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Morphology, flight performance, and water crossing tendencies of Afro-Palearctic raptors during migration

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Abstract Raptors primarily use soaring-gliding flight which exploits thermals and ridge lifts over land to reduce energetic costs. However during migration, these birds often have to cross water surfaces where thermal currents are weak; during these times, birds mainly use flapping (powered) flight which increases energy consumption and mortality risk. As a result, some species have evolved strategies to reduce the amount of time spent over water by taking extensive detours over land. In this paper, we conducted a meta-analysis of water-crossing tendencies in Afro-Palearctic migrating raptors in relation to their morphology, their flight performance, and their phylogenetic relationships. In particular, we considered the aspect ratio (calculated as the wing span squared divided by wing area), the energetic cost of powered flight, and the maximum water crossing length regularly performed by adult birds. Our results suggest that energy consumption during powered flight predominately affects the ability of raptors to fly over water surfaces [*Current Zoology* 61 (6): 951–958, 2015].

Keywords Water crossing, Aspect ratio, Powered flight, Migration, Raptors, Wing tip

Flight is the primary mode of movement in birds. Different flight styles have evolved under selective pressures. As a result, flight style, such as morphology, is a compromise between foraging, migration, dispersal, and reproduction (Hedenström, 2002; Åkesson and Hedenström, 2007). The most common flight style among birds is flapping (powered) flight which requires a high metabolic rate and energy expenditure changes depending upon the morphology of the bird (Pennycuick, 2008). For this reason, large and some medium-sized bird species avoid powered flight by exploiting thermal currents and ridge lifts over land (i.e. soaring-gliding flight; Newton, 2008). Soaring-gliding flight is significantly less energetically expensive than active flight (Baudinette and Schmidt-Nielsen, 1974; Hedenström, 1993).

Since migrating land birds often face long, non-stop flapping flights over water surfaces where thermal currents are very weak, especially in temperate zones, and they cannot land, their morphological adaptations can minimize the energetic expenditure required (Hedenström, 1993). On the other hand, species that do not have morphological characteristics that allow for long powered flight may have behavioral adaptations, such as avoiding large bodies of water by taking long detours over land (Alerstam, 2001: Agostini et al., 2002; Meyburg et al., 2002; Panuccio et al., 2012). In particular, Alerstam (2001) highlighted the importance of the "reduction of fuel transport costs across barriers" that "may well be of widespread importance for the evolution of detours in bird migration, especially where barrier distances are long". During long non-stop flights, migrants cannot feed or drink, and they only use body energy stores and body metabolic water while flying at a very high metabolic rate (Jenni-Eiermann et al., 2002; Klaassen, 1996; Pennycuick et al., 1996). Pennycuick and colleagues (2003) showed that "long over-water flights by land birds (even those that can rest on the water) need generous fuel reserves for an acceptable level of reliability".

Nearly half of diurnal raptor species are migratory (Bildstein, 2006). Raptors are large or medium sized land birds that primarily use soaring-gliding flight during migration. However, flight style varies among these species (Panuccio, 2011; Limiñana et al., 2013; Malmiga et al., 2014) and Kerlinger (1985, 1989) suggested that water-crossing tendencies of a given species depend on its wing shape. In particular, Kerlinger hypothesized that the aspect ratio (AR) of raptor wings is an impor-

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tant morphological characteristic in water-crossing behavior. The AR is a shape index for a wing(s) calculated as the wing span squared divided by wing area. According to this hypothesis, birds with relatively long and pointed wings (high aspect ratio) are better suited for flying over water surfaces than birds with relatively short and rounded wings (low aspect ratio), because the first ones decrease induced drag and thus the energetic cost of powered flight. Hedenström (1993) stated that a larger wing span reduces the cost of flight: "especially for soaring migrants there should be selection for long but also thin wings, which is equivalent to an increased aspect ratio". On the other hand, other research suggest that body mass can also affect energy consumption rates during powered flight (Pennycuick et al., 1996; Pennycuick, 2008); consequently, heavier raptor species are more reluctant to fly over open sea due to higher energy consumption rates during powered flight (Bildstein et al., 2009; Panuccio et al., 2012, 2013b).

The aim of this paper is to compare morphology and flight performances of Afro-Palearctic raptors in relation to their water-crossing tendencies during migration and discuss the results focusing on their consequences at behavioral and population levels. We used computational modeling (Pennycuick, 2008) to determine the relationship among aspect ratio, wing load, energy cost of powered flight, and water crossing length. In the analysis, we only considered Afro-Palearctic raptors since other species (e.g. Asian raptors) could migrate under different weather conditions affecting thermal strength and consequently the flight style during water surface crossings (see Yamaguchi et al., 2012). As reported by Bildstein (2006), "…. the trade wind zone stretching from 5° to 30° north and south of the equator permits migrants to travel long distances over water on sea thermals there.". This precludes a more extensive discussion of this topic.

1 Material and Methods

1.1 Data set

A total of 21 species of raptors were considered in our study. Data concerning body mass (BM), wing span (WS), wing area (WA) (Clark 1999, Bruderer and Boldt 2001), and maximum water crossing length (WCL) regularly performed by adult birds were collected from published literature (Kerlinger, 1989; Kjellén, 1992; Kjellén and Roos, 2000; Zalles and Bildstein, 2000; Hake et al., 2001; Meyburg et al., 2002, 2003, 2011, 2012; Meyburg and Meyburg, 2009; Panuccio et al., 2004, 2012; Agostini et al., 2000, 2001, 2004, 2012; Agostini and Panuccio, 2010; Ceccolini et al., 2009; Mellone et al., 2011a, 2011b; Limiñana et al., 2012; Trierweiler et al., 2014. Table 1). In order to provide theoretical information concerning energy consumption during powered flight, a published flight performance program based on flight mechanics "Flight computer model which calculates the rate at which a flying animal requires energy for whatever it is doing and it's based on classical aerodynamics" (Pennycuick, 2008) was used. Specifically, air speed was the value calculated one meter above sea level at the minimum power speed (V_{mp}), assuming no wind to homogenize the data analysis. V_{mp} is the speed for minimum mechanical power in level flight. Under the assumptions in "Flight", this is also the speed for minimum chemical power. Minimum chemical power was used for energy consumption during powered flight; Minimum chemical power is the rate at which fuel energy is required in aerobic flight when flying level at $V_{mp.}$ (Pennycuick, 2008). Moreover, the aspect ratio (wing span)^2 / (wing area) and wing load (weight / wing area) were calculated.

1.2 Statistical analyses

We used Pearson' s correlation tests to evaluate the relationships among the following variables: aspect ratio, wing load (body mass/wing area), and energy consumption during powered flight to evaluate the collinearity among possible predictors of the water crossing length. We used a Shapiro-Wilk test to determine whether data were normally distributed. Energy consumption during powered flight (PF) was log-transformed to meet the assumption of normality. Before modelling, we tested whether the observed variation in the water crossing trait was determined by a phylogenetic relationship among species. Since several possible phylogenetic comparative methods are available in the literature, we decided to compare results derived from at least two of the most used ones. At first we tested whether the phylogenetic signal (defined as the non-independence of a trait among species) was significantly different from 0 using a randomization procedure (Blomberg et al., 2003). If the ratio of the observed residual standard error on its randomized expected value among species (K) is < 1, the trait analyzed is not significantly influenced by the phylogenetic relationships. The phylogeny link among species was tested using the "phylosignal" function in the R package "picante" (Kembel et al., 2010). As a second phylogenetic method, we built 1000 phylogenetic trees using the website birdtree.org (Jetz et al., 2012, 2014, Rubolini et al., 2015). After that, we have computed a consensus tree

using MEGA 5.0 software (Fig. 1; Tamura et al., 2011). In the analysis, we have fitted and compared two Generalized Least Squares (GLS) linear models, one with phylogeny correlation structure (Grafen, 1989) and one without it, to explain variation in water crossing length (WCL) using energy consumption of powered flight and aspect ratio as fixed effects (phylogenetic tree available as supplementary material). GLS phylogeny models were compared with their respective GLS models built without weighing for the phylogenetic structure using a log-likelihood ratio test (Lewis et al., 2011). We applied the principle of parsimony in model comparison, i.e. - when the difference between two models were not significant, we selected the one using a smaller number of parameters. Before modeling, we checked for collinearity between AR and the log PF. We excluded the Eleonora's falcon *Falco eleonorae* from the analysis since it was an outlier (Fig. 2).

2 Results

Wing load was significantly correlated to both aspect ratio (rho = 0.49, *df* = 20, *P* = 0.027) and energy consumption during powered flight (rho = 0.64, *df* = 20, *P* = 0.002). Aspect ratio was not correlated to energy consumption during powered flight (rho = -0.20, *df* = 20, *P* = 0.372).

Water crossing length was not influenced by differences in phylogeny among species (*K* = 0.557, *P* = 0.072). The same result was obtained from the comparison between the GLS models (loglikelihood ratio = 2.259, *P* = 0.133). The selected, less complex, model without phylogeny structures showed a negative influence of energy consumption during powered flight on the water crossing length of birds (Fig.3) and no influence of the aspect ratio (Fig. 4, Table 2).

3 Discussion

Our results suggest that energy consumption during PF is the most important variable affecting water-crossing tendencies in raptors (Fig.3). Considering the aspect ratio (AR) which is the other variable affecting the water crossing length (WCL), we can find some substantial discrepancies (Fig. 4) in comparison with a previous study (Kerlinger, 1985). Since AR does not consider the shape of the wing tip, in particular if it is more or less pointed or rounded, it could be less suitable for

Table 1 Body mass (BM), wing span (WS), wing area (WA), aspect ratio (AR), energy consumption during powered flight (PF), wing loading (WL) and maximum water crossing length regularly performed during migration by adult of Afro-Palearctic raptors

Species	BM (kg)	WS (m)	WA (m²)	AR	PF (W)	WL	WCL (km)	References
Gyps fulvus	6.8	2.54	0.99	6.52	408	6.87	14	Zalles and Bildstein, 2000; Bildstein et al., 2009.
Aquila nipalensis	2.7	1.86	0.49	7.06	131	5.51	20	Meyburg et al., 2003, 2012.
Aquila pomarina	1.6	1.55	0.515	4.67	101	3.11	3	Meyburg et al., 2002; Meyburg and Meyburg, 2009.
Neophron percnopterus	1.8	1.59	0.55	7.12	85.4	5.07	130	Agostini et al., 2000, 2004; Ceccolini et al., 2001.
Circaetus gallicus	1.7	1.77	0.406	7.72	67.3	4.19	14	Mellone et al., 2011a; Panuccio et al., 2012.
Buteo rufinus	1.095	1.48	0.328	6.68	46.4	3.34	3	Zalles and Bildstein, 2000.
Buteo buteo	0.89	1.27	0.24	6.72	41.2	3.71	25	Kjellén, 1992; Kjellén and Roos, 2000.
Pandion haliaetus	1.125	1.6	0.313	8.18	37.9	3.59	500	Zalles and Bildstein, 2000; Hake et al., 2001.
Milvus migrans	0.875	1.43	0.28	7.3	31.6	3.13	250	Panuccio et al., 2004.
Pernis apivorus	0.79	1.3	0.236	7.16	30.6	3.35	280	Agostini et al., 2012; Panuccio et al., 2004.
Aquila pennata	0.735	1.24	0.2	7.69	29.1	3.68	14	Kerlinger, 1989; Zalles and Bildstein, 2000.
Circus aeruginosus	0.54	1.28	0.225	7.28	17.4	2.4	500	Agostini et al., 2001; Agostini and Panuccio, 2010.
Circus macrourus	0.375	1.09	0.16	7.43	12.2	2.34	350	Kerlinger, 1989; Zalles and Bildstein, 2000.
Falco eleonorae	0.37	0.94	0.051	17.3	10.5	7.25	1200	Mellone et al., 2011b.
Accipiter nisus	0.204	0.68	0.07	6.61	9.5	2.91	25	Kjellén and Roos, 2000; Zalles and Bildstein, 2000.
Circus pygargus	0.31	1.09	0.146	8.14	8.7	2.12	350	Zalles and Bildstein, 2000; Trierweiler et al., 2014.
Falco subbuteo	0.215	0.78	0.095	6.4	8.64	2.26	500	Zalles and Bildstein, 2000; Meyburg et al., 2011.
Accipiter brevipes	0.184	0.69	0.074	6.43	7.97	2.47	3	Kerlinger, 1989; Zalles and Bildstein, 2000.
Falco tinnunculus	0.18	0.76	0.069	8.37	6.01	2.61	500	Kerlinger, 1989; Zalles and Bildstein, 2000.
Falco vespertinus	0.162	0.73	0.073	7.3	5.71	2.22	350	Kerlinger, 1989; Zalles and Bildstein, 2000.
Falco naumanni	0.13	0.69	0.061	7.8	4.42	2.13	350	Zalles and Bildstein, 2000; Limiñana et al., 2012.

explaining the WCL of birds than the PF value. Indeed the expected positive influence of AR on WCL does not have a significant effect in our dataset (Fig. 4, Table 2). Conversely, PF values give us a direct measure of energy consumption during powered flight taking into account both the wing shape and the weight of the bird (Pennycuick, 2008). In particular among raptors with a broad distribution in Europe, some species with higher aspect ratios but more rounded wings perform shorter water crossings during migration (Table 1). For example, the short-toed snake eagle *Circaetus gallicus*, a species which crosses the Mediterranean Sea at the Strait of Gibraltar (approximately 14 km wide) and at the Bosphorus (1.5–3 km wide) has a higher aspect ratio but more rounded wings than several species undertaking crossings of more than 250 km through this water surface (Table 1). In particular, birds of this species breeding in Italy and Greece follow long, extremely detoured routes rather than directly crossing the Mediterranean

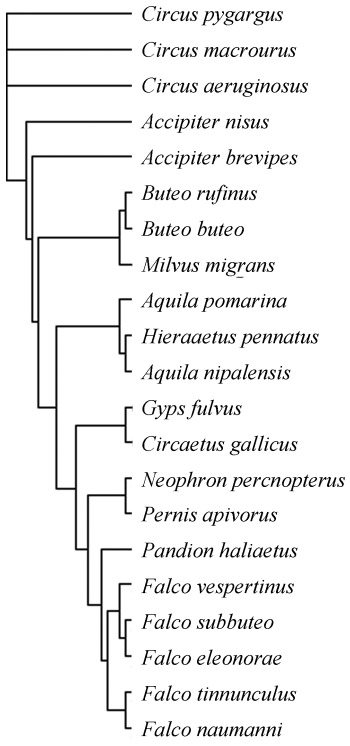

Fig. 1 Consensus tree performed with MEGA 5.0 software and based on 1000 phylogenetic trees

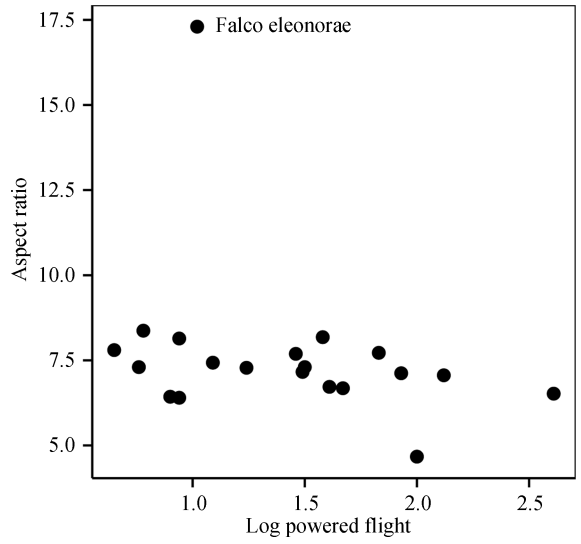

Fig. 2 Relationship between PF and AR for 21 different species of Afro-Palearctic raptors

Eleonora's falcon *Falco eleonorae* is highlighted as an outlier for the distribution of the AR values.

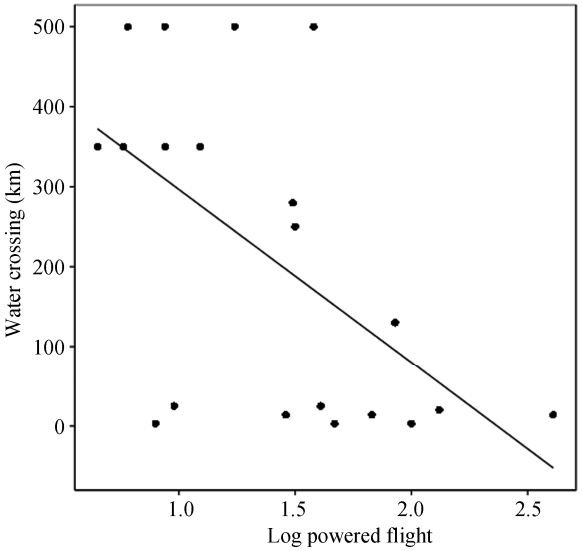

Fig. 3 Relationship between water crossing length and the logarithmic of powered flight for 20 species of Afro-Palearctic raptors (*Falco eleonorae* excluded)

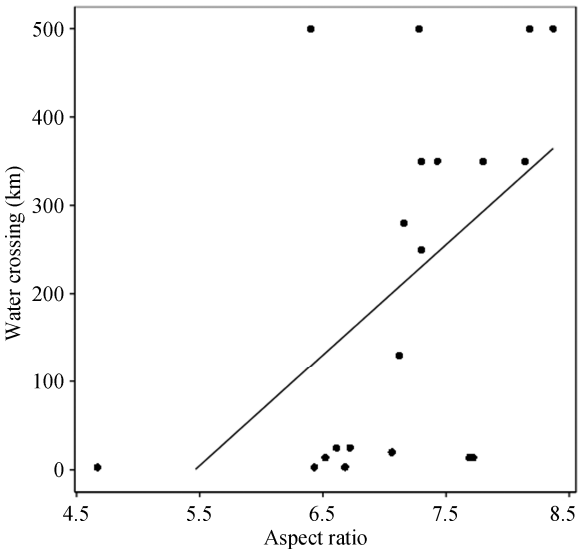

Fig. 4 Relationship between water crossing length and the aspect ratio for 20 species of Afro-Palearctic raptors (*Falco eleonorae* excluded)

Table 2 Linear model fitted using the Generalized Least Squares (GLS) approach applied to 20 species of Western Palearctic raptors

	Estimate	Std. Error	*t*-value	*P*-value
(Intercept)	-171.70	395.12	-0.434	0.669
Aspect Ratio	86.33	48.02	1.798	0.090
Log Powered Flight	-167.18	75.25	-2.221	0.040

Sea (Agostini et al., 2002; Mellone et al., 2011a; Panuccio et al., 2012). Their movements oppose the main migration direction of other birds in order to find straits where sea-crossings are narrower probably retracing the colonization process (Agostini and Mellone, 2008). This strategy could be explained by the high cost of powered flight (Panuccio et al., 2012. Table 1). In contrast, Egyptian vultures *Neophron percnopterus* breeding in southern continental Italy and Sicily, in spite of their higher cost of powered flight and lower aspect ratio than the short-toed snake eagles (Table 1), undertake the long sea crossing of the Channel of Sicily (approx. 150 km wide; Agostini et al., 2004; Ceccolini et al., 2009). Unlike short-toed snake eagles, Egyptian vultures breeding in southern Italy did not evolve a detoured migration from Western Europe. In Tunisia, there is a good number of breeding pairs of this species (Isenmann et al., 2005), and a high percentage of non-reproductive individuals (2nd to 4th calendar year birds) have been observed crossing the Channel of Sicily (Agostini et al., 2000, 2004). Therefore. it is possible that the small population breeding in southern Italy is not interacting with populations in Western Europe but, instead, with vultures located in North Africa. Consequently, the Channel of Sicily might not be a barrier long enough to induce the Italian population to become sedentary, but long enough to reduce the gene flow among populations in Tunisia and Italy exasperating its recent population decline (Newton, 1998). On the other hand, the absence of a migratory flyway between Crete and Lybia (Lucia et al., 2011; Panuccio et al., 2013a) suggests a threshold for crossing length beyond which an Egyptian vulture will endure. This hypothesis is corroborated by a study that tracked vultures from the Balkans using satellite telemetry; five out of seven individuals died while attempting to cross the eastern Mediterranean (www.lifeneophron.eu/en/Tagging.html; November, 15, 2013).

The booted eagle *Aquila pennata*, is another species with a broad distribution in Europe that crosses the sea at the Strait of Gibraltar and at the Bosphorus. Concerning aspect ratio and energy cost of powered flight we noted very similar values to those of the European honey buzzards *Pernis apivorus* and black kites *Milvus migrans* (Table 1). Unlike these other species, the booted eagle does not cross the central Mediterranean to reach its nesting areas located in Eastern Europe (Agostini, 2005); however, a significant population does breed in Tunisia (Isenmann et al., 2005). In addition, large numbers of booted eagles, mostly juveniles, reach the Italian peninsula and Sicily to spend the winter. These individuals take the same detoured route performed by short-toed snake eagles (i.e. from Western Europe via north-western Italy), but fly in the opposite direction; only a few individuals are observed attempting to cross the sea between western Sicily (southern Italy) and North Africa (Baghino et al., 2007; Panuccio et al., 2011). The Balkans booted eagles migrate through the Bosphorus, while very few individuals are observed migrating in southern Greece en route to Crete and Lybia (Lucia et al., 2010). Since historical information reported that the past numbers of booted eagles in Greece were not much more numerous than now (Handrinos and Akriotis, 1997), it has been proposed that booted eagles mostly winter in southern Greece and Crete (Panuccio et al., 2013a). Research in the central Mediterranean region showed that flocking behavior also plays a role in water crossing tendencies when flying over the open sea. For example, both European honey buzzards and black kites hesitate in front of the water barrier when they reach the Cap Bon Promontory (NE Tunisia) during spring migration. They tend to undertake the crossing when migrating in large flocks with the first individuals taking a decision (crossing or not) followed by the others in the flock (Agostini et al., 1994; Agostini and Duchi, 1994). Unlike European honey buzzards and black kites, booted eagles migrate in small flocks of < 5 individuals (Kerlinger, 1989). This behavior may explain why booted eagles do not cross the Central Mediterranean en route to Eastern Europe and instead undertake a long eastern detour as opposed to a time minimization strategy as expected at least during spring migration (Nilsson et al., 2013).

The flight characteristics and water-crossing tendencies of the Eleonora's falcon are unique. This species has an extraordinarily high AR which was excluded from the analysis. Eleonora's falcons breed on small rocky Mediterranean islands where they forage mainly on small, migratory birds; the falcons then migrate to Madagascar for the winter (Ferguson-Lees et al., 2001). Unlike other species of larger raptors breeding on islands, the Eleonora's falcon is not sedentary (Ferrer et

al., 2011). Gangoso et al. (2013) suggested that the ecological specialization of the falcon during the breeding season could prevent the shift from migratory to sedentary behavior. However, a recent study made using satellite telemetry showed that water surfaces are not a real barrier for this falcon. During migration, the falcons do not avoid ecological barriers, nor follow narrow corridors. In fact, it is the only species among Afro- Palearctic raptors to cross a 1000 km body of water to reach Madagascar (Mellone et al., 2013). This migration strategy could also explain why this species did not become sedentary both in Europe and Madagascar and why, unlike other migrating raptors, substantial numbers of 2nd cy birds return to their breeding colonies (Gangoso et al., 2013).

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Supplementary Materials

Consensus tree used for the statistical analysis:

((((((((((*Falco_subbuteo*, *Falco_vespertinus*), (*Falco_naumanni*, *Falco_tinnunculus*)), *Pandion_haliaetus*), (*Neophron_percnopterus*, *Pernis_apivorus*)), (*Gyps_fulvus*, *Circaetus_gallicus*)), (*Aquila_pomarina*, (*Aquila_nipalensis*, *Hieraaetus_pennatus*))), ((*Buteo_buteo*, *Buteo_rufinus*), *Milvus_migrans*)), *Accipiter_brevipes*), *Accipiter_nisus*), *Circus_aeruginosus*, *Circus_macrourus*, *Circus_pygargus*);")