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Differential autumn migration between sex and age groups in the Western marsh harrier: a longitudinal pattern analysis

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The Western marsh harrier *Circus aeruginosus* is a partial migrant with populations breeding in eastern and northern Europe migrating south and wintering mostly in sub-Saharan Africa. During autumn migration harriers move on a broad front heading SW and undertaking long sea-crossings en route to their wintering quarters. However, a substantial proportion of birds, mostly juveniles and adult females, migrate only shorter distances wintering in Europe and North Africa. In a 7-year study (2011–2017), between 26 August and 30 September, we compared the ratio and timing of the different sex/age classes of Western marsh harriers (adult male, adult female, juvenile) at two migration bottlenecks: the Strait of Messina (southern Italy) and Batumi (Georgia). At both sites, adult males migrated slightly earlier that adult females and earlier than juveniles. Among adults, males outnumbered females and this difference was more evident along the eastern flyway. At Batumi, a higher proportion of juveniles (first calendar year birds) was reported. The male-biased sex ratio reported at the Strait of Messina is very similar to that reported in broods of Western marsh harriers breeding in The Netherland and Poland. We suggest that the higher proportion of adult males recorded at Batumi could reflect the sex ratio in male-biased populations in western Russia.

KEY WORDS: Western marsh harrier, *Circus aeruginosus*, longitudinal pattern, differential migration, female mimicry.

INTRODUCTION

The Western marsh harrier *Circus aeruginosus* (hereafter WMH) is a partial migrant bird with mainly resident populations in western, southern Europe and

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North Africa (Ferguson-Lees & Christie 2001). Populations breeding in northern and eastern Europe instead migrate on a broad front, sometimes undertaking long sea crossings over the Mediterranean Sea. In so doing, they move along more or less parallel pathways showing a leapfrog migration, and overwinter in the southern parts of Europe and in Central-West Africa north of the Equator (Ferguson-Lees & Christie 2001; Agostini & Panuccio 2010; Panuccio et al. 2013b). In species showing this leapfrog migration, populations breeding furthest north spend the winter furthest south, while longitudinal patterns are not reversed: birds that breed furthest west tend to winter furthest west (Newton 2008). Several studies made on the migration of this species both by satellite telemetry and by direct visual observations at several migration watchsites of southern Europe suggest a more complex picture. In particular, a satellite telemetry study described both autumn and spring migration of Swedish WMHs showing that juveniles (first calendar year birds) migrated shorter distances and slower than adults, while no significant difference was found between adult males and adult females (Strandberg et al. 2008), although the analysis of recoveries of ringed birds suggests that males tend to migrate on longer distances (Wernham et al. 2002; Panuccio et al. 2013b). In addition, monitoring carried out at Falsterbo (Sweden; Fig. 1) during autumn migration showed that juveniles outnumbered adults, perhaps as a consequence of adults being less inclined to follow the mainland, while, among adults, females outnumbered males: it has been proposed that this may be explained by the polygyny of the species (Kjellén 1992). Conversely, monitoring made at several watchsites at lower latitudes, in Italy, Malta and Greece, showed the opposite, with adults outnumbering juveniles and adult males outnumbering adult females (Agostini & Logozzo 2000; Agostini et al. 2003, 2017; Panuccio et al. 2013a), while a recent study focusing on the passage of different age classes at Batumi (Georgia)

Fig. 1. — Location of the study areas in southern Italy (1 Strait of Messina) and Georgia (2 Batumi) (for comparison, 3 Strait of Gibraltar, 4 Bosphorus, 5 Falsterbo).

revealed that also along this easternmost flyway adults outnumber juveniles (Vansteelant et al. 2019). Finally, surveys made on WMHs wintering in Italy and central Europe showed that juveniles outnumber adults while, among adults, nearly all are females (Clarke 1995; Agostini & Logozzo 2000; Panuccio et al. 2005). To explain these results some authors suggested that, at least among WMHs migrating through this Mediterranean area, females, perhaps both juveniles and adults, might migrate shorter distances than males wintering at lower latitudes. Since larger females capture larger prey and, probably, are able to tolerate colder temperatures and fast longer than males, they might survive at higher latitudes during the winter on the basis of the Bergman's rule (Agostini & Logozzo 2000; Panuccio et al. 2005). Apparently, almost exclusively adult males belonging to resident populations spend the winter in Europe while nothing is known about autumn migration patterns in relation to sex classes in easternmost populations, accounting most of WMHs breeding in Europe with a notable increase reported since 1980s (BirdLife International 2004, 2018; Blanc et al. 2013; Panuccio et al. 2013b). The aim of this study is to fill this gap, by comparing the autumn migration patterns of this species at two watchsites in Italy (Strait of Messina) and Georgia (Batumi). In particular, we addressed the following questions: what is the sex ratio of WMHs during autumn migration? Does it differ between the two sites? What are the differences in the timing of autumn migration between sexes and age classes and between the two sites? Several recoveries of ringed birds showed that WMHs passing through the Central Mediterranean flyway belong to populations breeding in northern (Sweden, Finland and Baltic States) and central-eastern Europe (Germany, Poland, Czech Republic, Slovakia, Austria and Hungary), while most of those seen at Batumi probably come from breeding grounds in western Russia (Spina & Volponi 2008; Vansteelant et al. 2019).

METHODS

Study area and monitoring

The Italian watchsite was inland of the Strait of Messina (38°12′54″N, 15°49′25″E) on the Calabrian Apennines (southern continental Italy), on a flat highland (Aspromonte plateau, altitude 1000 m a.s.l.) west of the major mountain ridge in this area (Fig. 1). Here occurs the highest concentration of WMHs during autumn movements along the central Mediterranean flyway. Watchsite in Georgia was located northeast of Batumi, in a geographical bottleneck of a few kilometres width between the Black Sea to the west and the cloud covered Pontic Mountains to the east (Verhelst et al. 2011; Vansteelant et al. 2014; Wehrmann et al. 2019; Fig. 1). At Batumi, two count stations were chosen on an approximate east–west transect, 2 and 6 km east of the coast (41°41′05″N, 41°43′51″E and 41°41′08″N, 41°46′43″E) at 338 and 424 m above sea level. At both sites observations, aided with binoculars and telescopes, were carried out from 26 August to 30 September 2011–2017, each day from 9:00 a.m. until about 2 hr before sunset, and focused on the migration of adult males, adult females, and juveniles (first calendar year birds) based on the birds' plumage attributes (Forsman 1999, 2016), when possible. To limit a possible bias resulting from an easier identification of adult males, the numbers of adult females and juveniles were derived following the method used by Kjellén (1992) at Falsterbo. In particular, a proportion of WMHs was labelled "female/juvenile" meaning that they were either adult females or juveniles. Then, each day the group "female/juvenile" was divided between adult females and juveniles according to their proportions among identified individuals.

Data analysis

We used Linear Mixed Model (LMM) (Zuur et al. 2009) and Multiple Linear Model (MLM) (Legendre & Legendre 1998) to investigate the difference in the migration of WMHs between the

two sites. In particular, we ran two models. In the first (LMM), we used as response variable the number of WMHs passing per sex/age class per year per site (N = 42), whereas the sex/age class (adult male, adult female, juvenile), the site (Strait of Messina, Batumi) and their interaction were treated as fixed effects. To account for the use of repeated measures, the year was used as a random effect. In the second model (MLM), we used as response variable the median Julian date of the WMHs' migration. The year, the sex/age class (adult male, adult female, juvenile), and the site (Strait of Messina, Batumi) were used as covariates. The significance of the coefficients was calculated on the basis of the Wald test (Zuur et al. 2009). We used the Generalised Variance Inflation Factor (particularly GVIF$^{(1/2df)}$) with a threshold of 3 to exclude the variable collinearity (Fox & Monette 1992; Zuur et al. 2010; Pinke et al. 2012; Mizerek et al. 2016). The normality of the model's residuals was tested by the Kolmogorov-Smirnov test (Legendre & Legendre 1998) and the goodness-of-fit of the models obtained was assessed by the Pearson's χ^2 test (Legendre & Legendre 1998; Agresti 2007). The explained variance R^2 was used as a measure of the variation explained by the models, both for LMM and for MLM (Legendre & Legendre 1998; Nakagawa & Schielzeth 2013). The analysis was performed using the statistical software R v.3.3.2 (R Core Team 2016) and the packages "lme4" (Bates et al. 2019), "car" (Fox & Weisberg 2011), and "MuMIn" (Bartoń 2010).

RESULTS

At the Strait of Messina, a total of 14,382 WMHs were counted during the 7-year period, on average 2055 ± 187 (SE) birds per autumn season. A total of 7807 (54%) birds could be aged and sexed or at least labelled as "female/juvenile" (adult males = 2900; adult females = 984; juveniles = 1224; female/juvenile = 2699). In this sample, a total of 5211 (66.7%) adults and 2596 (33.3%) juveniles were estimated, as explained above. At Batumi, 37,804 individuals were counted, on average 5401 ± 312 (SE) birds per autumn season. Here, it was possible to determine age and sex or at least to label as "female/juvenile" a total of 13,039 birds (34.5% of the birds counted; adult males = 4465; adult females = 2355; juveniles = 4435; female/juvenile = 1784) and this allowed to estimate 7419 (56.9%) adults and 5620 (43.1%) juveniles, as explained above. At both sites, adult males and juveniles outnumbered adult females (Table 1). In particular, among adults, a total of 2311 (44.3%) and 2954 (39.8%) females were

Table 1.

Parameter estimates of the LMM comparing the number of migrating WMHs between sites and sex/age classes. The confidence intervals (CI) of the estimates are shown.

Variables	Estimate	SE	CI	χ^2	P
Intercept	5.702	0.122			
Site Batumi[1]	0.308	0.140	0.048, 0.569	43.682	< 0.001
Sex/age class M[2]	0.270	0.140	0.009, 0.531	19.786	< 0.001
Sex/age class J[2]	0.149	0.140	– 0.112, 0.409	19.786	< 0.001
Site Batumi × sex/age class M[1,2]	0.165	0.198	– 0.204, 0.533	6.950	0.031
Site Batumi × sex/age class J[1,2]	0.510	0.198	0.142, 0.879	6.950	0.031

[1]For the site, the reference level is the Strait of Messina.
[2]For the sex/age class, the reference level is the female.

Table 2.

Parameter estimates of the MLM to investigate the median date (Julian day) of WMHs migrating between the Strait of Messina and Batumi. The confidence intervals (CI) of the estimates are shown.

Variables	Estimate	SE	CI	χ^2	P
Intercept	4.607	2.128			
Sex/age class J[1]	0.008	0.005	– 0.002, 0.019	4.624	0.016
Sex/age class M[1]	– 0.007	0.005	– 0.018, 0.003	4.624	0.016
Year	0.0005	0.001	– 0.002, 0.003	0.201	0.657
Site[2]	– 0.014	0.004	– 0.022, – 0.005	10.852	0.002

[1]For the sex/age class, the reference level is the female.
[2]For the site, the reference level is the Strait of Messina.

estimated at the Strait of Messina and Batumi, respectively. As a result, the proportion of males was significantly higher at Batumi (60.2% vs 55.7%).

   The analyses showed that the site, the sex/age class and their interaction were significant, whereas the year was not. Therefore, at Batumi WMHs migrated earlier than at the Strait of Messina and higher proportion of juveniles was reported, also when compared only with that of adult males (Contingency table: χ^2 = 110; df = 1; $P < 0.001$). At both sites, adult males migrated earlier than adult females (Median dates: Strait of Messina, M = 16 September, F = 17 September; Batumi: M = 12 September, F = 15 September). Juveniles migrated later than adult females at the Strait of Messina but not at Batumi (Median dates: Strait of Messina, F = 17 September, J = 22 September; Batumi: F = 15 September, J = 15 September; Table 2, Fig. 2). In general, considering the minimum and the maximum median dates in the study period, the intervals in which the bulk of migration occurred were 11 and 18 days long at Batumi (10 September–20 September) and at the Strait of Messina (8 September–25 September), respectively.

   In the LMM there was not multicollinearity (GVIF[(1/2df)], site = 1.732, sex/age class 1.414, site × sex/age class 1.682) and the residuals were normally distributed (D = 0.104; P = 0.718). Moreover, its predicted values are significantly correlated with the observed one (r = 0.866; $P < 0.001$), the marginal R^2 is equal to 0.530 and the conditional R^2 is equal to 0.691. In the same way, the covariates used in the MLM showed the absence of multicollinearity (GVIF[(1/2df)], year = 1.000, sex/age class 1.000, site 1.000) and the residuals were normally distributed (D = 0.073; P = 0.966). In addition, its predicted values are significantly correlated with the observed one (r = 0.595; $P < 0.001$) and the R^2 is equal to 0.354.

DISCUSSION

   Our results show that differences in relation to sex classes in migrating WMHs are more evident at Batumi than at the Strait of Messina. In addition, with an average production of about two fledged young per breeding pair (Clarke 1995; Simmons 2000), juveniles are underrepresented at both sites. The male-biased sex ratio estimated at the Strait of Messina among adults, which confirms that of a previous study made in 1990s (Agostini & Logozzo 2000), was very similar to that reported in broods of birds breeding
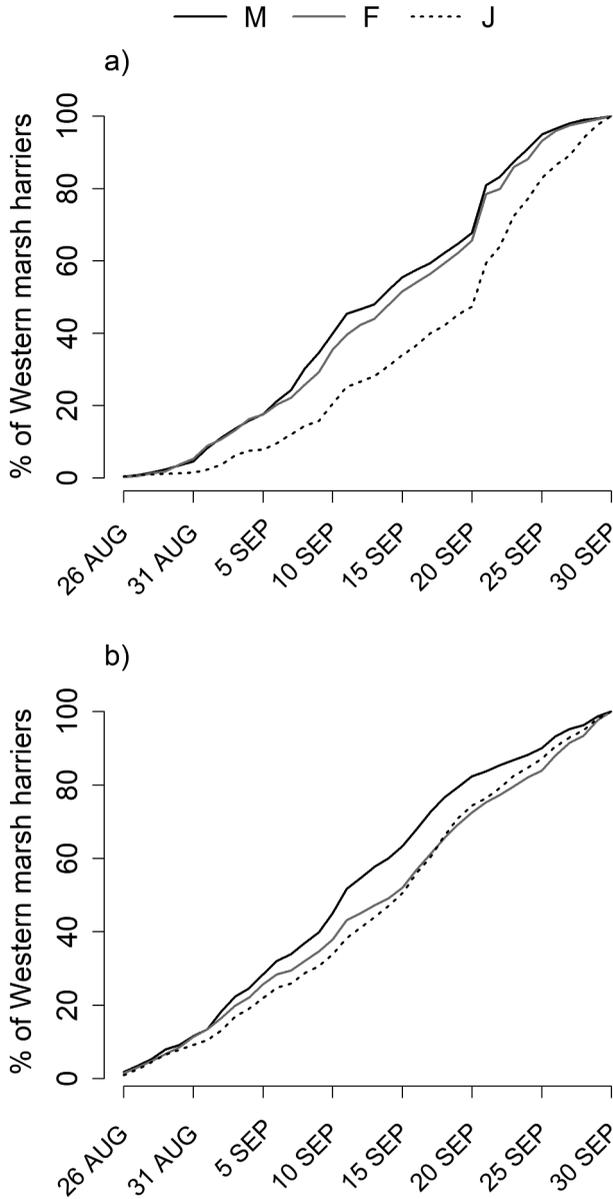
Fig. 2. — The cumulative percentage of migrating WMHs divided by sex/age categories obtained in the 7-year period at the Strait of Messina (a) and Batumi (b).

in The Netherlands and Poland (% of males 54.8 and 54.2, respectively; Witkowski 1989; Zijlstra et al. 1992). At Batumi, the proportion of males was even higher. Studies made by satellite telemetry have shown that migrating WMHs change their behaviour in relation to crosswinds showing drift, compensation and overcompensation during

different legs of their journeys (Klaassen et al. 2011; Vansteelant et al. 2020). However, in our case, it is unlikely that a higher proportion of adult males was reported at Batumi because of intersexual differences in response to crosswinds of birds migrating along the eastern coast of the Black Sea. As opposed to Kjellén (1992), who suggested that the higher proportion of adult females recorded at Falsterbo could be a consequence of a higher tendency to polygyny in that population, it has been suggested that a male-biased population in polygynous species could be explained by the benefit of rearing sons who later attract two or more females: a polygamous male WMH raises on average twice as many fledglings than a monogamous one (Zijlstra et al. 1992; Simmons 2000). Polygyny, nearly always bigamy, has been widely reported for this species, being more prevalent in certain regions and strictly related to the abundance of food (Clarke 1995; Simmons 2000). However, the study made on the male-biased populations in The Netherlands and Poland showed that the proportion of males produced increases during the season, and is not concentrated during the period of good food conditions as should be expected for the more rewarding sex (see also Dijkstra et al. 1990). Being male WMHs about 20% lighter than females and therefore the cheaper sex to rear using 20% less energy as nestlings (Riedstra et al. 1998), it has been suggested that their proportion could increase in denser populations in which competition for food increases (Simmons 2000). As mentioned above, most of the birds passing through the Batumi bottleneck are probably born or breed in Western Russia, where it has been estimated the presence of about the half of the whole European population of this species with a notable increase since 1980s (BirdLife International 2004, 2018). Future research should investigate both the population density and the sex ratio in broods of that region, as well among WMHs breeding in Sweden where a female-biased population is expected as suggested by Kjellén (1992). However, on the basis of observations made in Italy and central Europe revealing a female-biased population among adult WMHs wintering there, we cannot exclude that a higher proportion of adult females breeding in Western Russia might choose to migrate shorter distances wintering in eastern Europe affecting the male biased sex ratio reported at Batumi. Wide wintering areas of this species are located in eastern Europe, around north-western Black Sea as well as in the Balkan Peninsula (Ferguson-Lees & Christie 2001; Abuladze 2013), but there is lack of information about both numbers and proportion of age and sex classes of WMHs wintering there. However, because of the underrepresentation of juveniles at both migration sites, a juvenile-biased wintering population is expected, as observed in Italy and central Europe.

In a resident population in west-central France, a substantial proportion (34%) of adult males shows a permanent female mimicry while only 10% look like the typical field-guide male, so much so that this population appears as an outlier (Blanc et al. 2013). Adult males recorded in our study showed varying degrees of the grey plumage described by Forsman (1999, 2016) and their large number at both sites is in agreement with the conclusion that adult males showing a permanent female-like plumage are very rare elsewhere out of west-central France (see also Wehrmann et al. 2019). As mentioned above, the sex ratio we estimated at the Strait of Messina was very similar to that reported in broods in the Netherlands and Poland. Therefore, the potential bias resulting from female-like males being misidentified as females does not seem to be significant, since the passage of a substantial proportion of female-like males should have caused an evident distortion towards females in our estimations.

As regards migration phenology, at Batumi WMHs migrated slightly earlier than at the Strait of Messina probably because Batumi is situated more northerly (41°41′N

vs 38°12′N). As a matter of fact, at Falsterbo (55°39′N) the passage occurs earlier, peaking at the end of August (Kjellén 1992). At both sites, adult males migrated slightly earlier than adult females and at the Strait of Messina adult females earlier than juveniles. These results are in contrast with those of the study made at Falsterbo where juveniles migrated earlier than adults and, among adults, females earlier than males (Kjellén 1992). A recent study made at the Strait of Messina has shown that this species suspends moult during autumn migration, just growing the new feathers minimising the energy required for moulting (Ramirez & Panuccio 2019). Since WMHs largely use flapping flight during migration, gaps in the wings would also increase the energetic costs. Moreover, females showed a more advanced moult stage confirming that in this species they commence moult earlier than males (Kjellén 1992). In his study in southern Sweden, Kjellén suggested that this would explain why adult females also migrated earlier than adult males at Falsterbo. Then, why in our study adult males migrated slightly earlier? As mentioned above, the satellite study made on WMHs belonging to the Swedish population showed that juveniles migrated slower than adults, but did not show significant differences between autumn migration patterns of adult males and adult females (Strandberg et al. 2008). Future research on birds belonging to Eastern European populations should verify if possible intersexual differences concerning migration length, speed and direction might affect also their migration phenology at lower latitudes.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

AUTHOR CONTRIBUTION

N. Agostini made bird observations prepared data for analysis and wrote the first draft of the manuscript. M. Panuccio and G. Chiatante made bird observations and did all the statistical analyses. G. Dell'Omo helped with the study design.

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