie-Chickens to wind energy development. *The Condor: Ornithological Applications*, 117, 284–296. <https://doi.org/10.1650/CONDOR-14-98.1>
- Winder, V. L., McNew, L. B., Gregory, A. J., Hunt, L. M., Wisely, S. M., & Sandercock, B. K. (2014). Space use by female Greater Prairie-Chickens in response to wind energy development. *Ecosphere*, 5, 1–17. <https://doi.org/10.1890/ES13-00206.1>
- Wretenberg, J., Lindström, Å., Svensson, S., & Pärt, T. (2007). Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. *Journal of Applied Ecology*, 44, 933–941. <https://doi.org/10.1111/j.1365-2664.2007.01349.x>
- Zwart, M. C., Dunn, J. C., McGowan, P. J., & Whittingham, M. J. (2015). Wind farm noise suppresses territorial defense behavior in a songbird. *Behavioral Ecology*, 27, 101–108. <https://doi.org/10.1093/beheco/arv128>

How to cite this article: Gómez-Catasús J, Garza V, Traba J. Wind farms affect the occurrence, abundance and population trends of small passerine birds: The case of the Dupont's lark. *J Appl Ecol.* 2018;00:1–10. <https://doi.org/10.1111/1365-2664.13107>