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Effect of wind, thermal convection, and variation in flight strategies on the daily rhythm and flight paths of migrating raptors at Georgia's Black Sea coast

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ABSTRACT. Every autumn, large numbers of raptors migrate through geographical convergence zones to avoid crossing large bodies of water. At coastal convergence zones, raptors may aggregate along coastlines because of convective or wind conditions. However, the effect of wind and thermal convection on migrating raptors may vary depending on local landscapes and weather, and on the flight strategies of different raptors. From 20 August to 14 October 2008 and 2009, we studied the effect of cloud development and crosswinds on the flight paths of raptors migrating through the eastern Black Sea convergence zone, where coastal lowlands at the foothills of the Pontic Mountains form a geographical bottleneck 5-km-wide near Batumi, the capital of the Independent Republic of Ajaria in southwestern Georgia. To identify key correlates of local aggregation, we examined diurnal variation in migration intensity and coastal aggregation of 11 species of raptors categorized based on size and flight strategies. As reported at other convergence zones, migration intensity of large obligate-soaring species peaked during the core period of thermal activity at mid-day. When clouds developed over interior mountains and limited thermal convection, these large obligate-soaring species aggregated near the coast. However, medium-sized soaring migrants that occasionally use flapping flight did not aggregate at the coast when clouds over the mountains weakened thermal convection. Numbers of alternate soaring-flapping harriers (*Circus* spp.) peaked during early morning, with these raptors depending more on flapping flight during a time of day with poor thermal convection. Small sparrowhawks (*Accipiter* spp.) aggregated at the coast during periods when winds blew offshore, suggesting aggregation caused by wind drift. Thus, weather conditions, including cloud cover and wind speed and direction, can influence the daily rhythm and flight paths of migrating raptors and, therefore, should be accounted for before inferring population trends from migration counts.

RESUMEN. Efectos del viento, convección térmica y variación en estrategias de vuelo, ritmos diarios y rutas de vuelo de aves migrantes en la costa del mar negro en Georgia

Cada otoño un gran número de rapaces convergen en zonas geográficas a lo largo de su migración para evitar cruzar largos cuerpos de agua. En las zonas costeras de convergencia las rapaces se pueden agregar a lo largo de la línea costera debido a la conectividad o condiciones del viento. Sin embargo, el efecto del viento y de las convecciones térmicas en las aves rapaces migratorias pueden variar dependiendo de las condiciones locales del paisaje y el clima, y en la estrategia de vuelo de las diferentes rapaces. Del 20 Agosto al 14 Octubre 2008 y 2009, estudiamos el efecto de la formación de nubes y vientos cruzados en las rutas de vuelo de las rapaces migrantes a través de la zona de convergencia en el mar negro del este, en donde las tierras bajas costeras y el pie de monte de las montañas del Ponto forman un cuello de botella geográfico de 5 km de ancho cerca de Batumi, la capital de la república independiente de Ajaria en el sur de Georgia. Para identificar correlaciones claves de agregaciones locales, examinamos variación diurna en la intensidad de la migración y la agregación costera de 11 especies de rapaces que difieren en su tamaño y vuelo. Al igual que otras zonas de convergencia, la intensidad de migración de grandes especies planeadoras por obligación aumentan al medio día, mayor periodo de actividad térmica. Cuando las nubes se forman sobre el interior de las montañas y limitan la convección térmica, estas grandes especies planeadoras se ven obligadas a agregarse cerca de la costa. Sin embargo, planeadores migrantes de tamaños intermedios que ocasionalmente agitan sus alas para volar no exhibieron agregaciones costeras cuando las nubes sobre las montañas debilitan la convección

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térmica. Los números de individuos de *Circus* spp. que alternan entre planear y agitar las alas para su vuelo tiene un pico temprano en la mañana, en donde estas rapaces dependen más en agitar las alas para su vuelo durante la hora del día con pobre convección térmica. El pequeño *Accipiter* spp. se agrega en las costas durante los períodos cuando los vientos soplan hacia afuera de la costa sugiriendo una agregación causada por la deriva del viento. Así, las condiciones climáticas, incluyendo cobertura de nubes y velocidad y dirección del viento, pueden influir los ritmos diarios y las rutas de vuelo de las rapaces durante la migración y, por lo tanto, se deberían tener en cuenta antes de inferir tendencias poblacionales basadas en conteos durante la migración.

Key words: Batumi Raptor Count, birds of prey, coastal aggregation, convergence zone, migration, weather

During long-distance migration, many species of raptors travel almost exclusively by soaring in updrafts (Kerlinger 1989, Bildstein 2006, Newton 2008), using thermal convection (Leshem and Yom-Tov 1996a, Spaar 1997, Shamoun-Baranes et al. 2003), or orographic updrafts (Brandes and Ombalski 2004, Bohrer et al. 2012). Because thermal convection generally does not develop over large bodies of water outside the Trade-Wind Zones and Gulf Stream (Woodcock 1940, Stull 1988), soaring raptors typically make detours around large bodies of water (Meyer et al. 2000, Alerstam 2001, Meyburg et al. 2002, Bildstein et al. 2009). Raptors that simultaneously migrate between continents while avoiding geographical barriers reach high seasonal concentrations at geographical convergence zones (Zalles and Bildstein 2000, Bildstein 2006, Bensusan et al. 2007, Michev et al. 2011, Verhelst et al. 2011). Hundreds of thousands of raptors may be involved, often representing significant proportions of the regional or even global species populations (Bednarz et al. 1990, Leshem and Yom-Tov 1996a, Kjellén and Roos 2000, Bensusan et al. 2007, Verhelst et al. 2011).

Migratory movements of raptors depend on weather conditions, such as wind speed and direction and thermal convection, and their reaction to weather differs across morphologically distinct groups, ranging from obligate-soaring migrants (e.g., large eagles) and facultative-soaring migrants (e.g., harriers) to actively flapping migrants (e.g., small falcons; Kerlinger 1989, Spaar 1997, Spaar and Bruderer 1997a, b, Bildstein 2006, Shamoun-Baranes et al. 2010). Generally, soaring species fly faster with better soaring conditions (Kerlinger and Gauthreaux 1985a, Leshem and Yom-Tov 1996a, 1998, Shamoun-Baranes et al. 2003) and many have distinct diurnal and seasonal rhythms in migration activity, preferred modes of flight, and route choices that result from thermal convective dynamics at multiple scales (Kerlinger and Gauthreaux 1985b, Leshem and Yom-Tov

1996b, Spaar and Bruderer 1997a, Maransky et al. 1997, Shamoun-Baranes et al. 2006). Wind speed and direction can also influence travel speeds (Bruderer et al. 1994, Spaar and Bruderer 1997b, Bildstein 2006), flight altitudes (Murray 1964, Kerlinger 1984, 1989, Kerlinger and Gauthreaux 1984, 1985a, b), preferred flight modes (Maransky et al. 1997, Panuccio et al. 2010), and flight paths of raptors (Kerlinger 1984, Kerlinger and Gauthreaux 1984, Maransky et al. 1997, Meyer et al. 2000).

Understanding the effects of weather on flight paths and the spatial distribution of migrating raptors is particularly important where birds converge in space and time at high densities (Bildstein 2006, Kirby et al. 2008), e.g., to assess the potential impact of wind farm construction in a convergence zone (Barrios and Rodríguez 2004, Molina-Lopez et al. 2011) or to account for weather-induced variation in monitoring the population trends of migrants (Bednarz et al. 1990, McCarty and Bildstein 2005). However, the effects of atmospheric conditions, such as wind and thermal convection, on spatial migration dynamics at convergence zones may be highly site-specific because of differences in local land uses, topography, weather conditions, and the objectives of migrating raptors (Leshem and Yom-Tov 1996a, b, Bildstein 2006, Shamoun-Baranes et al. 2010). For example, Honey Buzzards (*Pernis apivorus*) migrating through Israel using soaring flight shift their flight paths during the day (Alon et al. 2004), taking advantage of differential development of thermal convection across a heterogeneous landscape (Shamoun-Baranes et al. 2003) and convergence lines associated with sea-breeze fronts (Alpert et al. 2000). In contrast, Honey Buzzards migrating through an isthmus in Italy compensate for wind drift by mixing gliding with flapping flight and so do not shift their flight path, possibly because they need to compensate for drift as they approach a sea-crossing (Pannuccio et al. 2010). Furthermore, some species use different

migration routes at different times. For example, Red-tailed Hawks (*Buteo jamaicensis*) migrating along the Appalachian mountains in the eastern United States can travel by soaring and gliding between broadly spaced thermals during early autumn, but later migrants use orographic updrafts along mountain ridges (Maransky et al. 1997). Ultimately, local conditions must be considered in the context of raptor migration strategies when trying to understand how weather conditions affect migration.

Our objective was to examine the role of wind and thermal convection in shaping diurnal dynamics in the spatial distribution of raptor flight paths at a migration convergence zone along the eastern Black Sea coast in the Republic of Georgia (Verhelst et al. 2011). The convergence zone is a geographical funnel for migrants bordered by the Black Sea coast to the west and the Pontic Mountains to the east. Raptors regularly shift flight paths between the mountain range and the coast when travelling through this convergence zone, leading to aggregations of raptors near the coast (Andrews et al. 1977). Cloud cover develops regularly over the Pontic Mountains during autumn migration (Kuchler 1975) and anecdotal evidence suggests that soaring migrants may aggregate at the Black Sea coast to avoid the cloud cover (Andrews et al. 1977) where thermal convection (Stull 1988) and the flight altitudes of soaring migrants may be limited (Kerlinger and Gauthreaux 1985a). We quantified diurnal patterns in migration intensity and coastal aggregation along the eastern Black Sea for 11 species of raptors, determined if and how wind and convective conditions accounted for coastal aggregations, and examined the effects of different raptor morphologies and flight strategies on migratory behavior. We expected that large soaring species dependent on thermal convection would exhibit strong mid-day peaks in migration intensity (Kerlinger 1989, Leshem and Yom-Tov 1996a, b). We also expected obligate-soaring species to aggregate more at the coast when clouds developed over the interior mountains in our study area (Kuchler 1975, Efimov and Anisimov 2011a, b).

METHODS

Study area. Raptors migrating to Africa from eastern European, Russian, and west-

ern Siberian breeding grounds circumvent the Caspian and Black seas by traveling through and around the Caucasus mountains. Many raptors track a westerly course, traveling in high numbers via lowlands along the Black Sea coast (Tholin 2010, Verhelst et al. 2011), whereas fewer are seen along the Caspian coast of Azerbaijan (Heiss and Gauger 2011). A strip of coastal lowlands forms a geographical bottleneck 5-km-wide near Batumi, the capital of the Independent Republic of Ajaria in southwestern Georgia, situated at the foothills of the Pontic Mountains (Fig. 1). Verhelst et al. (2011) reported that 800,000–1,000,000 migrating raptors of up to 35 species are observed in the area each autumn.

The region has a warm, humid climate and is covered by broad-leaved forests with an evergreen understory, generally described as subtropical vegetation (Kuchler 1975). Average maximum daily temperatures range from 20°C to 30°C from August through September and the area receives a large amount of annual precipitation (~2800 mm), much of which falls between mid-August and mid-September (Weatherspark 2013). Evapotranspiration over the forest canopy that covers the Pontic Mountains leads to the development of dense, cloud cover (Kuchler 1975). Because thermal convection does not easily develop after precipitation (excess water must first evaporate before air is warmed, Stull 1988) or when cloud cover shields the earth from incoming solar radiation (Kerlinger and Gauthreaux 1985a, Stull 1988), we expected stronger thermal convection over the coastal zone (first 2 km) than over the interior Pontic Mountains. This cloud cover contrast between mountains and coastline is stronger in the early half of the migratory season due to the higher average temperatures (>24°C; Kuchler 1975). Between 10 and 19 September, temperatures decline sharply and average ~18°C until the end of the migration season (Weatherspark 2013).

Winds are generally weak in the area, ranging from 0 to 10 m/s (Weatherspark 2013), and so usually do not disrupt thermal convection (Stull 1988). Winds average ~3 m/s and are mainly from the southeast (Weatherspark 2013) during the autumn. Until mid-September, onshore winds can be generated by sea-breeze circulation (Efimov et al. 2009) that strengthens thermal

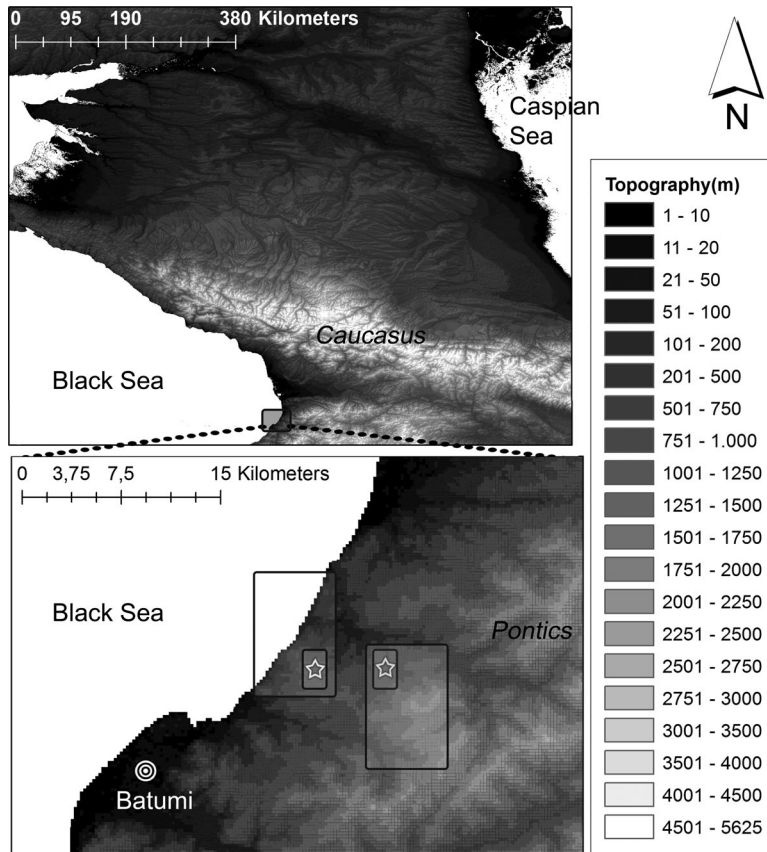


Fig. 1. Topography of the Batumi convergence zone (source: GMTED2010 at <http://earthexplorer.usgs.gov/>). Top: Regional topography of the Caucasus showing seas and mountains that constitute the convergence zone. Inset at the bottom indicates the location of our study area. Bottom: Topography of our study area at the foothills of the Pontic Mountains, near the city of Batumi (bulls-eye). All raptors that crossed a transect between survey stations 1 and 2 (stars, 2 and 6 km inland, respectively) were counted. Small gray insets around stations show areas from which sample counts were taken to calculate the coastal proportion of migrants (CPM). Weather conditions were estimated at Station 1. Large gray insets show approximate position of the sections of sky where cloud cover was visually estimated to calculate cloud contrast between coast and mountains.

convection in the coastal strip by transporting cold sea-air over land where it rapidly warms, forming a thermal front (Efimov et al. 2009, Efimov and Anisimov 2011a, b). Further, on-shore winds may weaken thermals above the interior mountains by bringing in moist air that enhances cloud development (Kuchler 1975). Sea-breezes in early autumn may also, therefore, contribute to the seasonal difference in cloud cover between the mountains and the coastal strip (Efimov and Anisimov 2011a, b).

Raptor migration data. The Batumi Raptor Count is a standardized raptor-migration

survey (www.batimiraptorcount.org). Data from the 2008 and 2009 surveys were used for this study. From 20 August to 14 October each year, the survey took place simultaneously from two stations located 2 and 6 km east of the Black Sea coast, respectively ($41^{\circ}41'05''N$ $41^{\circ}43'51''E$ and $41^{\circ}41'08''N$ $41^{\circ}46'43''E$, Fig. 1; Verhelst et al. 2011). At least three observers per station per day recorded all individuals and flocks that crossed an east–west transect running through these stations (bottom, Fig. 1). For each record, we noted time of passage and categorized the location of birds relative to the survey station

as overhead (between 50 m west and 50 m east from the station) or in one of six categories for raptors and flocks located 50–200 m, 200–2000 m, or >2000 m to either the east or west of the stations. Distance codes were estimated in the field by using landmarks at known distances and were used together with recorded times of passage to eliminate double counts of simultaneously observed flocks (Verhelst et al. 2011). We assumed no bias in counts by observers.

Quantifying migration dynamics. Because weather data were available every 2 h (see section entitled Weather data below), count data were pooled in blocks from 1 h before until 1 h after each weather observation. We then calculated the total migration intensity (TMI) as the total number of individuals observed within 200 m on either side of both stations (Fig. 1) during 2-h intervals. Solar noon shifted only 25 min throughout our study (from 20 August to 14 October), and we did not expect this shift to lead to an observable shift in the timing of daily peak migration.

Coastal aggregation was calculated as the proportion of raptors observed within 200 m around station 1 (Fig. 1) relative to the total number of birds observed within 200 m of the two stations combined. We restricted data to a range of 200 m around each survey station (Fig. 1, gray insets) to reduce count bias during periods where low visibility (e.g., during extensive and low cloud cover) prevented detection of distant birds. When calculating coastal proportion of raptors, we only included 2-h intervals for a given species if more than one individual was observed during that period.

Missing data. No counts took place during 12 d with stormy weather. Due to bad weather and other interruptions, several 2-h observation periods were missed at either one or both survey stations (191 missed out of 735 2-h periods). In our analyses, we only included observation periods if both survey stations were staffed simultaneously at the latest within 15 min of the intended start time and until at least 15 min before the intended end time of that observation period (258 of 544 periods). As a result, periods at the start and end of days (07:00–09:00 and 17:00–19:00) were poorly represented in our dataset. Additional missing entries in the dataset were random and not related to a specific time of day or weather condition.

Focal species. In our analyses, we included only those species with observations during at least 34 2-h intervals or where at least 700 individuals migrated through the area each year (Verhelst et al. 2011). Our analyses included 11 species, including, in order of decreasing abundance, Western Honey Buzzards (*Pernis apivorus*), Steppe Buzzards (*Buteo buteo vulpinus*), Black Kites (*Milvus migrans*), Eurasian Sparrowhawks (*Accipiter nisus*), Marsh Harriers (*Circus aeruginosus*), Booted Eagles (*Aquila pennatus*), Levant Sparrowhawks (*Accipiter brevipes*), Lesser Spotted Eagles (*Aquila pomarina*), Montagu's and Pallid harriers (*Circus pygargus* and *C. macrourus*), and Short-toed Eagles (*Circus gallicus*). We combined Montagu's and Pallid harriers because it was difficult to separate young and female birds of these species (Forsman 1999) and, because of their similar morphology, we expected them to react similarly to environmental conditions in the convergence zone (Spaar and Bruderer 1997a).

All species were categorized for comparison across functional groups, taking into account the average mass of each species and their preferred flight strategy (soaring or flapping flight). Based on mass (Forsman 1999, Ferguson-Lees and Christie 2001), we distinguished between large (>1 kg, large eagles), medium-sized (500 g to 1 kg), and small raptors (<500 g, small harriers and sparrowhawks). Next, eagles, buzzards, and Black Kites were considered obligate-soaring migrants (cf. Shirihai et al. 2000, Ferguson-Lees and Christie 2001, Bildstein 2006). Although Western Honey Buzzards and Black Kites occasionally use flapping flight, both species soar whenever possible (Spaar 1997). The small sparrowhawks were considered flapping migrants. Levant Sparrowhawks do routinely soar in large flocks during the daytime period of thermal convection in Israel (Spaar et al. 1998), but, at the Black Sea coast, large flocks of soaring Levant Sparrowhawks are rare and many are seen migrating in low flapping flight (W. Vansteelant, pers. obs.). Harriers were categorized as alternate soaring-flapping migrants (Spaar and Bruderer 1997a).

Weather data. Weather conditions were estimated at the coastal station every 2 h. For this analysis, we used visual estimates of cloud cover (0–8 scale) at two locations to determine the homogeneity of cloud cover along an east-west gradient in our study area. Raptors can

soar under convective cloud types (Smith 1985), but we did not classify cloud types because we were mainly interested in how fine-scale cloud cover differences across the convergence zone affected local raptor aggregation dynamics. Cloud cover was estimated for a segment of sky above the coastal survey station and for a segment above the Pontic Mountains (large insets, Fig. 1). The latter segment was located above the highest mountain peak in our study area (~5 km from the coastal station) to facilitate a repeatable estimation of cloud cover in a fixed field of view with reference to clear landmark. Alternative datasets such as cloud cover imagery from satellites and regional weather forecast did not provide a sufficiently high spatial resolution to quantify spatial differences in cloud types within the convergence zone.

Observers also estimated wind direction at cardinal and intercardinal compass points and estimated wind strength using the Beaufort scale (NOAA 2011), which we assumed to be a sufficiently accurate measure of average wind conditions at a resolution of 2 h. Analogous to the bird data, we assumed no observer bias in the weather data.

Processing weather data. Cloud contrast was calculated as the difference between the cloud-cover estimate (0–8) for the mountains versus the coast, whereby negative values indicate more cloudy conditions over the coast and positive values indicate relatively high cloud cover over the mountains. Cardinal wind directions were translated to degrees. The Beaufort (Bft) scale and exact wind speed (m/s) were linearly proportional to each other within the range of our observations (0–5 Bft). Thus, wind strength was multiplied with the sine of wind direction to calculate the crosswind strength (Bft) perpendicular to the principal southbound direction of migration. The sign of crosswinds was positive for winds blowing from east to west (easterly winds) which would have a positive effect on the proportion of raptors observed near the coast due to wind drift. Aggregation was expected to decrease with birds drifting to the east with winds from the west (westerly winds, negative crosswind component). Both crosswind strength and cloud contrast were treated as continuous (rather than ordinal) variables with an interval measurement level in our analysis.

Modeling approach. We first explored whether TMI and the coastal proportion of

migrants (CPM) varied significantly over the course of a day. Next, we explored whether cloud contrast and crosswinds showed distinct diurnal patterns. We initially fit a full model including cloud contrast and crosswinds as predictive variables per species. However, because only single effects were significant (Table S1), we eventually implemented single effect models to test whether cloud contrast or crosswinds explained the CPM.

Diurnal migration dynamics versus flight strategy. To detect the occurrence of diurnal migration dynamics, we fitted first- and second-order generalized linear regression models ($\alpha = 0.05$, GLM, Venables and Ripley 2002) for TMI and the CPM of every species separately, assuming, respectively, a Poisson and a quasi-binomial error distribution with hour of day (h and h²) as predictor variable(s). Second-order effects are only shown for those species where these were significant and explained more variation than linear models.

Diurnal patterns in cloud contrast and crosswinds. We also fitted first and second order generalized linear regression models with hour of day as a predictor variable and cloud contrast and crosswind as response variables. We investigated the correlation between cloud contrast and crosswind with Kendall tau ranked r (Hipel and McLeod 1994), a non-parametric alternative to Spearman's r .

Weather effects versus flight strategy. We tested the effect of cloud contrast and crosswinds (single effects) on coastal raptor aggregation using a GLM with a quasi-binomial error distribution, a logit link function, and giving weights to the observations by the log₁₀ of TMI ($P = 0.05$, GLM, Venables and Ripley 2002). Weights were used to account for variation in bird numbers during the collection period and were aimed at making the resulting models representative for most migrating birds (rather than representative for every observation-moment). Observations of coastal aggregation at moments with higher migration intensity are given more weight than observations with low intensity. Shapiro–Wilkinson's test of normality (W) was used to evaluate the distribution of the residual error in the GLMs (Venables and Ripley 2002). Finally, we selected the most adequate model for each species on the basis of AIC for quasi-likelihood estimation, i.e. QAIC (Burnham and Anderson 2002).

Seasonality in weather and aggregation.

Because of the seasonality in weather conditions noted previously, we defined an early and a late migration period (before and after 15 September, respectively) corresponding with a transition from warmer to cooler temperatures in our study area (Weatherspark 2013). Between early and late migration, we compared model results for two species with protracted migration seasons spanning the early and late autumn periods (Black Kites and Booted Eagles; Verhelst et al. 2011). We also tested for seasonality in the weather experienced by the birds by comparing mean cloud contrast and crosswinds between periods for each species (one-sided two-sample Student's *t*-tests). All statistical modeling was conducted in program R 2.14.0 (R Development Core Team 2010), using the ggplot2 package (Wickham 2009) for graphical representation of results.

RESULTS

TMI and the CPM observed within 200 m of both count stations for all 2-h time blocks are reported in Tables S2 and S3. We refer to Verhelst et al. (2011) for a summary of total seasonal counts and the phenology of raptors in our study area.

Diurnal migration dynamics versus flight strategy. Obligate-soaring species and Eurasian Sparrowhawks had mid-day peaks in TMI (Fig. 2; Table S2). Migration intensity of obligate-soaring migrants like Lesser Spotted Eagles (Fig. 2a) was up to 10 times higher at noon than during the morning or evening hours (note the logarithmic scale in Fig. 2). Short-toed and Booted eagles, both soaring migrants, tended to increase in numbers during the day (Figs. 2a and b). Harriers were most abundant in the morning and showed a marginal, but significant, decrease in migration intensity during the day, as was also true for Levant Sparrowhawks (Fig. 2e). Diurnal trends in migration intensity were significant ($P < 0.001$) for all species, including the seemingly weak trend lines for harriers (Figs. 2c and d). The flat trend line in the migration intensity of harriers is a plotting artifact due to the lower upward spread in the counts of harriers compared to the spread in counts of buzzards and kites.

Coastal aggregation often followed diurnal trends in TMI (Fig. 2). Obligate soaring mi-

grants mostly aggregated at the coast around mid-day (e.g., Short-toed Eagles, Black Kites, and Honey Buzzards; Figs. 2f and g; Table S3) or increasingly aggregated at the coast throughout the day (e.g., Booted Eagles, Fig. 2g). Diurnal trends of coastal aggregation were significant for all obligate-soaring species ($P < 0.001$), with the exceptions of Lesser Spotted Eagles ($P_{hr} = 0.10$) and Steppe Buzzards ($P_{hr} = 0.60$; Figs. 2f and g). In general, obligate-soaring species exhibited less coastal aggregation than other raptors. Average coastal aggregation was always high for Booted Eagles (>40%) compared to that of other medium-sized soaring migrants (Fig. 2g).

Harriers adopting a mixed soaring-flapping flight strategy and the flapping Eurasian Sparrowhawks aggregated most strongly at the coast during the morning (Figs. 2h–j; Table S3). The diurnal trends of coastal aggregation were significant for all alternate soaring-flapping and flapping species ($P < 0.001$), with the exception of a non-significant increase in coastal aggregation during the day by Levant Sparrowhawks ($P_{hr} = 0.30$, Fig. 2j).

Diurnal dynamics of cloud contrast and crosswinds. Over the course of an average autumn day at Batumi, an increasingly strong local cloud contrast develops due to cloud cover forming over the Pontic Mountains (Fig. 3). Strong cloud contrast in the afternoon coincides with the afternoon prevalence of westerly winds (Fig. 3), although the weak rank correlation between cloud contrast and crosswinds (Kendall tau ranked $r = -0.1$; $P < 0.001$) suggests cloud development also takes place with easterly winds.

Effect of cloud contrast and crosswinds on coastal aggregation. The response to local weather was consistent across species of the same functional groups (i.e., with similar body mass and flight strategy, Fig. 4; Table 1). Short-toed, Lesser Spotted, and Booted eagles aggregated significantly more at the coast with increasing cloud contrast (Figs. 4a and b; Table 1). Large and medium-sized obligate soaring species exhibited an increase of 10–70% in coastal aggregation in response to increasingly positive cloud contrast (Figs. 4a and b). The effect of cloud contrast was, however, not significant for Steppe Buzzards, Honey Buzzards, and Black Kites (Fig. 4b; Table 1). Alternate soaring-flapping harriers (Figs. 4c and d) and flapping sparrowhawks (Fig. 4e) had

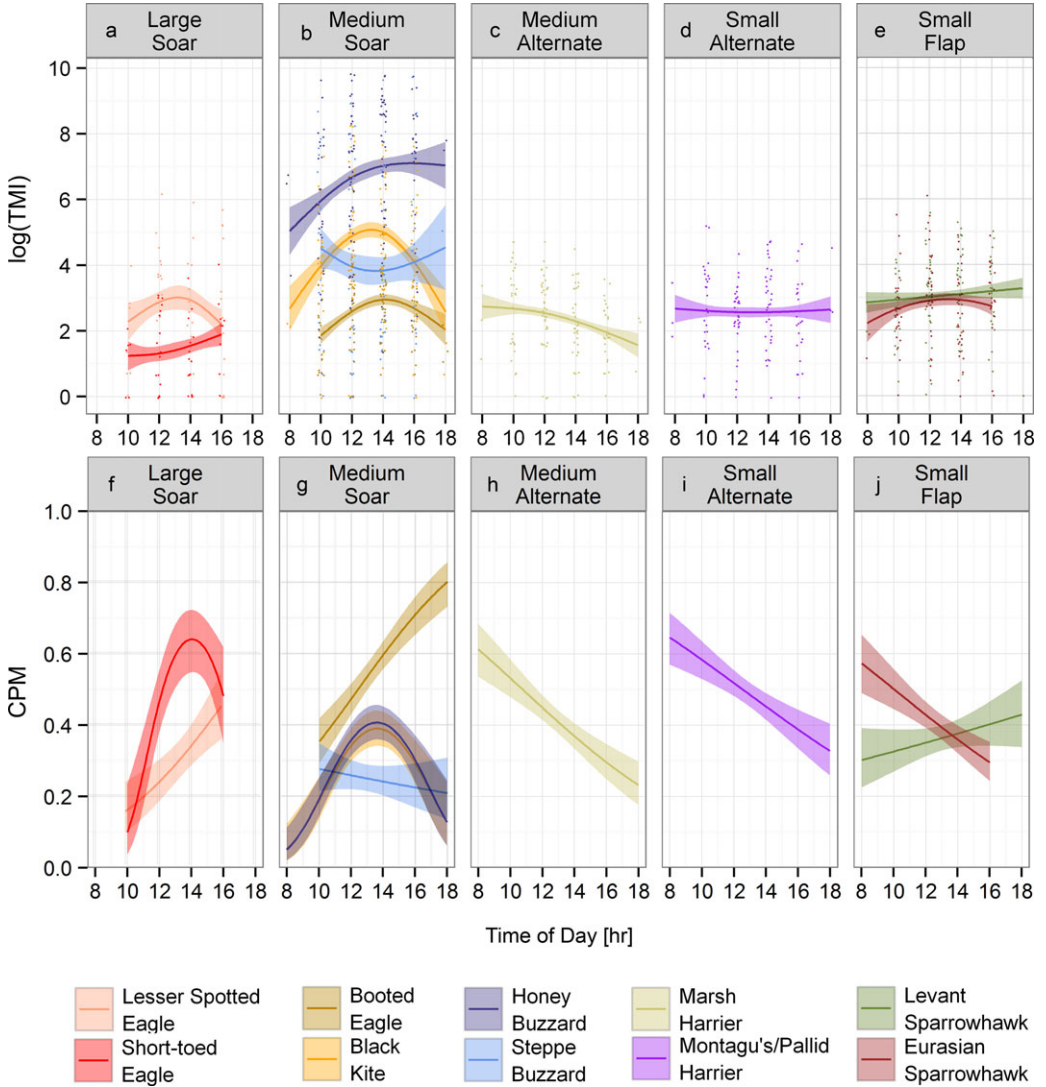


Fig. 2. Diurnal dynamics of migration in our study area for our 11 focal species (see legend). The diurnal trend in total migration intensity (TMI, top: a–e). and the coastal proportion of migrants (CPM, bottom: f–j) is shown (average trend = solid lines; shaded area = \pm SE) as function of time of day [h]. Regression models assumed a Poisson or a quasi-binomial error structure for modeling TMI and CPM, respectively, and, for each graph, we modeled a second-order polynomial unless a linear regression model was more significant. Each subplot represents one of five functional groups of species that share similar size (large, medium, or small) and flight modes (obligate soaring, mixed, or flapping). TMI (top) was plotted on a logarithmic scale to avoid trends for the least abundant species that would be compressed when plotted with the most abundant species in the same plot. Note that the trends for CPM of Honey Buzzards and Black Kites overlap almost exactly.

weaker, non-significant responses to cloud cover (Table 1).

Crosswinds did not affect the coastal aggregation of either large or medium-sized soaring

migrants (Figs. 4f and g; Table 1) or alternate soaring-flapping harriers (Fig. 4h; Table 1). Wind did significantly affect the two smallest species (i.e., sparrowhawks; Table 1), with

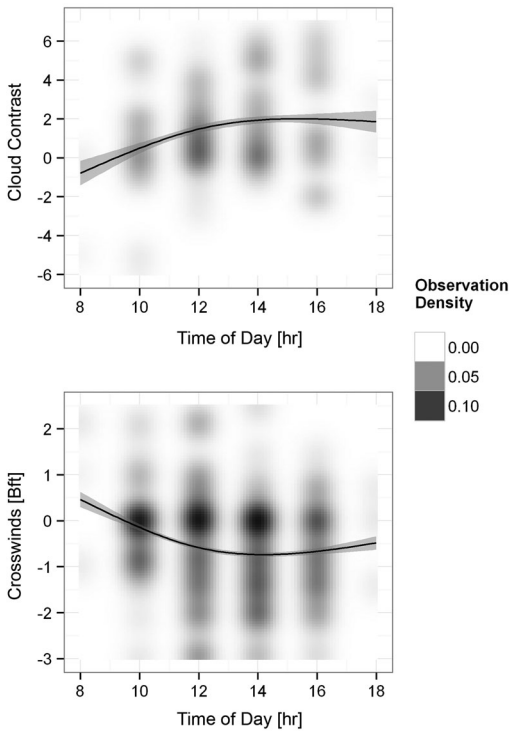


Fig. 3. Diurnal weather patterns at Batumi during migration surveys between 20 August and 14 October 2008 and 2009. Top: second-order diurnal evolution of cloud contrast ($CC = -1.49 + 17.48 \times h - 9.46 \times h^2$; $P < 0.001$) as a function of time of day. Bottom: second-order diurnal evolution of crosswind ($CW = -0.54 - 5.99 \times h + 5.14 \times h^2$; $P < 0.001$), with wind speed estimated using the Beaufort scale (Bft). Shaded areas around average trends represent \pm SE. For each environmental variable, we calculated kernel densities of total observation frequency at each 2-h interval between 08:00 and 18:00 for every interval value of the variable. Positive cloud contrast indicates conditions with greater cloud cover over the interior mountains than over the coastal lowlands. Positive crosswinds were winds blowing from the east (toward the coast).

both observed at the coast more frequently with stronger easterly crosswinds (Fig. 4j; Table 1).

Seasonality in weather effects. Atmospheric conditions were more homogenous across the convergence zone during the late migration period (after 15 September) than during the early migration period, with generally weak crosswinds (Avg. $CW_{\text{early}} = -0.84 < \text{Avg.}$

$CW_{\text{late}} = -0.04$; 1-sided $t_{1041.41} = -11.3$, $P < 0.001$) and, more importantly, low levels of cloud contrast (Avg. $CC_{\text{early}} = 2.0 > \text{Avg. } CC_{\text{late}} = 0.7$; 1-sided $t_{1560.48} = 9.3$, $P < 0.001$). We found a significant positive effect of cloud contrast on coastal aggregation during the early part of the season for Booted Eagles, but not during the last half of the season ($\beta_{\text{early}} = 0.3$, $P < 0.01$; $\beta_{\text{late}} = 0.2$, $P = 0.1$). Black Kites did not respond to cloud cover during either period ($\beta_{\text{early}} = 0.1$, $P = 0.40$; $\beta_{\text{late}} = 0.2$, $P = 0.30$). Coastal aggregation increased with easterly crosswinds during the late migration period for Booted Eagles ($\beta_{\text{early}} = -0.2$, $P = 0.50$; $\beta_{\text{late}} = 0.4$, $P = 0.04$) and Black Kites ($\beta_{\text{early}} = -0.02$, $P = 0.70$; $\beta_{\text{late}} = 0.4$, $P = 0.04$).

DISCUSSION

Dynamics of diurnal migration intensity in relation to flight strategy. We observed a mid-day peak in abundance of most obligate-soaring raptors, as also observed at other convergence zones along the eastern Palearctic flyway (Shirihai et al. 2000) and for other species (Kerlinger 1989, Bildstein 2006). The largest species in our study, Short-toed, Lesser-spotted, and Booted eagles, restricted their daily periods of flight compared to smaller migrants, consistent with previous reports that large obligate-soaring migrants restrict their activity to the core period of thermal activity (Kerlinger 1989, Leshem and Yom-Tov 1996b, Bildstein 2006). The migration intensity of Short-toed Eagles in our study increased linearly during the day, contrasting with the typical mid-day peaks in abundance of this species at other locations (Spaar 1997, Shirihai et al. 2000, Spaar et al. 2006). However, this unexpected trend was likely an artifact of the low number of 2-h observation periods ($N = 34$) for this species and the concomitant lack of evening observations (after the 2-h period from 15:00 to 17:00) that could be retained to detect the expected evening decrease in abundance of this species.

Alternate soaring-flapping harriers were most abundant in the morning in our study as also reported in Israel (Spaar and Bruderer 1997a). This morning peak in abundance suggests that harriers readily migrate using flapping flight at times with poor thermal convection (Spaar and Bruderer 1997a). This ability to fly during periods of poor convection should allow harriers

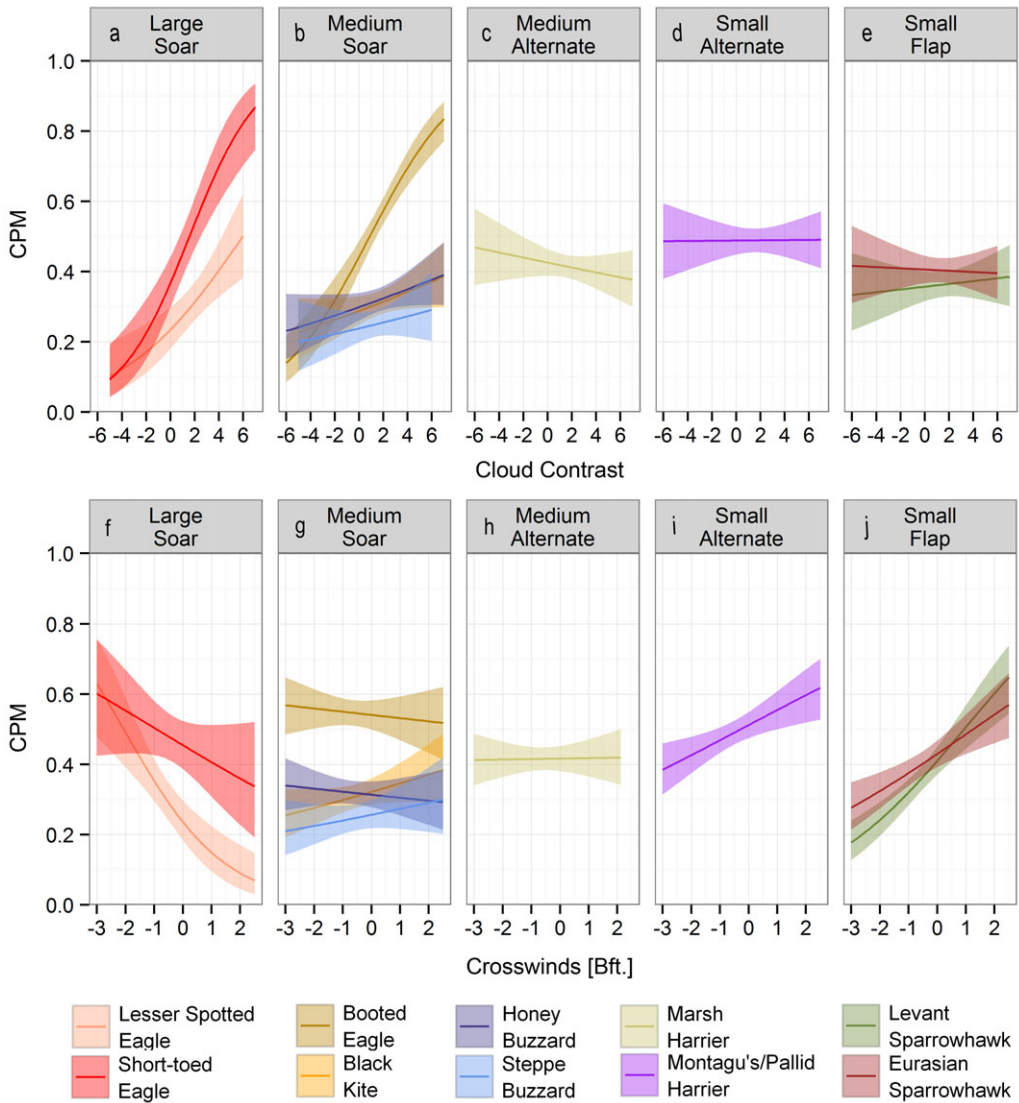


Fig. 4. Species-specific coastal aggregation (CPM) at the eastern Black Sea shore in response to local weather conditions. The effect of cloud contrast (top, a–e) and crosswinds (bottom, f–j) on coastal aggregation of raptors (solid lines \pm SE) as determined by linear logistic regression is shown for each of the 11 focal species (see legend). Each subplot represents one of five functional groups of species that share similar size (large, medium, or small) and flight styles (obligate-soaring, mixed, or flapping). Note that graphs are curved despite linear model structure as a consequence of the (back-) transformation of data by the logit link function during logistic regression. Positive cloud contrast indicates greater cloud cover over the interior mountains than over the coastal lowlands. Positive crosswinds are offshore winds blowing from east to west, with wind speed estimated using the Beaufort scale (Bft).

to migrate over a broad geographical front rather than converging in a small geographical area. Nevertheless, the numbers of harriers observed in our convergence zone (Verhelst et al. 2011)

far exceed the numbers seen elsewhere along the eastern Europe–Africa flyway (Bijlsma 1983, Welch and Welch 1988, Shirihai et al. 2000). As such, environmental factors such as habitat

Table 1. Weather effects on coastal aggregation of each raptor species determined by linear logistic regression. Sample sizes (in parentheses) indicate the number of 2-h periods during which observations were made. Results are for single effect models of cloud contrast (CC) and crosswinds (CW), respectively. Superscripts with estimates of intercept and effect size indicate significance levels, with marginally significant results at $P < 0.10$ (+) and significant results at $P < 0.05$ (*) and $P < 0.001$ (**). Best models for each species are those with the lowest QAIC.

Type	Species	Model	Intercept	β_{CC}	β_{CW}	QAIC
Large Soaring	Short-toed Eagle (34)	CC	-0.744*	0.247 ⁺	-	55.3
		CW	-0.551 ⁺	-	-0.187	59.5
	Lesser Spotted Eagle (45)	CC	-1.294**	0.236*	-	18.1
		CW	-1.149**	-	-0.41	18.5
	Booted Eagle (116)	CC	0.074	0.251**	-	39.9
		CW	0.382*	-	-0.125	43.4
Medium Soaring	Black Kite (121)	CC	-0.739**	0.04	-	54.6
		CW	-0.604**	-	0.172	54.2
	Honey-buzzard (136)	CC	-0.876**	0.044	-	82.9
		CW	-0.843**	-	-0.063	83.0
	Steppe Buzzard (82)	CC	-1.379**	-0.023	-	28.8
		CW	-1.386**	-	0.127	28.6
Medium Alternate	Marsh Harrier (125)	CC	-0.308*	-0.024	-	104.7
		CW	-0.334*	-	0.012	104.8
Small Alternate	Montagu's/Pallid Harrier (120)	CC	-0.103	-0.009	-	55.2
		CW	-0.1	-	0.032	55.2
Small Flapping	Levant Sparrowhawk (98)	CC	-0.711**	-0.002	-	41.5
		CW	-0.506*	-	0.359*	39.3
	Eurasian Sparrowhawk (98)	CC	-0.412*	0.04	-	57.8
		CW	-0.282*	-	0.281*	55.8

availability for feeding during migration (Niles et al. 1996) likely drive the regional convergence of harriers toward our study area.

Diurnal dynamics of coastal aggregation in relation to weather and flight strategies. Obligate-soaring migrants responded to cloud development over the interior mountains by flying closer to the Black Sea coast. Short-toed, Lesser Spotted, and Booted eagles responded the strongest, likely because they are more dependent on convection to sustain high ground-speeds during travel than smaller soaring raptors (Spaar 1997, Shirihai et al. 2000). Apart from Booted Eagles, three other medium-sized soaring migrants (Honey Buzzards, Steppe Buzzards, and Black Kites) showed no increase in coastal aggregation in response to cloud contrast. Honey Buzzards and Black Kites occasionally use flapping flight, allowing them to fly further and longer than larger eagles when there is weaker convection (Spaar 1997, Bildstein 2006). The stronger flight capacity of these medium-sized species also allowed them to travel earlier in the morning and later in the

evening than large eagles in our study area and elsewhere (Kerlinger 1989, Spaar 1997). Finally, Steppe Buzzards rarely approached the coast and thereby behaved differently than other soaring migrants in our study. This is surprising because Steppe Buzzards typically depend on soaring flight (Spaar and Bruderer 1997b; see the "Exceptional cases" section for further discussion of this seemingly aberrant behavior).

Aggregation of small and flapping sparrowhawks at the coast increased with easterly winds (i.e., blowing offshore), suggesting that wind drift caused this aggregation. Along the east coast of the United States, accipiters have also been observed in higher numbers when winds are blowing offshore (Mueller and Berger 1967). However, Murray (1964) and Kerlinger and Gauthreaux (1984, 1985b) showed that these higher counts occurred because accipiters were flying lower to reduce the effect of drift, making them easier to detect by observers. Further study is needed to determine if the coastal aggregation of accipiters we observed is also an artifact of higher coastal detection rates, i.e., if

they fly lower near the coast during periods with offshore winds.

Interestingly, easterly crosswinds, and not cloud development, were the main correlate of coastal aggregations of two medium-sized soaring species (Booted Eagles and Black Kites) during the last half of the autumn season. We expected this would be the case based on the increasing homogeneity of cloud cover, and thus the increasing homogeneity of thermal convective conditions across our study area in late autumn (Kuchler 1975, Efimov et al. 2009). Nevertheless, to infer drift due to wind from the significant effect of crosswinds on Black Kites and Booted Eagles, we must first consider whether the observed aggregations were not due to a bias in detection rates due to birds flying lower with offshore winds (Murray 1964, Kerlinger and Gauthreaux 1984, 1985b). We suspect such a bias is unlikely for medium-sized to large soaring species because nearly all birds flying within 200 m of our observatory were detected by observers with the naked eye and repeated efforts to find otherwise undetected high-flying raptors with binoculars have rarely proved successful (W. Vansteelant, pers. obs.). We, therefore, tentatively conclude that Booted Eagles and Black Kites drifted with offshore winds to aggregate at the coast during the last half of the migration season, and only did so during that period because of the strong seasonality in convective and wind conditions in our study area. Similar observations of shifting flight paths in response to seasonal variation in atmospheric conditions have been reported for Red-tailed Hawks migrating along the Appalachian Mountains in North America (Maransky et al. 1997) and for other soaring raptors migrating through Israel (Leshem and Yom-Tov 1998). Furthermore, juvenile raptors are generally more prone to drift (Thorup et al. 2003) and juvenile Black Kites and Booted Eagles also migrate up to two weeks later than adult birds (Ferguson-Lees and Christie 2001). Consequently, drift-prone juveniles likely made up the bulk of the Booted Eagles and Black Kites observed in late autumn in our study.

In contrast to the strong effect of wind drift on raptor movements at more windy locations such as the Gibraltar Strait or other sea-crossings (Meyer et al. 2000, Yamaguchi et al. 2011), the effect of drift in our study was likely small for most raptors because they could easily compen-

sate for the weak winds in our study area (>80% observations were 0–2 Bft). Similarly, Kerlinger (1984, 1989) suggested that drift only had an effect when winds were sufficiently strong, e.g., >5 m/s for actively flapping Sharp-shinned Hawks (*Accipiter striatus*).

Influence of landscape on coastal aggregation. The weak and non-significant response to cloud development and wind conditions by harriers and sparrowhawks in our study may be best explained by the fact that these species select their routes mainly to fuel their flights by feeding, in contrast to obligate-soaring raptors that do not regularly feed during migration (Niles et al. 1996, Bildstein 2006, Liminana et al. 2007, Trierweiler 2010). The importance of habitat preferences in the choice of migration routes of fly-forage migrants is evidenced by the use of traditional stopover sites for resting and refueling by harriers during migration (Panuccio et al. 2006, Kitowski 2007, Trierweiler 2010).

The eastern Black Sea convergence zone likely provides foraging and stopover opportunities for fly-forage migrants because numerous day-active passerines (e.g., swallows, pipits, wagtails, and bee-eaters) migrate near the coast and some food-rich wetlands can be found along the coast (Ptushenko 1959). The high morning abundance and coastal aggregation of harriers (with large flocks >2000 Montagu's Harriers before 10:00, 4 September 2008, Verhelst et al. 2011) and sparrowhawks in our study area support this hypothesis. This coastal food supply is a likely reason why non-obligate soaring raptors such as harriers and Eurasian Sparrowhawks converge in such high numbers along the Black Sea coast, whereas they are considered broad-front migrants elsewhere along the eastern Europe–Africa flyway (Shirihai et al. 2000, Bensusan et al. 2007, Michev et al. 2011).

Soaring migrants may also shift their flight paths in response to factors other than weather conditions. For example, in Israel, Honey Buzzards migrating over the Negev shift their flight paths toward the Central Mountains in the evening to find roost sites (Tsovel and Alon 1991, Alpert et al. 2000). It is likely, therefore, that species like Honey Buzzards, Black Kites, eagles, and Steppe Buzzards leave from, and return to, the interior mountains in our study area during mornings and evenings (despite regular persistence of cloud cover over the interior

mountains during evenings) because they roost inland. This may be because (large) raptors are sensitive to human disturbance (Richardson and Miller 1997) and so avoid human settlements in the coastal zone for roosting (W. Vansteelant, pers. obs.).

Exceptional cases. We found that Booted Eagles aggregated at the coast in high numbers at all times of the day compared to other soaring species, and similar observations have been reported elsewhere around the Black Sea (Andrews et al. 1977) and Mediterranean basin (Premuda et al. 2007). Although coastlines can provide an important visual leading line for orientation during migration (Bildstein 2006), it is not clear why Booted Eagles follow coastlines so strongly compared to other obligate-soaring migrants.

Steppe Buzzards and Levant Sparrowhawks in our study rarely responded to cloud development by aggregating at the coast, contrasting with their active response to convective conditions elsewhere, e.g., Israel (Leshem and Yom-Tov 1996b, Spaar et al. 1998, Bildstein 2006). However, during at least three of 10 exploratory single-day counts 6 km east of our study area (from 24 August to 8 September and 12–30 September), up to 20,000 Steppe Buzzards and a maximum of 1000 Levant Sparrowhawks were recorded flying over the interior mountains under clear skies while migration intensity of these two species was low at our survey sites. These anecdotal observations suggest that the migratory corridor of Steppe Buzzards and Levant Sparrowhawks is broader than that of other species in our study and that this corridor was insufficiently covered during our study, making it difficult to detect relative displacements in the flight paths for these species in response to weather. In Israel, the main migration corridor of these species is also broader than that of other raptors (Alon et al. 2004). This broad migration front appears in Israel, and probably also in our study area, because Steppe Buzzards and Levant Sparrowhawks migrate into Africa predominantly via an easterly route over the Bab-el-Mandeb Strait at the southern end of the Red Sea in Yemen (Welch and Welch 1988) rather than over the westerly route of our other focal species that cross into Africa at the Suez Strait (Bijlsma 1983, Leshem and Yom-Tov 1998, Shirihai et al. 2000, Meyburg et al. 2002).

CONCLUSIONS

Our results suggest that weather conditions should be accounted for before inferring population trends from migration counts (McCarty and Bildstein 2005) and more work is needed to elucidate the effect of weather on the ability of observers to detect migrating raptors. Given the anecdotal observation of coastal raptor aggregations by Andrews et al. (1977) in northeast Turkey, the weather effects observed in our study likely apply to the entire southeastern Black Sea coastline. If so, our results may have implications concerning the planned construction of power lines 20 km south of our study area (Mott McDonald 2012). Because such structures pose collision and electrocution risk for migrating raptors (Bevanger 2008, Kirby et al. 2008), developers should assess the potential impact of these power lines on migrating raptors, identifying high-risk zones, especially near the coast, and evaluating possible mitigation measures.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Weather effects on coastal aggregation of each species determined by linear logistic regression. Results are reported for

models including cloud contrast (CC) and crosswinds (CW) and an interaction term as predictive variables. Superscripts with estimates of intercept and effect size indicate significance level, with marginally significant results at $P < 0.10$ (+) and significant results at $P < 0.05$ (*) and at $P < 0.001$ (**).

Table S2. Total migration intensity (TMI) per 2-h interval (h) and per day of year (DOY) for 11 species of raptors observed within 200 m range of two survey stations situated 2 and 6 km from the Black Sea coast. Species columns give TMI as calculated in 2008 and 2009, respectively. Day of year (DOY) 233 is 21 August and DOY 284 is 11 October.

Table S3. Coastal proportion of migrants (CPM) per 2-h interval and per day of year (DOY) for 11 species of raptors observed within 200 m of two survey stations located 2 and 6 km from the Black Sea coast, respectively. Species columns give CPM's as calculated in 2008 and 2009, respectively. Day of year (DOY) 233 is 21 August and DOY 284 is 11 October.