Movements and habitat use by immature Cinereous Vultures (Aegypius monachus) from the Caucasus

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Looking out for birds

Movements and habitat use by immature Cinereous Vultures (*Aegypius monachus*) from the Caucasus

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Capsule Juvenile and immature Cinereous Vultures from the Caucasus move large distances across undeveloped open-dry habitats in response to snowfall or high summer temperatures.

Aim To study local and long-range movements of Cinereous Vulture (*Aegypius monachus*), and investigate the influence of environmental variables on spatial and temporal distributions of the species on a large scale.

Methods We use 4-year-long location data from 6 juvenile Cinereous Vultures fitted with satellite-received transmitters to track their movements and obtain habitat suitability models.

Results A few months after fledging, Cinereous Vultures may migrate from the Caucasus as far south as the Arabian Peninsula. Their movements are concentrated in undeveloped open-dry habitats. High temperatures push the vultures to higher latitudes and altitudes, while reverse seasonal movements are triggered by the extent of snow cover.

Conclusions Our study shows the importance of the Arabian Peninsula and Iran as wintering areas for Cinereous Vultures. Long-distance movements by immature cinereous vultures are determined by climate seasonality, and in light of climate-warming scenarios for the next 100 years, there might be a shift in timing of the onset of the species seasonal movements and a change in the duration and geography of its wintering and summering.

The Cinereous (or Eurasian Black) Vulture (*Aegypius monachus*) is a scarce to rare scavenger that has a large southern Palearctic breeding distribution that extends from Spain to Russia, Mongolia, and China (del Hoyo *et al.* 1994; Ferguson-Lees & Christie 2001). Its conservation status is Near-threatened (IUCN 2011).

European, but few Asian, populations are well monitored (IUCN 2011). European Union legislation and conservation actions have contributed to the recovery and positive trend of the species in Europe, particularly Spain. Breeding populations in Eastern Europe and throughout much of the Caucasus are small and are generally stable. The current distribution of Cinereous Vulture in Europe is small in historical terms, and is limited almost entirely to protected areas.

Globally, the main threats to Cinereous Vultures are human-related, including the targeted and inadvertent poisoning of individuals and groups of birds and the loss of food resources for local and regional populations (BirdLife International 2009). Declines in food resources such as Saiga antelope (*Saiga tartartica*) in Central Asia and declines in sheep numbers in the Caucasus due to the removal of state subsidies in the post-Soviet period have had a negative effect on the populations there (BirdLife International 2009). Despite its Soviet history, this impact is not obvious in Azerbaijan, where the pastoral tradition is stronger and numbers of sheep have not declined as severely as in neighbouring Caucasus nations. Cutting of nest trees and other direct disturbances in Georgia (Gavishelishvili *et al.* 2006), and killing for feathers in China (GRIN 2010) are local threats.

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Although several aspects of the species' biology are reasonably well studied in Europe, within the Mediterranean basin, both non-breeding and adult cinereous vultures do not perform migratory movements (cf. Carrete & Donázar 2005, Vasilakis et al. 2008). However, migratory movements of Cinereous Vultures have been documented for populations breeding in the northern part of their Asian distribution, including the Caucasus (Gavashelishvili & McGrady 2006a) and in Mongolia (Kim et al. 2007, Batbayar et al. 2008; Kenny et al. 2008), but details of wintering areas are generally absent.

For conservation purposes it is important to understand the annual movement ecology of species, including movement geography and strategies, and the location of their wintering and summering grounds (Martin et al. 2007), during pre-breeding and breeding phases of their life cycle. We used data from satellite received-transmitters to (a) detail movements over multiple years for juvenile and immature Cinereous Vultures, (b) analyse large-scale data on land cover, terrain and climate to determine habitat preferences shown by the vultures and (c) create habitat suitability maps for the species' temporal and spatial distributions based on these preferences.

METHODS

Migratory movements and home-ranges

We fitted six nestling Cinereous Vultures with battery- and solar-powered satellite-received radio-transmitters (platform terminal transmitters, PTTs) in Georgia and Armenia in 2004, 2006, 2007 and 2009 (Table 1). PTTs were fitted as backpacks and, in the case of those that were battery-powered, programmed for a duty cycle that would potentially provide data for at least 3 years. Deployment of PTTs occurred when nestlings were as large as they could be without being a threat to fledge prematurely – that is, ~2.5 months old. The transmitters incorporated movement, battery voltage and temperature sensors, providing us with insights into the ultimate fate of the tag and vulture. The movements of Vulture CV1 (a bird tagged as a nestling in 2004 in Chachuna Sanctuary, Georgia) have already been described (Gavashelishvili & McGrady 2006a). Vultures CV2, CV5 and CV6 hatched from the same nest in Khosrov Nature Reserve, Armenia, in 2006, 2007 and 2009, respectively.

Vultures were fitted with a variety of tags from North Star Science & Technology, LLC (Baltimore, MD,

USA) and Microwave Telemetry, Inc. (Columbia, MD, USA) (Table 1). The three transmitters deployed in 2004, 2006 and 2009 were tracked via the 6-satellite Argos Doppler system, a non-GPS system that assigns a nominal accuracy or 'location class' (LC) to each location estimate (LC-3, LC-2, LC-1, LC-0, LC-A, LC-B). Because the accuracy of LC-0 and LC-B locations are highly variable (Britten et al. 1999, Vincent et al. 2002), we used only LCs-3, -2, -1 and -A to detail vulture movements. We removed obviously erroneous location fixes using maximum flight speed as a filter. The maximum flight speed was determined using data from a Cinereous Vulture tagged with a GPS PTT (see below).

The three transmitters deployed in 2007 were GPS PTTs, with best quality locations accurate to ~15 m. Of these three transmitters, only the 70 g solar-powered GPS PTT was able to record speed and elevation data.

To distinguish between non-migratory and migratory states, we used the criterion offered by Limiñana et al. (2008). During the non-migratory state after the PTT-tagged vultures became independent from their parents, we estimated seasonal home ranges, using the Animal Movement (Hooge & Eichenlaub 1997) extension to ArcView 3.x software package (ESRI Inc., Redlands, CA, USA). We derived 95% and 100% Minimum Convex Polygon (MCP) home ranges and 50%, 90% and 95% Fixed Kernel home ranges (KHR) for each of the tagged vultures. We defined the onset and span of migration as the time period from the date a bird moved from one home range to the next one.

Habitat use

Our main objective was to determine whether the timing of establishment and use of seasonal home ranges could be explained by environmental predictors other than food availability. We assumed that environmental conditions during non-migratory movements were important for flight and foraging. We then assumed that these conditions within each of the seasonal 100% MCP home ranges were equally optimal, and median values of predictor variables within each of the 100% MCPs would represent the optimal conditions for the species presence. We used the median instead of the mean because the median can be used as a measure of location when a distribution is skewed, and is less sensitive to outliers that may be the result of measurement errors, accidental events or proximity to

Table 1. Details of PTTs deployed on six Cinereous Vulture nestlings in the Caucasus.

Bird ID PTT ID	PTT type	PTT manufacturer	PTT specifications	Site of deployment	Latitude, longitude, elevation	Date of deployment (months of operation)	No. of useable locations	Current status
CV1 47807	80g battery-powered PTT	North Star	a duty cycle of 8 h on, 32 h off	Chachuna Sanctuary, Georgia	41.22888, 45.87733, 497 m	18 July 2004 (12)	294	Stopped transmitting near Astrakhan, Russian Federation on 17 July 2005
CV2 65797*	80g battery-powered PTT	North Star	a duty cycle of 8 h on, 32 h off	Khosrov Nature Reserve, Armenia	39.99817, 44.87766, 1587 m	1 August 2006 (9)	147	Stopped moving in April 2007 and later found dead in southeastern Iran at N27.3950, E57.5280
CV3 75460	105g GPS-based LC4	Microwave Telemetry	Transmit to ARGOS every 10th day. GPS: 12:00 Noon local time every day	Chachuna Sanctuary, Georgia	41.23029, 45.871, 519 m	31 July 2007 (38)	692	Stopped transmitting near Lagodekhi, Georgia on 11 October 2010
CV4 75459	105g GPS-based LC4	Microwave Telemetry	Transmit to ARGOS every 10th day. GPS: 12:00 Noon local time every day	Khosrov Nature Reserve, Armenia	40.02933, 44.92034, 1883 m	7 August 2007 (42)	793	Stopped transmitting in western Azerbaijan on 26 January 2011
CV5 75458	70g solar GPS PTT	Microwave Telemetry	Transmit to ARGOS every 4–6 h. GPS: start time: 05:00, end time: 15:00, step: 1 h	Khosrov Nature Reserve, Armenia	39.99817, 44.87766, 1587 m	8 August 2007 (21)	1453	Stopped transmitting in western Azerbaijan on 5 May 2009
CV6 65797*	80g battery-powered PTT	North Star	a duty cycle of 8 h on, 32 h off	Khosrov Nature Reserve, Armenia	39.99817, 44.87766, 1587 m	31 July 2009 (18)	242	Still transmitting

* This PTT was recovered from dead CV2, refurbished and redeployed on CV6.

suitable habitat. In calculating median values, we merged those home ranges that intersected each other both in space and time, even if they belonged to different individuals. We also assumed that although the age of our study vultures increased during the research, their tolerance limits of environmental variables remained similar across the years of our study. These assumptions and the sampling scheme were adopted to allow a skewed response to predictor variables and minimize bias that might result from over- or under-representation of some individual(s) or geographic areas(s) in the overall sample.

We estimated vulture habitat needs by relating the locations of their 100% MCPs to various environmental data, using free online digitalized data and managed these using ArcGIS Desktop 9.3 software package (ESRI Inc., Redlands, CA, USA) and ERDAS IMAGINE 9.1 (Leica Geosystems Geospatial Imaging, LLC). The selection of environmental variables was based on documented species–habitat associations (Cramp & Simmons 1980, Gavashelishvili et al. 2006, Gavashelishvili & McGrady 2006b) and our field experience, and with regard to their availability (Table 2). We did not use elevation in this

Table 2. Variables used for modelling habitat suitability for Cinereous Vulture distribution in the study area.

Variable	Description
Ruggedness (m)	Standard deviation calculated in 3 × 3 cell overlapping neighbourhoods of a SRTM elevation grid of 1-km cells (Jarvis et al. 2008)
Land cover	Categorical variable identifying 17 land-cover classes (see Table 5), extracted from 500-m MODIS data 'MCD12Q1'*
Percent tree cover (%)	% of tree canopy cover, extracted from 500-m MODIS data 'MOD44B'*
Daytime temperature (°C)	Mean daytime temperature of an 8-day interval, extracted from 1-km MODIS data 'MYD11A2'*
Nighttime temperature (°C)	Mean nighttime temperature of an 8-day interval, extracted from 1-km MODIS data 'MYD11A2'*
Snow-free land	Presence–absence of snow-free land, extracted from 500-m MODIS data 'MOD10A2'*
NDVI	Normalized Difference Vegetation Index as proxy for seasonal vegetation density, extracted from 1-km NDVI 10-day time-series maps, provided by the VEGETATION Program (SpotImage/VITO: www.vgt.vito.be)

* NASA: http://www.echo.nasa.gov/reverb/about_reverb.htm
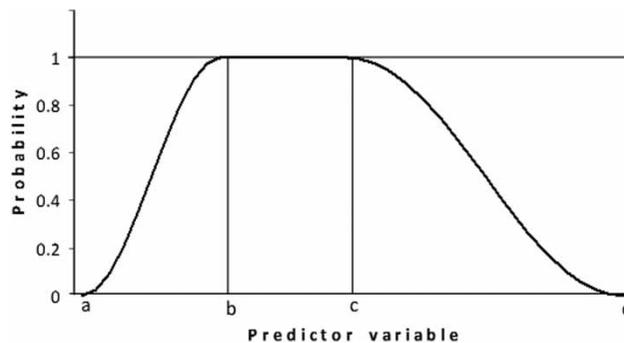
Figure 1. Sigmoidal membership functions (see text for details).

process because the effect of elevation is well explained by climate variables and vegetation density.

At every location determined via telemetry, we measured values of the environmental variables for the MODIS and NDVI time intervals in which the location was recorded. These values and those of the other predictor variables were then used to develop a general 8-day interval Fuzzy Envelope Model of vulture habitat suitability, using the sigmoidal (cosine) membership functions whose values (i.e. habitat suitability scores) vary between 0 and 1 (Schmucker 1982). We used this fuzzy presence-only algorithm because of the assumptions we made about our data. The sigmoidal functions require the positions (along the predictor variable x axis) of control points a, b, c and d that govern the shape of the curve (Fig. 1). These functions or 'fuzzy sets' (μ) per predictor variable x are calculated as follows:

Bell-shaped function

if $a < x < b$, $\mu = [COS(0.5 \times \pi \times (1 - ((x - a)/(b - a))))]^2$
if $b < x < c$, $\mu = 1$
if $c < x < d$, $\mu = [COS(0.5 \times \pi \times ((x - c)/(d - c)))]^2$

otherwise $\mu = 0$

Monotonically increasing function
if $x < a$, $\mu = 0$
if $a < x < b$, $\mu = [COS(0.5 \times \pi \times (1 - ((x - a)/(b - a))))]^2$
if $x > b$, $\mu = 1$

Monotonically decreasing function
if $x < c$, $\mu = 1$
if $c < x < d$, $\mu = [COS(0.5 \times \pi \times ((x - c)/(d - c)))]^2$
if $x > d$, $\mu = 0$

To define values for *b* and *c*, we calculated median values for each home range and assigned *b* and *c* to minimum and maximum median values, respectively. For each predictor variable we assigned *a* and *d* to the minimum and maximum values, respectively, of all home range locations. Final vulture habitat suitability models were derived by multiplying the sigmoidal membership functions.

Moreover, to avoid the repeated spatial sampling of predictor variables we used locations that were > 1415 m from neighbouring locations because our analyses were performed on predictor variable grids whose cell sizes varied between 90 and 1000 m. Because the coarsest cell size in our analysis was 1000 m and to avoid repeated sampling in a grid of 1000 × 1000m cells, the minimal distance will be $\text{SQRT}(2 \times 1000^2) = 1414.2$ m. Temporal autocorrelation among locations can lead to biased relationships between independent and dependent variables (Swihart & Slade 1985). For example, temporary or stochastic events such as abundance of food or better satellite visibility in marginal vulture habitats may result in many temporally close location fixes that will not reflect true habitat preferences. Bias with temporal autocorrelation can be minimized by collecting locations at regular time intervals over a long timescale (Robertson *et al.* 1998). Therefore, we used location fixes at > 24-h intervals after the tagged birds migrated from natal areas. The time frame in which vultures were radiotracked meant that vultures could access various landscape types in all seasons, and full cycles of long-distance movements were recorded. Therefore, we consider the time frame sufficiently long to reveal unbiased ecological relationships between vulture distribution and predictor variables. Thus, we reduced our overall sample size to 2896 training presence locations to develop the fuzzy envelope habitat suitability models.

Modelling suitable habitats from a set of several predictor (independent) variables should be done cautiously. Inclusion of all available variables in the modelling typically results in high predictive power at local spatial and temporal scales. However, this all-variable approach fails to reflect realistic species-specific tolerance limits and interactions between predictor variables that make sense for the response of the independent variable at broader spatial and temporal scales (Scott *et al.* 2002). Any modelling methods assume (a) tolerance limits and (b) correlations among independent variables measured at training locations to reflect true underlying ecological

relationships. Models based on this assumption may perform well within the extent of training locations but prove wrong outside the extent. We derived sigmoidal functions based on our observed data and used all possible combinations of the fuzzy sets and categorical variables to select important predictor variables that would yield the 8-day interval model with the best predictive power. We checked the predictive accuracy of our models against an independent data set of presence–absence locations (i.e. test locations). We obtained one set of the presence–absence test locations by generating 100 random points within the areas where our previous study (Gavashelishvili & McGrady 2006b) revealed no signs of Cinereous Vulture presence, and 100 random points that the study identified as a regular foraging area for the species. The extent of these test locations represented well the Caucasus Ecoregion (latitudinal range: 36.2–47.3°, longitudinal range: 36.5–51.5°). We measured values of predictor variables at these locations at each of MODIS 8-day and NDVI 10-day intervals for the year 2006 – that is, the time period during which the previous study was conducted (Gavashelishvili & McGrady 2006b). In this way we obtained in total 4600 presence and 4600 absence test cases (number of 8-day intervals × test locations). An additional set of absence test cases was obtained based on the assumption that seasonal changes in environmental conditions within home ranges caused seasonality in vulture presence within them. To obtain additional absence test points, first we identified home ranges that were only seasonally established, and then measured values of predictor variables at telemetry locations within them at each of MODIS 8-day and NDVI 10-day intervals for the time periods during which vultures were absent from these home ranges. Thus we obtained 14,609 additional absence test cases that would help us understand which predictor variables accounted for the establishment and timing of home ranges.

The predictive accuracies of our models were defined using the receiver operating characteristic (ROC) curve, or more specifically the area under the ROC curve (AUC) (Hanley & McNeil 1982, Zweig & Campbell, 1993). The ROC curve analysis was performed using SPSS v.16 for Windows (SPSS Inc., Chicago, IL, USA). Instead of widely used presence–absence model building methods, we employed the fuzzy envelope as a method based on presence-only data mainly because it was difficult to fit presence–absence methods to our assumptions.

To make a final demonstrative map of habitat suitability for the distribution of immature Cinereous Vultures across the Caucasus, Middle East, and parts of Central Asia and Eastern Europe (latitudinal range: 12.3–50.0°, longitudinal range; 25.0–70.0°, hereafter the study area) over the time period of our study (i.e. 2004–2010), we created predictor layers where cells were assigned average values for scale predictor variables and majority values for categorical predictor variables over this time period. We used the ArcGIS 9.3 module Spatial Analyst (ESRI, Redlands, USA) to create these layers and project the best 8-day interval habitat suitability model onto them for every 8-day interval within the study area. Each of the MODIS 8-day intervals was aligned with an NDVI 10-day interval that had the largest overlap with the MODIS 8-day interval.

RESULTS

Migratory movements and home ranges

Vultures were tracked for 9–42 months. As of November 2011 one tag was still transmitting (CV6). Transmitters produced 3915 locations (range per individual: 147–1453) that were used in our analyses. Extent of the movements of all six vultures covered a large geographic space (latitudinal range: 21.8–46.7°, longitudinal range: 39.8–57.6°) (Table 3).

Figure 2 shows the migratory movements, wintering and summering locations of Cinereous Vultures tracked via satellite in 2004–2011. All individuals left their natal area between 2 and 26 November.

All individuals migrated in the autumn after hatching, wintered in Iran and Saudi Arabia, and then migrated north the following spring, initiating spring migration about the time of hatching of Cinereous Vultures in the Caucasus (March–April). After that first migration cycle seasonal movement patterns were more variable among individuals. One vulture (CV4), migrated north to western Azerbaijan in its first spring and overwintered there (home-range centroid: N40.69150, E46.44675) for three consecutive winters. Another vulture (CV3), after wintering farther south in its first two winters overwintered in western Azerbaijan in 2009–2010. CV5 showed fidelity to its wintering and summering grounds (which was not its natal area) in two consecutive years. CV1 returned to its natal area for about 1 month in the summer after fledging, but later in the summer moved farther north. Although the vultures CV4 and CV5 were hatched in nests 5 km apart in 2007 and they left their natal area one day apart, their movements were different.

Vulture CV4 from Armenia and the vulture CV3 from Georgia started their southbound migration in November and reached their winter grounds on almost the same day, even though the centres of their winter locations were 700 km apart and distances travelled

Table 3. Flight characteristics of the six juvenile Cinereous Vultures fitted with transmitters. Ground altitude is from the 90-m SRTM data (Jarvis et al. 2008).

Flight characteristics	Individual	n	Mean	sd	Min.	Max.
Ground altitude (m) asl	CV6	242	629	634	12	1,627
	CV5	1,453	920	512	3	3,009*
	CV4	793	869	646	13	2,751
	CV3	692	1,543	886	0	3,503
	CV2	147	1,202	547	205	2,772
	CV1	294	516	423	−22	2,689
Flight altitude (m) asl	CV5	1,123	989	502	3	2,040
Flight height (m) above ground	CV5	1,123	97	194	0	1,551
Altitude (m) asl at nightroost	CV5	207	854	450	3	2,016
Altitude (m) asl gained in 1 h	CV5	201	170	371	0	1,853
Altitude (m) asl lost in 1 h	CV5	210	178	358	0	2,008
GPS speed (km/h)	CV5	335	44	23	1	103
Distance (m) travelled in 1 h	CV5	469	4,687	40,267	0	45,138
Distance (m) travelled in 24 h	CV5	60	23,183	33,454	24	100,000
	CV4	588	16,828	22,892	13.65	200,000
	CV3	570	35,714	55,305	14.1	300,000

* At this elevation the satellite system failed to provide flight altitude. As a consequence, maximum ground altitude is greater than that of flight altitude.
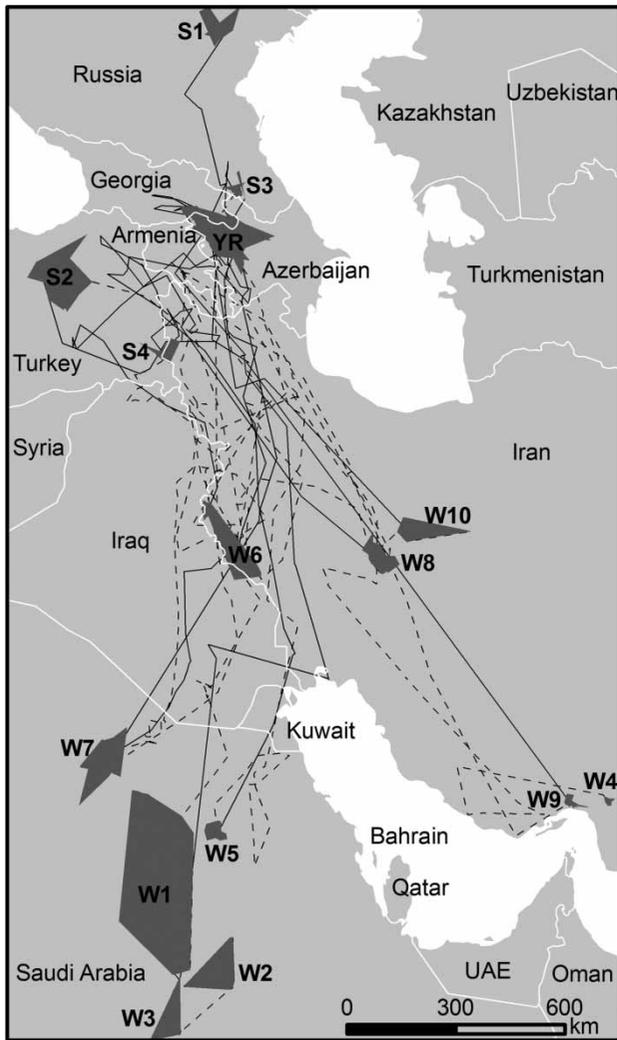
Figure 2. Movement paths and pooled home ranges of six immature Cinereous Vultures tagged with satellite-received radio-transmitters, which were established after they became independent from their parents. Solid lines = northbound paths; dashed lines = southbound paths. Black polygons = MCP home ranges. Season: W, winter; S, summer; YR, year-round. W1, CV1 from 27 December 2004 to 22 March 2005; W2, CV1 from 27 December 2004 to 22 March 2005; W3, CV1 from 27 December 2004 to 22 March 2005; W4, CV2 from 1 December 2006 to 20 April 2007; W5, CV3 from 23 December 2007 to 10 March 2008; W6, CV4 from 23 December 2007 to 6 April 2008; W7, CV5 from 27 December 2007 to 14 April 2008 and from 14 November 2008 to 8 April 2009; W8, CV3 from 10 November 2008 to 14 February 2009 and CV6 from 26 November 2010 to 31 March 2011; W9, CV6 from 5 December 2009 to 17 April 2010; W10, CV6 from 26 November 2010 to 31 March 2011; S1, CV1 from 26 May to 17 July 2005; S2, CV3 from 7 April to 16 September 2008; S3, CV3 from 7 May to 11 October 2010; S4, CV3 from 6 March to 14 May 2009; YR, CV3 from 5 January to 5 May 2010, CV4 from 7 May 2008 to 26 January 2011, CV5 from 24 April to 24 October 2008 and CV6 from 27 April to 31 July 2011. All maps shown in this manuscript have been projected to Mollweide; False Easting: 0; False Northing: 0; Central Meridian: 45°; WGS: 1984.

considerably different (983 km versus 2505 km, respectively).

Cinereous Vultures that migrated travelled a mean of 2135 km (range: 254–5319 km) between the centroids of their wintering and summering grounds. Mean difference in latitude between summering and wintering areas was 10.563° (range: 0.319–22.638°). Individuals took an average of 36 days to migrate (range: 1–120 days). Migration routes were not straight, and had a mean sinuosity of 2 (range: 1.12–4.8) (see Appendix). Although CV3, CV4 and CV5 were all hatched in 2007 and CV4 and CV5 left their natal area within a day of one other, they wintered in widely separate locations.

We were able to determine fledging date for three vultures fitted with GPS tags in 2007. All left their nests between 25 August and 1 September. In the weeks immediately after fledging juveniles stayed close to their nests, and as time passed they made ever-greater excursions out from their nests. Prior to migrating, juveniles fitted with GPS tags ranged over large areas (mean 95% MCP = 369 km^2, range: 115–813 km^2; mean 100% MCP = 1078 km^2, range: 471–2182 km^2; $n = 3$). The migration of the tagged birds started 2–3 months after fledging. We assumed that this was the point when juveniles became independent from their parents and thus the age of independence to be 5.7–7 months after hatching. Even though CV2, CV5 and CV6 were raised in the same nest in different years, the areas in which they spent their first winter were far from one another (i.e. 100–1415 km). In summer and winter, vultures ranged over large areas (summer range 100% and 95% MCP = 6700–21870 km^2 and 3000–13598 km^2, respectively; winter range 100% and 95% MCP = 2639–14298 km^2 and 1559–13536 km^2, respectively) (Table 4).

During summer and winter vultures sometimes undertook large excursions and sometimes settled temporarily in more than one area over the course of a season. For example, during the winter of 2008–09, CV3 undertook a 1586-km journey to the Iran–Iraq border from its wintering grounds near Esfahan, Iran. On 6 March 2009 this bird settled into a summering area for 70 days on the Iran–Turkey border (100% MCP = 4151 km^2, 95% MCP = 1625 km^2), then moved 1650 km north to Dagestan in the northeastern Caucasus, Russian Federation, where it stayed until 5 January 2010 (100% MCP = 2553 km^2, 95% MCP = 1427 km^2).

Five birds spent at least one summer or winter in western Azerbaijan, close to one another. Centroids of

Table 4. Mean home-range sizes in km^2 (and standard deviations in brackets) of the three juvenile Cinereous Vultures that carried GPS-PTTs after they became independent from their parents. MCP, = minimum convex polygon; KHR, = fixed kernel home range.

Home -range	100%MCP	95%MCP	50%KHR	90%KHR	95%KHR
Summer	7033 (8191)	3912 (5053)	574 (519)	2665 (2318)	3847 (3120)
Winter	7814 (4386)	5434 (4636)	514 (360)	2472 (1674)	3870 (2541)

summer home ranges were within 4 km of each other, and those of winter home ranges were within 24 km. Overall, all centroids were within 50 km of one another. Minimum and maximum distances between winter and summer centroids were 28 and 50 km, respectively.

Habitat use

Based on all telemetry locations (3621 in total), vulture movements were concentrated in open-dry habitats (Table 5). Because they were absent from water surfaces, permanent wetlands, permanent snow and ice, and their few occurrences in urban areas and forest (11 and 4 locations, respectively) coincided with migration periods, we masked out these areas from the habitat suitability map. More than 95% of locations within each of the 100% MCP home ranges were in snow-free areas.

Table 6 shows the sigmoidal response of our observations to each environmental variable. Despite

Table 5. Frequency distribution of vulture locations relative to MODIS land- cover types based on the IGBP classification scheme (n = 3621).

Land-cover class	Frequency	Percent	Cumulative percent
Barren or sparsely vegetated	1149	31.7	31.7
Grasslands	957	26.4	58.2
Closed shrublands	375	10.4	68.5
Woody savannas	365	10.1	78.6
Open shrublands	329	9.1	87.7
Croplands	218	6.0	93.7
Cropland or natural vegetation mosaic	151	4.2	97.9
Savannas	62	1.7	99.6
Urban and built-up	11	0.3	99.9
Mixed forest	2	0.1	99.9
Deciduous broadleaf forest	2	0.1	100
Deciduous needleleaf forest	0	0	100
Evergreen needleleaf forest	0	0	100
Evergreen broadleaf forest	0	0	100
Permanent wetlands	0	0	100
Permanent snow and ice	0	0	100
Water	0	0	100

the bell-shaped response to temperatures, we used curves of monotonically increasing nighttime and decreasing daytime temperatures for our further analyses, thus accounting for the daily extremes of temperatures. With these observed relationships and arrangements we generated five fuzzy sigmoidal sets and one dichotomous set of snow-free land. We then tested the predictive accuracy of all possible combinations of these sets (n = 6), with the number of the sets in a combination varying from 3 to 6 (k = 3–6, Table 7). Considering the knowledge of most species-environment relationships, we assumed that less than 3 of these predictor variables would not be informative enough for species distribution at a broad scale.

ROC plot analysis based on test data suggested that the habitat suitability models that included snow-free land, the bell-shaped function of NDVI, the monotonically increasing function of nighttime temperature and the monotonically decreasing functions of daytime temperature and percent tree cover (AUC = 0.89) performed best (Table 7). However, the exclusion of nighttime temperature from the analysis did not affect the predictive power of the model. Projections of models suggested that vultures should move to higher latitudes or altitudes in the summertime and vice versa in the wintertime (Fig. 3).

The habitat suitability model suggested that high daytime temperatures accounted for the absence of our radiotagged Cinereous Vultures from their wintering areas in Saudi Arabia, Iran and Iraq, while snow extent explained their absence from their summering areas in Iran, Russian Federation and Turkey. Low NDVI values explained the absence of the vultures from water surfaces and deserts while high values accounted for their absence in summer from densely vegetated areas (i.e. the Black Sea region). High vegetation density in the study area increases in the summertime due to the growth of crops and seasonal herbs. Our model identified highly suitable areas in some parts of the study area, e.g. the southern Arabian Peninsula and northeastern Africa, where Cinereous Vultures are not known to occur.

Table 6. Control points of sigmoidal membership functions calculated from 15 home ranges established by 6six radio-tagged Cinereous Vultures. *a* and *d*, minimum and maximum values, respectively; *b* and *c*, minimum and maximum median values, respectively (see the text for details).

Variable	Function type	a	b	c	d
Ruggedness (m)	Monotonically decreasing	0	0	36	80
Percent tree cover (%)	Monotonically decreasing	0	0	6	66
Daytime temperature (°C)	Bell-shaped	−12.35	12.85	44.85	53.41
Nighttime temperature (°C)	Bell-shaped	−22.37	−5.15	12.85	26.07
NDVI	Bell-shaped	−0.06	0.028	0.468	0.832

DISCUSSION

Our results show that juvenile Cinereous Vultures from the Caucasus, like those from Mongolia (Batbayar *et al.* 2008), wander far from their natal areas. Unfortunately, the limited lifespan of our PTT batteries (< 4 year) did not allow us to track the vultures till their maturity – that is, the time when they establish territories to start or attempt breeding. Knowledge of the whereabouts of their first breeding grounds would make it clear whether their movements showed dispersal (movement away from a natal area to breed in a new area) or migration (seasonal movement from breeding ground to wintering ground, then back to breeding ground again). None of the vultures established home ranges in their natal areas. However, two of them briefly visited their natal areas in the following years after fledging. They all demonstrated no consistent pattern of fidelity to summering or wintering areas over the years. Based on these patterns, we can only speculate that our vultures showed a mix of both dispersive and migratory behaviour.

Although the vultures we tracked came from two different natal areas, all but one (CV2, which was killed before its first northbound migration) spent at least one season in western Azerbaijan near Georgia's southeastern border. This area contains one of the largest continuous pasturelands of which we are aware in the region, and supports the highest year-round density of extensively farmed livestock in the Caucasus Ecoregion. Vultures benefit from high livestock mortality typical of this kind of farming and the availability of dead domestic animals being dumped away from urban areas (Gavashelishvili & McGrady 2006c).

Our habitat suitability model suggests that immature Cinereous Vultures avoid water surfaces, permanent wetlands, urban areas, densely vegetated areas and prefer snow-free land, a finding that is consistent with data from elsewhere (e.g. Cramp & Simmons 1980).

These preferences may be related to better soaring conditions and easier food detection and availability. Cinereous Vultures like other large soaring birds depend heavily upon thermal updrafts (Hiraldo & Donazar 1990), the strength and regularity of which is negatively correlated with the amount of moisture in the ground and vegetation density (Stull 1988). Where low ground moisture and poorly vegetated areas occur, soaring conditions for large birds, including Cinereous Vultures, are best. Soaring flight is essential because even small increases in energy expenditure can have a large impact on the foraging ranges of heavy birds (e.g. Ruxton & Houston 2002). Also, because of their size and dominance at a carcass (Gavashelishvili & McGrady 2006b) or their low population density in the study area, Cinereous Vultures may be less pressed to forage in wetter areas where soaring-flight conditions are poorer. Our study also indicates a preference by Cinereous Vultures for open areas (i.e. low canopy cover and vegetation density), as with other large vultures that detect food visually (Cramp & Simmons 1980). Open areas provide better visibility. Good visibility over a large area around a carcass enables vultures to easily detect it and identify potential danger from afar and escape (whether those dangers be from humans or terrestrial predators), and this results in them being less wary of landing (Gavashelishvili & McGrady 2006b). Our radiotagged vultures also avoided urban and developed areas, during both non-migratory and migratory states, probably due to a variety of anthropogenic threats and low food availability typical of these areas.

Our study suggested that daytime temperature was more important than nighttime temperature in determining vulture seasonal movements in the study area. High daytime temperatures pushed the vultures to higher latitudes and altitudes (i.e. relatively cooler areas) while reverse seasonal movements were triggered not by low nighttime or daytime temperatures but the extent of snow cover. Temperature extremes are some

Table 7. Combinations of fuzzy and presence–absence sets of 6 environmental variables and the predictive accuracy of each *k*-combination (*k* = 3–6). (>), monotonically increasing sigmoidal function of a scale variable; (<>), bell-shaped sigmoidal function of a scale variable; (<), monotonically decreasing sigmoidal function of a scale variable; yes/no, positive or negative outcome of a dichotomous variable.

No	Number of variables	Percent tree cover	NDVI	Nighttime temperature	Daytime temperature	Ruggedness	Snow-free land	AUC
1	4	<	<>		<		yes/no	0.89
2	5	<	<>	>	<		yes/no	0.89
3	6	<	<>	>	<	<	yes/no	0.85
4	5	<	<>		<	<	yes/no	0.85
5	3	<	<>		<			0.84
6	5	<	<>	>	<	<		0.84
7	4	<	<>	>	<			0.84
8	4	<	<>		<	<		0.84
9	3	<	<>				yes/no	0.83
10	5	<	<>	>		<	yes/no	0.83
11	4	<	<>	>			yes/no	0.83
12	4	<	<>			<	yes/no	0.83
13	4	<	<>	>		<		0.80
14	3	<	<>	>				0.80
15	3	<	<>			<		0.80
16	5	<		>	<	<	yes/no	0.75
17	4	<		>	<		yes/no	0.75
18	4	<			<	<	yes/no	0.75
19	3	<			<		yes/no	0.75
20	5		<>	>	<	<	yes/no	0.72
21	4		<>	>	<		yes/no	0.72
22	4		<>		<	<	yes/no	0.72
23	3		<>		<		yes/no	0.72
24	4			>	<	<	yes/no	0.70
25	3			>	<		yes/no	0.70
26	3				<	<	yes/no	0.70
27	4	<		>	<	<		0.69
28	3	<		>	<			0.69
29	3	<			<	<		0.69
30	4		<>	>	<	<		0.66
31	3		<>	>	<			0.66
32	3		<>		<	<		0.65
33	4	<		>		<	yes/no	0.64
34	3	<		>			yes/no	0.62
35	3	<				<	yes/no	0.61
36	4		<>	>		<	yes/no	0.63
37	3		<>	>			yes/no	0.63
38	3		<>			<	yes/no	0.63
39	3		<>	>		<		0.61
40	3			>	<	<		0.56
41	3			>		<	yes/no	0.56
42	3	<		>		<		0.55
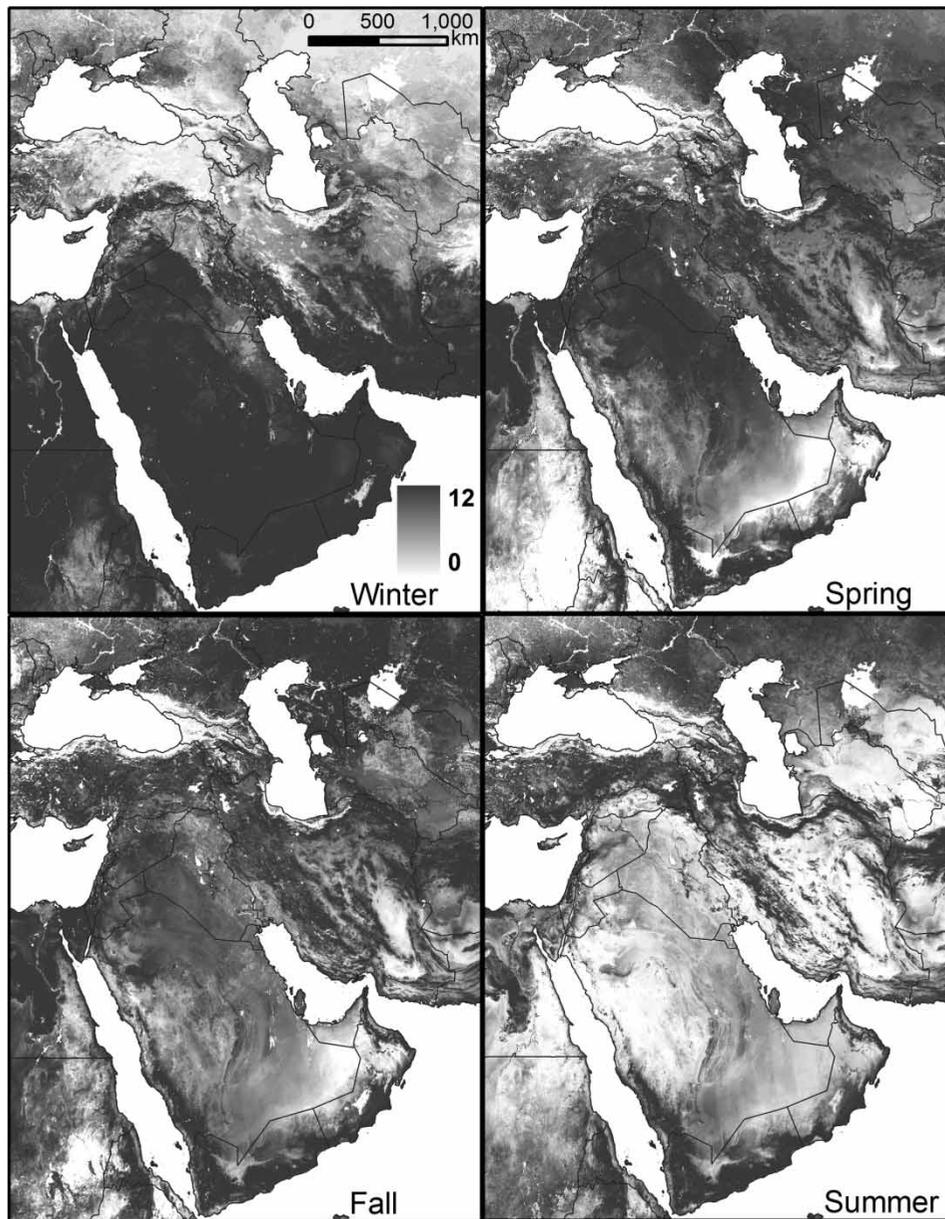
Figure 3. Quarterly habitat suitability maps for the distribution of immature Cinereous Vultures at the age of 5.7–42 months across the Caucasus, Middle East, and parts of Central Asia and Eastern Europe. Winter = sum of 8-day suitability maps from December to February; Spring = sum of 8-day suitability maps from March to May; Summer = sum of 8-day suitability maps from June to August; Fall = sum of 8-day suitability maps from September to November. Darker areas indicate higher habitat suitability.

of the major climatic variables that account for global distributions of many species (Tarkhnishvili *et al.* 2012). However, our variable selection procedure attached more importance to maximum temperatures than minimum ones (Table 7). The most likely reason for this outcome is that our data set under-represented the species' lower tolerance limits for nighttime and daytime temperatures. Minimum nighttime and daytime temperatures measured at our training and test locations were above −25°C and −19°C, respectively, while in the species northernmost distribution in northern Mongolia and the Altai-Sayan, Russia, where adult and immature Cinereous Vultures occur year-round (Karyakin *et al.* 2009; see Acknowledgements), minimum nighttime and daytime temperatures are −46.3°C and −33.7°C, respectively, based on our

MODIS data. Consequently, in the future we recommend that our model be refined by masking it at nighttime temperature $\geq -46.3°$C and daytime temperature $\geq -33.7°$C. Ranges of all the other variables at our locations covered those measured within the species range (IUCN 2011).

Our model identified highly suitable areas for Cinereous Vultures in southern parts of the Arabian Peninsula and northeastern Africa (Fig. 3) – that is, areas where Cinereous Vultures are not known to occur currently, especially year-round. The reasons for the species apparent absence from these areas might be lack of data, poor food availability, human impact (e.g. poisoning) or competition with its closest genetic relative and ecological counterpart Lappet-faced Vulture (*Torgos tracheliotos*; Seibold & Helbig 1995) that occurs in these areas.

In light of our results and different climate-warming scenarios that assume a likely surface temperature increase of 1.4–5.4°C for the next 100 years (IPCC 2007), we predict that the distribution of Cinereous Vultures will expand to higher latitudes and altitudes, especially during summer, and that there will be a shift in timing of the onset of seasonal migration and a change in the duration of wintering and summering. More specifically, under these climate-warming scenarios, spring daily temperatures will substantially increase in the current southernmost wintering areas, while precipitation will remain unchanged. This will dramatically reduce vegetation density or NDVI which is currently (typically) low for these areas. The formation of snow cover in the current northernmost summering areas will begin 1–2 months later. The incorporation of these trends into our suitability model suggests that northbound migrations or shifts to higher altitudes will start 1–2 months earlier from the current southernmost wintering areas while southbound movements from the current northernmost summering areas will start 1–2 months later. One could argue that the species might not necessarily respond to climate change by shifting its geographical range, but rather by maintaining or improving its fitness through evolutionary change mainly based on intergenerational selection. Because a species with a shorter generation length has a higher rate of evolutionary changes, we think that the rates of evolutionary response for the long-lived species of this kind (life span ~40 years) will be much slower than the predicted rate of current climate change.

This study provides some insight into understanding the movement ecology of Cinereous Vultures prior to becoming breeders, including geography and environmental signals accounting for their movements, and the location of their wintering and summering grounds. It provides new information on the timing, location and extent of summering and wintering grounds of Cinereous Vultures in the Caucasus and the Middle East. Hopefully, the outcomes of our study and methods that we used will contribute to the conservation of the ecosystems important to Cinereous Vultures and similar species. As climate changes, predictions of how it might affect year-round ranging of Cinereous Vultures are particularly important in view of their apparent dependence on protected areas for breeding and the herding practices.

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Appendix. Migration routes of Cinereous Vultures tracked by satellites. Variables are measured between migration start and end locations.

Direction	Variable	CV1	CV2	CV3	CV4	CV5	CV6
Natal area to Winter 1	Straight line (km)	1364	1725	1549	745	1259	1688
	Tracked line (km)	1688	3143	2504	983	1782	1892
	Sinuosity	1.238	1.822	1.617	1.320	1.415	1.121
	Duration (days)	42	38	39	29	32	30
	Difference in latitude (°)	12.824	12.474	14.611	7.069	11.648	12.602
Winter 1 to Summer 1	Straight line (km)	2415		1448	817	1380	1777
	Tracked line (km)	3515		3064	1789	1688	1823
	Sinuosity	1.456		2.116	2.190	1.223	1.026
	Duration (days)	64		29	32	10	42
	Difference in latitude (°)	22.638		13.09	7.679	12.672	13.943
Summer 1 to Winter 2	Straight line (km)			1108	Stayed on first summer location	1380	1001
	Tracked line (km)			5319	(still transmitting as of mid February 2011)	1599	1154
	Sinuosity			4.8005		1.1587	1.153
	Duration (days)			56		22	31
	Difference in latitude (°)			6.643		12.672	8.162
Winter 2 to Summer 2	Straight line (km)			955		1336	
	Tracked line (km)			2870		1781	
	Sinuosity			3		1.333	
	Duration (days)			120		27	
	Difference in latitude (°)			8.444		12.073	
Summer 2 to Winter 3	Straight line (km)			165			
	Tracked line (km)			289			
	Sinuosity			1.752			
	Duration (days)			1			
	Difference in latitude (°)			1.542			
Winter 3 to Summer 3	Straight line (km)			55			
	Tracked line (km)			254			
	Sinuosity			4.6			
	Duration (days)			2			
	Difference in latitude (°)			0.319			