

Narrow sea crossings present major obstacles to migrating Griffon Vultures *Gyps fulvus*

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The flight behaviour of Griffon Vultures *Gyps fulvus* was studied at a major migration bottleneck, the Strait of Gibraltar in southernmost Spain, during the autumns of 2004 to 2007. The 14-km-wide sea channel significantly impeded the southern migration of the species into Africa, with many birds attempting repeated passage for weeks before crossing, and others not crossing at all and overwintering in Southern Spain. Water-crossing attempts were restricted to times between 11:00 and 14:00 h on days with light or variable winds, or on days with strong winds from the north or west. No crossing attempts were made on days with strong winds from the south or east. Vultures attempted to cross the Strait in large flocks and never attempted to do so alone. Although 29% of the birds soared during crossing attempts, at least until they flew beyond visible range of approximately 4 km, most engaged in considerable flapping flight when attempting to cross. Overall, birds flying over water flapped more than 10 times as frequently as those flying over land prior to crossing attempts. Vultures did not flap continuously, but intermittently in brief bouts of flapping interspersed with periods of gliding or soaring flight. The number of flaps per bout over water was significantly greater than the number of flaps per bout over land. Vultures flying over water that flapped at rates of 20 flaps or more per minute typically aborted attempted crossings and returned to Spain in intermittent flapping and gliding flight. There are numerous reports of Vultures falling into the Strait and drowning while attempting to cross, as well as reports of returning Vultures collapsing on the beach having reached Spain in spring (Barrios Partida 2006). Our observations indicate that passage of Griffon Vultures at the Strait of Gibraltar is limited by the species' over-water flapping-flight abilities, including its inability to flap continuously for even short periods of time. We suggest that even relatively short sea crossings represent significant obstacles to migrating Vultures and discuss the implications of this limitation on the distribution and abundance of the species.

Keywords: flapping rates, gliding, raptor migration, soaring, water-crossing behaviour.

Unlike many groups of migratory birds, birds of prey migrate largely by day, often in soaring flight (Newton 2008). Many raptors depend critically upon soaring flight to complete their migratory journeys (Bildstein 2006), and generally fly in flocks while migrating, presumably because doing so enhances the efficiency with which they find

updraughts to soar in (Kerlinger 1989, Bildstein 2006). Energy-efficient soaring flight appears to be a key innovation in the group (*sensu* Simpson 1953) in permitting large numbers of birds of prey to complete long-distance migratory movements with little or no refuelling en route (Kerlinger 1989, Bildstein 2006).

Some migratory raptors, including Ospreys *Pandion haliaetus*, several small hawks (e.g. Chinese Sparrowhawk *Accipiter soloensis*, Grey-faced

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Buzzard *Butastur indicus*), and several falcons (e.g. Amur Falcon *Falco amurensis*), regularly migrate long distances over water while soaring in the Trade-Wind Zones in sea thermals (*sensu* Pennycuick 1983, Bildstein 2006), and these and other raptors, including Western Honey Buzzards *Pernis apivorus* and many harriers *Circus* spp., sometimes migrate over water using both soaring and flapping flight (Kerlinger 1989, Agostini *et al.* 2005, Bildstein 2006). However, most long-distance migratory birds of prey, particularly obligate soaring migrants, appear reluctant to fly even short (i.e. < 25 km) distances over water, and instead migrate mainly, if not entirely, over land (Kerlinger 1989, Agostini 2005, Bildstein 2006). Many of the latter concentrate at isthmuses and short water crossings called migration bottlenecks (Brown & Amadon 1968, Evans & Lathbury 1973, Kerlinger 1984, 1985, 1989, Finlayson 1992, Meyer *et al.* 2000, Bildstein 2006). The reluctance to cross water, particularly among obligate soaring migrants, is thought to be due to the risk of fatigue associated with increased flapping flight, and the possibility of drifting off course due to crosswinds (Kerlinger 1989).

Previous studies of water-crossing behaviour have suggested that the decision whether to cross a water body is influenced by lifetime experience (i.e. differences in juveniles vs. adults at water crossings), local weather conditions, and, possibly, flocking behaviour. In general, juveniles appear more likely to make longer water crossings than adults (Agostini & Logozzo 1995, Viverette *et al.* 1996, Agostini *et al.* 2002, Hake *et al.* 2003). Furthermore, many migrants are more willing to cross water on following or light winds (Panuccio *et al.* 2002, Agostini *et al.* 2005) and are less likely to do so with opposing winds or strong crosswinds, particularly when the latter might cause the birds to drift over large bodies of open water (Kerlinger 1984, 1985, 1989, Meyer *et al.* 2000). Obligate soaring migrants, in particular, appear reluctant to make water crossings, and have been known to retrace their movements to avoid crossing them or to wait for ideal weather conditions before attempting a crossing (Allen & Peterson 1936, Kerlinger 1984, 1985, 1989, Finlayson 1992). In addition, flocking behaviour may enhance the likelihood of water-crossing behaviour in obligate soaring migrants at least in part because increased flock size increases the probability that the group will contain one or more individuals with a pronounced

tendency to continue migrating over water (cf. Agostini & Duchi 1994, Agostini *et al.* 1994).

Both New World (i.e. Cathartid) and Old World (i.e. Accipitrid) Vultures have relatively broad, low-aspect-ratio wings typical of species that regularly engage in thermal, cross-country soaring at low speeds over land, rather than the tapering, high-aspect-ratio wings of species such as pelicans *Pelecanus* spp. and frigatebirds *Fregata* spp., which typically soar over water (Pennycuick 1983). It has been suggested that all soaring birds would evolve high-aspect-ratio wings 'if soaring performance was the only requirement to be satisfied', but that selection for take-off performance often compromises this (Pennycuick 1983, p. 321). Indeed, Vultures flap vigorously when taking off from roosts, nest-sites and carcasses (McGahan 1973a, 1973b, K. Bildstein pers. obs.) and many species position their roosting and nesting sites in ways that minimize such flapping (Mundy *et al.* 1992). That wing shape might limit water-crossing behaviour in Vultures is supported by the fact that the only two Vultures that, at least occasionally, undertake relatively long (> 100-km) flights over water, the Turkey Vulture *Cathartes aura* and Egyptian Vulture *Neophron percnopterus* (Mundy *et al.* 1992, Agostini 2005), have relatively long, tapering wings with higher aspect-ratios than most other Vultures (Ferguson-Lees & Christie 2001).

Here we report on the flight behaviour of (Eurasian) Griffon Vultures *Gyps fulvus* during autumn migration at the Strait of Gibraltar in Southern Spain, where an estimated 4000–5000 Vultures cross into Africa each year (Camiña 2004, L. Barrios pers. comm.). Spanish populations of the Griffon Vulture have increased for two decades (Parra & Tellería 2004), and the annual passage of Vultures across the Strait of Gibraltar appears to have increased as well (L. Barrios pers. comm.).

Griffon Vultures are obligate-soaring migrants whose populations in Spain are partially migratory, with juveniles in the region being particularly prone to long-distance southward movements into Africa (Bernis 1983, Griesinger 1996, 1998). The species migrates later in the autumn than do most raptors and some individuals overwinter in Southern Spain rather than continuing on into Morocco and beyond (Garrido & Sarasa 1998, Garrido *et al.* 2002). Numbers of Griffon Vultures on the Spanish side of the Strait of Gibraltar increase through autumn as individuals wait to cross the Strait until conditions that favour soaring flight occur (Finlayson 1992).

Most crossing attempts are made at the narrowest stretch of the Strait, midway between Tarifa and Punta del Carnero (Finlayson 1992). Even so, many individuals attempting to cross turn back upon reaching the coastline (Bernis 1983).

We quantify the flight behaviour of Griffon Vultures attempting to cross the Strait of Gibraltar during the autumns of 2004 to 2007. Specifically, we report the flapping rates of individuals prior to and during attempted water crossings, as well as those of individuals returning to the Spanish coast after aborting a crossing. We also document the likelihood of crossing attempts as a function of local winds. Our findings are discussed in terms of physical limitations on the migrations of raptors, and how, in turn, such restrictions affect the geography and likelihood of raptor migration.

METHODS

Study area and observations

Griffon Vultures were observed along the northern shoreline of the Strait of Gibraltar, in the state of Cadiz, Southern Spain. The Strait is an approximately 20-km-long channel that connects the Atlantic Ocean and the Mediterranean Sea and that separates continental Europe (Southern Spain) from Africa (Northern Morocco) by as little as 14 km. Limestone mountains, including the 426-m-high Rock of Gibraltar at the eastern end of the Strait, and the 851-m-high Jebel Musa, in northernmost Morocco near the narrowest part of the Strait, dominate the landscape. Local flora consists of a mosaic of mainly Mediterranean scrub and pastureland. The human landscape includes scattered suburban and urban developments, including the town of Tarifa, and the small cities of Algeciras and Gibraltar (Finlayson 1992, Bildstein 2006).

Weather at the Strait is characterized by strong easterly (*levante*) and westerly (*poniente*) winds that blow on approximately 85% of autumn days, and that typically gust to over 100 km/h (Bernis 1980). Both wind speed and direction vary considerably among years, with easterly winds dominating in some years and westerly winds in others. Mean rainfall is approximately 60 mm in October and 120 mm in November (Finlayson 1992).

We recorded the flight behaviour of Vultures from a series of promontories 0.5–3 km north of the Strait, across approximately 30 km, between the outskirts of the small villages of El Pelayo

(approximately 36°03'N, 5°30'W) in the east and Camarinal (36°06'N, 5°43'W) in the west. Observation sites changed within and among days depending upon the locations of flying Vultures.

We used focal-animal sampling (Altmann 1974) and watched single individuals with 10 × 50 binoculars for 30 s each, using an alarm timer to establish the length of each observation period. All observations were limited to rainless periods. We reduced the likelihood of recording the same individual twice during each period by limiting the number of observations of individuals made in any one flock to no more than 10% of the total number of birds in the flock. For each observation we recorded the observation point, date and time of day, percent cloud cover and wind conditions and temperature on the ground using a portable thermometer and anemometer. Because wind conditions faced by flying Vultures appeared to differ considerably from those measured by us on the ground, we also used the modified wind speed and wind direction at 10 m, modelled from the National Oceanic and Atmospheric Association's Global Forecast System (GFS) available at the Windguru website (<http://www.windguru.cz>) to assess the impact of wind on water-crossing behaviour.

For each observation, we recorded the type of flight the bird was engaged in as 'circle soaring' in thermals, 'linear soaring' along mountain slopes or over water, or 'gliding'. We recorded the number of times birds flapped during each observation, as well as the numbers of flaps per 'flapping bout' (i.e. a period of continual flapping interspersed with brief to prolonged periods of soaring or gliding, during which the birds set their wings in a largely horizontal posture; Hankin 1913, p. 14). We also recorded the number of 'wing dips' made by the bird. Wing dips, which sometimes occurred twice in rapid succession, and have been called 'double dips' by some (e.g. Hankin 1913, p. 86), occur more slowly and appear to be more deliberate than individual flaps. They may act to increase the speed of both gliding and soaring (Koford 1953). We also recorded whether the bird was flying alone or in a flock and, if the latter, the size of the flock. Flocks were defined as groups of two or more Vultures flying in coincidental flight paths ≤ 75 m from each other. Finally, we recorded whether the bird was (1) flying over land before attempting or not attempting to cross the Strait, (2) flying over water while attempting to cross, (3)

returning toward Spain over water having aborted a crossing attempt or (4) returning over land having reached the Spanish coast following an aborted crossing attempt.

Data analyses

All statistical analyses were conducted using STATISTICA 7.1 software (Statsoft Inc. 2005). Because Vultures did not flap or wing dip, or both, during most 30-s observations, we used non-parametric procedures for most statistical testing. Flapping rates were compared among flight types using Kruskal–Wallis tests (Zar 1996), and wing-dipping using Mann–Whitney *U*-tests in pairwise comparisons of different flight situations (i.e. over water vs. over land). We also used this procedure to test for differences in flaps per bout over land vs. over water, and flaps per bout over water in Griffon Vultures and Turkey Vultures, the latter being a species with greater over-water abilities than the former.

The influence of wind on the numbers of attempts to cross water was assessed using 2×2 contingency tables and chi-square statistics (Zar 1996). In addition, we analysed the relationship between flock size, weather conditions, and propensity of Vultures to cross the strait using binary logistic regression, with over-land vs. over-water observations as the dependent variable and weather conditions (air temperature, wind speed, wind direction) and flock size as independent variables. We used Hosmer–Lemeshow goodness-of-fit tests (Hosmer & Lemeshow 2000) to assess the fit of all possible models to the data, and selected a set of candidate models with non-significant chi-square values (indicating good fit) for further assessment. Among the candidate models, we selected the model that minimized Akaike's Information Criterion (AIC) to estimate parameter values (Burnham & Anderson 2002). Parameter estimates were interpreted as indications of effect size and direction, and odds ratios (OR) with 95% confidence intervals (CI) were used to characterize the influence of independent variables on the probability of a water crossing. Odds ratios > 1.0 with 95% CI not overlapping 1.0 were interpreted as evidence of a significant increase in probability of crossing, whereas OR < 1.0 with 95% CI not overlapping 1.0 were interpreted as evidence of a significant decrease in probability of crossing.

RESULTS

Griffon Vultures were observed for 26 days in October and November, 2004 to 2007, yielding 193 30-s observations on 3 days in 2004, 349 observations on 7 days in 2005, 546 observations on 6 days in 2006, and 435 observations on 10 days in 2007. On most days of observation, several dozen to several 100 Griffon Vultures approached the coast from inland between 09:25 and 12:09 h (mean = 10:48 h). Most birds travelled within and between flocks of Vultures numbering several to more than 100 birds that coalesced or split over time. Many flocks flew to within < 0.5 km of the coast before returning to areas ≤ 5 km inland. Serious over-water passage attempts (those during which part or all of a flock was at least momentarily over the Strait) were restricted to periods between 10:59 and 14:18 h (mean = 12:49 h, $n = 167$).

Overall, we recorded 1523 30-s observations of the flight behaviour of Griffon Vultures. Most observations ($n = 1259$) occurred when birds were flying over land, either before attempting or refusing water crossings ($n = 1203$), or after returning inland following an aborted water crossing ($n = 56$). A total of 264 observations occurred when the bird was over water, either heading toward Morocco ($n = 167$), or returning to Spain after aborting a crossing ($n = 97$).

Flocking and crossing attempts

Vultures approached to within 3 km of the coast on 24 of 26 days of observations, but attempted actual crossings on only 11 days. Vultures attempted to cross the Strait in large flocks (mean = 59 ± 4.6 , $n = 167$) and never attempted to do so alone. On days when crossings were attempted, many flocks reached the coast before turning and retreating inland. When flocks did attempt crossings, Vultures that began to flap almost always turned and flew back toward Spain within 15 s of beginning to flap. Once 5–10% of birds in a flock began flapping and retreated, the remaining individuals in the flock turned and returned to the coast, some in soaring flight and others in intermittent flapping flight. Although individuals from such flocks often joined other flocks that were about to initiate a crossing, most travelled several kilometres inland as individuals before regrouping, and on two occasions were seen

perching on rocky outcrops several kilometres inland. We were unable to determine the extent to which flocks that had flown out of sight turned around and returned to Spain. However, birds often reappeared over the Strait within several minutes of the disappearance of a flock.

Flapping rates

Vultures flying over water, either as they attempted to cross the Strait (mean = 18.69 flaps per 30-s period) or as they attempted to return to the Spanish coast having aborted a crossing (mean = 15.94), flapped at more than 10 times the rate of those flying over land before attempting to cross (mean = 1.22), and more than twice as frequently as those flying over land when returning from an aborted crossing attempt (mean = 7.45) (Fig. 1, Table 1). Furthermore, whereas only 14% of Vultures flying over land flapped once or more during a 30-s observation, 71% of those flying over water did so.

Over water, Vultures flapped least when circle soaring ($H_{2,130} = 14.60$, $P = 0.007$), but this was not the case over land ($H_{2,1154} = 1.59$, $P = 0.45$) (Table 1). Both over water and over land, Vultures flapped more when gliding than during soaring (over water, gliding mean = 18.25 ± 1.27 , soaring mean = 12.50 ± 3.04 ; over land, gliding mean = 1.95 ± 0.27 , soaring mean = 1.27 ± 0.34),

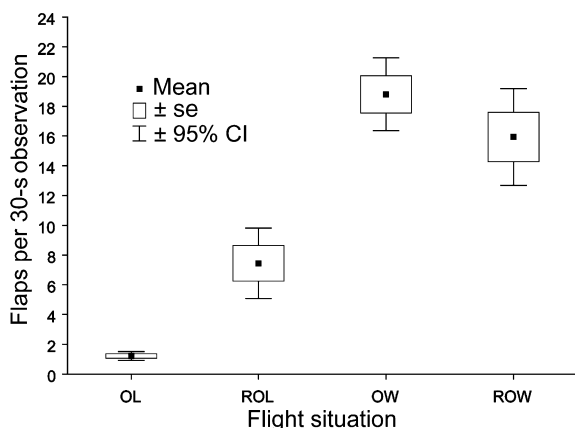


Figure 1. Numbers of times Griffon Vultures flapped during 30-s observations when flying over land prior to crossing attempts (OL, $n = 1203$), returning over land after aborting a water crossing (ROL, $n = 56$), flying over water toward Africa (OW, $n = 167$), returning over water after aborting a water crossing (ROW, $n = 56$).

although these differences were not significant (Table 1).

Wing-dipping

Wing-dipping was more frequent during gliding than during soaring over land (gliding mean = 0.28 ± 0.04 , soaring mean = 0.08 ± 0.01 ; $U = 85166$, $Z = 3.40$, $P = 0.0007$), but the difference was not significant over water (gliding mean = 0.04 ± 0.03 , soaring mean = 0.11 ± 0.11 ; $U = 1309.5$, $Z = -0.04$, $P = 0.96$) (Table 1).

Vultures flying over land wing-dipped significantly more than those flying outbound over water (over land vs. over water, $U = 89\ 852$, $Z = 2.19$, $P = 0.028$), but not significantly more than those returning to land over water (over land vs. returning over water, $U = 53\ 737$, $Z = 1.28$, $P = 0.199$) (Fig. 2). There was no significant difference in wing-dipping between birds flying over land prior to crossing vs. immediately after a crossing event ($U = 31\ 784$, $Z = 0.70$, $P = 0.48$) (Fig. 2).

Numbers of flaps per bout

The number of flaps per bout was significantly greater over water than over land (5.32 ± 0.15 vs. 4.05 ± 0.23 ; $U = 67\ 231$, $Z = -15.22$, $P < 0.001$). Maximum bout length was 14 flaps over water and nine over land (Fig. 3).

Winds and crossing attempts

Crossing attempts were significantly more likely when winds were light and variable, or when winds were > 5 knots from the northern or western quadrants, than when winds were from the southern or eastern quadrants ($\chi^2 = 75.4$, $P < 0.001$, $df = 1$; $\chi^2 = 89.1$, $P < 0.001$, $df = 1$, respectively) (Fig. 4).

Regression models

Of the regression models considered, only one independent variable, wind direction, explained significant variation in crossing data (Appendix 1), with winds from the northern and western quadrants positively influencing crossing attempts ($P \leq 0.0001$, OR = 1.127, lower confidence limit = 0.778, upper confidence limit = 1.632) and winds from the eastern or southern quadrants negatively

Table 1. Numbers of flaps and wing dips during 30-s observations of Griffon Vultures flying over land prior to crossing attempts, over water during crossing attempts, and returning over water or over land after aborting a crossing attempt, at the Strait of Gibraltar, 2004 to 2007.

Situation	Flight type	n	Mean \pm se (%)	
			Flaps	Wing dips
Over land	Gliding	403	1.19 \pm 0.23 (86) ^a	0.29 \pm 0.04 (79)
	Straight soaring	264	1.26 \pm 0.32 (87)	0.14 \pm 0.02 (87)
	Circle soaring	487	0.61 \pm 0.15 (88)	0.08 \pm 0.01 (93)
	All types	1154	1.22 \pm 0.15 (86)	0.16 \pm 0.01 (87)
Over water	Gliding	94	19.41 \pm 1.65 (33)	0.04 \pm 0.03 (97)
	Straight soaring	8	11.00 \pm 2.48 (13)	
	Circle soaring	28	4.64 \pm 1.72 (50)	0.11 \pm 0.11 (96)
	All types	130	18.69 \pm 1.25 (29)	0.04 \pm 0.02 (97)
Returning over land	Gliding	53	7.68 \pm 1.05 (38)	0.08 \pm 0.05 (94)
	Straight soaring	1	4	2
	Circle soaring	2	3.00 \pm 3.00 (50)	
	All types	56	7.45 \pm 1.21 (38)	0.11 \pm 0.06 (93)
Returning over water	Gliding	69	16.67 \pm 1.97 (35)	0.07 \pm 0.04 (95)
	Straight soaring	6	14.50 \pm 2.50 (50)	
	Circle soaring	16	11.56 \pm 3.62 (38)	0.06 \pm 0.06 (95)
	All types	91	15.94 \pm 1.66 (37)	0.06 \pm 0.03 (95)

^aPercent observations with no flapping or dipping.

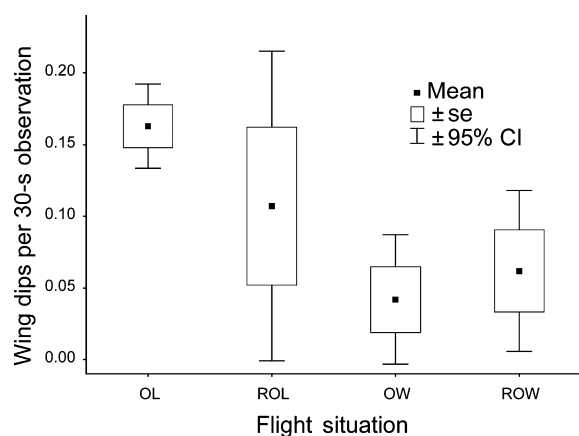


Figure 2. Numbers of times Griffon Vultures wing-dipped during 30-s observations when flying over land prior to crossing attempts (OL, $n = 1203$), returning over land after aborting a water crossing (ROL, $n = 56$), flying over water toward Africa (OW, $n = 167$), returning over water after aborting a water crossing (ROW, $n = 56$).

influencing crossing attempts ($P \leq 0.0001$, OR = 0.206, LCL = 0.129, UCL = 0.327). Other independent variables (i.e. flock size, air temperature and wind speed) and the interactions among them and wind direction, did not influence the probability of crossing attempts (Appendix 1).

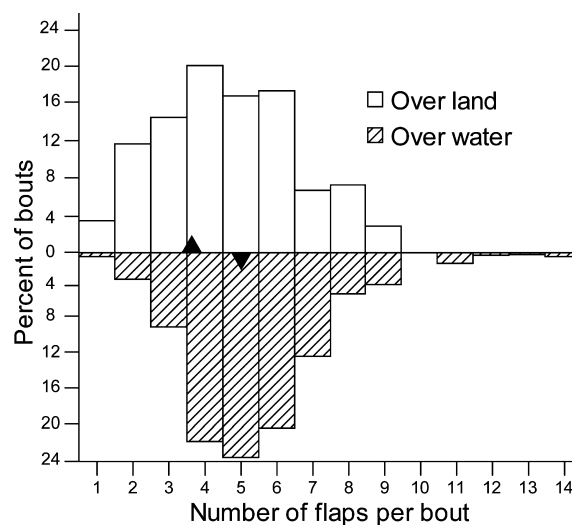


Figure 3. Numbers of flaps per flapping bout over land ($n = 54$ 30-s observations) vs. over water ($n = 111$).

DISCUSSION

Raptor migration scientist P. Kerlinger (1989, p. 262) stated that 'The mechanism by which hawks decide whether to cross a water barrier is not known...'. Kerlinger went on to speculate that individual migrants might fly along the shoreline or out over water for short distances to sample

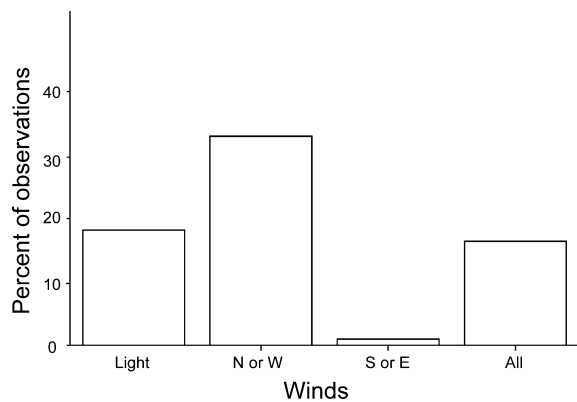


Figure 4. Percent of flight observations that occurred over water during light winds (light, $n = 417$), winds from the northern or western quadrant (N or W, $n = 558$), winds from the southern or eastern quadrant (S or E, $n = 548$), and all winds (all, $n = 1523$) combined.

conditions before attempting crossings at migration bottlenecks. Our observations of flapping rates over land and over water support the idea that obligate soaring migrants sample conditions prior to water crossings. The Griffon Vultures observed attempted crossings on less than half the days of observation. When crossings were attempted, most were aborted before the birds travelled out of sight over the Strait. The typical series of events involved multiple approaches toward the coast by flocks of Vultures, with many flocks returning inland as many as five or six times before attempting to cross. Although we did not quantify it, it was our impression that more birds crossed on days when fewer flocks turned back before reaching the coast than on days when repeated approaches and retreats were seen.

Like Western Honey Buzzards and Black Kites *Milvus migrans* at the Cap Bon Peninsula in Tunisia (Agostini *et al.* 1994, Agostini 2005), Griffon Vultures hesitated before water crossing and exhibited a strong tendency to remain in flocks as they approached the Strait. Indeed, flocking behaviour appeared to increase the likelihood of water crossing attempts significantly.

Logistic regression analysis relating probability of crossing to weather and flock size variables allowed calculation of odds ratios, which estimate the unique effect of a variable on the probability of a crossing attempt. The most important predictor of crossings among the variables measured (wind direction, wind speed, air temperature and flock size) was the occurrence of winds from the

eastern or southern quadrants, which reduced the probability of a crossing by nearly 80%. Winds from the western or northern quadrants, although positively associated with crossing attempts, did not significantly increase the probability of attempts, nor did air temperature or flock size.

Kerlinger (1984) and Meyer *et al.* (2000) suggested that birds making water crossings did so at higher altitudes than those following the coast. We did not quantify the heights of individuals within flocks attempting to cross the Strait. However, Vultures soared to higher altitudes, sometimes perhaps in excess of 2 km, on days when crossings were attempted, and all of the Vultures that aborted crossings returned to the Spanish coastline at noticeably lower altitudes than when they left the coast. Vultures initiating crossing at high altitudes would have greater potential energy available to them and, if able to maintain a gliding ratio of at least 1 : 7 (i.e. about half of the best gliding ratios recorded for Vultures in general; Pennycuik 1972, Pennycuik & Scholey 1984), theoretically would be able to complete the 14-km passage with little or no flapping. However, there was no evidence that Griffon Vultures attempted to take advantage of lee waves while crossing, a phenomenon others (e.g. Evans & Lathbury 1973) have suggested as important for some migrants at the site.

Many researchers (Kjellén 1992, Agostini & Logozzo 1995, Meyer *et al.* 2000, Agostini *et al.* 2002) have indicated that juvenile rather than adult Honey Buzzards are more likely to make water crossings. Although we were not able to age every Vulture we watched, all of those that were aged were juveniles.

Aborting a water crossing during migration has been reported for Broad-winged Hawks *Buteo platypterus* and Turkey Vultures at Whitefish Point, Michigan, USA, where the crossing involved is approximately 18 km (Kerlinger 1985). Individual Turkey Vultures soared when they departed but intermittently flapped and glided when they returned following aborted attempts.

Previous observation of migrating raptors at the Strait suggested that the proportion of over-water crossings, compared to flights that paralleled the coast southwest, increased toward the end of the migratory season for Western Honey Buzzards and Peregrine Falcons *Falco peregrinus*, but not for Marsh Circus *aeruginosus* and Montagu's Harriers *C. pygargus*, for which crossings were more likely

in weak winds (< 4 m/s), and less likely in headwinds (Meyer *et al.* 2000). Our results support the idea that light and following winds enhance the likelihood of water crossings, a phenomenon that Meyer *et al.* (2000) linked to energy minimization. Being blown out to sea during water crossings appears to be a genuine risk for migrating raptors (Zu-Aretz & Leshem 1983, Kerlinger & Gauthreaux 1984, Kerlinger 1989, Bildstein 2006). Presumably, this phenomenon also helps to explain why individuals avoid water crossings in crosswinds.

That Griffon Vultures are willing to attempt a 12–13-km water crossing near the northern end of the Gulf of Suez in Egypt (Goodwin 1949), but not at the 120-km wide Sicilian Channel in the Central Mediterranean (Thiollay 1977), suggests that there are limits to their ability to cross water. Furthermore that only three Griffon Vultures crossed the 30-km Bab-el-Mandeb at the southern end of the Red Sea during 2 years of autumn counts there (Welch & Welch 1988), suggests that the limit for regular water crossings may be close to being reached at the ≥ 14 -km Strait of Gibraltar.

By comparison, Turkey Vultures regularly migrate across the 24-km Strait of Juan de Fuca between Vancouver Island, Canada and northwestern Washington State in the USA (Hunn & Mattocks 1981) and at least occasionally also appear to cross the 140-km wide Straits of Florida (Darrow 1983). The species also was reported as a vagrant in sub-Antarctic South Georgia in 3 of 4 years in the early 1990s (Prince & Croxall 1996), an over-water journey of at least 1000 km from the nearest known population on the Falkland Islands. This species, which regularly commutes up to at least several kilometres over water between feeding and roosting sites in both the Falkland Islands (K. Bildstein pers. obs.) and Coastal Peru (Pennycuick & Scholey 1984), has significantly greater over-water flapping rates and bout lengths in the southern winter (i.e. May and June) at 51°S in the Falklands than do Griffon Vultures at the Strait of Gibraltar in far more thermally conducive conditions in northern autumn (October and November) at 36°N (Turkey Vulture versus Griffon Vulture: flapping rates, $n = 22$, mean = 34.2 ± 1.05 and $n = 167$, mean = 18.7 ± 1.25 , respectively; $U = 797.5$, $Z = 4.31$, $P = 0.0002$; bout lengths, $n = 22$, mean = 9.39 ± 0.63 and $n = 112$, mean = 2.63 ± 0.11 , respectively; $U = 11.0$, $Z =$

7.33 , $P = 0.0000$). These differences, together with differences in the water-crossing abilities of the two species, indicate that water-crossing behaviour is limited anatomically and physiologically in some Vultures and that flapping rates and bout lengths may offer useful and quantifiable metrics in assessing the extent of these limitations. They also suggest that flapping ability may be linked, at least in part, to the fact that Turkey Vultures are the most common and widespread of all scavenging birds of prey (Ferguson-Lees & Christie 2001).

The extent to which water-crossing ability may be limiting growth in Iberian populations of Griffon Vultures remains unknown. That large numbers of young Vultures fail to cross the Strait annually, after having attempted to do so, suggests that this population may soon, if not already, be limited by the difficulties they face in reaching potential wintering areas in West Africa. Overwintering in southernmost Spain rather than crossing the Strait of Gibraltar into Africa is almost certainly costly to young Vultures. Southernmost Cadiz hosts some of the highest densities of overwintering Vultures in Spain, when the sizeable local breeding population (Parra & Tellería 2004) is augmented by dispersing young from elsewhere in Iberia (Griesinger 1998, Garrido *et al.* 2002). As the latter's presence in winter is not believed to be related to particularly abundant food resources, competition for food is likely to be high at that time of year. That many of the birds apparently depend on rubbish dumps in the area places them at particular risk from pathogens and sub-lethal poisoning (Garrido *et al.* 2002). Wind-power development in the region is substantial, and there is a growing body of evidence that Griffon Vultures, in particular, are vulnerable to collisions with wind turbines in the region (cf. Barrios & Rodriguez 2004). The extent to which these factors, together with intrinsic limitations on migratory abilities, will affect populations in the region is unclear. Houston (1976) estimated that individual Rüppell's Vultures *Gyps rueppellii* might be able to survive for up to 3 weeks without feeding, during which they would lose 20% of their body mass (Houston 1993). The extent to which weight loss might enhance the likelihood of an attempted water crossing, either by an increased incentive to find adequate feeding areas, via a shift in flight mechanics including increased or soaring and powered-flight capacities (Pennycuick 1969: p. 546), or both, remains an unanswered question.

We were unable to accurately count the numbers of Griffon Vultures that crossed the Strait, as birds often reappeared over the Strait within several minutes of the disappearance of a flock attempting to cross. The same pattern has been reported at the Cap Bon Peninsula in Tunisia (Agostini 2005). This should be taken into account when attempts are made to monitor populations at such bottlenecks, as such behaviour (i.e. attempting to but not successfully crossing a water barrier and retreating to the mainland to try again) can act to inflate migration counts in such situations.

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APPENDIX

Model fit statistics for binary logistic regression. Models with Hosmer–Lemeshow \hat{C} statistics Hosmer–Lemeshow \hat{C} statistics having $P \leq 0.05$ were not considered to fit the data well.

Variables in model	AIC	\hat{C}^a	P
Flock size (FS)	986.21	24.97	0.0016
Air temperature (AT)	1000.65	43.94	< 0.0001
Wind direction (WD)	945.68	0.00	1.000
Wind speed (WS)	983.30	185.67	< 0.0001
FS, AT	974.54	26.45	0.0009
FS, WD	900.43	41.77	< 0.0001
AT, WD	920.69	81.86	< 0.0001
AT, WS	964.38	116.07	< 0.0001
FS, WS	946.47	59.89	< 0.0001
WD, WS	946.45	112.79	< 0.0001
FS, AT, WD	884.64	26.36	0.0009
AT, WD, WS	922.17	102.91	< 0.0001
FS, AT, WS	933.83	101.60	< 0.0001
FS, WD, WS	900.98	24.40	0.002
FS, WD, AT, WS	885.84	37.10	< 0.0001

^aHosmer–Lemeshow test statistic (see Methods).