



Wing size but not wing shape is related to migratory behavior in a soaring bird

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Both wing size and wing shape affect the flight abilities of birds. Intra and inter-specific studies have revealed a pattern where high aspect ratio and low wing loading favour migratory behaviour. This, however, have not been studied in soaring migrants. We assessed the relationship between the wing size and shape and the characteristics of the migratory habits of the turkey vulture *Cathartes aura*, an obligate soaring migrant. We compared wing size and shape with migration strategy among three fully migratory, one partially migratory and one non-migratory (resident) population distributed across the American continent. We calculated the aspect ratio and wing loading using wing tracings to characterize the wing morphology. We used satellite-tracking data from the migratory populations to calculate distance, duration, speed and altitude during migration. Wing loading, but not aspect ratio, differed among the populations, segregating the resident population from the completely migratory ones. Unlike what has been reported in species using flapping flight during migration, the migratory flight parameters of turkey vultures were not related to the aspect ratio. By contrast, wing loading was related to most flight parameters. Birds with lower wing loading flew farther, faster, and higher during their longer journeys. Our results suggest that wing morphology in this soaring species enables lower-cost flight, through low wing-loading, and that differences in the relative sizes of wings may increase extra savings during migration. The possibility that wing shape is influenced by foraging as well as migratory flight is discussed. We conclude that flight efficiency may be improved through different morphological adaptations in birds with different flight mechanisms.

The size and shape of the wings of birds determine their maneuverability and their efficiency to perform flapping, gliding, and soaring flight (Swaddle and Witter 1998). Because of this, wing morphology should be linked with several movement parameters such as the distance of migration, flight altitude and speed during migration, among others. If the selection pressure imposed by migration on wing morphology is stronger than that of other ecological aspects of the species this link should be especially evident in response to seasonal migrations. The relationship between wing morphology and movement ecology, has been assessed both within (Senar et al. 1994, Yong and Moore 1994, Egbert and Belthoff 2003, Fiedler 2005, Milá et al. 2008, Neto et al. 2013, Watanabe 2016) and among species (Winkler and Leisler 1992, Keast 1996, Lockwood et al. 1998). Those studies have highlighted the ways in which wing loading and wing shape influence flight characteristics, energetic cost, or both (Yong and Moore 1994, Swaddle and Witter 1998). Overall, longer and narrower wings (i.e. those with high aspect ratios), with low wing loading and a pointed shape, have been associated with higher energetic efficiency of flight (i.e. per unit time). This wing morphology tends to be common among birds that undertake long-distance migrations (Lockwood et al. 1998, Watanabe 2016, but see

Winkler and Leisler 1992). By contrast, shorter and wider wings, with low aspect ratio, and a more rounded shape have generally been associated to higher maneuverability and mostly found in less migratory and non-migratory birds (Keast 1996, Swaddle and Witter 1998).

Most studies assessing the influence of wing morphology on flight dynamics have been conducted on songbirds (Swaddle and Witter 1998, Egbert and Belthoff 2003, Fiedler 2005, Milá et al. 2008) and in non-passerine birds with flapping or gliding flights (Baudinette and Schmidt-Nielsen 1974, Spaar and Bruderer 1997, Lockwood et al. 1998). In comparison, little is known about how wing morphology affects the flight of soaring birds (but see Watanabe 2016). Soaring flight is a very efficient energy-saving mechanism (Hedenstrom 1993, Ruxton and Houston 2004, Duriez et al. 2014, Watanabe 2016) that is highly dependent on body size (Spaar and Bruderer 1997) and environmental conditions (Spaar and Bruderer 1997, Mallon et al. 2015, Miller et al. 2016). Understanding the constraints that wing morphology imposes to the movements of soaring species, can help us predict the way in which environmental changes can affect those species, and their ability to cope or adapt to those changes. This is particularly important in species whose life history includes migrations, but also for species

with scavenging habits, which involves the dependence on ephemeral food sources that forces the birds to cover large areas searching for food.

The turkey vulture *Cathartes aura* is an obligate soaring migrant that has successfully occupied environments across almost all of the American continent, ranging from central Canada in the north to Tierra del Fuego in the south (Kirk and Mossman 1998). Throughout its distribution, the species is found in a broad range of environments, from deserts to forests, where it finds its food both by smell and by sight (Houston 1986, Kirk and Mossman 1998, Platt et al. 2015). The turkey vulture is also the only large-scale migratory species among the 23 species of vultures in the New World that exhibits a wide range of migratory behavior: from completely resident populations to completely migratory ones (Woods and Woods 1997, Kirk and Mossman 1998), making it an excellent model to test the relationship between wing size and wing shape and the degree to which populations migrate.

Here, we test the hypothesis that wing morphology is linked to migratory movements through two general predictions; 1) if turkey vultures show the same pattern than most other bird species, aspect ratio will be higher and wing loading lower in migratory populations than in resident populations; 2) if higher aspect ratio favors the exploitation of thermals and the opposite is true for wing loading, then, birds with higher aspect ratio and lower wing loading may get higher in thermals, allowing them to cover longer distances during the gliding phase of the flight. This would result in birds travelling longer distances per day and thus increasing the overall migration speed. Therefore the distance travelled and speed and altitude of flight during migration will be positively related to the aspect ratio and negatively related to the wing loading, and the opposite relationship will be found for the duration of migration. To test these predictions we trapped, satellite tagged and took wing measurements of turkey vultures across the entire distribution of the species on the American continent and compared morphological and movement parameters among populations.

Material and methods

Studied populations

We studied morphological characteristics of 127 turkey vultures from five populations belonging to four different subspecies (Kirk and Mossman 1998) across the American continent (Fig. 1). The five populations cover different breeding areas and a range of migratory habits. Three of the populations were complete migrants: central Canada (53°0'16"N, 106°18'47"W; *C. a. meridionalis*), western USA (33°23'20"N, 112°40'59"W; *C. a. meridionalis*) and Patagonia (south-western Argentina, 41°11'14"S, 71°8'40"W; *C. a. jota*); one was a partial migrant from the eastern USA (40°38'20"N, 76°1'6"W; *C. a. septentrionalis*); and one was a sedentary population from Islas Malvinas (Falkland Islands) (51°20'22"S, 60°7'22"W; *C. a. falklandica*). We tracked the movement patterns only for the migratory populations because we wanted to compare variation in wing morphology with migration behavior.

Body measurements

Wing loading and aspect ratio are two morphological variables related to relative shape and size, independent of the actual size of the birds, that we related to the movement parameters. Wing loading was calculated as an individual's body mass (g) divided by the total wing area (cm²) and the aspect ratio as the squared wing span divided by the total wing area. For each trapped bird, we measured body mass and wing chord and traced on paper one wing in a fully spread position. For the Patagonian population we measured the half wing span defined as the length from the spinal cord to the distal tip of the spread wing. As we did not have the same measurements for the rest of the populations, we calculated the wing span by doubling this measurement. We calculated the body width for each bird from Patagonia as the difference between their measured wing span and twice the wing length measured from their tracings. We calculated wing span for each bird from all the other populations by adding the average body width for the birds from Patagonia to twice their wing length. This generalization of the body width could hinder the differences in morphological parameters among populations by increasing the real wing span in the smaller birds and reducing it in the larger ones. However, we are confident that this is not an issue as the body width represented ~ 10% of the wing span of the birds from Patagonia and its variation represented only 3% of their wing span. Homogenization of the body width for all the birds makes the differences found to be attributable only to the wing length.

Total area was calculated by doubling the wing area and adding the area of the body between the wings. The wing area was measured by overlapping the tracing to a grid and counting the number of 1 cm² squares contained into it. The area of the body between the wings was calculated from the average body width calculated from the birds from Patagonia and the length of body at the insertion of the wing, measured from the tracing of each bird.

Wing measurements were taken at the breeding sites, except for the population breeding in Central Canada whose measurements were taken at their wintering site in Maracaibo, Venezuela (10°32'17"N, 71°32'11"W). For this population the body mass was corrected by adding the mean body weight loss (mean body weight: 1711 g (Canada) – 1520 g (Venezuela): 191 g) after the migration. Both, wing tag re-sightings and satellite tracks indicate that birds wintering in Venezuela breed in central Canada (Dodge et al. 2014, Bildstein unpubl.).

Movement parameters

We obtained movement parameters for each migratory population using GPS satellite transmitters on a total of 27 birds (central Canada: n = 10, eastern USA: n = 3, western USA: n = 9, Patagonia: n = 5). Solar-powered transmitters (PTT-100 model, Microwave Telemetry, Columbia, MD, USA and Model 40 GPS, Northstar Science and Technology, King George, VA, USA) were set to collect GPS locations every 1 or 3 h. We calculated five movement parameters to characterize the populations during migrations: total migration distance (km), average migration speed (km h⁻¹),



Figure 1. Breeding sites of the studied populations of turkey vultures *Cathartes aura* and the migratory paths of migrant populations.

duration (days), average altitude above the sea level (aasl, m) and average altitude above the ground (aag, m).

We used movement parameters recorded during the outbound migration because we had a greater number of complete seasonal tracks than for return migration. We defined the start of migration when a bird initiated a one way displacement and the distance between consecutive days was higher than 50 km. The opposite was used to define the end of the migration. We defined stopover days as days for

which displacement was less than 20 km once a migration had started. The duration of the migration, average migration speed, and flight altitude during migration may be affected by the stopover days, thus we only considered the days of actual migratory movements (i.e. excluding stopover days) for the flight parameters. We used the same criterion to define the duration of the migration. We calculated the distance traveled during the whole outbound migration as the addition of distances travelled each day, and the daily

speed as the distance travelled daily divided by 16 h, discarding an average of 8 night hours per day when the birds most likely did not fly. We averaged the daily speed for the whole migration in the analyses.

We expressed the flight altitude as both altitude above sea level (aasl) and altitude above the ground (aag). The flight aasl was obtained from GPS units on satellite-tracked birds. We calculated the flight aag by subtracting to the aasl

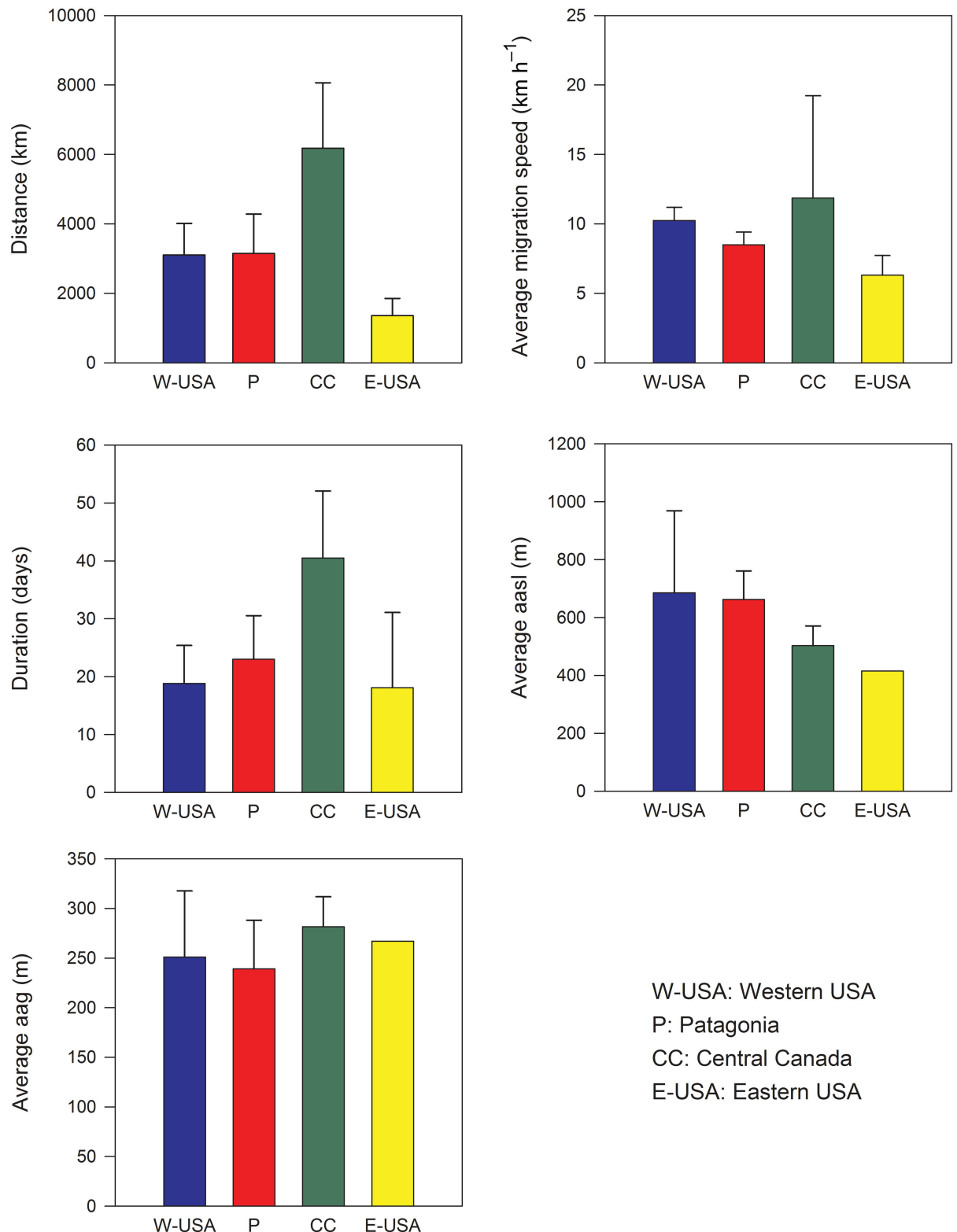


Figure 2. Mean ± SD of the movement parameters analysed for each population of turkey vulture *Cathartes aura* with migratory movements.

the ground altitude (Land Processes Distributed Active Archive Center 2015) extracted for each individual location from the annotation system Env-DATA of Movebank (Dodge et al. 2013, Wikelski and Kays 2015). To avoid using altitude data for perched birds and unrealistic data collected by the GPS units (Ladetto et al. 2000), we excluded altitudes (both, aasl and aag) for which the speed of movement was 0 and/or when aag had negative values. We used the average individual value of all the altitude data registered during the whole outbound migration for analyses. For birds with more than one outbound migration, we used mean values for each movement parameter.

Data analysis

We explored the segregation of birds from the five populations according to morphological variables: body weight, wing chord, wing span, total area, wing loading and aspect ratio; through a principal components analysis. We present the distribution of birds according to the two first eigenvectors and the contour line probability (0.95 of confidence level) around each population (Wickham 2009). We compared morphological variables among populations using ANOVA and post-hoc Tukey tests.

For comparisons among populations, we calculated average population values for each one of the five movement parameters and used them as dependent variables to be explained by the morphological variables (Fig. 2). We performed a multivariate regression model (Fox 2015) using the `lm` function to determine the influence of wing loading and aspect ratio on the five movement parameters. All the analyses were done using R software 3.2.2 (R Core Team).

Data available from Movebank Data Repository (movebank.org, study ID 217784323): <doi:10.5441/001/1.37r2b884> (Bildstein et al. 2016).

Results

Wing morphology of populations

Morphometric measurements segregated the resident population from Malvinas from the fully migrant populations from western USA, Patagonia and central Canada (Fig. 3). This segregation occurs through PC2, which is mostly determined by body mass and wing loading (Table 1). Birds belonging to the partially migrant population from eastern USA overlapped with the resident and completely migrant populations (Fig. 3). Birds coming from Patagonia, in the southern cone of the continent, presented a higher aspect ratio compared with all the other populations (Table 2; $F = 3.22$, $p = 0.01$). Wing loading differed among all populations, except between two of the completely migratory populations whose breeding grounds are located at opposite and extreme latitudes north and south of the equator (i.e. central Canada and Patagonia; Table 2).

Wing size and shape associations with movements

We found wing loading to be negatively related to the distance (estimate = -20098 , $t = -5.27$, $p < 0.001$), duration (estimate = -73.6 , $t = -3.91$, $p < 0.001$), average migration

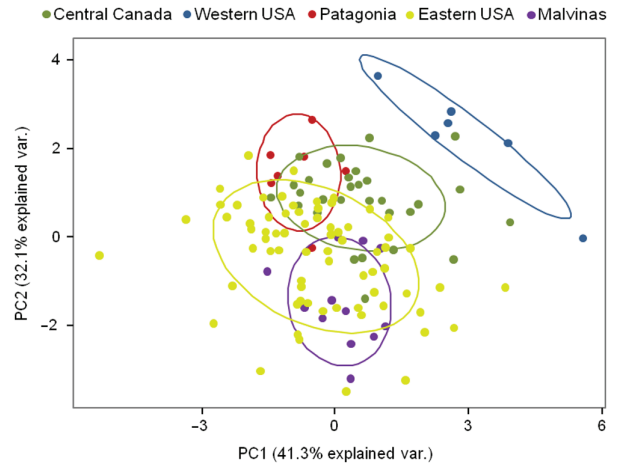


Figure 3. Distribution of individual birds from the five populations of turkey vulture *Cathartes aura* according to the two first eigenvectors (PC 1 and PC 2) obtained from the principal component analysis performed on morphological variables.

speed (estimate = -28.4 , $t = -6.69$, $p < 0.001$) and aasl (estimate = -1045.3 , $t = -7.62$, $p < 0.001$) during migration, but not to aag (estimate = 7.9 , $t = 0.35$, $p = 0.72$; Fig. 4). None of the movement parameters were related to differences in aspect ratio (Fig. 5).

Discussion

Our work is the first intra-species study relating morphological characteristics to the migratory habits of different populations of an obligate soaring bird. To our knowledge, for the first time, we show that for a soaring species, the migratory habits can be related to wing morphology. Despite intra-species studies showing a lack of relationship between body mass and distance of migration for soaring birds (Watanabe 2016), our results show that wing loading is linked with migration distance, duration, speed and altitude above sea level, according to the predictions. Previous work, mostly focused on species with flapping flight, showed a strong trend for migratory birds to have wings with lower aspect ratio than the resident ones (Lockwood et al. 1998, Fiedler 2005, Milá et al. 2008, Neto et al. 2013). By contrast, aspect ratio did not relate to any of the movement parameters in turkey vultures, suggesting differences in morphological requirements related to the energetic optimization according to the flight mechanism.

Table 1. Variable loadings for the first three eigenvectors (PC1, PC2 and PC3) included in the principal component analysis performed with morphological variables of turkey vultures *Cathartes aura*.

Variable	PC1	PC2	PC3
Body mass	-0.40	-0.54	0.19
Wing span	-0.54	0.28	0.07
Wing loading	-0.13	-0.66	0.34
Aspect ratio	-0.35	0.36	0.49
Wing area	-0.52	0.12	-0.28
Wing chord	-0.27	-0.21	-0.72

Table 2. Morphological variables of turkey vultures *Cathartes aura* from the five studied populations. Values are mean \pm SD.

Population (n)	Body mass (g)	Wing chord (cm)	Calculated wing span (cm)	Total area (cm ²)	Wing loading (g cm ⁻²)	Aspect ratio
Western USA (6)	1318.3 \pm 21.4*	49.9 \pm 1.4 ^a	161.1 \pm 10.0 ^a	3933.3 \pm 354.2 ^a	0.34 \pm 0.03*	6.61 \pm 0.37 ^a
Patagonia (7)	1788.6 \pm 82.7 ^a	51.2 \pm 5.6 ^a	176.7 \pm 3.7 ^b	4372.0 \pm 200.1 ^b	0.41 \pm 0.02 ^a	7.15 \pm 0.32*
Central Canada (30)	1711 \pm 165.9*	52.1 \pm 2.3 ^a	168.8 \pm 6.4 ^{a,b}	4235.6 \pm 250.1 ^{a,b}	0.40 \pm 0.03 ^a	6.73 \pm 0.17 ^a
Islas Malvinas (14)	2120.4 \pm 153.0*	51.1 \pm 1.1 ^a	166.4 \pm 4.2 ^{a,c}	4156.8 \pm 160.5 ^{a,b}	0.51 \pm 0.04*	6.67 \pm 0.24 ^a
Eastern USA (70)	1940.7 \pm 169.5 ^a	54.8 \pm 1.7*	170.0 \pm 8.1 ^{b,c}	4309.6 \pm 285.0 ^b	0.45 \pm 0.04*	6.71 \pm 0.37 ^a

Same letter indicates non-significant differences. * indicates differences with all the other groups.

Wing loading and aspect ratio are two morphological parameters broadly used to characterize the morphology of birds, especially in relation to their flight characteristics (Yong and Moore 1994, Lockwood et al. 1998, Milá et al. 2008, Watanabe 2016). The calculation of both of these parameters requires the use of the wing span measurement (Pennycuik 2008). Our wing loading and aspect ratio calculations are derived from a wing span measurement that was obtained using an average body width for all the birds. This did not preclude us from making inter-population comparisons as the calculation of morphological parameters was done in the same way for each population, and allows us to attribute the differences to the wing characteristics. On the other hand, the relationship between the morphological variables and the flight parameters was done using average values of the flight variables for each population. Considering similarity in the migratory behavior in the birds from each population (Dodge et al. 2014), we believe that our approach is reliable and allowed us to find differences in morphology that can be related to the movement characteristics of the populations.

Despite the fact that some interspecific studies indicated a low correlation between wing morphology and flight characteristics (Wang and Clarke 2015), several intra-species and inter-species studies of non-soaring species found that aspect ratio is higher in migratory than in resident birds (Fiedler 2005, Milá et al. 2008, Neto et al. 2013, Watanabe 2016), leading some to propose that soaring flight might also be favored by long and narrow wings, meaning wings with high aspect ratio (Hedenstrom 1993). However, aspect ratio does not change among populations with different migratory habits nor relate with any movement parameters in turkey vultures. By contrast, wing loading relates to all the movement parameters studied, except the altitude above the ground. Birds with lower wing loading, meaning with relatively bigger wings, seem to fly farther, faster, during longer journeys and at higher altitude above the sea level. The lack of differences in the flight altitude above the ground despite differences in wing loading may suggest two possible explanations. On the one hand, that the flight altitude is limited by the air density, which reduces at higher altitudes, regardless the distance to the ground. On the other hand, that the link with the ground, possibly related to the food search behavior has a strong influence in the flight pattern (Shepard et al. 2011), particularly in this species that use the smell to find the food (Houston 1986, Platt et al. 2015).

As a more energetically demanding flight mechanism, flapping flight may lead to changes in the wing shape producing meaningful energetic savings that provide adaptive advantages related to migratory movements. In the case of

soaring birds, the energetic cost of flight is reduced (Ruxton and Houston 2004, Watanabe 2016). It is possible that for this soaring species its actual wing shape allows an adaptively enough low cost flight and that subsequently only changes in the relative size of the wings may add extra savings that can be key for the environment they use, or alternatively, that the relative size of wings is a character more prone to evolve than the shape.

The wide distribution of this species makes it possible that the climatic influence on body size leads to a latitudinal change in wing loading (Rensch 1938). In our data, there is not a clear pattern since the population from the lowest latitude (western USA) is the smallest one. However the biggest birds are not from the highest latitude, but from the resident population. This is not surprising in an analysis including migratory populations, which are exposed in the breeding and wintering sites to selective pressures that may counteract each other, blurring the effects of the Bergmann's rule (Salomonsen 1955, Meiri and Dayan 2003). In addition, for terrestrial soaring birds, the wing shape may relate to the selective pressure of the foraging strategy and habitat. Soaring flight is highly dependent on environmental conditions (Spaar and Bruderer 1997, Shepard and Lambertucci 2013), and low aspect ratio and wing loading in general give birds the ability to exploit weak thermals (Hedenstrom 1993, Ákos et al. 2010, Shepard and Lambertucci 2013). This may be particularly significant for scavenging birds, as the ephemeral nature of their food resources often requires them to search large areas, and because the possibility of using weak thermals early in the day increases their chances of getting food (Kendall 2014). Therefore, both wing size and wing shape could respond to the optimization of foraging ability through soaring flight. It is notable that despite belonging to the same family and sharing the same scavenging feeding habits the wing loading of Andean condors, California condors, and American black vultures, is higher than that of turkey vultures (D'Elia and Haig 2013, Shepard and Lambertucci 2013), the latter being the only complete large scale migratory species of New World vultures.

We studied one of the most abundant vulture species in the world (Houston 1994), which migrates long distances and occurs in most of the American continent in habitats with different characteristics. The high abundance and large distribution of this species indicate a high adaptability of the species to a very diverse suite of environments, and of each subspecies to their own local environment during residence periods as well as along the migratory path (Houston 1994). The constraints and needs imposed by the wing morphology, as the environmental requirements to fly

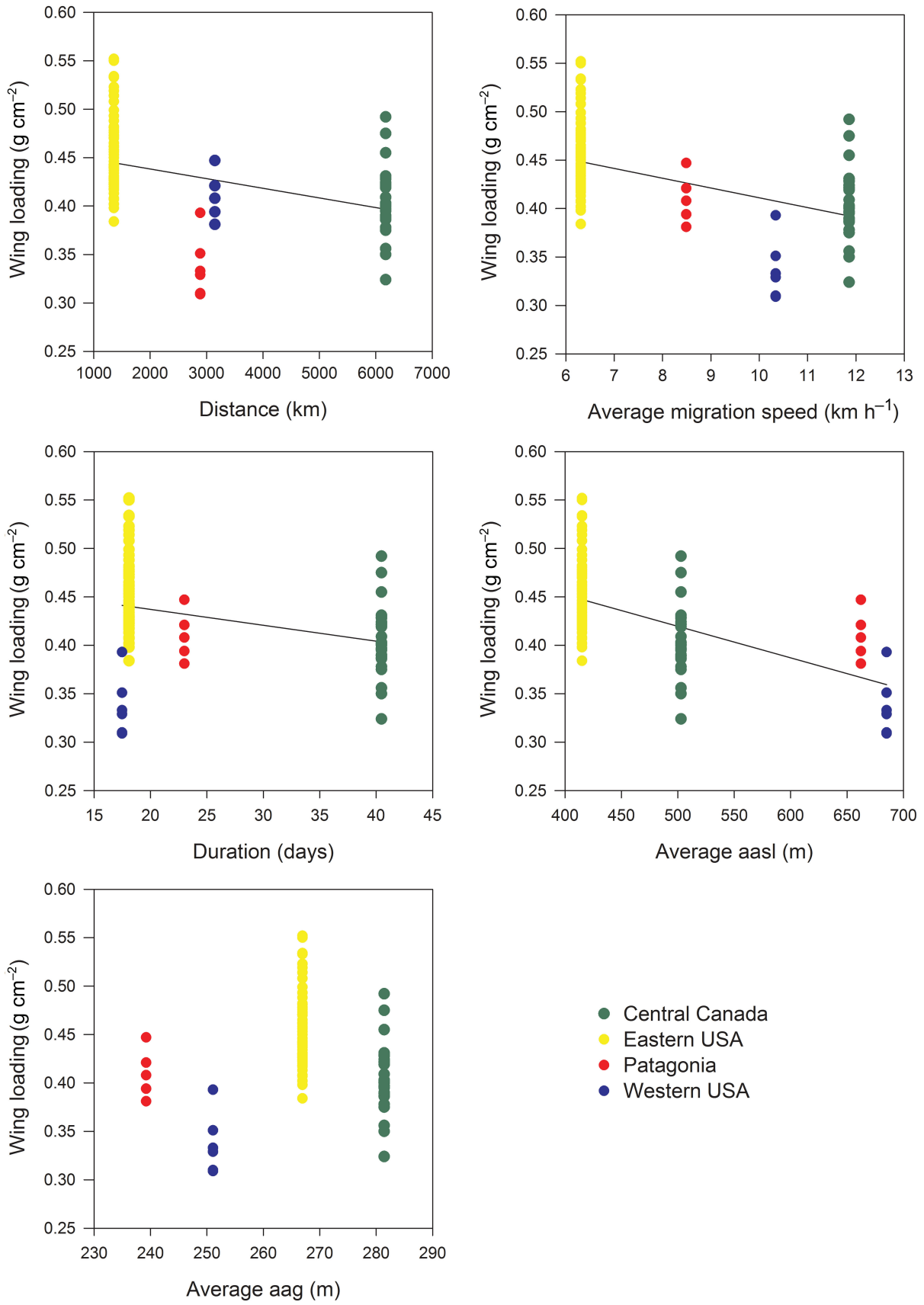


Figure 4. Relationship between wing loading of individual turkey vultures *Cathartes aura* and flight parameters of each population.

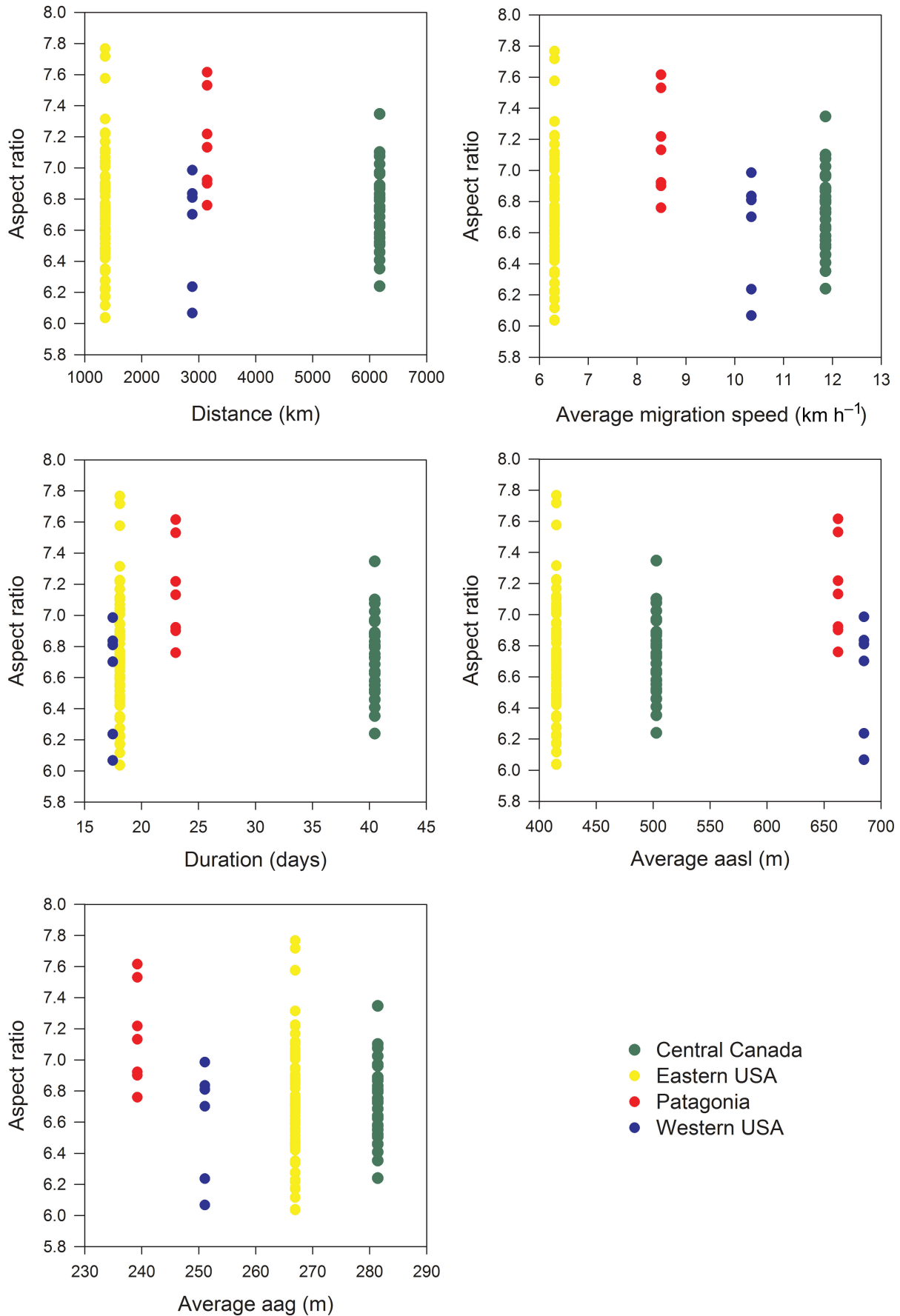


Figure 5. Relationship between aspect ratio of individual turkey vultures *Cathartes aura* and flight parameters of each population.

and the need for stopover and roosting sites, may influence the selection of the migratory route and the risks the birds face during their migration. Morphology with its influence on movements must be determinant in providing this species the versatility necessary to succeed across its entire range. For instance, reductions of the wing loading in this species may give the birds the possibility to get higher in thermals and to lose altitude more slowly during the gliding phase of soaring (Ákos et al. 2010, Mallon et al. 2015), allowing them to increase the speed and distance of migration. This prevalence of wing loading over wing shape in relationship to migratory parameters in an obligate-soaring, contrasting with those of flapping birds, suggests that different selective pressures can influence the wing morphology of birds with different flight mechanisms.

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