Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: https://www.tandfonline.com/loi/tbis20

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To cite this article: Fulvio Genero, Marcello Franchini, Yannick Fanin & Stefano Filacorda (2020): Spatial ecology of non-breeding Eurasian Griffon Vultures *Gyps fulvus* in relation to natural and artificial food availability, Bird Study

To link to this article: https://doi.org/10.1080/00063657.2020.1734534

Published online: 12 Mar 2020.

BIRD STUDY
https://doi.org/10.1080/00063657.2020.1734534

Spatial ecology of non-breeding Eurasian Griffon Vultures *Gyps fulvus* in relation to natural and artificial food availability

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ABSTRACT

Capsule: The movements and spatial ecology of non-breeding Eurasian Griffon Vultures *Gyps fulvus* in northern Italy, Croatia and Austria do not seem to be affected by feeding station use.

Aims: The purpose of this study was to assess how the creation of a feeding station at the Riserva Naturale Regionale del Lago di Cornino (Forgaria nel Friuli, northeast Italy) during the 1980s might have affected the spatial and behavioural ecology of the Eurasian Griffon Vulture.

Methods: Using global positioning system (GPS) satellite tracking, we studied movements of nine non-breeding Eurasian Griffon Vultures within the Riserva Naturale Regionale del Lago di Cornino in Italy, the Hohe Tauern in Austria and the Kvarner Gulf in Croatia.

Results: Both the average foraging range size and the time spent by the birds in Italy were comparable to those recorded in Croatia and Austria, where the vultures depend on unpredictable food resources. A significant difference in terms of foraging range size was recorded among seasons. In winter it seems to be smaller as a consequence of reduced movements performed by the individuals due to harsh climate conditions.

Conclusions: Our results suggest that the creation of a feeding station in Forgaria does not seem to have affected the spatial ecology of the Eurasian Griffon Vulture. However, due to the limited sample size and the young age of the individuals monitored, which have a long dispersal period, the findings presented should be considered as preliminary. Further research needs to be implemented to inform decisions regarding the management of supplementary feeding stations to promote the recovery and conservation of scavenger species, particularly in areas in which they have declined massively.

ARTICLE HISTORY
Received 13 August 2019
Accepted 15 January 2020

The 1979 Birds Directive was the first major European Union (EU) law passed that focuses on the protection and conservation of European birds (Carrete *et al.* 2006). Traditional practices, especially in remote areas, included the abandonment of carcasses in the field providing the maintenance of ecological processes affecting soil, vegetation and consumers (including invertebrates and large vertebrates) (DeVault *et al.* 2003). Avian scavenger species responded positively to this practice as they benefit from livestock carcasses especially in those areas where wild ungulates are absent (Mundy *et al.* 1992, Donázar *et al.* 1996, Olea & Mateo-Tomás 2009). For many years, farmers obtained a financial advantage from vultures feeding on the carcasses, obviating the cost of disposal at dump sites (García-Ripollés & López-López 2011). However, since the outbreak of the neurodegenerative disease in cattle in late 1990s called bovine spongiform encephalopathy and its form in humans called new variant Creutzfeldt-Jacob disease (nvCJd), a mandatory regulation of the European Union made the removal and cremation of all livestock carcasses obligatory to prevent the risk of disease transmission (Tella 2001, Donázar *et al.* 2009, Margalida *et al.* 2010). With such food reduction, scavenger populations have been negatively affected in terms of both their survival and reproduction. The decrease in terms of breeding success, reduced population growth, increased mortality in young age classes and increased number of cases of vultures attacking and killing cattle, suggest that the decrease in the availability of food resources produced a harmful effect on vulture populations (Tella 2001, Camiña & Montelío 2006, Donázar *et al.* 2009, Margalida *et al.* 2010). Because of this negative impact, the current restrictive European sanitary legislation (European Union Directive EU999/2011) has been implemented together with a series of regulations that allow supplementary feeding to be used as a strategy for the conservation of avian scavengers in southern Europe (CE 322/2003, CE 830/2005, CE 1069/2009, CE 142/2011) (Donázar *et al.* 2009, Margalida *et al.* 2012). The implementation of such policies in several

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Mediterranean countries has seen the disposal of dead animals only in specific locations, so-called vulture restaurants or supplementary feeding stations (Cortés-Avizanda *et al.* 2010, Margalida *et al.* 2010) that may prove useful for the recovery of various species (González *et al.* 2006, 2009). This new scenario of food concentration has led to large aggregations of the largest and most common avian scavenger species such as Eurasian Griffon Vultures *Gyps fulvus* (hereafter Griffon Vulture), a long-lived scavenger bird classified as 'Least Concern' by the International Union for the Conservation of Nature (BirdLife International 2017) and currently listed as a priority species by the European Union (Annex I of the European Birds Directive), the survival of which depends on the availability of medium and large carcasses (Tella 2001, Donázar *et al.* 2009, Margalida *et al.* 2010). Food shortages (Olea & Mateo-Tomás 2009, Ogada *et al.* 2012), intoxication by pharmaceutical products (Prakash *et al.* 2012), pesticides (Hernández & Margalida 2008), electrocution (Sarrazin *et al.* 1994, Gangoso & Palacios 2002) and collisions with both power lines and wind turbines (Gangoso & Palacios 2002, Tellería 2009, Carrete *et al.* 2009, 2012, García-Ripollés & López-López 2011, de Lucas *et al.* 2012a, 2012b). direct persecution, lead intoxication from hunting ammunition, deliberate poisoning (Margalida & Mateo 2019, Margalida *et al.* 2019), diseases and habitat loss (Ogada *et al.* 2012) are the main factors which have led to a decline in avian scavengers in Europe and worldwide over the last century, and still present serious hazards for their conservation today. By modifying the availability of natural food resources, ecological restoration projects and other management practices may lead social vultures, that naturally search for unpredictable food resources, to face the risk of an ecological trap (Schlaepfer *et al.* 2002, Battin 2004, Gilroy & Sutherland 2007) leading, in the worst cases, to population decline (Fletcher *et al.* 2012). It has been demonstrated that predictable food resources provide benefits in terms of survival but also drawbacks, as the unnatural concentration of individuals may increase the risk of predation or the spread of infectious diseases (Anderson & Anthony 2005, Piper 2004, Robb *et al.* 2008, Thompson *et al.* 2008, Cortés-Avizanda *et al.* 2009, 2016). Furthermore, supplementary feeding stations may promote both intra- and interspecific competition (Moreno-Opo *et al.* 2015a, 2015b, 2016). Moreover, it has been demonstrated that manipulating size, amount and appearance of food inputs affects the feeding behaviour of different vulture species (Moreno-Opo *et al.* 2015a). Finally, it has been shown that competition produces a detrimental effect mainly over younger birds (Duriez *et al.* 2012, Monsarrat *et al.* 2013) and shy species (Cortés-Avizanda *et al.* 2012) or may alter their natural behaviour, causing dependence upon feeding stations (Donázar *et al.* 2009, Phipps *et al.* 2013, Kane *et al.* 2016). For example, in a natural context, vultures are expected to interact with conspecifics to obtain information regarding the location of food (Prior & Weatherhead 1991, Buckley 1997, Harel *et al.* 2017), while in the presence of artificial feeding stations vultures rely more on personal, memory-based information in their search for food (Deygout *et al.* 2009, 2010). However, to date, this approach has received little attention from conservation biologists and needs to be assessed further.

Here we present the results of a Griffon Vulture satellite tracking programme, on non-breeding individuals, begun in 2006 in Friuli Venezia Giulia (northeast Italy). The study aimed to assess the effect on the vultures spatial and behavioural ecology produced by the creation of a feeding station in Forgaria nel Friuli (Italy), comparing the activity pattern and spatial data of vultures in Italy with those recorded in Croatia and Austria where individuals are forced to move more in their search for unpredictable food resources. The general hypothesis was that the feeding site would influence the spatial and behavioural ecology of the species. Thus, we predicted that: (*i*) both the foraging ranges and core areas recorded in Italy would be smaller compared to those recorded in Croatia and Austria as the vultures would not need to move as far in their search for food, (*ii*) the 50/95 kernel density estimation (KDE) ratio would be larger in Italy, as the presence of the feeding station would have allowed a more efficient exploration of the territory and (*iii*) the vultures would spend more time in Italy than in Croatia and Austria, especially during the coldest months of the year during which unpredictable food resources are more difficult to find.

Methods

Study species

Species distribution in Italy

Historically, in Italy, the Griffon Vulture bred in Sicily, Sardinia and, probably, in various parts of the Alps, the Apennines and other suitable areas. The Italian Griffon Vulture population underwent a marked decline in the twentieth century. A single small colony survived on Sardinia (Genero 1992). To date, the presence of the Griffon Vulture in Italy has been closely tied to conservation projects that have allowed the creation of five separate colonies in Sardinia, Friuli Venezia Giulia, Abruzzo, Sicily and Calabria. Between 1992 and 2018 more than 400 Griffon Vultures were released in Italy and, as a result of such reintroduction programmes, the number in Italy increased progressively, reaching 800–1000 birds, with some 200 breeding pairs (Genero, unpubl. data). Moreover, the creation of a feeding station at Forgaria nel Friuli (Italy) during the 1980s progressively attracted birds which have now formed a new stable nesting colony (the only one in the Italian Alps) (Genero 2009, 2016, 2017). Additionally, since the creation of the feeding station, the vultures have changed their traditional flyways when moving between Croatia and other areas (Mihelič & Genero 2005).

Species distribution in Croatia and Austria

In Croatia, Griffon Vultures are found on the islands and some mainland areas. The Kvarner Archipelago represents the northernmost natural colony of Griffon Vultures in eastern Europe, with about 140 breeding pairs (Sušić 2013). In this part of the world, its distribution declined massively at the beginning of the twentieth century (BirdGuides Ltd 2006) as a result of a decline in sheep grazing (Rebrović 2017) together with the deliberate poisoning of livestock carcasses (Muzinic 2007). Nowadays, the breeding population is restricted to four islands: Cres, Krk, Plavnik and Prvić (Kapelj & Modrić 2017). Croatian Griffon Vultures cover long distances in autumn, reaching the wintering grounds in southeast Europe and even as far as the Middle East and North Africa (Sušić 2000). The summering area is vast and includes the Julian and Carnic Alps, the southern Slovenian Alps and part of the Hohe Tauern National Park (Austria) (Genero 2009, 2016, 2017). In Austria, the vultures mainly visit the area during the spring and summer months searching for unpredictable food resources (Glutz *et al.* 1971, Genero 2009, 2016, 2017). Nevertheless, the number of birds present has declined continuously (Danko *et al.* 2014).

Study area

The study area encompassed the Kvarner Gulf (Croatia 44°54′N 14°36′E), the Riserva Naturale Regionale del Lago di Cornino (Forgaria nel Friuli, Friuli Venezia Giulia Region, Italy 46°13′N 13°01′E), and the Hohe Tauern National Park (Austria 47°05′N 12°39′E) (Figure 1). Geomorphological and ecological conditions vary considerably within these areas, especially in the Kvarner Gulf where anthropogenic activities over the centuries have led to a reduction in vegetation cover to create open areas dedicated to intensive pastoralism. In this area Griffon Vultures are found mostly on the islands. The northern part includes the islands of Cres and Krk and, partially, the Velebit mountain chain on the mainland. These areas are crucial for vultures in terms of food resources and presence of cliff-nesting sites. Temperature varies by season reaching an annual mean of 16.6°C. Capture sessions were carried out within the Riserva Naturale Regionale del Lago di Cornino, at the extreme southeast edge of the Carnic Alps. The area covers about 487 ha and altitude ranges from 170 to 700 m above sea level. The climate is temperate, humid and characterized by variable seasonal temperatures reaching a mean of 12.3°C per year. The Hohe Tauern is a mountainous area of the central-eastern Alps in which the pastures are traditionally used during summer for free-range rearing of cattle and sheep. The area's climate is variable among seasons reaching a mean annual temperature of 5.8°C. The distance between the Friulan and Croatian colonies is about 160–200 km, while that between the Friulan and Austrian ones is about 90–120 km.

Food resources vary between the different study areas. In Croatia and Austria, the Griffon Vultures rely totally upon unpredictable food resources, while in Italy they feed mostly at the feeding station. In Croatia, they are essentially dependent on areas with a long tradition of sheep husbandry. In Croatia, the sheep population totals about 630 000 individuals (Ćurković *et al.* 2016) of which about 38 500 are concentrated within Primorje-Gorski Kotar county that includes the largest islands of Cres and Krk (Guggenberger & Ringdorfer, unpubl. data). In Austria, on the other hand, the food supply is represented by both wild and domestic ungulates (mainly cattle and sheep). Cattle are abundant within the area (approximately13 500) while sheep are less common (a little over 1000 head) (Guggenberger & Ringdorfer, unpubl. data).

Characteristics of the feeding station

The feeding station is located within the Riserva Naturale Regionale del Lago di Cornino (Forgaria nel Friuli) at 200 m above sea level. The station itself covers 0.5 ha and is surrounded by stone walls and thermophilous forests. Carcasses of both wild (Red Deer *Cervus elaphus*, Roe Deer *Capreolus capreolus* and Wild Boar *Sus scrofa*) and domestic ungulates (pigs and cattle) were stocked three times per week to maximize the benefit for the target species. Carcasses of road-killed ungulates represent 30–35% of the total amount and are previously subjected to sanitary inspections for lead poisoning. As far as livestock carcasses are concerned, close attention is dedicated to veterinary pharmaceutical products used by livestock farmers to

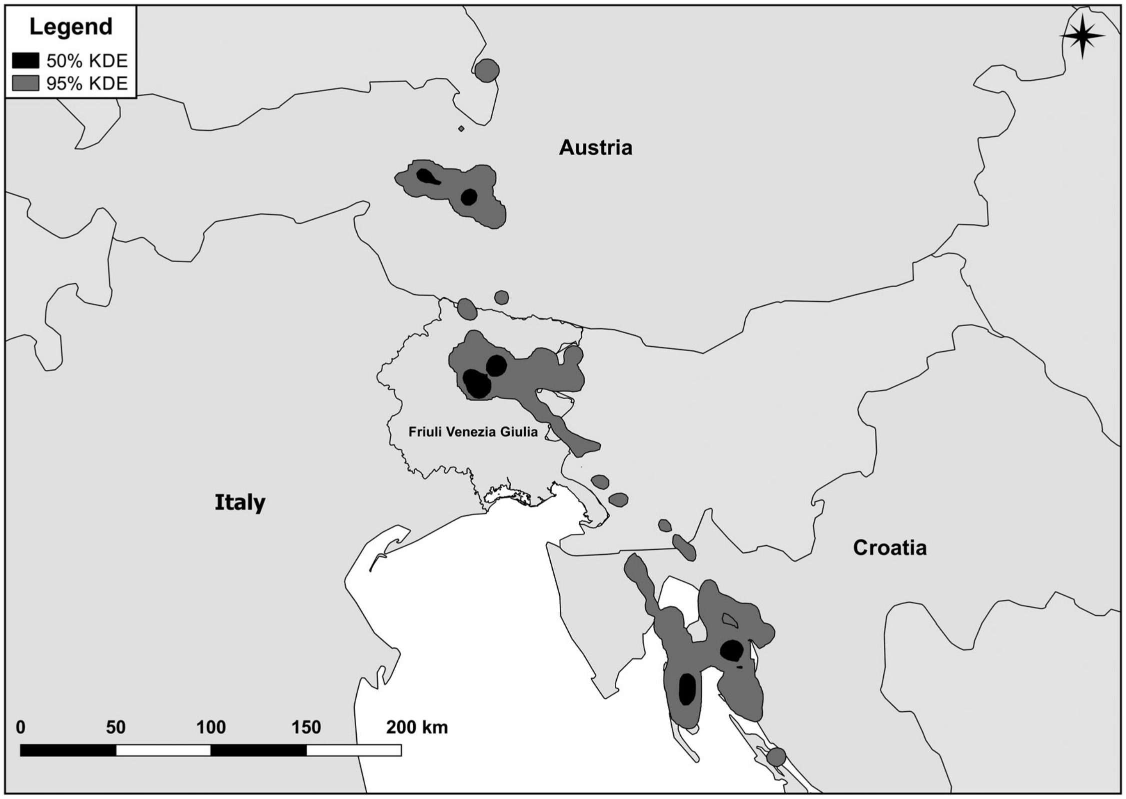

Figure 1. Map showing the 95% (foraging range) and 50% (core area) KDE calculated, based on Griffon Vultures' movements within the study areas. Spatial data were obtained from nine individuals (one non-breeding floating adult, four sub-adults and four immatures) monitored from 2006 to 2014 for a total of 2825 days and 16829 recorded fixes.

avoid, for example, the risks related to diclofenac contamination (Prakash *et al.* 2012). The risk of lead poisoning through the ingestion of pellets or fragments of lead-based bullets was avoided by excluding ungulates killed during the hunting season, carcasses in which visible gunshot wounds were present and individuals hunted using lead ammunition. The average total food supply averaged 55 tonnes per year but varied among years and seasons. Each season was classified as follows: autumn (October, November and December), winter (January, February and March), spring (April, May and June) and summer (July, August and September). Considering the period in which Griffon Vultures were monitored (2006–14) the greatest amount of food was put out during spring (median = 3215 kg range = 1690–5690 kg) followed by summer (median = 3170 kg range = 0–5795 kg) autumn (median = 2723 kg range = 0–4520 kg) and least in winter (median = 2258 kg range = 790–4030 kg).

Vulture captures

Capture sessions were carried out close to the feeding station using a 4 × 5 × 1.57 m lightweight wooden framed walk-in cage trap with a remote-controlled door (70 × 80 cm), in which the wooden frame consisted of a wire mesh reinforced with steel cables (Diekmann *et al.* 2004). The cage trap was baited with domestic or wild ungulate carcasses to attract vultures (Bamford *et al.* 2009). Each Griffon Vulture captured was ringed with official metal (Institute for Environmental Protection and Research/Euring) and/or alphanumeric green plastic rings (35–45 mm high and 25–28 mm in diameter) and, in addition, birds were bleached on the wings and/or tail feathers to facilitate individual recognition. The age class was identified according to plumage characteristics and using ringing data obtained from Sušic (1994). Once marked, each individual was equipped with global positioning system (GPS) transmitters and, finally, released. Vultures were equipped with GPS PLUS 1C BIRD GPS-GSM tracking units (Vectronics Aerospace Gmbh-Germany) using a Teflon ribbon backpack-style harness enclosed in flexible plastic tubing to prevent skin abrasion (Diekmann *et al.* 2004). Each unit weighed 190 g (about 2.5% of the mean mass of an individual) and was encased in hardened epoxy resin to make it safe and waterproof. A cotton thread was used to secure the harness which would eventually degrade, allowing the harness to fall off when the transmitters stopped working. The transmitters had a life expectancy that varied from two to four years. Units were set to record GPS locations (with 25 m accuracy), date, time, altitude above sea level, temperature and mortality logging, positional dilution of precision, battery charge and validation test. Data were transmitted daily by short message service (SMS) (7 fixes per SMS) to an online database via the Global System for Mobile Communications (GSM) network. The first four Griffon Vultures were equipped with non-solar units providing, a mean (±sd), 5 locations per day (±0.91). In the final two years of the study, however, solar-powered units were used and, thus, GPS locations were recorded more regularly every hour during summer (from 5:00 to 18:00 and at 22:00 hours, Coordinated Universal Time) and three times a day during winter (7:00, 10:00, 12.00 hours). The update frequencies varied between seasons, based on the solar energy available. The bias related to the difference in terms of GPS data collected between the vultures monitored from 2006 to 2013 (birds 85, 2161, 5985, 5986) and those monitored from 2013 to 2014 (birds 13121, 13122, 13123, 13124, 13125) did not affect the data analysis as we considered a global spatial and temporal analysis without considering the difference among individuals.

Spatial analysis

Spatial analysis was carried out using ArcGIS Software (version 9.3). The birds' daily activity patterns were computed based on the frequency of segments for which an effective movement was recorded, considering the nominal accuracy of the GPS (approximately 25 m) and assuming 50 m of altitude. To describe individual space use, both 95% KDE and 50% KDE were calculated and represented by isopleths (Urios *et al.* 2010). The 95% KDE corresponds to the foraging range (set to 95% such that the most extreme points were removed) while the 50% KDE represents the core area of activity. The calculation was arrived at using a fixed KDE with smoothing factor H = 5000, raster cell size = 500 and quartic to estimate the isopleths with a fine spatial resolution. For spatial analysis, GPS locations were projected using the Universal Transverse Mercator (UTM) coordinate system (World Geodetic System, WGS 84 UTM Zone 33N). As we mostly dealt with immature and sub-adult Griffon Vultures, that have notoriously long dispersal periods (Heredia 1991, Gil *et al.* 2010, 2014, Urios *et al.* 2010, Gavashelishvili *et al.* 2012, Yamaç & Bilgin 2012, Spiegel *et al.* 2013, Margalida *et al.* 2016, García-Jiménez *et al.* 2018, Martens *et al.* 2018) to describe the individuals' space use we referred to foraging range and core area, rather than home range and core area. Using GPS locations, we, furthermore, calculated the total distance travelled per day and season by each vulture.

Explanatory variables

Data were analysed in terms of movements, foraging range (95% KDE), core area (50% KDE), 50/95 KDE ratio and number of days spent by the birds in each area (Austria, Croatia, Italy) and during the seasons within each area. So, 95% KDE, 50% KDE, 50/95 KDE ratio and time spent at the various sites represent the dependent variables whilst the area and season were the independent variables. The 50/95 KDE ratio represents the difference between the core area and the foraging range and provides information concerning the spatial use of an area by the individuals. The 50/95 KDE ratio can take values ranging from 0 to 1. The closer the value to 0, the bigger is the difference between the core area and foraging range. This means that each activity is mostly concentrated within a small area. On the contrary, the closer is the value to 1, the smaller is the difference between core area and foraging range revealing, hence, a more efficient exploration of the territory (Genero 2017). For the Croatian data, we performed a comparison between the foraging range that included both marine and terrestrial land surface areas and a foraging range that included only the terrestrial area. Nevertheless, in further analysis, we considered only the foraging range size referring to the terrestrial surface, as the marine surface was not used for foraging and/or nesting. The seasonal analysis was performed by classifying the seasons as above. Inter-annual variation was not considered as, for logistic reasons, data were collected more regularly and mainly during the final years of the study. In this sense, the difference in terms of sample size did not allow us to carry out a comparison.

Statistical analysis

Statistical analysis was performed using R Software (version 3.5), setting the alpha value at 0.05. The normality distribution of data was assessed using a Shapiro–Wilk normality test while both parametric and non-parametric Levene tests (within the R package 'lawstat') were used to assess variance homogeneity.

To test the difference in terms of distance travelled by vultures within each study area a multiple comparison analysis testing in analysis of variance (ANOVA) with Tukey's range test was performed, while to test the same difference between seasons a Kruskal–Wallis test was used.

To test the effect of each independent variable (area and season) over the dependent variables (i.e. 95% KDE, 50% KDE, 50/95 KDE ratio and time spent at the various sites) both linear mixed models and generalized linear mixed models with Laplace approximation (Zuur *et al.* 2009) and negative binomial distribution were used, considering the identity of each individual as a random factor, and the area and season as fixed factors. The goodness of fit of each model was assessed by calculating the marginal R squared (R^2_m) and the conditional R squared (R^2_c), using the R package MuMIn, following Nakagawa & Schielzeth (2013). The family distribution of the dependent variable was assessed using the R package fitdistrplus. Differences between areas and seasons within each area were assessed through Tukey's range test, while comparisons between the same seasons among areas (i.e. autumn (Italy) *vs.* autumn (Croatia) *vs.* autumn (Austria)) were made using a multiple comparison analysis testing in ANOVA with Tukey's range test or through a two-sample *t*-test.

For Croatia, to test the difference between the foraging range that encompassed both marine and terrestrial surfaces and that one that covered only the terrestrial environment, a multiple comparison analysis testing in ANOVA with Tukey's range test was performed.

To test the correlation between the proportion of time spent at a certain distance from either predictable and/or unpredictable feeding site/s and foraging range size measured within the study areas, a Spearman's correlation coefficient was used.

Results

Distance travelled by vultures

We analysed the movements of nine Griffon Vultures, four of which were immatures (two/three years), four sub-adults (four/five years) and one non-breeding floating adult (more than five years old). The data collection period spanned the years 2006–14 for a total number of 2825 tracking days (Table 1). Because of the long dispersal periods typical of both immature and sub-adult individuals (Heredia 1991, Gil *et al.* 2010, 2014, Urios *et al.* 2010, Gavashelishvili *et al.* 2012, Yamaç & Bilgin 2012, Spiegel *et al.* 2013, Margalida *et al.* 2016, García-Jiménez *et al.* 2018, Martens *et al.* 2018) we created an accumulation curve illustrating the relationship between the number of tracking days and foraging range size of each monitored bird (Figure 2). Data obtained from GPS locations showed that Griffon Vultures covered a mean (±sd) distance of 25.41 (±15.97) km per day. Information regarding the distance travelled per day by each vulture was provided in Table 1. Considering the dispersal movements within each area we showed that in Croatia the vultures explored more ($n = 55$, mean ± sd = 489.15 ± 326.29 km), while in Italy ($n = 78$, mean ± sd = 332.20 ± 262.91 km) and Austria ($n = 22$, mean ± sd = 256.23 ± 173.53 km) movements were reduced. A significant difference was obtained between Croatia and Italy (ANOVA, se = 56.63, $t = 4.11$, $P < 0.001$) and between Croatia and Austria (ANOVA, se = 52.68, $t = -2.97$, $P < 0.01$). We showed that individuals moved more during spring ($n = 36$, mean ± sd = 1521.95 ± 589.29 km), followed by summer ($n = 66$, mean ± sd = 882.83 ± 571.32 km), autumn ($n = 38$, mean ± sd = 648.52 ± 478.17 km) and winter ($n = 15$, mean ± sd = 479.56 ± 406.91 km). However, no significant difference (Kruskal–Wallis H test, $P > 0.20$) was found between seasons.

Foraging range and core area

Figure 1 shows the foraging range and the core area used by Griffon Vultures (95% KDE and 50% KDE, respectively) within each study area. Our findings revealed that no significant difference in terms of either foraging range (Tukey's range test, $P > 0.20$) and/or core area (Tukey's range test, $P > 0.20$) was found between areas (Figure 3). For Croatia, comparing the

Table 1. Data obtained from Griffon Vultures equipped with GPS transmitters. Foraging range (95% KDE) and core area (50% KDE) values were obtained considering the sum of the overall home ranges and core areas calculated within each study area. Abbreviations: KDE = Kernel density estimation.

			Transmissions dates		Tracking days	Fixes per month	Spatial data (km^2)		Distance travelled per day (mean ± sd km)
ID	Age	Origin	start	end			95% KDE	50% KDE	
85	Immature	Croatia	14.06.2012	03.03.2013	176	167	2479.59	554.41	7.69 ± 9.01
2161	Adult	–	22.05.2006	07.11.2006	120	155	1964.99	440.64	13.26 ± 14.58
5985	Sub-adult	–	22.06.2009	22.02.2010	195	167	2716.46	687.11	11.52 ± 8.91
5986	Sub-adult	–	23.06.2009	22.04.2010	278	109	1411.56	300.33	20.04 ± 13.74
13121	Immature	Croatia	29.05.2013	31.12.2014	515	4556	8589.63	1543.40	33.30 ± 18.36
13122	Immature	Croatia	15.07.2013	31.12.2014	464	3855	7399.20	1285.46	25.28 ± 17.26
13123	Sub-adult	Croatia	11.06.2014	31.12.2014	204	1934	4534.86	860.60	42.53 ± 21.97
13124	Sub-adult	Croatia	29.05.2013	08.10.2014	493	3318	8506.18	1507.11	39.09 ± 21.85
13125	Immature	Croatia	17.07.2013	06.08.2014	380	2568	4180.77	697.79	35.97 ± 18.08

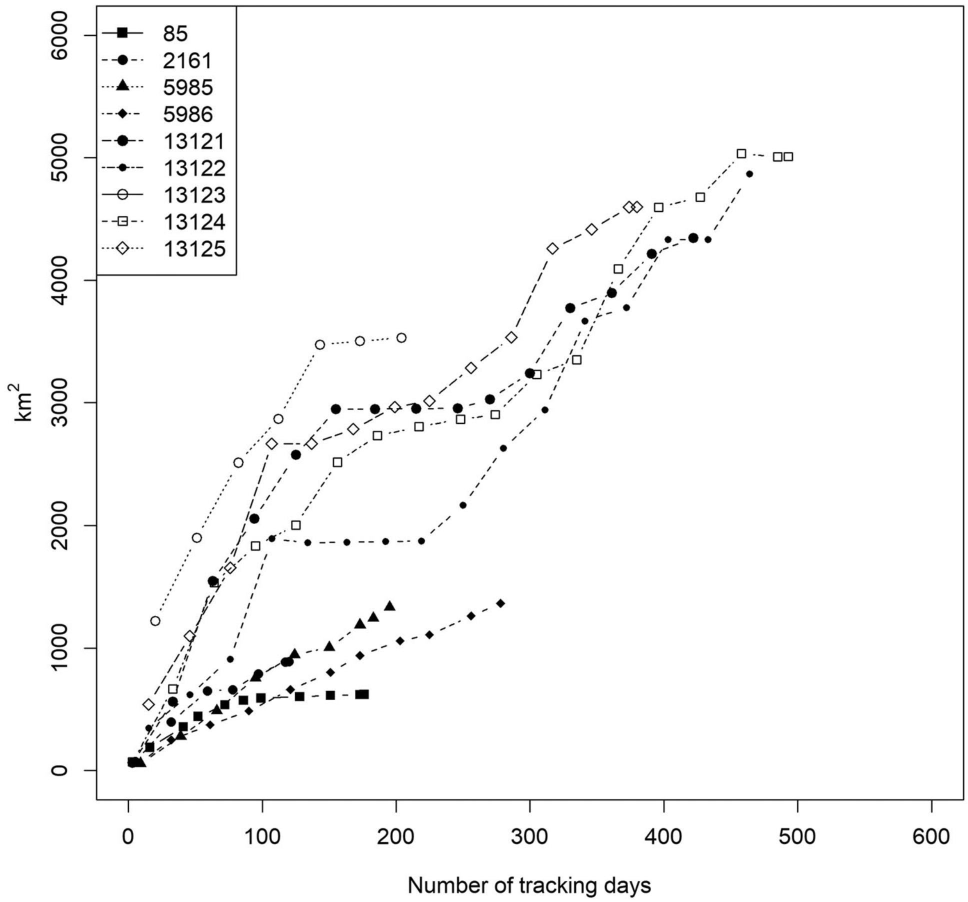

Figure 2. Relationship between number of tracking days and foraging range (95% KDE) size (km^2) for each individual monitored.

foraging range value including both marine and terrestrial surfaces ($n = 55$, mean ± sd = 450.20 ± 234.09 km^2) with that encompassing only the terrestrial area ($n = 55$, mean ± sd = 285.07 ± 139.45 km^2), a significant difference (Tukey's range test, se = 36.41, t = 4.53, $P < 0.01$) was obtained.

In Croatia no significant differences were found between seasons from both foraging range (Tukey's range test, $P > 0.70$) and core area (Tukey's range test, $P > 0.10$) seasonal comparisons (Figures 4 and 5). In Italy, a significant difference in terms of foraging range was found comparing autumn ($n = 23$, mean ± sd = 208.66 ± 110.18 km^2) with both spring ($n = 15$, mean ± sd = 299.48 ± 84.88 km^2) (Tukey's range test, se = 0.13, $z = 2.76$, $P = 0.02$) and summer ($n = 31$, mean ± sd = 324.38 ± 118.53 km^2) (Tukey's range test, se = 0.10, z = 4.09, $P < 0.001$). The same significant difference was obtained comparing winter ($n = 9$, mean ± sd = 192.65 ± 32.04 km^2) with either spring (Tukey's range test, se = 0.16, $z = -2.63$, $P = 0.04$) and/or summer (Tukey's range test, se = 0.15, $z = -3.26$, $P < 0.01$) (Figure 4). From the seasonal comparison of core areas we found a significant difference between autumn ($n = 23$, mean ± sd = 44.13 ± 27.79 km^2) and summer ($n = 31$, mean ± sd = 67.36 ± 25.70 km^2) (Tukey's range test, se = 0.12, z = 3.52, $P < 0.01$) and between winter ($n = 9$, mean ± sd = 34.23 ± 10.27 km^2) and summer (Tukey's range test, se = 0.17, $z = -3.74$, $P < 0.01$) (Figure 5). In Austria, no significant difference was found between spring and summer in terms of both foraging range (Tukey's range test, $P > 0.20$) (Figure 4) and core area (Tukey's range test, $P > 0.90$) (Figure 5). Regarding Austria, no GPS data were collected during either autumn or winter as the vultures spend the winter months in warm areas.

From a seasonal comparison between study areas, we obtained a significant difference (Tukey's range test, se = 31.01, $z = 3.60$, $P = 0.01$) between Italy ($n = 31$, mean ± sd = 324.38 ± 118.53 km^2) and Austria ($n = 16$, mean ± sd = 212.62 ± 94.48 km^2) in terms of foraging range recorded during summer (Figure 4). Furthermore, a significant difference was obtained between Italy (n = 31, mean ± sd = 67.36 ± 25.70 km^2) and Austria ($n = 16$, mean ± sd = 43.27 ± 19.96 km^2) (Tukey's range test, se = 6.63, $z = 3.63$, $P = 0.01$), and between Italy and Croatia ($n = 19$, mean ± sd = 44.78 ± 21.93 km^2)

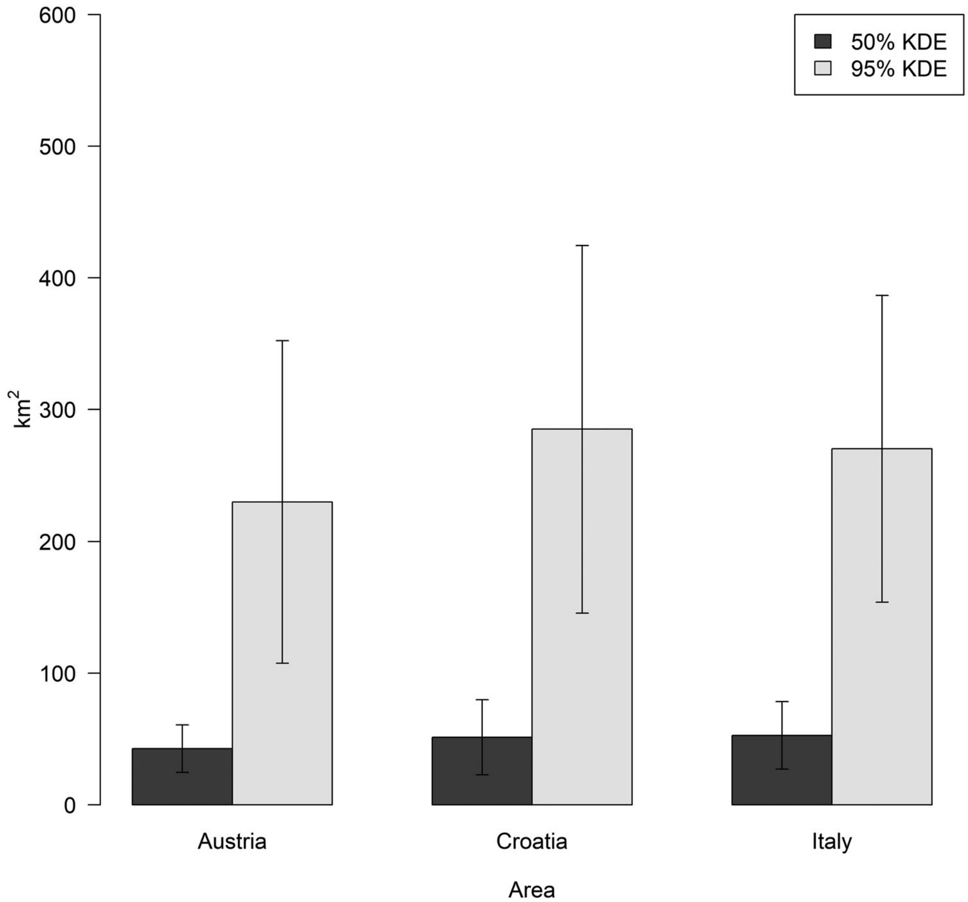

Figure 3. Mean ± sd foraging range (95% KDE) and core area (50% KDE) size (km^2) used by Griffon Vultures within each study area.

(Tukey's range test, se = 6.67, $z = 3.38$, $P = 0.02$) in terms of core area recorded during summer (Figure 5).

50/95 KDE ratio

No significant difference (Tukey's range test, $P > 0.70$) was found in the 50/95 KDE ratio between areas. As far as the seasonal comparison was concerned, we observed that in Croatia a significant difference was found between autumn ($n = 14$, mean ± sd = 0.24 ± 0.08) and summer ($n = 19$, mean ± sd = 0.16 ± 0.06) (Tukey's range test, se = 0.12, $z = -3.39$, $P < 0.01$) (Figure 6). In Italy, a significant difference was found comparing autumn ($n = 23$, mean ± sd = 0.22 ± 0.08) with spring ($n = 15$, mean ± sd = 0.17 ± 0.04) (Tukey's range test, se = 2.03, $z = -2.57$, $P = 0.04$) and comparing summer ($n = 31$, mean ± sd = 0.22 ± 0.06) with spring (Tukey's range test, se = 1.92, $z = 2.57$, $P =$ 0.04) (Figure 6). In Austria no significant difference (Tukey's range test, $P > 0.20$) was found between spring and summer (Figure 6).

From a seasonal comparison between study areas, a significant difference between Italy ($n = 31$, mean ± sd = 0.22 ± 0.06) and Croatia ($n = 19$, mean ± sd = 0.16 ± 0.06) (t-test, $t = -3.27$, df = 35.10, $P < 0.01$) and between Austria ($n = 16$, mean ± sd = 0.22 ± 0.06) and Croatia (t-test, $t = -2.79$, df = 32.11, $P < 0.01$) was obtained in terms of 50/95 KDE ratio recorded during summer.

Time spent at the various sites

No significant difference was found between study areas for the time spent at different sites (Tukey's range test, $P > 0.10$). As far as the seasonal comparison was concerned, in Croatia, no significant difference was found (Tukey's range test, $P > 0.30$) between seasons and the same result was obtained in Italy in which no significant difference between seasons was found (Tukey's range test, $P > 0.10$) (Figure 7). In Austria, a significant difference (Tukey's range test, se = 0.38, $z =$ 1.98, $P = 0.04$) was found between spring ($n = 5$, mean ± sd = 9 ± 7) and summer ($n = 16$, mean ± sd = 20 ± 11) (Figure 7). Moreover, no significant correlation (Spearman's rank correlation, rho = 0.21, $P > 0.10$) between the proportion of time spent at a certain distance from both the predictable and unpredictable feeding site/s and foraging range size measured in each

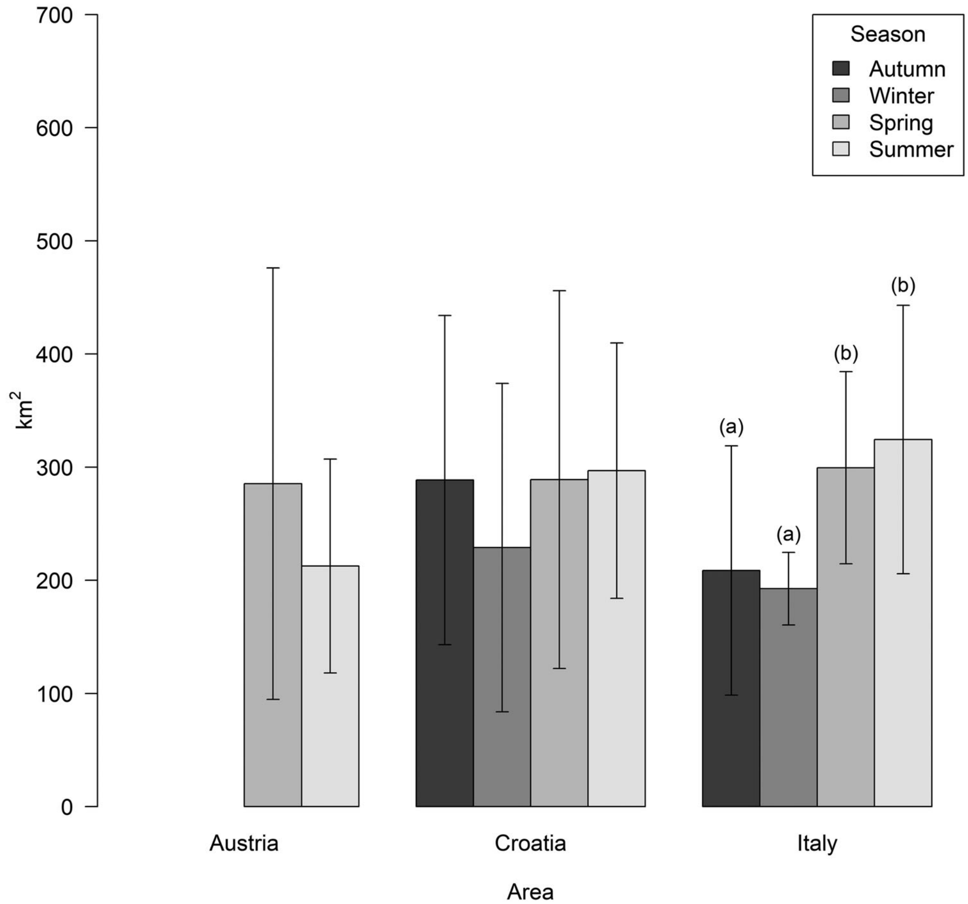

Figure 4. A comparison of seasonal foraging range (mean ± sd 95% KDE) used by Griffon Vultures within each study area. Different letters over the bars represent a significant difference ($P < 0.05$) in pairwise comparisons.

area was found. From a seasonal comparison between study areas, no significant difference (Tukey's range test, $P > 0.60$) was found.

Discussion

In this study, we analysed the spatial ecology of nine non-breeding Griffon Vultures in the eastern Alps and Adriatic region including Italy, Croatia and Austria, in relation to the presence of a feeding station in Forgaria nel Friuli (Italy) with the aim of determining its potential effect on movements of individuals within the study area and in terms of both foraging range (95% KDE) and core area (50% KDE) size. Furthermore, the time spent by vultures at the various sites was analysed. The movements of bird species within and among areas can be affected by either intrinsic (e.g. species morphology, experience and migration strategy) (Alerstam & Hedenström 1998, Thorup *et al.* 2003, Klaassen *et al.* 2012) and/or extrinsic factors (e.g. landscape properties and meteorological variables) (Klaassen *et al.* 2008, López-López *et al.* 2010, Mellone *et al.* 2011, Bohrer *et al.* 2012). Our results showed that Griffon Vultures moved mainly between Croatia and Alpine areas and towards Austria only during the warmer seasons of spring and summer. The foraging areas appeared easily identifiable and relatively constant for most of the individuals and included three important sectors: the islands of Krk, Cres, Plavnik, Prvič and part of the Velebit mountain chain in Croatia, both the pre-Alps and southern Alps including the Friulan and Slovenian Alps and, lastly, the Hohe Tauern in Austria. This is the first time in which the spatial ecology of a small non-breeding Griffon Vulture population inhabiting the Italian and Slovenian alpine areas has been studied in detail showing the modalities, frequency of movements and use of foraging areas and roosting places. GPS locations showed that, in Croatia, the vultures regularly explored certain areas of Cres island (almost completely avoiding neighbouring Lošinj), Prvič and Plavnik, the southern part of Krk and the coastal area of the Velebit mountain chain. The Hohe Tauern in Austria was mainly frequented during spring and summer months (Perco *et al.* 1983, Genero 1985, 1986, 1992, 2009, 2016, 2017), while Italy now represents a traditional summering area in which

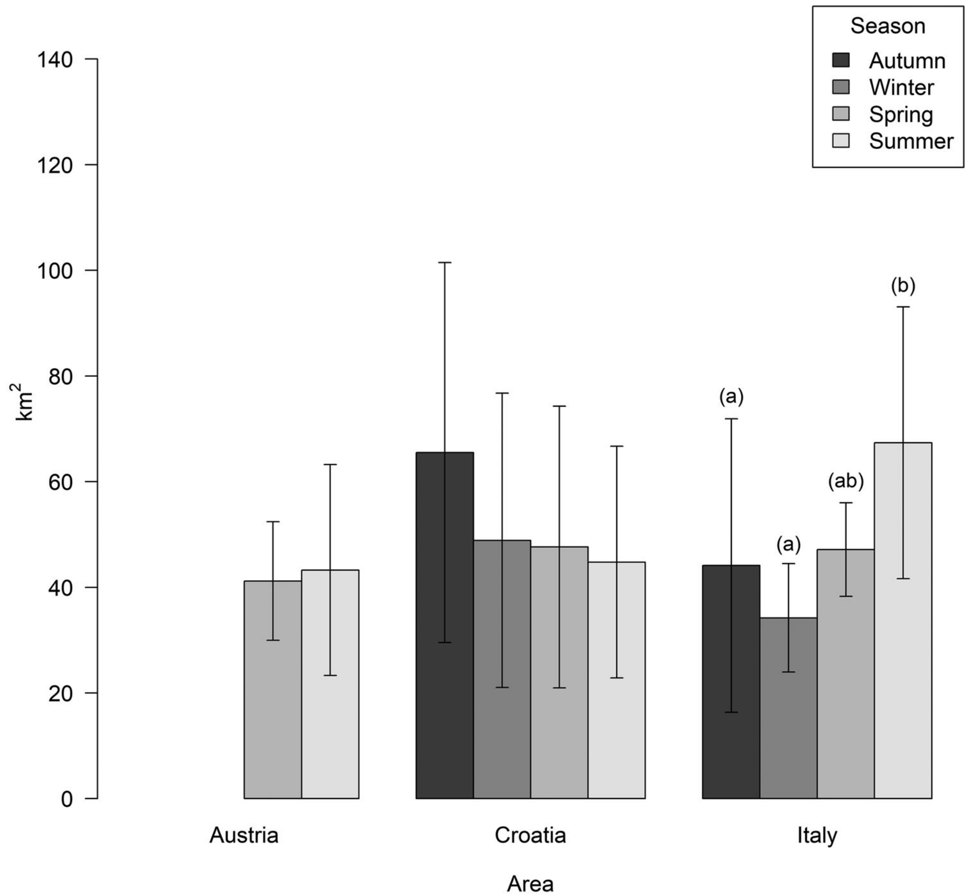

Figure 5. A comparison of seasonal core area (mean ± sd 50% KDE) used by Griffon Vultures within each study area. Different letters over the bars represent a significant difference ($P < 0.05$) in pairwise comparisons.

Griffon Vultures move mainly around the feeding station but regularly explore the neighbouring Alpine areas. Movements within and between areas occurred most frequently during late spring and summer rather than autumn or winter, seasons in which movements are generally reduced due to difficult flying conditions and fewer hours of daylight (Blondel *et al.* 2010, Mellone *et al.* 2012, Dodge *et al.* 2014) that may reduce the time available for foraging forcing, hence, vultures to move less and to restrict their foraging activity to smaller areas (Margalida *et al.* 2013). The significant difference recorded in terms of distance travelled by vultures within each area between Croatia and both Italy and Austria may be due to the difference in terms of food resources available in relation to the surface that birds need to cover searching for food. That is that in Italy, due to the presence of the feeding station, individuals are not forced to cover long distances. In Austria, feeding activity is concentrated mainly in small mountainous areas of the Hohe Tauern National Park while in Croatia, since free-range rearing sheep practices are concentrated mainly in insular areas, vultures are forced to move more in search of unpredictable food resources (Genero 2009, 2016, 2017). Consequently, since the distance travelled by vultures includes also the movements performed among islands, the difference in terms of total distance travelled between area resulted as significant. Moreover, the significant difference obtained between Croatia and Austria could have been influenced by the difference in terms of GPS locations between the two areas, as Austria is frequented only during spring and summer (Glutz *et al.* 1971, Perco *et al.* 1983, Genero 1985, 1986, 1992, 2009, 2016, 2017). The accumulation curve shown in Figure 2 revealed a marked difference in terms of foraging range size recorded among vultures in relation to the number of days over which they were tracked. Such differences could be due to: (*i*) disparity in terms of the monitoring period between individuals, especially during the first years of the study, (*ii*) the age class of the birds involved. With the exception of one non-breeding floating adult (ID 2161) monitored during 2006, the other birds being immatures or sub-adults, meant that, as reported in various studies (Heredia 1991, Gil *et al.* 2010, 2014, Urios *et al.* 2010, Gavashelishvili *et al.* 2012, Yamaç &

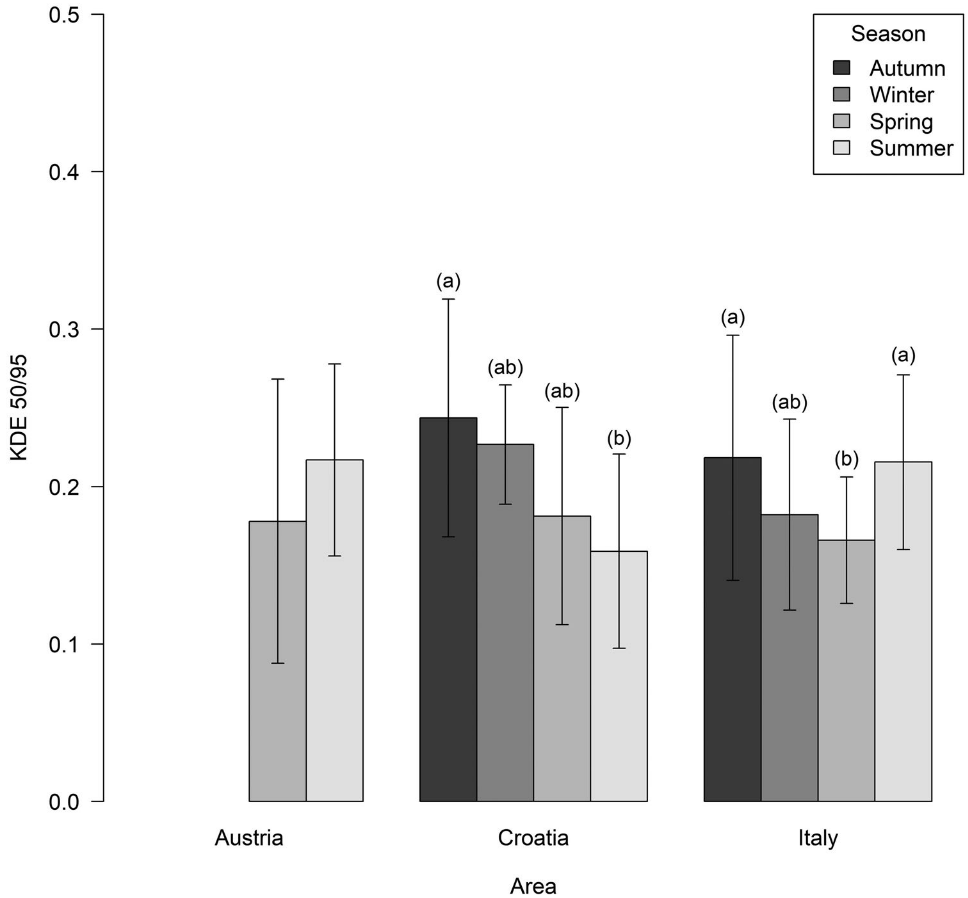

Figure 6. A comparison of seasonal range use (mean ± sd 50/95 KDE) used by Griffon Vultures within each study area. Different letters over the bars represent a significant difference ($P < 0.05$) in pairwise comparisons.

Bilgin 2012, Spiegel *et al.* 2013, Margalida *et al.* 2016, García-Jiménez *et al.* 2018, Martens *et al.* 2018), they were generally highly mobile during their long dispersal period.

The management of feeding stations is not a trivial matter. Factors including their location and the frequency with which they need to be stocked may have a notable effect on animal behaviour (López-López *et al.* 2013, 2014a, 2014b, Monsarrat *et al.* 2013, Zuberogoitia *et al.* 2013, Gil *et al.* 2014, Moreno-Opo *et al.* 2015a, 2015b, Yarnell *et al.* 2015). In addition, such predictable food resources may have an impact that differs between immature and adult individuals, depending upon how they are managed. Duriez *et al.* (2012) showed that adult vultures tend to be dominant over the youngest individuals at artificial feeding stations located close to colonies and regularly supplied with food. Similarly, Monsarrat *et al.* (2013) found that vultures regularly searched for stocked, predictable food resources mainly during hard conditions, either due to low natural food availability in summer or because of poor flight conditions during the winter. This said, the competition between adult and immature vultures at feeding stations regularly stocked with large amounts of food (depending on season, between one and ten carcasses daily) forced the youngest individuals to search for food in other areas and to concentrate their foraging activities on feeding stations stocked with less food (on average, one carcass per month) where competition with adults was lower. In this sense, conservationists should make careful use of feeding stations to manage the different age classes effectively (Kane *et al.* 2016). No significant difference was found when comparing both foraging ranges and core areas among the three monitoring areas, suggesting that vultures seem not to be affected by the presence of the feeding station created in Forgaria. This result is in contrast with those obtained by Gil *et al.* (2014) for Bearded Vultures *Gypaetus barbatus* in which they showed that non-breeding individuals included predictable sources of food into their home range and that these were particularly important for young birds (under 3 years old), that often remained near feeding stations for longer periods. This behaviour seems to be common even for Griffon and Egyptian Vultures *Neophron percnopterus* for which GPS data showed

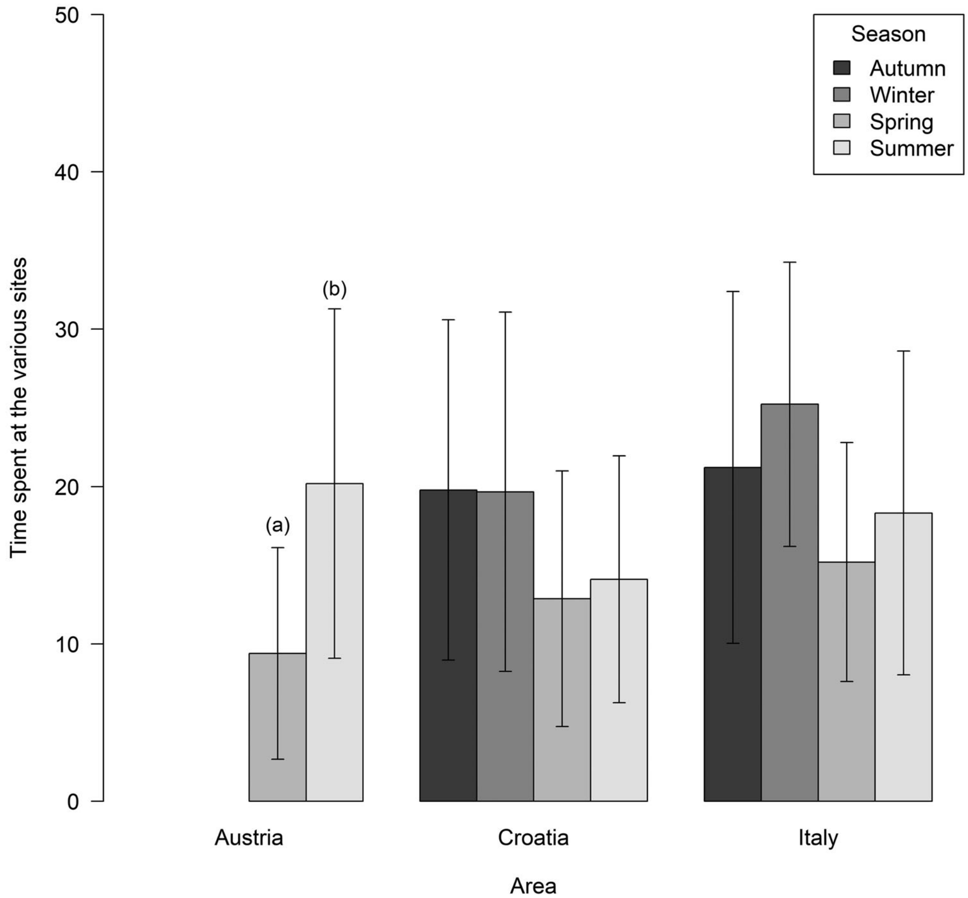

Figure 7. A comparison of mean (±sd) number of days spent by Griffon Vultures at each study area in each season. Different letters over the bars represent a significant difference ($P < 0.05$) in pairwise comparisons.

how individuals were temporarily linked to particular feeding stations, which affected their ranging behaviour (López-López *et al.* 2013, 2014a, 2014b, Monsarrat *et al.* 2013, Zuberogoitia *et al.* 2013). Nevertheless, our findings are in accordance with those obtained by García-Ripollés *et al.* (2011) in which they showed that vultures ranged extensively mainly in areas where traditional stock-raising practices and pasturing were common, while vulture restaurants were visited occasionally. Moreover, a similar result was presented by Margalida *et al.* (2017) in which they showed that the European policies on livestock carcass management did not modify the foraging behaviour of Egyptian Vultures. In our case, the absence of a significant effect may be attributable to the dietary plasticity of the species and to the good habitat quality that compensates for the sudden effects of food shortages derived from the implementation of sanitary policies and questioning, hence, the usefulness of feeding stations in those areas characterized by good environmental conditions.

For Croatia, the significant difference obtained when comparing the foraging range including both marine and terrestrial surfaces and the one that considered only the terrestrial area, could be related to various factors such as the search for food, exploration of the territory, and/or interaction with conspecifics that may explain the vast distances recorded (Margalida *et al.* 2013, Arrondo *et al.* 2018). A study performed by Monsarrat *et al.* (2013) on GPS tracked Griffon Vultures in France described a median home range of $962 \pm 623\ km^2$ and a core area of $109 \pm 80\ km^2$, calculated using the KDE method. The difference with our study in terms of foraging range in each area may be related to several factors: (*i*) the higher number of birds tracked ($n = 27$) that also included young individuals with a greater tendency to dispersal (Heredia 1991, Gil *et al.* 2010, 2014, Urios *et al.* 2010, Gavashelishvili *et al.* 2012, Yamaç & Bilgin 2012, Spiegel *et al.* 2013, Margalida *et al.* 2016, García-Jiménez *et al.* 2018, Martens *et al.* 2018), (*ii*) a larger number of feeding stations with high and low levels of food provision, distributed in a study area at higher altitude, frequented in a range of ways by vultures of different age classes, (*iii*) the different tracking period, as the study was concentrated within a shorter time period, (*iv*) a different approach used for foraging range calculation as they calculated the entire foraging range within the same area, while we calculated foraging range values among three different areas without considering surfaces we defined as displacement areas. This said, in general, both the foraging and/or home range comparisons among studies must be considered with caution as factors such as topography, vulture population size, availability of both predictable and unpredictable food resources and the number of GPS locations obtained in relation to the number of individuals monitored could play a key role in influencing foraging/home range size. The 50/95 KDE ratio comparison revealed that there was no significant difference between study areas. The low values recorded highlighted the fact that Griffon Vultures tended to concentrate their activities in areas in which food resources were abundant, thus leading to lower territorial exploration (Genero 2017). When examining the average number of days spent by vultures in each area, we found no significant difference between study areas, suggesting that the presence of the feeding station in Forgaria del Friuli may not have affected the time vultures spent at the site. Furthermore, the absence of a significant correlation between the proportion of time spent at a certain distance from both the predictable and unpredictable feeding site/s and foraging range size measured within each study area seems to support these statements.

In autumn, movements were generally reduced probably due to poor flight conditions (Blondel *et al.* 2010, Mellone *et al.* 2012, Dodge *et al.* 2014). Consequently, foraging ranges were generally smaller compared to those recorded during the spring and summer and this difference was more evident in Italy than Croatia, where a significant difference between autumn and both spring and summer was noted. The spring core area measured in Italy was significantly smaller than the summer one, while in Croatia the largest core area was recorded during the autumn, but no significant difference between seasons was identified. We showed that in both Italy and Croatia. Vultures tended to stay within their respective areas for more time during autumn than spring and/or summer probably due to the more difficult climate conditions (Blondel *et al.* 2010, Mellone *et al.* 2012, Dodge *et al.* 2014). However, the average core area value recorded in Croatia suggests that, despite poor flying conditions, vultures were forced to move further to search for unpredictable food resources. The largest 50/95 KDE ratio was measured during autumn in both Croatia and Italy, showing more extensive exploration of the area. Nevertheless, the difference between seasons was more evident in Croatia most likely because of the absence of a regularly stocked artificial feeding station that forces vultures to cover larger distances in their search for food, even during the coldest seasons where climate conditions make flight difficult (Blondel *et al.* 2010, Mellone *et al.* 2012, Dodge *et al.* 2014).

Conditions for vultures are harsher in winter; low temperatures reduce thermal soaring, strong winds may create orographic currents close to mountains and there are fewer hours of daylight for foraging (Blondel *et al.* 2010, Mellone *et al.* 2012, Dodge *et al.* 2014). Together, these factors may reduce the time available for vultures to move and restrict their foraging activity to smaller foraging ranges and core areas (Margalida *et al.* 2013, Kang *et al.* 2019). Moreover, the number of winter days spent by vultures in both Italy and Croatia was greater when compared to that measured during other seasons. The 50/95 KDE ratio comparison among seasons revealed a higher value during winter and this difference was more evident in Croatia than in Italy where the vultures were forced to exploit the area as much as possible in the search for unpredictable food resources.

During spring, the foraging pattern was similar to that recorded in summer. Indeed, as reported in other studies (Dodge *et al.* 2014, García-Jiménez *et al.* 2018) and by data obtained from GPS locations, good flight conditions and longer daytime hours may have allowed vultures to move more within the area. Both the foraging range and core area were almost equal between the three study areas. However, a significant difference in terms of the foraging range size was recorded between spring and both autumn and winter within the Italian study area. The number of days spent by vultures in both Italy and Croatia was smaller compared to that recorded during the colder times of year, autumn and winter, probably for two reasons: firstly, better flying conditions allowed vultures to explore the area more effectively and to concentrate their main activities in small areas and, secondly, spring represents the season in which a high number of vultures are present at the feeding station (Table 2). As a result, given that the youngest individuals are negatively affected by the presence of adults (Duriez *et al.* 2012, Monsarrat *et al.* 2013), our birds may have

Table 2. Number of Griffon Vultures counted on the feeding point in each season during the monitoring period (2006–2014).

Season	mean	sd	median
Autumn	80	42	72
Winter	61	32	56
Spring	75	38	70
Summer	81	48	80

been forced to explore the area looking for other food resources.

In summer, as supported by the information obtained from GPS data, ideal flight conditions may have allowed the vultures to spread their activity to a wider area. Comparison between areas showed that there was a significant difference in terms of foraging range size between Italy and Austria and in terms of the core area size between Italy and both Austria and Croatia. The greatest values, recorded in Italy, may be related to food resource availability and competition among individuals. In Italy, the main food resource available was provided by the feeding station at Forgaria nel Friuli in which the youngest individuals may suffer competition with adults, particularly during the summer season when vulture density at the feeding station was higher (Table 2). Thus, they were forced to move in search of food in other areas. Moreover, the number of days spent by vultures in Croatia and Italy was lower compared to that measured during autumn and winter. Furthermore, a significant difference in terms of the time spent within the area was found between spring and summer in Austria, where vultures tended to stay for longer periods during the summer months, in relation to the traditional husbandry practices. The 50/95 KDE ratio recorded during summer in Italy was significantly higher compared to that measured in either spring or winter and, what is more, was higher compared to that recorded in Croatia and Austria although this difference was only significant between Italy and Croatia. This result may be influenced by the vultures' movements. In fact, during summer the birds tended to move up to Austrian and Italian Alpine areas, searching for unpredictable food resources in the form of fallen livestock living under free-range conditions (Genero 2009, 2016, 2017). The arid climate in Croatia during summer forces livestock farmers to concentrate animals in only a few areas, thus, reducing food resources for vultures. Furthermore, the need to search for alternative food resources to avoid competition with the adult individuals may have encouraged birds to exploit the area more widely.

Management implications

This is the first quantitative study in which both the spatial and behavioural ecology of non-breeding Griffon Vultures have been assessed in relation to a feeding station created in Forgaria nel Friuli (Italy), using GPS satellite tracking and thus showing the modalities, frequency of movements, and use of foraging areas in the eastern Alps and Adriatic region. The feeding station created in Forgaria del Friuli during the 1980s provided *ad libitum* food throughout the year for vultures and progressively attracted the birds which have now formed a new stable nesting colony that represents the only one in the Italian Alps (Genero 2016). In this study, we found that vultures tended to concentrate their activities around the most favourable areas with abundant predictable (feeding site-based) and unpredictable (pastoralism-based) food resources. Our findings highlighted that the presence of the feeding site seems to not significantly affect the vultures' foraging behaviour. In fact, since individuals also moved across open habitat searching for unpredictable food resources, they may not have radically modified their natural opportunistic behaviour. However, the long dispersal period of both immature and sub-adult Griffon Vultures (Heredia 1991, Gil *et al.* 2010, 2014, Urios *et al.* 2010, Gavashelishvili *et al.* 2012, Yamaç & Bilgin 2012, Spiegel *et al.* 2013, Margalida *et al.* 2016, García-Jiménez *et al.* 2018, Martens *et al.* 2018) in addition to the competition for resources that they could have suffered from adult vultures (Duriez *et al.* 2012, Monsarrat *et al.* 2013) may have forced the young individuals to move more within and between areas. Furthermore, considering the low number of vultures tracked, it is not possible to define strong conclusions as the small sample size may have affected the lack of significance of some results. Another aspect to consider in the future would be the food supply, on which we had no data due to logistic reasons (e.g. livestock carcasses removed by helicopter, or difficult to find), issues concerning landowner privacy.

The use of feeding stations to promote the recovery of vultures has been questioned by both conservationists and wildlife managers due to the potential negative effects that may be produced (Boutin 1990, Carrete *et al.* 2006, Robb *et al.* 2008, Monsarrat *et al.* 2013, López-López *et al.* 2014a, Moreno-Opo *et al.* 2015a, 2015b, 2016, Cortés-Avizanda *et al.* 2016, Fluhr *et al.* 2017). Feeding stations have been effective and important tools for conservation and reintroduction of avian scavengers, especially in those areas in which they have declined massively. However, they have been used worldwide, often without considering the scientific evidence supporting the suitability of this practice. Among the negative consequences we have large aggregations of individual birds, disruption of intraguild processes, promotion of both intra- and interspecific competition among individuals, and reduction in terms of productivity due to density-dependent factors (Carrete *et al.* 2006, Ferrer *et al.* 2014, 2018, Moreno-Opo *et al.* 2015a, 2015b, 2016, Cortés-Avizanda *et al.* 2016). Feeding stations may also lead to increased depredation risk on small- and medium-sized vertebrates because they promote the aggregation of predators in the vicinity of the feeding station, and they might even affect processes of natural selection and render populations maladapted to their environments (Cortés-Avizanda *et al.* 2016). Furthermore, the use of artificial feeding sites may be questioned in relation to the dietary plasticity of vultures in the presence of suitable habitats (Margalida *et al.* 2017). However, some vulture species present higher dietary plasticity than others. For instance, Griffon and Cinereous Vultures *Aegypius monachus* are known to differ in their trophic resource used. In fact, while Griffon Vultures are mostly dependent on livestock carcasses, the diet of Cinereous Vultures includes also the remains of small- and medium-sized vertebrates such as European Rabbits *Oryctolagus cuniculus* (Arrondo *et al.* 2018). Moreover, even the format (whole, divided, meat/bone remains, bones) and the scattering (concentrated or dispersed) of the carcasses used may affect the feeding behaviour of the vulture species considered (Moreno-Opo *et al.* 2015a). In this sense, the use of feeding stations should be strongly considered in those areas characterized by low habitat quality and, particularly, to promote the recovery of those vulture species, such as Griffon Vultures, that are strongly dependent on the carcasses of domestic ungulates.

Acknowledgements

We thank Mr Andrea Madinelli, Dr Alessandro Visintin and the working group for support provided during capture sessions; the local administrators of the Riserva Naturale Regionale del Lago di Cornino who allowed us to work in this area; all those working in the Hohe Tauern National Park, in particular Dr Thomas Guggenberger and Dr Ferdinand Ringdorfer for information on livestock densities; all those involved at the Parco Natura Viva (VR) as well as Dr Daniel Hegglin, Dr Michael Knollseisen, Mr Alfonso Godino, Dr Stefano Pesaro, Dr Goran Sušic, Prof. Giuseppe Bogliani, Prof. Christian Walzer, Prof. Olivier Duriez and Dr Mita Drius for both technical and financial support. Finally, we wish to thank Dr Marco Virgilio for climatic data within the Riserva Naturale Regionale del Lago di Cornino. The present study was carried out in accordance with relevant national and international guidelines and conformity to the legal requirements. Birds captured were marked before their release and blood samples were taken in compliance with the Ethical Principles in Animal Research.

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