Increasing wild boar density explains the decline of a Montagu's harrier population on a protected coastal wetland

J. Crespo, J. Jiménez, A. Martínez–Abraín

Abstract

Increasing wild boar density explains the decline of a Montagu's harrier population on a protected coastal wetland. We studied the rapid decline in the number of breeding pairs (geometric growth rate λ = 0.86; 14 % annual decrease) of a semi–colonial ground–nesting bird of prey, the Montagu's harrier (*Circus pygargus*), after twelve years of rapid population growth (λ = 1.15; 15 % rate of annual increase) in a protected coastal wetland in Eastern Spain. The study was conducted from 1992–2017, and the range of values in population size was: 2–37 breeding pairs. We contrasted 20 biologically–sound hypotheses (including local and regional factors) to explain the trend over time in the annual number of pairs. The most parsimonious model included a surrogate of wild boar (*Sus scrofa*) density in the region during the previous year and the annual number of Montagu's harrier pairs breeding inland in the study province during the focal year. Syntopic western marsh harriers (*C. aeruginosus*) were not found to have any effect on the numbers of Montagu's harriers either in our modelling or when we performed a quantitative and qualitative study both for years t and t–1. Our final 'best' models did not include spring rainfall, regional forest fires or local land use changes. The impact of wild boars on breeding success, together with conspecific attraction, could have resulted in the dispersal of coastal wetland birds to larger populations in dense inland shrub lands where levels of wild boar nest predation were more likely lower.

Key words: Ground–nesting birds, Regional dynamics, Protected wetlands, Nest predation, *Circus pygargus, Sus scrofa*

Resumen

El aumento de la densidad de jabalíes explica la reducción de una población de aguilucho cenizo presente en un humedal costero protegido. Hemos estudiado el rápido descenso del número de parejas reproductoras (tasa de crecimiento geométrico λ = 0,86; 14 % de disminución anual) de un ave semicolonial que nidifica en el suelo, el aguilucho cenizo (*Circus pygargus*), tras 12 años de rápido crecimiento demográfico (λ = 1,15; 15 % de tasa de aumento anual) en un humedal costero protegido situado en el este de España. El periodo de estudio fue 1992–2017, con un intervalo de valores del tamaño de población de 2–37 parejas reproductoras. Hemos contrastado 20 hipótesis razonables desde el punto de vista biológico (teniendo en cuenta factores locales y regionales) para explicar la tendencia del número anual de parejas. El modelo más parsimonioso incluyó un indicador de la densidad regional del jabalí (*Sus scrofa*) durante el año anterior y el número anual de parejas de aguilucho cenizo que se reprodujeron en el interior de la provincia del estudio, durante el año en cuestión. En nuestro modelo no se observó que el aguilucho lagunero occidental (*C. aeruginosus*) sintópico tuviera efecto alguno en el número de aguiluchos cenizos; tampoco lo tuvo en los análisis cuantitativos y cualitativos relativos a los años t y t–1. Las precipitaciones de primavera, los incendios forestales en la región y los cambios en el uso del suelo a escala local tampoco aparecieron en nuestros mejores modelos finales. Los efectos de jabalíes en el éxito reproductor, junto con la atracción de individuos conespecíficos, podrían haber provocado la dispersión de las aves de los humedales costeros a poblaciones más numerosas presentes en zonas arbustivas de interior, donde probablemente la depredación de nidos por jabalí sea inferior.

Palabras clave: Aves que nidifican en el suelo, Dinámica regional, Humedales protegidos, Depredación de nidos, *Circus pygargus, Sus scrofa*

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Introduction

Protected areas are created to secure the long–term persistence of species therein. However, animal populations in protected areas sometimes decline abruptly or are unexpectedly extirpated after years of successful breeding (Martínez–Abraín et al., 2003; Oro et al., 2004). Explanations for this phenomenon are not always evident at the local level because drivers of population decline are often multifaceted and can operate at different temporal and spatial scales (Vickery et al., 2014). For example, changes in landscape structure, in conjunction with climate change, have been listed among the most frequent causes of breeding failure in birds (Gaston et al., 2003; Luck, 2003; Hilbert et al., 2004). More specifically, habitat degradation (including the indirect effect of human infrastructure) and habitat loss (via changes in land use) are currently the main threats to raptor populations (Thiollay, 2006; Martínez–Abraín et al., 2009). Land use changes may include not only changes in agricultural practices but also the total abandonment of such activity in association with human depopulation of rural areas (Hansen et al., 2002). The consequences of such change may bring about wide and unexpected consequences at the regional level (Martínez–Abraín et al., 2020). Disentangling the relevance of local versus regional/global processes on the long–term persistence of vertebrate populations is currently a major challenge for applied ecology.

We studied the possible causes of the rapid decline in the number of pairs of Montagu's harrier (*Circus pygargus)* in a population nesting in a coastal protected wetland. Initially, our expectations were that two local factors could be the main drivers of the decline: a) changes in land use in and around the protected wetland that might affect both the persistence of foraging and nesting habitat for Montagu's harriers (Arroyo et al., 2002; Arroyo and García, 2005); and b) the increasing number of breeding pairs of the larger western marsh harrier (*Circus aeruginosus*) possibly causing competitive exclusion (Kitowski, 2008; Krupinski et al., 2012). Western marsh harriers were absent from 1992 to 1999 but colonized the site in 2000 (one pair) and grew to five pairs in 2016. However, a broader analysis of the question led us to consider that not only local but also regional factors could be involved. Ecological consequences of the human depopulation of rural areas are now emerging and are behind many population changes that have no clear proximate explanations (Martínez–Abraín et al., 2019, 2020). One major consequence of rural exodus is shrub and tree encroachment on former agricultural land, with the consequent expansion of wildlife associated to shrublands and forests and decline in species from open landscapes (Inger et al., 2015). One of the species most favoured by this process is the wild boar (*Sus scrofa*), a mammal that was locally extinct in the study region in the 19th century but started recolonizing the region in the 1940s (Jiménez, 2012). Wild boars have rebounded and expanded rapidly in the Iberian Peninsula over recent decades (Sáez–Royuela and Tellería, 1986; Delibes–Mateos et al., 2009) and in the entire European continent since the beginning of

last century (Apollonio et al., 2010; Barrios–García and Ballari, 2012; Massei et al., 2014; Morelle et al., 2016). As a consequence, they have become a new agent of ecological disturbance in many ecosystems (i.e. forests, wetlands, dune fields, urban areas) and are creating a new paradigm for human–wildlife coexistence (Acevedo et al., 2011, 2014). In addition to wild boars, other regional factors must be taken into account: a) the possible role of dispersal from coastal wetland populations to other larger populations due to conspecific attraction typical of social birds (Martínez–Abraín et al., 2001); b) the regeneration of breeding habitat offering better protection from wild boar predation (mainly inland shrublands of kermes oak *Quercus coccifera*) after the major forest fires in the province during the 1980s; and c) changing rainfall patterns due to global climate change, as spring rainfall could be related to the level of flooding in the wetland and hence to breeding success (Corbacho et al., 1997) and lower prey capture rate (Schipper, 1973).

Material and methods

Study species and study population

Montagu's harrier is a semi–colonial ground–nesting raptorial bird that nests mostly in natural steppes and broad river valleys and plains within its global distribution range (Cramp and Simmons, 1980). In humanized landscapes of Europe, Montagu's harriers often occupy anthropogenic habitats (e.g. cereal fields) that unintentionally reproduce many of the features of the species' original habitat ('substitution habitats' *sensu* Martínez–Abraín and Jiménez, 2016). In Spain, around 90% of Montagu's harriers breed in farmland (from a sample of 2,114 pairs out of 7,389 breeding pairs estimated in 2006; Arroyo and García, 2007). Similar nesting preferences have been reported for France and Portugal (Ferrero, 1995; Salamolard et al., 1999). These harriers can also use small wetlands for nesting, although the archetypical harrier species in wetlands is the western marsh harrier. The conservation status of Montagu's harriers in the Spanish Red List of Birds (Madroño et al., 2004) is 'vulnerable'. A population decrease of 23–27% in relation to the population in 2006 was estimated in the most recent Spanish census in 2017, indicating a declining trend at the country level (Arroyo et al., 2019).

The study population was located in a protected coastal marsh in eastern Spain (Cabanes–Torreblanca Natural Park, 40° 10' N, 0° 11' E), within the province of Castellón (fig. 1). This is probably a suboptimal habitat for a ground–nesting species originally from steppe habitats as the site presents high risk of flooding if spring precipitation is high. The species might actually be present in this and other coastal marshes in the region as ecological refugees (Kerley et al., 2012, Martínez–Abraín and Jiménez, 2016, Martínez–Abraín et al., 2021) rather than by preference. This population, similarly to other populations of this species in the region, has been thoroughly monitored by the regional Department of the Environment (i.e. Conselleria de Agricultura, Desarrollo

Table 1. Description of the variables used for modelling the number of breeding pairs of Montagu's harriers at our coastal study site. Scale, scale at which the variable acts (R, regional; L, local); Type, nature of the variable (C, climatic; H, habitat; E, ecological). The variable 'Fires' was also modelled with time delays ranging from 1 to 6 years. Overall, 12 explanatory variables were used for the modelling of number of pairs.

Tabla 1. Descripción de las variables empleadas para elaborar los modelos que permiten determinar el número de parejas reproductoras de aguilucho cenizo en nuestro sitio de estudio costero. Scale, escala a la que actúa la variable: R, regional; L, local. Type, tipo de variable: C, climática; H, del hábitat; E, ecológica. En el modelo también se ha incluido la variable "Fires" con un retardo de entre 1 y 6 años. En total se emplearon 12 variables explicativas para la modelización estadística del número de parejas..

Variable	Scale	Type	Description
Aprp	R	C	Amount of rainfall in April in the protected area (l/m^2)
Wildb1	R	E	Number of wild boars hunted regionally during the previous year
Ciraer	L	E	Total number of western marsh Harrier pairs in the protected area in the focal year
Ciraer1	L	E	Total number of western marsh Harrier pairs in the protected area in the previous year
Montagh	R	E	Total number of Montagu's harrier pairs of the inland population in the focal year
Montagh1	R	E	Total number of Montagu's harrier pairs of the inland population in the previous year
Fires	R	H	Annual surface area (ha) of forest fires in the province of Castellón during the period 1986–2017

Rural, Emergencia Climática y Transición Ecológica) on a yearly basis. Field surveys and ringing of chicks by authorized and knowledgeable staff are conducted every year during the breeding season (April–July). Estimates of breeding (territorial) pairs are performed by seeking adults with territorial behaviour (or transporting nest material) and by direct nest search (Arroyo and García, 2007). Nests were placed in unflooded areas rich in *Juncus maritimus* and *Arthrocnemum fruticosum*.

Study variables and statistical analyses

We analysed the change in number of nesting pairs at the study site, considering a large number of biologically–sound variables with potential influence on the ecology of Montagu's harriers (table 1). The number of wild boars hunted in the province of Castellón (hunting bags) was used as a proxy of regional wild boar abundance, as in works by other authors (Massei et al., 2014). The number of hunting licenses in the province was used as surrogate to assess the change over time in hunting pressure. Importantly, wild boar hunting bags are increasing in Europe even though the number of hunting licenses is stable or declining (Massei et al., 2014), a scenario similar to that observed in our region where licenses declined from 1991–2017 (table 1s in supplementary material). The number of wild boars hunted per year was provided by the Fishing and Hunting Service of the Regional

Department of the Environment, and the number of hunting licenses was extracted from the website of this same institution (www.agroambient.gva.es). Changes in agricultural practices in the area surrounding the protected site (used by harriers to forage mainly on passerine chicks among fruit–tree orchards; G. Ros and J. Tena pers. com., see also Guixé and Arroyo, 2011) were graphically explored by comparing aerial photographs in this zone from 1996 to 2017, and by calculations from Corine Land Cover (https://visor.gva.es/visor/), quantifying variations in the surface (ha) of the different land cover classes from 1990 to 2012. For this purpose, we defined a buffer zone including all low–altitude land (< 100 m a.s.l.) around the protected area (with the rivers Sant Miquel and Xinxilla as northern and southern limits, respectively). The surface area of the buffer zone was 6,582 ha in comparison with the 848 ha of the protected wetland. Montagu's harriers are known to have foraging range sizes of over 10,000 ha in cereal steppes (Guixé and Arroyo, 2011). Data on land use changes around the protected area were not introduced in our modelling because quantitative information was only available for four years (1990, 2000, 2006 and 2012), and was hence taken into consideration in a qualitative way. Rainfall data for the study site (Torreblanca station, 40º 12' 41" N, 00º 11'01" E, 35 m a.s.l.) were provided by the Spanish Meteorological Agency (www.aemet.es). The number of western marsh harrier breeding
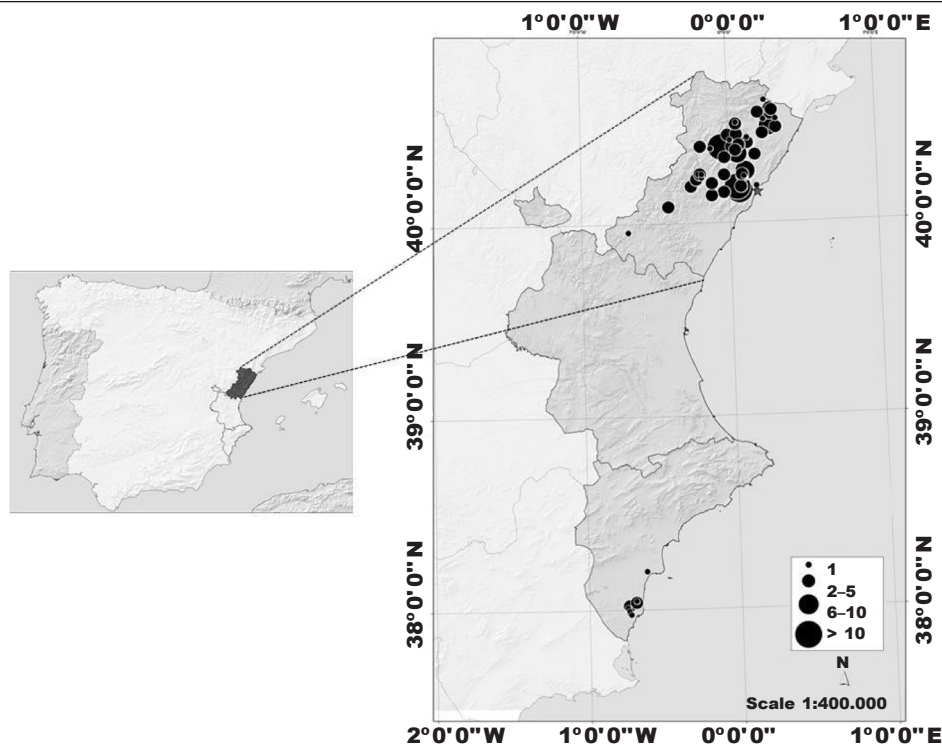
Fig. 1. Location of the study site (✱, Prat de Cabanes–Torreblanca Nature Park) within the context of the province of Castellón (shaded in black in the lower left panel), Comunidad Valenciana: ● location and relative size of Montagu's harrier colonies within the study province and region.

Fig. 1. Ubicación del área de estudio (✱, Parque Natural Prat de Cabanes–Torreblanca) en la provincia de Castellón (sombreada en la imagen inferior izquierda), Comunidad Valenciana: ● ubicación y tamaño relativo de las colonias de aguilucho cenizo en la provincia y la región del estudio.

pairs and the number of Montagu's harrier breeding inland in Castellón province were provided by the regional department of the environment. The likely influence of western marsh harriers was also tested qualitatively (presence/absence) for years t and t–1. The annual land surface burned regionally by forest fires in Castellón province from 1986 to 2017 was extracted from the website of the Ministry of Agriculture and Fisheries, Food and Environment (http://www.mapama.gob.es/es/).

We simultaneously tested multiple hypotheses explaining temporal variability in our dependent variable (i.e. number of pairs) by means of generalized linear mixed models with Poisson error distribution (link = log) and year as a random term. Years without available data for any of the response variables (n = 2; table 2s in supplementary material) were not considered in our modelling. Correction for small sample size of Akaike's index (AICc) was performed, and models with a difference in AICc of less than 2 units were considered to be statistically equivalent (Burnham and Anderson, 2002). The model with the lowest AICc value was considered the most parsimonious. Analyses were conducted using the R software environment (R Core Team, 2019).

Twenty models were considered. Models with time lags of up to 6 years relating surface area burned regionally were considered to account for possible delays in the response of Montagu's harriers to generation of suitable breeding habitat inland (shrublands) after forest fires (table 3s in supplementary material). Geometric growth rates (λ) were calculated by means of the equation for discrete exponential growth ($\lambda = (N_t/N_0)^{(1/t)}$).

Results

The coastal harrier population increased from 12 pairs in 1992 to 37 pairs in 1999 (geometric growth rate, λ = 1.15; 15 % annual increase). However, this increase was followed by a steep decline to just 2 pairs in 2017 (λ = 0.86; 14 % annual decrease) despite legal protection of the site since 1989. For comparison, the annual population growth rate of the inland Montagu's harrier population was 1.1 (10 % annual increase) for 1991–2016. Figure 2 shows the contrasting patterns of change in the number of pairs between these two populations.
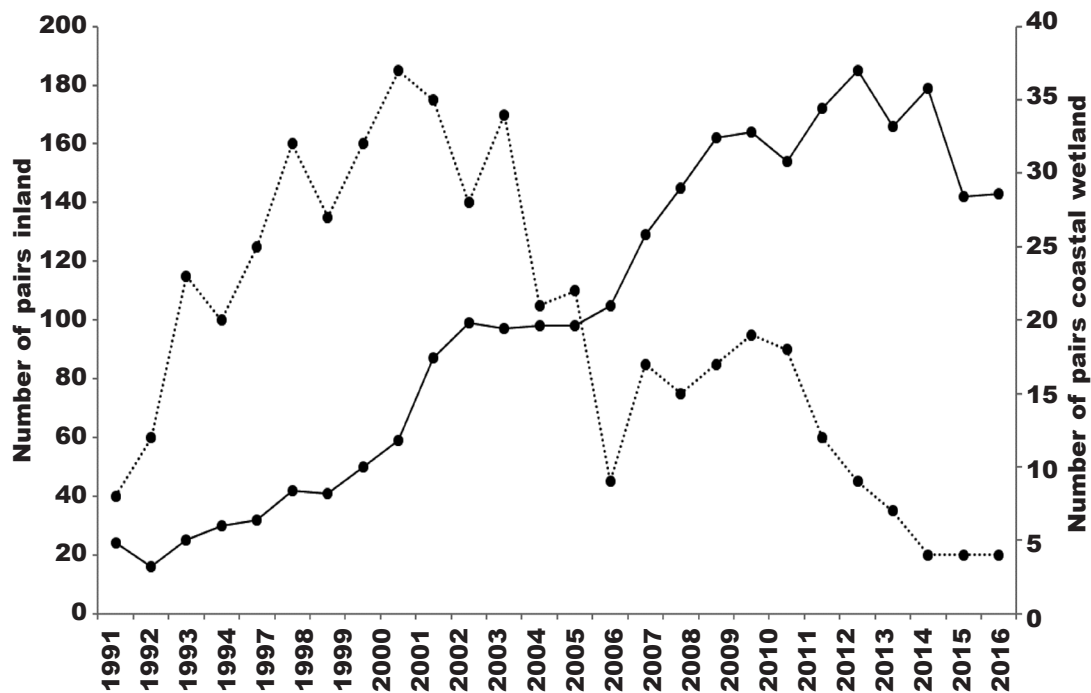
Fig. 2. Annual number of pairs of Montagu's harrier (*Circus pygargus*) on the inland (shrubland) population of the study region (Comunidad Valenciana) during the period 1991-2016 (solid line and solid black dots), compared to the growth of the coastal wetland population (broken line and solid black dots). Data source: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

*Fig. 2. Número anual de parejas de aguilucho cenizo (*Circus pygargus*) en la población interior (arbustiva) de la región de estudio (Comunidad Valenciana) durante el período 1991-2016 (línea continua y puntos negros), en comparación con la evolución temporal de la población del humedal costero (línea discontinua y puntos negros). Fuente de los datos: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.*

The surface of land devoted to fruit tree cultivation around the protected marsh remained approximately stable from 1990 to 2000 (ca. 4,750 ha). It decreased to 3,300 ha from 2000 to 2006 and to 2,800 ha from 2006 to 2012. Fruit trees were mostly transformed into a diverse crop mosaic (increase from 230 ha to 1,280 ha from 1990 to 2012) and only a small proportion of the land was abandoned (increase from 7 to 266 ha for the same period as above).

The results of our modelling (table 2) showed that the two most parsimonious models included wild boar density (during the previous year) together with the number of Montagu's harrier pairs breeding inland during the focal year (relative model probability of 0.51). These were followed by the model including only wild boar density during the previous year (relative model probability of 0.29). Differences in AICc for all the other models were higher than 2. Multi–model inference indicated that models containing wild boar density as an explanatory variable had a cumulated relative probability of 0.9.

Figure 3 shows the inverse linear relationship (r = –0.73; 95 % CI –0.45, –0.87) between the annual number of coastal harrier breeding pairs and the density of wild boars during the previous year. The annual population growth rate of Montagu's harriers showed a decrease (λ = 0.66; 14 % annual decrease) from 2007–2017 when annual regional hunting bags were above 4,000 wild boars. Our modelling did not detect any effect of the local number of western Marsh Harrier pairs (considered either quantitatively or qualitatively), forest fires at the regional level (with several time delays explored) or the amount of precipitation in April.

Discussion

Major changes in agricultural practices did not coincide in time with major changes in harrier trends. Whereas surface devoted to fruit tree cultivation remained roughly stable from 1990 to 2000 (4,740 ha
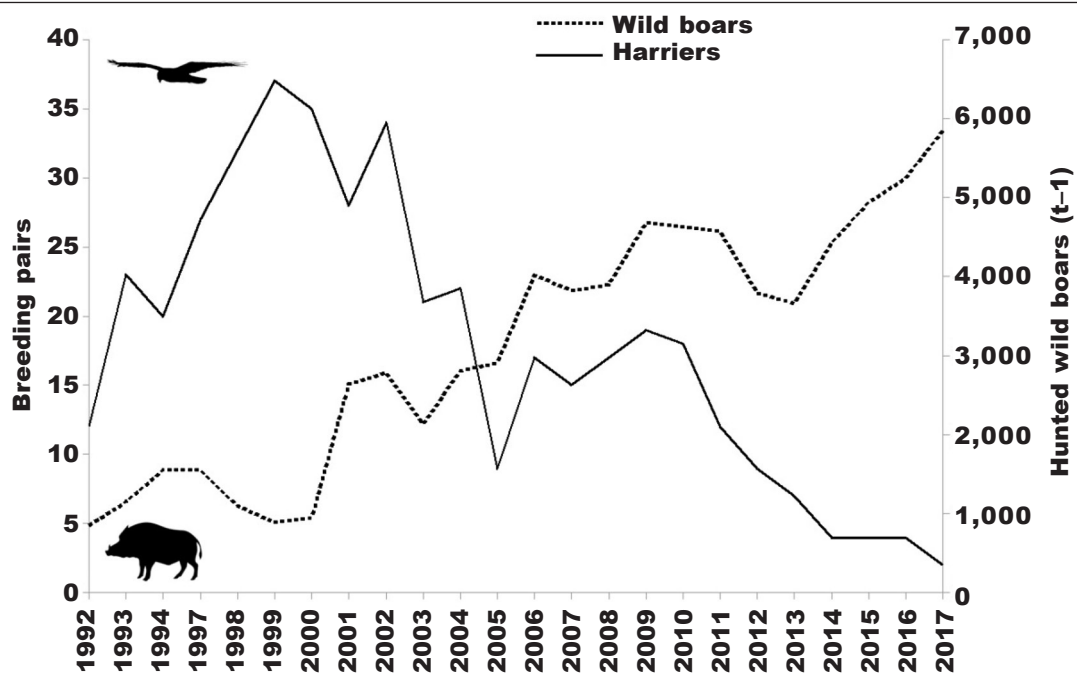
Fig. 3. Number of Montagu's harrier breeding pairs at our coastal study site (black solid line) over time in relation to regional wild boar hunted during the previous year (t–1) (dotted dash line) for the period 1992–2017. Data source: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Fig. 3. Número de parejas reproductoras de aguilucho cenizo en nuestro lugar de estudio costero (línea negra) a lo largo del tiempo con respecto a los jabalíes abatidos en la región durante el año anterior (t–1) (línea punteada) en el período 1992–2017. Fuente de los datos: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

in 1990 vs. 4,726 ha in 2000), harriers experienced an abrupt change in trend from 2000 on. Additionally, the fruit tree surface declined 30 % from 2000 to 2006, and harriers decreased from 35 pairs in 2000 to only 9 in 2005 and 17 in 2006. Even if fruit trees are instrumental as a source of passerine chicks for harriers, changes in agricultural crops alone cannot explain the change in population trend from a continuous increase to a rapid decline. The crop patchwork and abandoned lands that substituted the orchards were most likely a good source of food for harriers too (mostly passerines, but also large insects, lizards and small mammals according to the results of an unpublished study performed by the park staff from 1997 to 2004; Ros and Tena, 2004). Since changes in the foraging habitat could not explain the observed decline in the harrier population we focused on the analysis of perturbations in the nesting habitat. By the early 1990s, wild boars were still scarce in the region. Their overall low abundance most likely allowed the settlement and rapid growth of the Montagu's harrier population, as has been suggested previously for similar areas (Väli, 2017). However, the population growth and expansion of wild boar over the last

15 years could have caused the rapid decline in the coastal colony of Montagu's harrier. The role of wild boars as nest predators on ground–nesting birds in Mediterranean coastal wetlands has been previously reported (Herrero et al., 2004), and their predation of harrier nests has been recorded at the study site, with at least seven nests predated from 2007 to 2015 (Staff of the Cabanes–Torreblanca Natural Park, own unpublished data).

The mechanism by which wild boar could have impacted the wetland population might involve permanent dispersal of birds to other breeding populations where the wild boar density or their impact on nests is lower. In effect, many protected wetlands in Spain have become an ecological refuge for wild boars because water, food and shelter are guaranteed therein (Galán, 2015, Barasona et al., 2021). According to unpublished data from the regional government (based on surveys targeting hunters from 2015 to 2020), densities of wild boars killed in the hunting states located inside the coastal nature park (where wild boars were absent 30 years ago) were ca. four times higher than those in adjacent hunting areas outside the coastal wetland within the same munici-

Table 2. Multiple hypotheses testing of the change in number of Montagu's harrier breeding pairs (N) over time as a function of several explanatory variables (see table 1). Only the three most parsimonious models are shown. The remaining set of models tested are shown in table 3s in supplementary material: K, number of estimable parameters; AICc, Akaike's Information Criterion corrected for small sample size; LL, Log likelihood; ΔAICc, difference in AICc between each model and the most parsimonious model; w$_i$, Akaike's weight; r^2, variance–function–based coefficient of determination. The best models are highlighted in bold. Models with ΔAICc < 2 were considered statistically equivalent.

Tabla 2. Múltiples hipótesis para explicar el cambio en el número de parejas reproductoras de aguilucho cenizo (N) a lo largo del tiempo en función de varias variables explicativas (véase la tabla 1). Sólo se muestran los tres modelos más parsimoniosos. El resto de los modelos se muestra en la tabla 3s del material complementario: K, número de parámetros estimables; AICc, criterio de información de Akaike corregido para un tamaño muestral reducido; LL, logaritmo neperiano de la verosimilitud; ΔAICc, diferencia en el AICc entre cada modelo y el modelo más parsimonioso; wi, pesos de Akaike; r², coeficiente de determinación. Los mejores modelos se destacan en negrita. Los modelos con una ΔAICc < 2 se han considerado estadísticamente equivalentes.

Hypotheses	K	AICc	LL	ΔAICc	wi	r^2
N~Wildb1 + Montagh	3	190.81	-91.80	0	0.51	0.53
N~Wildb1	2	191.96	-93.69	1.15	0.29	0.49
N~Wildb1 + Montagh1	3	194.01	-93.41	3.20	0.10	0.50

palities (10.6 individuals/km^2 vs. 2.7 individuals/km^2) (C. Gómez, Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, pers. com.). Dispersal could have been triggered by the continuously decreasing breeding success of harriers (see fig. 1s in supplementary material), likely caused by wild boar directly predating on nests. Conflicts between predator abundance and harriers' breeding success have been described previously (Simmons, 2000; Wiącek, 2015; Ludwig et al., 2016; Väli, 2017). Cases of abandonmnet of territories and dispersal, motivated by successive failures caused by predation, have been reported previously in harriers (Soutullo et al., 2006; McMillan, 2014) and other social bird species (Fernández–Chacón et al., 2013; Payo–Payo et al., 2017). Moreover, rapid population responses of Montagu's harriers to disturbance have been described in the study region (Oro et al., 2012). Wild boar population growth and expansion represent a regime perturbation theory with a likely threshold density value for prey such as harriers to disperse and leave the coastal wetland. This process may promote decision–making in dispersal with positive density dependence via social copying and the additional impact of the Allee effect on anti–predatory defence (Arroyo et al., 2004; Kitowski, 2008; Wiącek, 2015). As a consequence, runaway dispersal of harriers from the coastal wetland would follow a non–linear pattern after a tipping point of progressive deterioration of environmental conditions caused by wild boar (Oro, 2020).

Because we only marked chicks in the monitoring program, we do not have data concerning the movements of adult birds (breeding dispersal). Howe-ver, there is evidence of dispersal of birds from our coastal study population to other harrier populations, as three birds ringed as chicks (two females and one male) were observed breeding in inland populations four and six years after ringing. Moreover, three individuals (also ringed as a chicks) performed long–distance dispersal and were observed during the breeding season hundreds of kilometers away in Loja (Granada), Totana (Murcia) and Castuera (Badajoz), two, three and five years after marking, respectively (Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, internal reports). Although breeding dispersal is likely to be less common than natal dispersal (which is known to be high in the focal species; see Limiñana et al., 2011), long distance movements (> 100 km) of females have been reported following breeding failure (Arroyo et al., 2004). Dispersal could have targeted areas with lower levels of wild boar predation, which could be the case of the dense shrublands of kermes oak. Montagu's harriers are known to select dense vegetation habitats for nesting as protection from predators (Claro, 2000, Limiñana et al., 2006). Dense shrublands could explain the growth of inland harrier populations despite the regional population growth of wild boars. Importantly, the differential trend of coastal and inland colonies also suggests that mortality in wintering grounds cannot explain the decline of the coastal colony (fig. 2).

The local trend of other ground–nesting species in the protected wetland such as the collared pratincole (*Glareola pratincola*) showed a marked decline as of 2006, coinciding with the rapid increase in numbers of wild boars (r = –0.64; 95 % CI –0.32,

–0.85). However, this was not the case for other local ground–nesting species (the black–winged stilt *Himantopus himantopus*) This difference, however, could be explained by the different nesting habitats of each species. Pratincoles nest on cobble dunes by the sea front whereas stilts nest on flooded terrain, which may provide some protection against wild boar predation, as in the case of western marsh harriers. The parallel growth over time of collared pratincoles and Montagu's harriers is shown in figure 2s supplementary material. The impact of wild boar on ground–nesting waterbirds, including pratincoles, has recently been reported (Barasona et al., 2021). Their impact on other vertebrate groups, such as amphibians and reptiles, has also been reported in the literature recently (Jolley et al., 2010; Barrios–García and Ballari, 2012; Galán, 2012, 2015; Carpio et al., 2016; Graitson et al., 2018; Barasona et al., 2021). Moreover, predation by wild boar and naturalized domestic pigs has been recognized as a major risk factor for imperiled species worldwide (Massei and Genov, 2004; Engeman et al., 2016; McClure et al., 2018; Wehr et al., 2018). Finally, our results highlight that predation of ground–nesting bird species by wild boars may be habitat–specific, and that dispersal to lower–predation sites or habitats is likely a major buffering mechanism to avoid nest predation (see Barros et al., 2016 for an example with seabirds).

In summary, our results illustrate a sequence of changing scenarios associated with changes in the landscape and in human use of the territory at a regional level. The abandonment of agriculture and livestock farming and the early protection of coastal wetlands (in the 1980s) favoured the colonization of these areas by Montagu's harriers as they found refuge therein. Subsequently, shrub and tree encroachment favoured the expansion of wild boar outside their mountain refuges, until they recolonized the coastal areas, from where intense human activity (i.e. agriculture, livestock, hunting) likely expelled them centuries ago. The protection of coastal wetlands, including the exclusion of traditional human activities such as livestock raising and vegetation burning, has led to the recovery of spontaneous vegetation and to the growth of coastal wild boar populations, which thrive in humid areas. The movement of both harriers and wild boars out of their respective historical refuges may largely explain the rapid and unexpected changes that have occurred at the local study site and at other similar protected wetlands in the region.

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Supplementary material
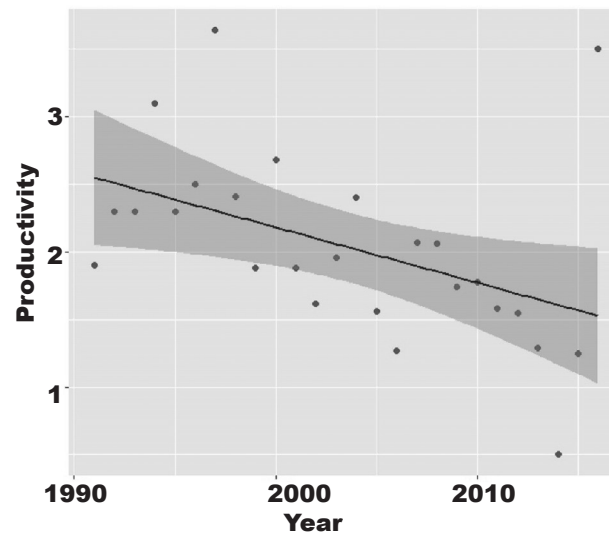
Fig. 1s. Change over time of the breeding success (productivity, estimated as number of chicks at the age of ringing) of Montagu's harriers at the study coastal wetland population for the period 1991–2016. Data source: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Fig. 1s. Cambio a lo largo del período 1991–2016 del éxito reproductor (productividad, estimada como el número de pollos en edad de ser anillados) del aguilucho cenizo en la población del humedal costero estudiado. Fuente de los datos: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.
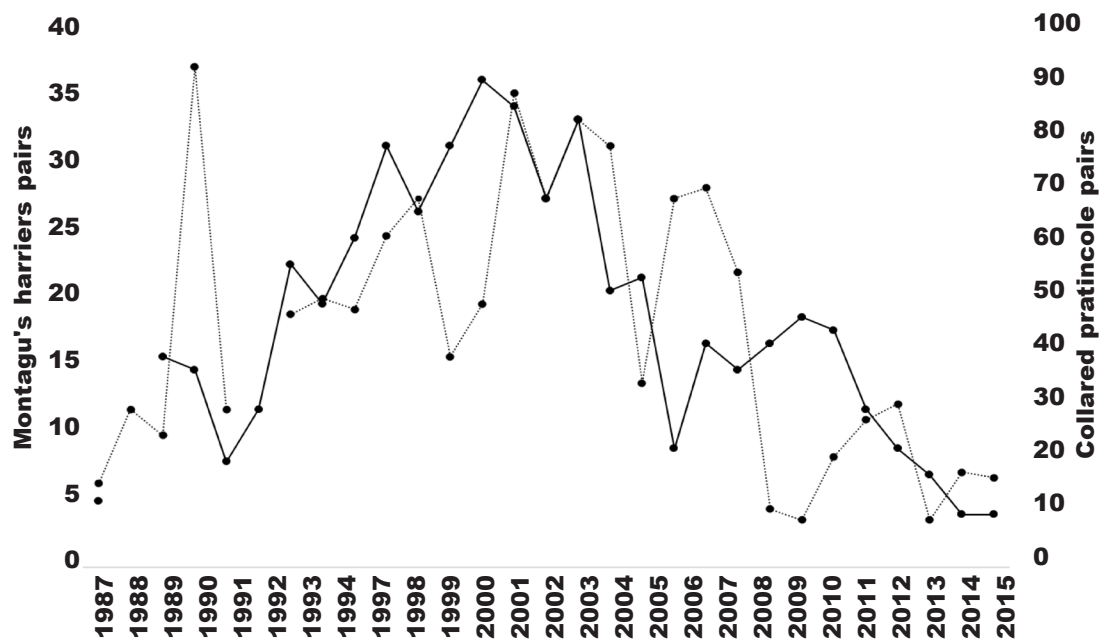
Fig. 2s. Number of annual pairs of Montagu's harriers and collared pratincole at the coastal wetland study site (Cabanes–Torreblanca) from 1987 to 2015. Data source: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Fig. 2s. Número de parejas anuales de aguilucho cenizo y de canastera común en el humedal costero estudiado (Cabanes–Torreblanca) durante el período 1987–2015. Fuente de los datos: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Table 1s. Number of wild boars hunted regionally (H) and number of hunting licenses (HL) issued per year (1991–2017) in the province of Castellón (Comunidad Valenciana): NA, not available. Data source: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Tabla 1s. Número de jabalíes abatidos (H) en la región y número de licencias de caza expedidas (HL) al año (1991–2017) en la provincia de Castellón (Comunidad Valenciana): NA, no disponible. Fuente de los datos: Conselleria de Agricultura, Desarrollo Rural, Emergencia Climática y Transición Ecológica, Generalitat Valenciana.

Year	H	HL	Year	H	HL
1991	NA	27592	2005	4018	21919
1992	1150	28367	2006	3820	21730
1993	1550	27681	2007	3895	NA
1994	1550	26727	2008	4680	11742
1995	NA	26878	2009	4625	19509
1996	NA	28688	2010	4569	19001
1997	1100	26399	2011	3795	18015
1998	890	24383	2012	3661	16646
1999	949	37779	2013	4423	16563
2000	2639	24499	2014	4935	16208
2001	2784	24523	2015	5245	15226
2002	2133	23345	2016	5847	15011
2003	2804	22528	2017	6433	15298
2004	2909	21726			

Table 2s. Data set used for statistical analyses: P, pairs; Y, year; A, Aprp; W, wildb1; C, Ciraer; F, fires; M, Montagh. (See table 1 for variable description).

Tabla 2s. Matriz de datos utilizados para los análisis estadísticos (véase arriba para las abreviaturas y la tabla 1 para consultar la descripción de las variables).

P	Y	A	W	C	C1	F1	F2	F3	F4	F5	F6	M	M1
12	1992	150	850	0	0	1,986.30	816.60	152.60	280.20	3879.40	2241.70	16	24
23	1993	557	1150	0	0	8,976.30	1,986.30	816.60	152.60	280.20	3879.40	25	16
20	1994	455	1550	0	0	11,941.10	8,976.30	1,986.30	816.60	152.60	280.20	30	25
27	1997	438	1550	0	0	136.70	721.20	48,889.00	11,941.10	8,976.30	1,986.30	41	42
32	1998	186	1100	0	0	451.10	136.70	721.20	48,889.00	11,941.10	8,976.30	50	41
37	1999	285	890	0	0	517.56	451.10	136.70	721.20	48,889.00	11,941.10	59	50
35	2000	243	949	1	0	859.53	517.56	451.10	136.70	721.20	48,889.00	87	59
28	2001	214	2639	0	1	601.00	859.53	517.56	451.10	136.70	721.20	99	87
34	2002	788	2784	0	0	3,488.18	601.00	859.53	517.56	451.10	136.70	97	99
21	2003	1113	2133	2	0	229.62	3,488.18	601.00	859.53	517.56	451.10	98	97
22	2004	896	2804	1	2	364.12	229.62	3,488.18	601.00	859.53	517.56	98	98
9	2005	207	2909	2	1	220.65	364.12	229.62	3,488.18	601.00	859.53	105	98
17	2006	48	4018	1	2	1,450.02	220.65	364.12	229.62	3488.18	601.00	129	105
15	2007	2203	3820	3	1	120.30	1,450.02	220.65	364.12	229.62	3,488.18	145	129
17	2008	44	3895	2	3	7,800.66	120.30	1,450.02	220.65	364.12	229.62	162	145
19	2009	425	4680	3	2	317.38	7,800.66	120.30	1,450.02	220.65	364.12	164	162
18	2010	350	4625	1	3	1,177.05	317.38	7,800.66	120.30	1,450.02	220.65	154	164
12	2011	637	4569	2	1	30.83	1,177.05	317.38	7,800.66	120.30	1,450.02	172	154
9	2012	145	3795	2	2	270.00	30.83	1,177.05	317.38	7,800.66	120.30	185	172
7	2013	943	3661	3	2	11,015.07	270.00	30.83	1,177.05	317.38	7,800.66	166	185
4	2014	219	4423	0	3	260.79	11,015.07	270.00	30.83	1,177.05	317.38	179	166
4	2015	9	4935	2	0	436.74	260.79	11,015.07	270.00	30.83	1,177.05	142	179
4	2016	358	5245	5	2	490.99	436.74	260.79	11,015.07	270.00	30.83	143	142
2	2017	163	5847	3	5	1,583.40	490.99	436.74	260.79	11,015.07	270.00	148	143

Table 3s. Complete list of models testing biologically–sound hypotheses. All models had year as a random term in addition to fixed variables.

Tabla 3s. Lista completa de los modelos empleados para probar hipótesis con sentido biológico. Todos los modelos tuvieron año como término random además de las variables fijas.

mod1<-glm(nid~1,family=poisson(log),data=circus)

mod2<-glm(nid~ppabr, family=poisson(log),data=circus)

mod3<-glm(nid~cirpre,family=poisson(log),data=circus)

mod4<-glm(nid~jabpre,family=poisson(log),data=circus)

mod5<-glm(nid~ciraer,family=poisson(log),data=circus)

mod6<-glm(nid~inland,family=poisson(log),data=circus)

mod7<-glm(nid~inlandpre,family=poisson(log),data=circus)

mod8<-glm(nid~inctant,family=poisson(log),data=circus)

mod9<-glm(nid~inctant2,family=poisson(log),data=circus)

mod10<-glm(nid~inctant3,family=poisson(log),data=circus)

mod11<-glm(nid~inctant4,family=poisson(log),data=circus)

mod12<-glm(nid~inctant5,family=poisson(log),data=circus)

mod13<-glm(nid~inctant6,family=poisson(log),data=circus)

mod14<-glm(nid~ciraer+inland,family=poisson(log),data=circus)

mod15<-glm(nid~ppabr+ciraer,family=poisson(log),data=circus)

mod16<-glm(nid~ppabr+inland,family=poisson(log),data=circus)

mod17<-glm(nid~cirpre+inlandpre,family=poisson(log),data=circus)

mod18<-glm(nid~jabpre+inlandpre,family=poisson(log),data=circus)

mod19<-glm(nid~jabpre+cirpre,family=poisson(log),data=circus)

mod20<-glm(nid~jabpre+inland,family=poisson(log),data=circus)