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Rapid expansion of the golden jackal in Greece: research, management and conservation priorities

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ABSTRACT: A rapid and extensive range expansion of the golden jackal has recently been documented in continental Europe, raising new policy and legal questions and creating an urgent need to understand the mechanisms underlying this distribution change. Because of human persecution, the jackal population in Greece went through a serious bottleneck and is therefore now listed as endangered. We used data from field work and publicly accessible sources as well as general linear models to assess the evolution of jackal presence and to identify important variables that could predict occupancy probability and potential expansion, and priority conservation and management areas for the species in Greece. Our results indicate a rapid expansion of approximately 320 % of the golden jackal range in Greece in less than 5 jackal generations. Distance to their previous distribution range and the presence of wolves had a negative effect, while percentage of wetlands, arable land and permanent crops had a positive effect in predicting the probability of jackal occupancy in Greece. Potential areas of expansion were identified mainly in the western and central parts of the Greek mainland and the island of Euboea. Only 22.6 % of the potential priority conservation areas for the jackal in Greece are currently under legal protection, and of these, 23.8 % are suitable for targeted management actions. Based on these results we define concrete research, conservation and management priorities for golden jackals in Greece.

KEY WORDS: *Canis aureus* · Endangered species · Generalized linear models · Greece · Population expansion · Priority conservation areas · Priority management areas

1. INTRODUCTION

Species distributions usually represent a combination of various biological conditions (e.g. resource availability, climatic tolerance, predation pressure) that enable an individual or a population to thrive. If these conditions change, a species may respond with a distribution shift (i.e. distribution contraction or expansion) in order to maintain optimal living conditions (Hovick et al. 2016). Rapid distribution shifts are normally expected from species that are highly mobile and/or capable of dispersing through unsuit-

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able habitat, and from species that are considered to be generalists as opposed to specialists (McCracken et al. 2018). Anthropogenic pressure and climate change have been identified as primary drivers of shifts in species distributions, and therefore, there has been an increased interest recently in documenting and understanding the underlying mechanisms of (rapid) distribution shifts related to land-use changes (McRae et al. 2008) and climate warming (Chen et al. 2011).

The golden jackal *Canis aureus* is a habitat generalist (Yusefi et al. 2021) and one of the canids with the widest global distributions, covering large parts of Asia and southern, central and eastern Europe (Hoffmann et al. 2018). In continental Europe, the distribution of the species has recently been very dynamic, undergoing phases of contraction, recovery and expansion (Arnold et al. 2012). This range expansion has been particularly extensive in the last 2 decades, raising new policy and legal questions, and the urgent need to understand the mechanisms underlying this distribution change in order to define pragmatic priorities for research, management and conservation (Trouwborst et al. 2015). Some of the suggested mechanisms facilitating the expansion of the golden jackal in Europe include climate change (Arnold et al. 2012), anthropogenic changes (Spassov & Acosta-Pankov 2019), land use changes (Šálek et al. 2014) and mesopredator release processes following the disappearance or reduction of large apex predators, such as the grey wolf *Canis lupus* (Krofel et al. 2017, Newsome et al. 2017).

In Greece, the golden jackal reaches its southernmost distribution in Europe. The fate of the population in this country was similar to that of other European populations: golden jackals in Greece experienced a dramatic population and distribution decline towards the end of the last century, which was driven primarily by intense human persecution. This led to the golden jackal being confined to only 7 disjunct areas in the country (Giannatos et al. 2005) and listed nationally as endangered (Giannatos 2009). By the time of the latest nationwide monitoring of the species in 2013 to 2018, some subpopulations in the country had recovered and a small range expansion had been documented, mainly in the northeastern part of the country; overall, the trend of the golden jackal range in Greece was characterized as stable (Giannatos 2015 with an update in 2019).

Considering the recent range expansion of *C. aureus* in Europe in general (Arnold et al. 2012) and in Greece's neighboring countries in particular (e.g. North Macedonia, Ivanov et al. 2016), we initiated a study in 2013 to collect data on jackal presence in Greece in order to: (1) assess the evolution of the presence of the species in the country between 2001 and 2022, i.e. over a timeframe of approximately 5 to 6 jackal generations (Hoffmann et al. 2018); (2) identify land-use, topographic, climatic and biotic variables that could predict the probability of occupancy of *C. aureus* in Greece; (3) identify potential expansion, and priority conservation and management areas in the country and (4) collate all the survey results with information available on the species in the country to define research, management and conservation priorities for the golden jackal in Greece.

2. METHODS

2.1. Data used

We used 2 different databases. The first database consisted of the publicly available datasets on golden jackal distribution reported by the Hellenic Republic to the European Union within the framework of the Article 17 Habitats Directive (European Environment Agency, 2nd report https://cdr.eionet.europa.eu/gr/eu/art17/envrfzupg/; 3rd report: https://cdr.eionet.europa.eu/gr/eu/art17/envvkfa_q/; 4th report: https://cdr.eionet.europa.eu/gr/eu/art17/envxrm90g/). This database (hereafter, 'EEA1, EEA2, EEA3 dataset') includes data on the jackal distribution (i.e. presence–absence) during 3 different time frames (i.e. EEA1 dataset 2001–2006; EEA2 dataset 2007–2012; EEA3 dataset 2013–2018) at a 10 × 10 km Universal Transverse Mercator (UTM) grid cell resolution. The second database used in the study comprised data on golden jackal presence in Greece (hereafter, 'GJP dataset') collected between 2013 and 2022 using various methods and sources: (1) Data collected within the framework of the 'Hellenic Bear Register' (i.e. a project focusing on the study of large carnivores in Greece; see www.hellenicbearregister.com/) using standard monitoring techniques for assessing jackal presence in the country (Giannatos et al. 2005, Giannatos 2015 with an update in 2019, Hostnig et al. 2018, Kominos et al. 2018c, Hatlauf & Böcker 2022), including the deployment of trap cameras, visual observations, acoustic monitoring and the inspection of road kills. (2) Citizen science: data on jackal presence were collected through a citizen science project, the 'Hellenic Brown Bear Rescue and Information Network' (HBBRIN), established by the non-governmental organization ARCTUROS. This methodology has been used successfully to study spatial patterns and define conservation priorities for large carnivores in Greece (Bonnet-Lebrun et al. 2020). (3) Social media (e.g. Facebook) and publicly accessible citizen science databases (e.g. iNaturalist [www.inaturalist.org], Observation.org [Observation International and local partners 2022], Global Biodiversity Information Facility [GBIF.org 23 August 2022]). The majority of presence records used in the study (66%) met the C1 criterion (i.e. reliable evidence based on photo, video, dead find, live catch, genetic evidence or sound recording) of the recommendations for the documentation and assessment of golden jackal records in Europe (Hatlauf & Böcker 2022). We also included some records (44%) meeting the C2 criterion (i.e. evidence confirmed by experienced persons) when these observations were located within the current species distribution.

We restricted our analyses and findings to the Greek mainland and the island of Euboea, i.e. excluding other insular populations, such as that from Samos (Giannatos 2015 with an update in 2019), due to the expected ecological and demographic differences between the mainland and islands. We assumed that the former populations were connected with other southern Balkan jackal populations (Rutkowski et al. 2015), whereas the latter has obvious dispersal limitations. The island of Euboea was included in the study due to its proximity to the mainland and its connection to it through a narrow land strip.

2.2. Data analysis

To assess changes in the presence of the golden jackal in our study area in Greece we used the data from the EEA1 dataset to establish the baseline situation. The timeframe of these data (2001–2006) coincides with the time when the distribution of the species in the region is considered to have been approximately at its minimum (Spassov & Acosta-Pankov 2019). We then identified and calculated the number of cells that were gained (hereafter, occupied cells) and lost with respect to the baseline situation during 2 monitoring phases: Phase A: 2007–2012 (EEA2 dataset) and Phase B: 2013–2022 (EEA3 dataset merged with the GJP dataset).

To study the land-use, topographic, climatic and biotic factors that could influence the probability of occupancy of golden jackals, we used data from the EEA2 and EEA3 datasets to train our models, and fitted generalized linear models (GLMs) with a binary response, using 10 × 10 km cell occupancy as the response variable (1 = occupied cells; 0 = non-occupied cells). Based on the maximum size of the home range of the species in the Balkans (32.5 km^2, Fenton et al. 2021), we considered that occupancy at 10 × 10 km implies negligible spatial autocorrelation and that this is an adequate scale for our study, consistent with jackal biology and commonly used in their management. We defined occupied cells as the cells that were newly occupied with respect to the previous phase (i.e. with respect to the EEA1 dataset for the EEA2 dataset and with respect to the EEA2 dataset for the EEA3 dataset). Cells where the species had never been reported and which were within a Euclidean distance of 60 km (based on information on the individual dispersal distance, Lanszki et al. 2018) from the species distribution in the previous phase were considered non-occupied cells. To reduce the likelihood of including false negatives, we excluded cells adjacent/connected to occupied cells from the analyses. Finally, we merged all occupied and non-occupied cells to obtain a single presence/pseudo-absence 'training dataset' for model fitting. This dataset contained 156 presences/270 pseudo-absences originating from the EEA2 dataset and 23 presences/136 pseudo-absences originating from the EEA3 dataset. For model validation, we used an independent dataset (i.e. 'test dataset') that consisted of the occupied cells from the GJP dataset (i.e. presences, n = 66) and of randomly selected cells within a radius of 60 km around each of these occupied cells, while excluding adjacent/connected cells (i.e. pseudo-absences, n = 66).

We considered 15 variables potentially predicting the probability of occupancy by jackals in Greece (see Table 1 for a detailed description of the variables and how they were calculated). All variables were averaged over each 10 × 10 km cell, as this is the resolution used in the reporting for the Habitats Directive and the national species management plans. In order to account for potential changes in the variables most likely to vary across time, we used different versions of the source layers for each component of the training and test datasets (Table 1), and assumed no change for the other variables. The Pearson correlation (R) for all pairs of predictor variables was below 0.65 and the variance inflation factor (VIF) was below 5.0 (Table S1 in the Supplement at www.int-res.com/articles/suppl/n051p001_supp.pdf). We fitted GLMs testing all possible additive combinations of predictor variables (R package MuMIn, Bartoń 2020), selected the models with a difference in Akaike's information criterion corrected for small sample sizes (ΔAIC_c) below 2.0 as the best fitting

Table 1. Description and sources of the predictor variables potentially influencing the probability of occupancy of golden jackals in Greece. The relative importance variable (RIV) and number (n) of models containing each variable for the best fitting models (i.e. $\Delta AIC_c < 2.0$; n = 14) predicting probability of occupancy of golden jackals in Greece are also presented. For each variable the standardized estimate of the highest ranked model including that variable is presented. Important variables are highlighted in **bold**

	Variable (unit)	Description	RIV	n	Standardized estimate
1	Forest (%)[a]	Broad-leaved, coniferous and mixed forest	0.05	1	−0.13
2	Shrublands (%)[a]	Moors and heathland, sclerophyllous vegetation and transitional woodland-shrub	0.13	2	0.21
3	Pastures and grasslands (%)[a]	Pastures and natural grasslands	**0.93**	**13**	**0.53**
4	Wetlands (%)[a]	Inland marshes, peat bogs, salt marshes, salines, intertidal flats	**1.00**	**14**	**1.46**
5	Naturalized crops (%)[a]	Heterogeneous agricultural areas with significant natural vegetation and complex cultivation patterns	0.12	2	0.15
6	Permanent crops (%)[a]	Vineyards, olive groves, and fruit and berry plantations	**1.00**	**14**	**0.55**
7	Arable land (%)[a]	Non-irrigated and permanently irrigated arable land	**1.00**	**14**	**0.82**
8	Roughness (Index)[b]	Terrain roughness index	**0.80**	**11**	**0.64**
9	Density of rivers (km/km^2)[c]	Density of rivers	0.06	1	−0.12
10	Density of roads (km/km^2)[c]	Density of motorway, primary, secondary and tertiary roads	0.06	1	−0.12
11	Human density ($people/km^2$)[d]	Gridded estimates of population density (log-transformed)	0.23	3	−0.31
12	Minimum temperature (°C)[e]	Minimum temperature of coldest month	–	0	–
13	Annual precipitation (mm)[e]	Accumulated annual precipitation	**0.80**	**11**	**0.53**
14	Distance to previous range (km)[f]	Distance to the jackal distribution during the previous period	**1.00**	**14**	**−2.77**
15	Wolf presence (0/1)[f]	Presence (1) vs. absence (0) of wolves according to distribution range	**1.00**	**14**	**−1.58**

[a]Modified from Corine Land Cover (CLC) seamless vector data, version 2020_2021 (https://land.copernicus.eu/pan-european/corine-land-cover) using CLC 2006 for the EEA2 dataset, CLC 2012 for the EEA3 dataset and CLC 2018 for model projections (EEA: European Environment Agency, see Section 2.1)

[b]Derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model (United States Geological Survey 2006)

[c]Derived from OpenStreetMap data in layered GIS format (www.openstreetmap.org/#map=6/38.359/23.810)

[d]Derived from the Gridded Population of the World (GPW), population density v4.11 (Center for International Earth Science Information Network 2018) using data from 2005 for the EEA2 dataset, data from 2015 for the EEA 3 dataset and data from 2020 for model projections

[e]Derived from the CHELSA timeseries data (Karger et al. 2017), averaged for years 2007–2012 for the EEA2 dataset and for years 2013–2019 for the EEA3 dataset' and the model projections

[f]Derived from the Article 17, Habitats Directive layers for Greece, using the 2nd (2001–2006), 3rd (2007–2012) and 4th report (2013–2018), respectively, for calculating the distance to previous golden jackal distribution for EEA2, EEA3 and projections, while for assigning presence of wolves, we used the 3rd report for EEA2 and the 4th report for EEA3 and projections

models, and estimated the relative importance of each variable and the relative weights for the best models using functions implemented in the MuMIn package. We evaluated these models (R package dismo, Hijmans et al. 2011) using the test dataset as independent model validation data. We then projected the predictions (i.e. probability of occupancy estimates) of the best fitting models across our study area over the last decade (using the predictor variable sources specified in Table 1) and calculated a weighted average for each cell to obtain a single map of occupancy probabilities in the country. Subsequently, we re-projected the predictions but considered a spatially homogeneous distance to the previous distribution of golden jackals (i.e. while the rest of the predictor variables remained equal), thus obtaining a map of occupancy probabilities excluding distance to the population source as a limiting factor. We identified potential priority conservation areas by defining cells with a predicted probability >0.5 as areas with high probability of occupancy and intersecting them with the current distribution of protected areas (i.e. Natura 2000 Network [N2000]) in Greece. Finally, we defined potential priority management areas as the areas within the potential priority conservation areas with arable land, and naturalized and permanent crops. This was done because Greece, in an effort to promote biodiversity conservation, has included a measure (Π3-70-1.1) specifically targeting the protection and management of golden jackal habitat in the Strategic Planning of the next Common Agricultural Policy (CAP, 2023-2027) (see www.agrotikianaptixi.gr/sites/default/files/protasi_stratigikoy_shedio_kap_17.10.22.pdf). In this measure, 10% of arable/cultivated lands within protected areas should be left unharvested.

3. RESULTS

As part of the data collection (2013–2022) for the GJP dataset we collected 129 observations of golden jackals in Greece that were considered sufficiently accurate for the scope of the study (Table S2, Fig. S1). The observations came from publicly accessible citizen science databases (n = 94), field work (n = 25) and social media (n = 10), and included 93 visual observations (Fig. 1A), 26 cases of acoustic monitoring and 10 camera trap records (Fig. 1B). The data collected also included 18 cases of jackals killed in road accidents

Fig. 1. Examples of the data on golden jackal presence collected in Greece (2013–2022). (A) Photograph of a visual observation of a golden jackal (©S. Karipidis). (B) Image from a camera trap (©ARCTUROS). (C) A golden jackal killed in a road accident (©A. A. Karamanlidis). (D) A golden jackal at the Rehabilitation Centre of ARCTUROS (©A. A. Karamanlidis)

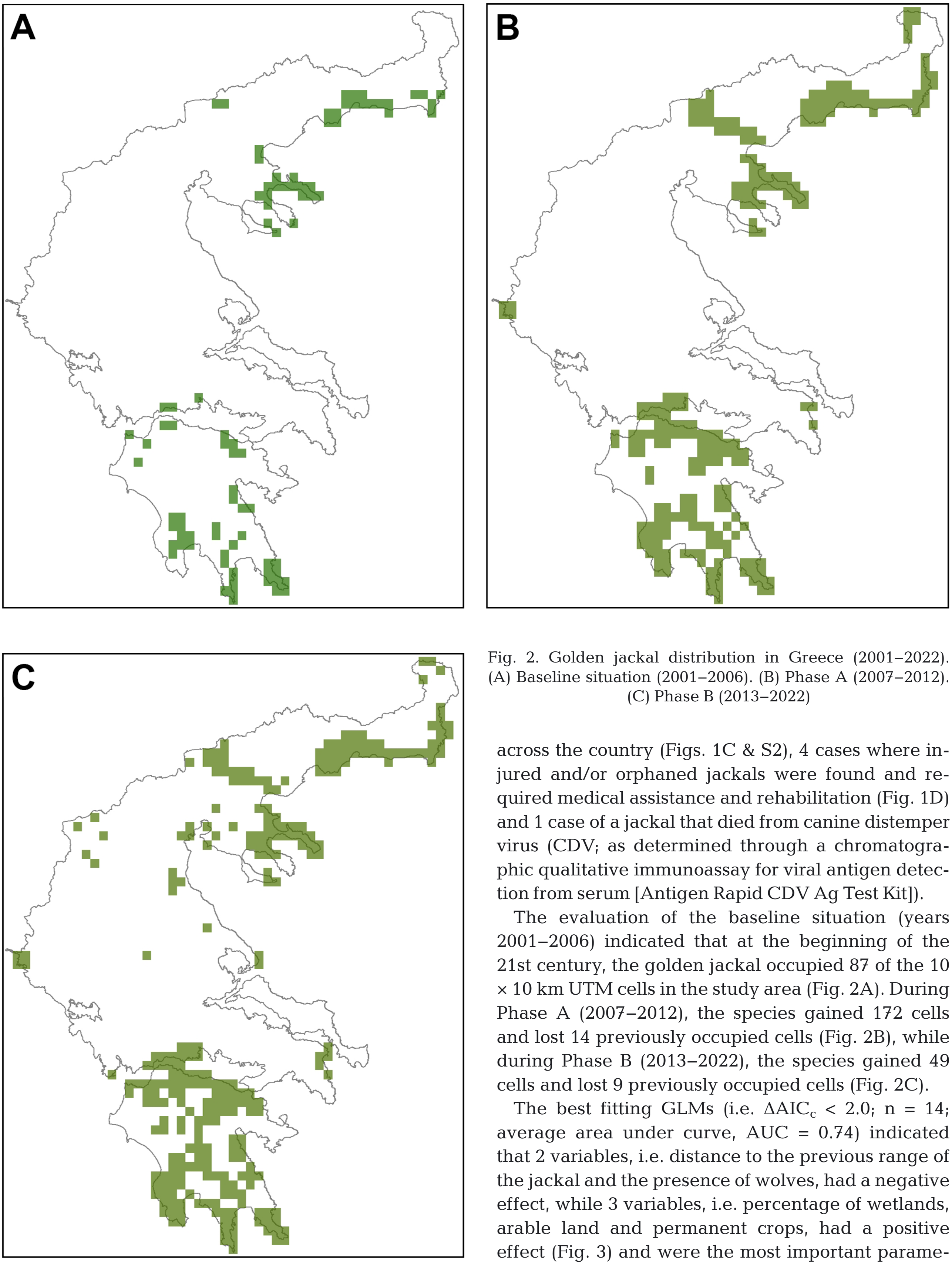

Fig. 2. Golden jackal distribution in Greece (2001–2022). (A) Baseline situation (2001–2006). (B) Phase A (2007–2012). (C) Phase B (2013–2022)

across the country (Figs. 1C & S2), 4 cases where injured and/or orphaned jackals were found and required medical assistance and rehabilitation (Fig. 1D) and 1 case of a jackal that died from canine distemper virus (CDV; as determined through a chromatographic qualitative immunoassay for viral antigen detection from serum [Antigen Rapid CDV Ag Test Kit]).

The evaluation of the baseline situation (years 2001–2006) indicated that at the beginning of the 21st century, the golden jackal occupied 87 of the 10 × 10 km UTM cells in the study area (Fig. 2A). During Phase A (2007–2012), the species gained 172 cells and lost 14 previously occupied cells (Fig. 2B), while during Phase B (2013–2022), the species gained 49 cells and lost 9 previously occupied cells (Fig. 2C).

The best fitting GLMs (i.e. $\Delta AIC_c < 2.0$; n = 14; average area under curve, AUC = 0.74) indicated that 2 variables, i.e. distance to the previous range of the jackal and the presence of wolves, had a negative effect, while 3 variables, i.e. percentage of wetlands, arable land and permanent crops, had a positive effect (Fig. 3) and were the most important parame-

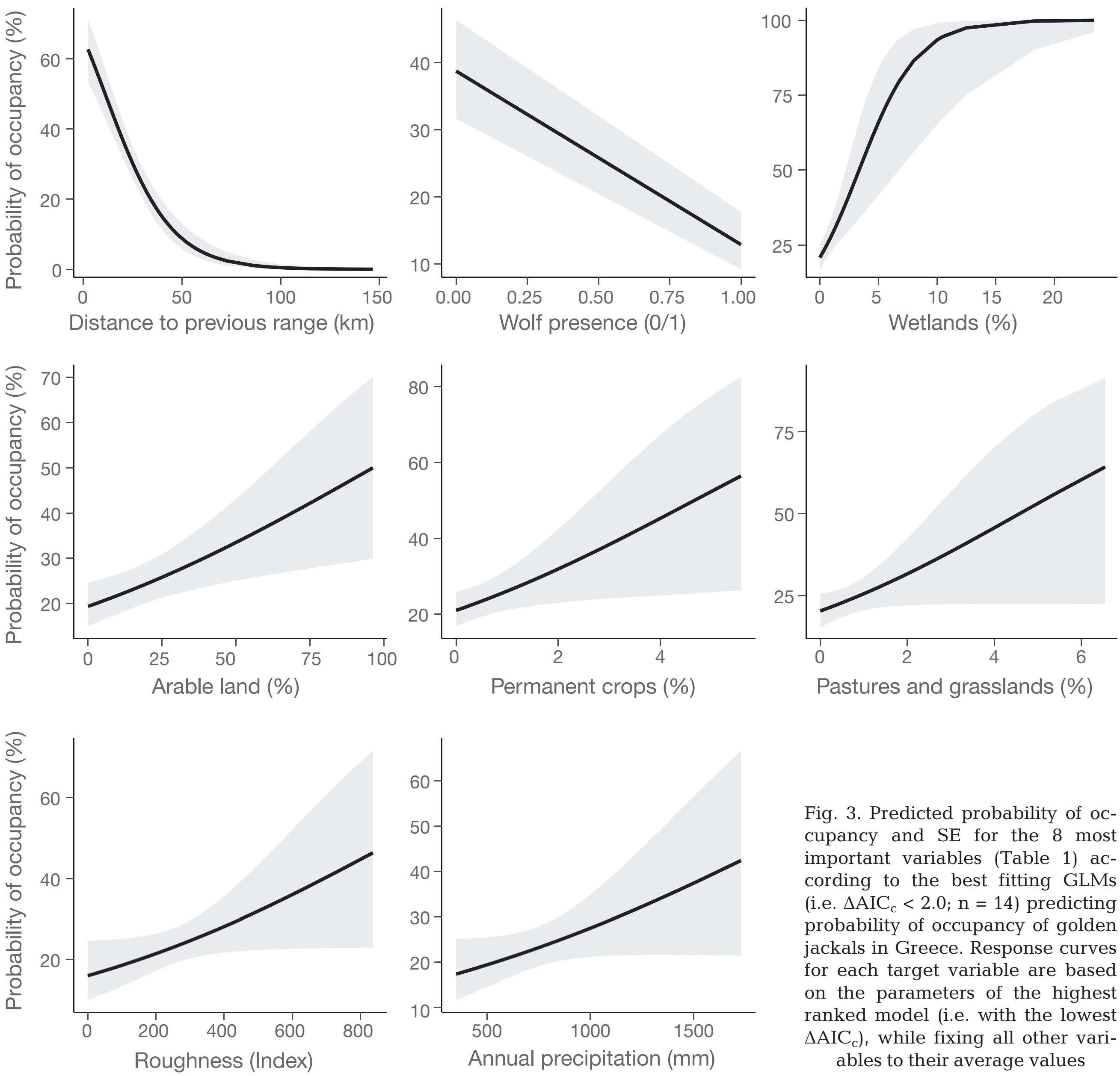

Fig. 3. Predicted probability of occupancy and SE for the 8 most important variables (Table 1) according to the best fitting GLMs (i.e. $\Delta AIC_c < 2.0$; n = 14) predicting probability of occupancy of golden jackals in Greece. Response curves for each target variable are based on the parameters of the highest ranked model (i.e. with the lowest ΔAIC_c), while fixing all other variables to their average values

ters predicting probability of occupancy of golden jackals in Greece. Percentage of pastures and grasslands, terrain roughness and annual precipitation were of lesser importance, in all cases positively affecting the probability of occupancy of golden jackals in the country (Tables 1 & S3).

The model projections of the probability of occupancy of the golden jackal in Greece indicated that areas with high probability of occupancy (i.e. $p > 0.5$; Fig. 4A) are consistent with the current distribution of the species (Fig. 2C). However, when re-projecting the best-fitting models considering a spatially homogeneous distance to the previous distribution of the golden jackal, the models indicated additional, potential areas for expansion in Greece (Fig. 4B), mainly in the western and central parts of the mainland and the island of Euboea. The intersection of this map with the N2000 in Greece resulted in a map of potential priority conservation areas for the jackal and indicated that 22.6% of the high probability occupancy areas (Fig. 5A) are under legal protection (12 361 km^2 out of a total of 54 598 km^2). Within these potential priority conservation areas, 23.8% (2945 km^2 out of 12 361 km^2) contain arable land, and naturalized and permanent crops, and could be considered as potential priority management areas for the jackal

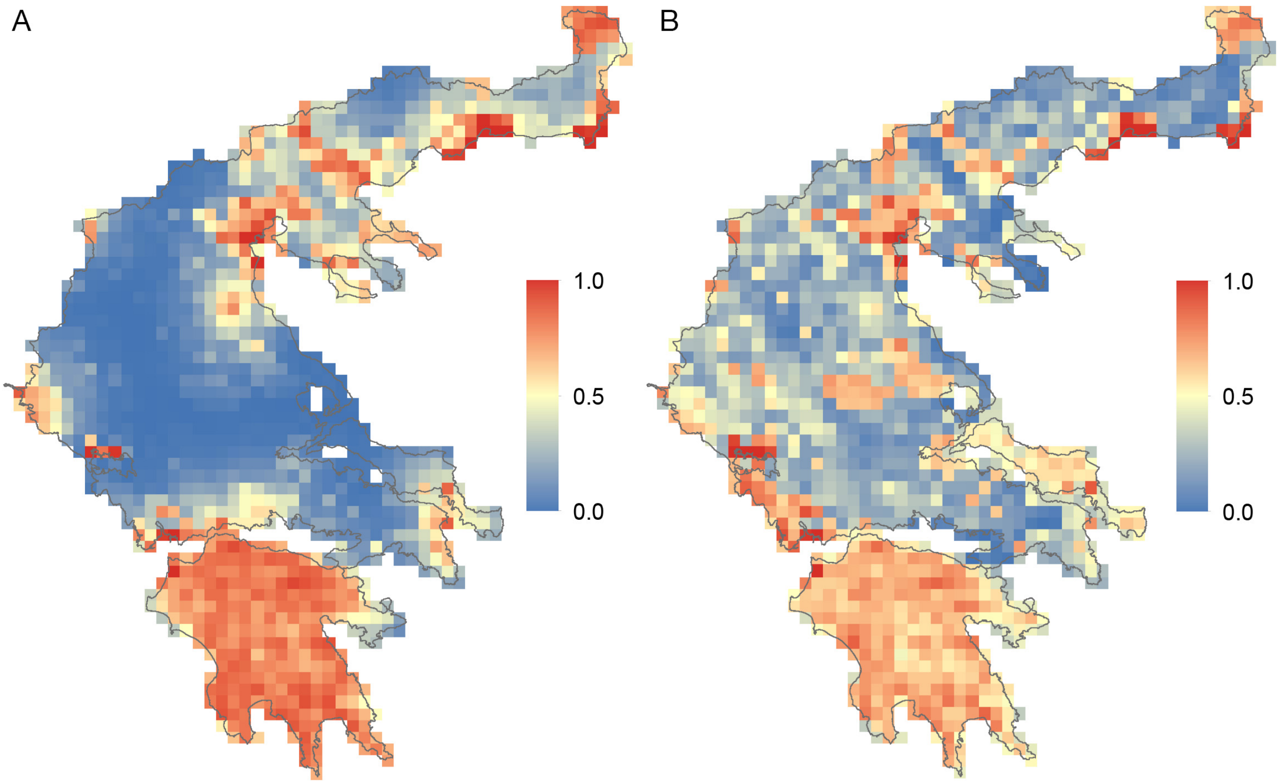

Fig. 4. (A) Average probability of occupancy of golden jackals in the study area in Greece according to the best-fitting GLMs, considering distances to the previous distribution range, and (B) taking into account the minimum spatially homogeneous distance to the previous distribution range

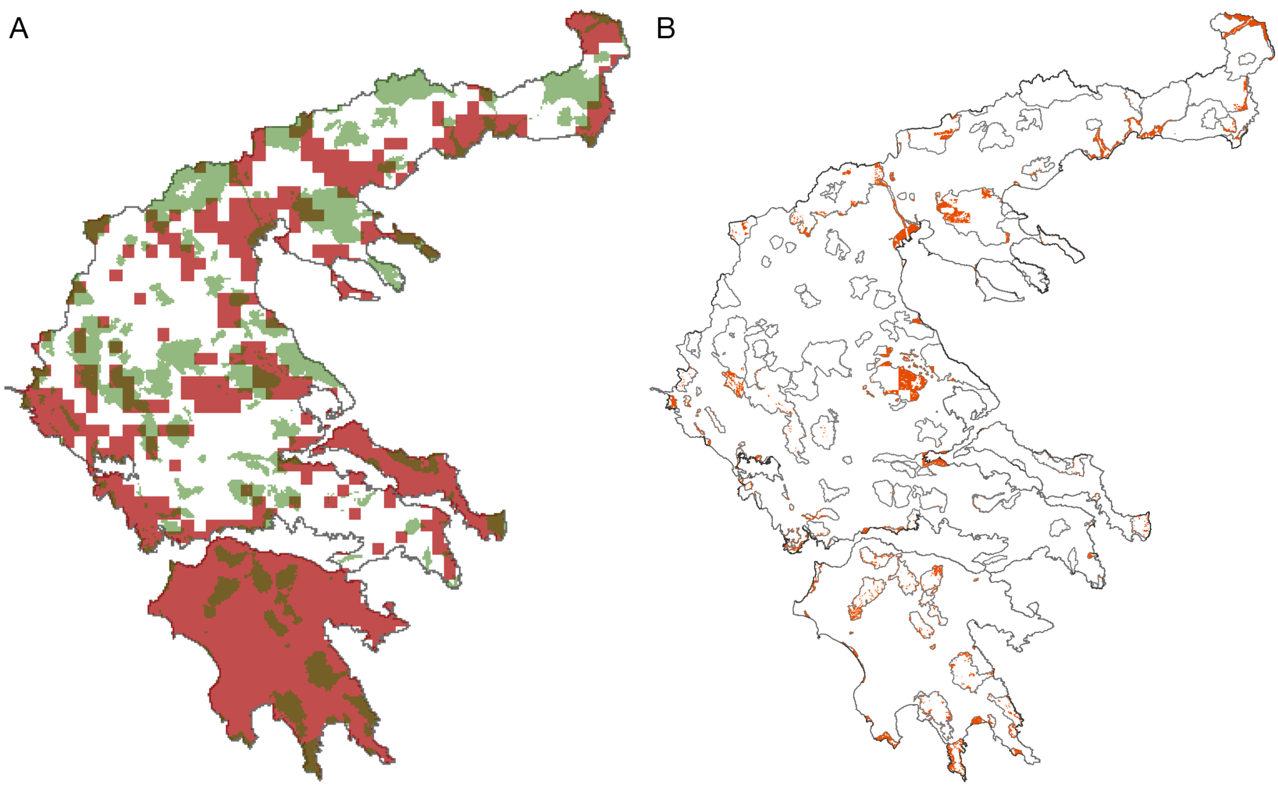

Fig. 5. (A) The study area in Greece presenting the distribution of the Natura 2000 network (green) and the high probability occupancy areas for the golden jackal ($p > 0.5$; red), based on models considering a spatially homogeneous distance to the previous distribution of the golden jackal. (B) The study area in Greece presenting the priority management areas identified within the potential priority conservation areas in the country (see panel A)

within the framework of the implementation of the CAP (Fig. 5B, Table S4).

4. DISCUSSION

The golden jackal has made a remarkable comeback in Europe over the past 2 decades, thus creating a new conservation reality for the species, which is associated with considerable management and policy challenges (Trouwborst et al. 2015). This situation also applies to Greece, where the biology, population dynamics and distribution of the species are still not fully understood.

4.1. Golden jackal expansion in Greece

Our results indicate that, as in neighboring countries such as Northern Macedonia (Ivanov et al. 2016) and Bulgaria (Stoyanov 2012), golden jackal occupancy/distribution in Greece has been increasing in the last 2 decades. This expansion has taken place not only in the northeastern parts of the country, as previously reported (Giannatos 2015 with an update in 2019), but also in the northern, western, southern and central parts of the mainland. It is possible that the recent recovery of the species, at least in northern and northwestern Greece, may be related to the expansion of its populations in the neighboring countries of Albania and Northern Macedonia. Starting from a very limited distribution at the beginning of the century (Spassov & Acosta-Pankov 2019), the species now occupies approximately 28 500 km^2 in Greece, an expansion of approximately 327 % in just 16 yr (i.e. end of baseline situation in 2006 to the present), or 4 jackal generations. In Central Europe, a similar rapid expansion has been facilitated by the innate traits of the species, such as high dispersal ability (Lanszki et al. 2018) and/or high dietary plasticity (Lanszki et al. 2022). Additional studies on the dispersal abilities and the dietary habits of the species in the newly occupied areas in Greece are necessary to elucidate the role of these innate traits in the expansion of the species in this country.

4.2. Factors predicting golden jackal occupancy in Greece

Our results suggest that a number of variables are suitable for predicting the current probability of occupancy of jackals in Greece. The most important predictor variables essentially cover 3 distinct areas: (1) habitat type (i.e. 'Arable land', 'Pastures and grassland', 'Wetlands'); (2) presence of a large apex predator ('Wolf presence'); (3) geography ('Distance to previous range').

The recent success of the golden jackal in recolonizing western and northern Europe, which has resulted in the species inhabiting such varying habitats as marshlands, continental mixed forests and Mediterranean coastal areas, has been, at least partially, attributed to the high behavioral plasticity (i.e. adaptability) of the species (Ranc et al. 2018). This adaptability has allowed the species to utilize a variety of anthropogenic resources and consequently effectively colonize/inhabit human-modified landscapes (Šálek et al. 2014, Ćirović et al. 2016). This also appears to be the case for golden jackals in Greece, where our study indicates that open, but at the same time human-dominated, habitat such as arable lands, pastures and grasslands, as well as wetlands, appears to be positively associated with the probability of occupancy of golden jackals, especially in areas with rough terrain. Rough terrain has also been found to be an important predictor of occupancy in other golden jackal populations (Shahnaseri et al. 2019). The availability in these heterogeneous agricultural landscapes of anthropogenic food sources and the abundance of small mammals (e.g. voles and mice), which are the preferred prey of the golden jackal (Lange et al. 2021), provide an explanation for the preference of this type of habitat. A positive association with heterogeneous agricultural landscapes has previously been recorded for golden jackals in the Balkan Peninsula (Šálek et al. 2014), and also in Greece (Giannatos 2004). Based on the results of this study, the decision of the Hellenic government to protect heterogeneous agricultural landscapes within the framework of the implementation of the CAP seems justified; the potential priority management areas identified in the study (Fig. 5B) should be used as guidance for the implementation of the measure and for improving habitat suitability for the golden jackal in Greece.

Our results indicate furthermore that probability of occupancy of jackals in Greece is positively associated with the availability of wetlands. Wetlands have been identified as preferred golden jackal habitat, both in the core range of the species in the Balkan Peninsula (Trbojević et al. 2018) and in recently occupied areas in northern Europe (Kowalczyk et al. 2020). Wetlands have previously been identified as important habitat for golden jackals in Greece (Giannatos et al. 2005, Lanszki et al. 2009), confirming the importance of this type of habitat for the survival of the species in this country and highlighting the necessity of effectively protecting it.

We also found that annual precipitation was an important positive predictor of the occupancy probability of jackals in Greece. Precipitation is a strong predictor of abundance of small mammals, such as voles *Microtus* spp., which constitute the main natural prey for the species in southeastern Europe (Lange et al. 2021). Therefore, seasonally higher prey availability in areas with higher precipitation (Jareño et al. 2015) could explain our results; increased use of natural prey has also been documented in the recovering wolf population in Greece (Petridou et al. 2018).

Due to the top-down suppression of wolves on jackals, wolf presence has been identified as a potential factor negatively influencing jackal presence, especially within the core distribution of the species in the Balkans (e.g. Bosnia-Herzegovina, Trbojević et al. 2018). It has also been suggested to be a critical factor in the recent expansion of the golden jackal in Europe. Persecution and decline of wolf numbers across the continent may have facilitated this expansion in the past (Krofel et al. 2017). However, ongoing, natural wolf recovery (e.g. Szewczyk et al. 2019) may limit this potential, as this biological constraint is strongly mediated by humans. Our results also suggest that wolf presence is a limiting factor in the probability of occupancy of golden jackals in Greece. Despite indications of the recent range expansion of wolves in the country (i.e. 4th report of the Hellenic Republic to the European Union within the framework of the Article 17 Habitats Directive), it is still unclear whether this expansion involves the permanent establishment of the wolf in new areas (i.e. as opposed to 'simply' dispersal) and whether golden jackals will be able to colonize areas with a lower probability of interspecific competition. Both species must therefore be closely monitored.

4.3. Potential areas of expansion and conservation for golden jackals in Greece

One of the main aims of the study was to identify potential areas of expansion and new areas for the conservation of jackals in Greece. The results of our modelling efforts have identified the areas of high probability of occupancy (i.e. potentially critical habitat); in some of these areas, e.g. in northwestern (Kominos et al. 2018a,c) and central Greece (Fig. S1), jackal presence has already been recorded. In some other areas with high probability of occupancy (e.g. the island of Euboea), golden jackals have not yet been documented; a permanent monitoring scheme for the species, similar to the ones existing for other large carnivores in the country (e.g. 'Hellenic bear Register') should be considered a conservation priority for golden jackals in Greece. Furthermore, the results of the study have indicated that less than a quarter of the critical habitat of golden jackals in the country is formally protected within the N2000. This percentage should be considered low, especially when compared to the similar protection afforded to the critical habitat of the other 2 large carnivores in Greece (i.e. grey wolves, Votsi et al. 2016, and brown bears *Ursus arctos*, Bonnet-Lebrun et al. 2020). Creating new areas for the conservation of the species in the country will require a thorough understanding of habitat suitability and connectivity, which is not available at the moment. Acquiring it should be considered a conservation priority for this species.

4.4. Other conservation issues

The data we collected (i.e. Table S1) also included cases of jackals injured/killed in road accidents, those in need of medical assistance and rehabilitation, and a jackal that died from CDV. We believe that all 3 categories of cases must be considered in the conservation planning. The relatively high number of fatal jackal–vehicle collisions (n = 18) that have been recorded nationwide (Fig. S2) indicates that this is a potentially important source of human-induced mortality for the species in Greece, which is in accordance with previous research in the country (Kominos et al. 2018b) and in other expanding jackal populations in Europe (e.g. Italy, Frangini et al. 2022). Road mortality has been a conservation concern for other large carnivores in Greece (e.g. brown bear, Psaralexi et al. 2022), prompting close monitoring of the effects of linear transportation infrastructure on wildlife to identify and establish effective mitigation measures (e.g. Karamanlidis et al. 2012). Similar research efforts should also be considered for jackals in Greece. Partially as a result of traffic accidents, there has also been an increasing need for the rehabilitation of jackals in the country, so a dedicated rehabilitation program based on the principles of another large carnivore rehabilitation program in Greece (Komnenou et al. 2016) has been established. Finally, the recording of a case of CDV, originating from the same area of the only previously known anecdotal report of CDV in jackals in Greece (ARC-

TUROS unpubl. data) should not escape the attention of local conservation authorities. Although never reported previously in Greece, CDV has been reported from jackals in Israel (Shamir et al. 2001) and is generally recognized as a conservation issue for wild canids (Åkerstedt et al. 2010).

5. CONCLUSIONS: MANAGEMENT AND CONSERVATION PRIORITIES FOR GOLDEN JACKALS IN GREECE

Golden jackal populations have been expanding recently in Greece. Because of their potential for conflicts with humans (i.e. depredation of livestock, Yom-Tov et al. 1995), which is likely to increase in the near future and in turn compromise this recovery, it is of utmost importance to evaluate habitat requirements, landscape connectivity and protection of biological corridors to guide conservation of the species (Shahnaseri et al. 2019). Based on the findings of our study, we suggest the following priority management and conservation actions for the golden jackal in Greece:

(1) Scientific research: A thorough understanding of the biology, ecology and population dynamics of the species in Greece is still lacking. Particular attention should be given to elucidating aspects of jackal dispersal ability, which in turn will enable an assessment of habitat connectivity in the country. This information will ultimately enable the prioritization of critical habitat to be formally protected and managed for the golden jackal in Greece.

(2) Habitat protection: As anthropogenic landscapes are likely to increase in Greece in the near future, habitat protection should focus on protecting the last remaining 'natural' areas for the golden jackal in the country, i.e. primarily wetlands. Given their importance for biodiversity and the existence of relevant legal frameworks (Verhoeven 2014), this action should be promoted within the general framework of the conservation of biodiversity in the country. Furthermore, considering the importance of arable land and cultivated fields for the survival of the species, the measure designed by Greece within the next CAP to improve habitat suitability for the jackal in the country should be considered a management priority.

(3) Understanding wildlife mortality: This is crucial in defining effective conservation strategies, particularly for linear infrastructure (Ascensão et al. 2019). The present study indicates high levels of jackal mortality in Greece associated with roads. Given that road mortality also affects grey wolves and bears in Greece and is a factor generally jeopardizing their overall survival (Grilo et al. 2015), monitoring this factor should be implemented within the framework of the overall conservation of large carnivores in the country.

(4) All previous information should be used to reassess and improve the current formal protection afforded to the species under the N2000. As in other parts of Europe (Rosso et al. 2018), where the N2000 is instrumental in protecting biodiversity, the current setup of the N2000 in Greece seems insufficient to adequately protect the golden jackal.

All the aforementioned priority management and conservation actions should be used to update the action plan for the golden jackal in Greece (Giannatos 2004) (following the formal processes that have been established for the preparation and ratification of species action plans in the country, e.g. brown bear, Mertzanis et al. 2020), which, together with other actions (such as public awareness and education, and rehabilitation) will ensure the survival of the golden jackal in Greece.

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