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Biometrics of Iberian Dippers *Cinclus cinclus*: environmental sources of among-population variation

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Biometry of Iberian Dippers *Cinclus cinclus* has typically been addressed from a geographic perspective, often considering small local populations. In this work, we explored environmental correlates of among-population phenotypic variation in Dipper morphology throughout Iberia. We tested for effect of river slope, altitude, temperature and precipitation (summarized using Principal Component Analyses, PCA) on absolute and relative (controlling for tarsus length) wing length and tarsus length. We used data of 222 Dippers captured from 35 rivers in eight breeding areas in N and S Iberia. All biometric variables were larger for older birds and males, though tarsus length was not affected by age. Wing length was longer in S Iberia, even when controlling for tarsus length. All biometric variables co-varied negatively with one of the PCA components of abiotic factors, owing to large-scale environment differences between N and S Iberia (zone). The abiotic factors predicted mean tarsus length of birds within zones, with tarsus increasing with increasing river slope and decreasing temperatures and precipitation. Furthermore, Dippers from S Iberia were not larger but had longer absolute and relative wings than those from N Iberia. Altogether, these findings imply that the morphological diversification of Iberian Dippers is affected by the environment and that body size-wing length allometric relationship differs between N and S Iberia.

Key words: adaptation, biometry, Dipper, *Cinclus cinclus*, environmental abiotic factors, Iberia

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INTRODUCTION

Studying how size and shape of animals are determined by selective pressures, such as habitat (Schluter 1993, Langerhans *et al.* 2003), mates (Székely *et al.* 2000), foraging (Marchetti *et al.* 1995, Alonso *et al.* 2006) or migration (Mönkkönen 1995, Calmaestra & Moreno 2001) can be of key importance to understand the ultimate causes promoting the biometric and morphological diversification of populations, and, finally, the processes involving speciation (e.g. Benkman 1993).

The Dipper *Cinclus cinclus* is a very suitable species for studying morphological diversification. This polytypic Palaearctic passerine breeds from W Europe to E Asia (Cramp 1988), and in the W Palaearctic it is present between Fennoscandia and S Europe, reaching also the main mountain ranges of N Africa (Cramp 1988, Wilson & Breitenmoser-Würsten 1997). It is associated to well-oxygenated waters of rivers with beds of stones where it finds macroinvertebrates that constitute its main diet (Cramp 1988, Tyler & Ormerod 1994). Dipper populations vary from sedentary to migratory, with migration distances increasing with latitude (Cramp 1988).

Within Iberia, the species has been suggested to be sedentary, performing only some post-breeding or post-juvenile movements, often from high- to lowlands in autumn or winter (Cramp 1988, Tellería *et al.* 1999). This, as well as its confined occurrence in mountain rivers, suggests that populations from Iberia might be

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quite isolated among each other. Therefore, Dipper is a suitable model species for evaluating how environmental conditions affect morphology.

Two subspecies are currently suggested to breed in Iberia (though their status is still unresolved from a taxonomic viewpoint; Campos *et al.* 2005a): *C. c. cinclus* in NW Iberia, and *C. c. aquaticus* in S and E Iberia (Ormerod & Tyler 2005; for further details see Campos *et al.* 2005a). Noteworthy, several studies have investigated biometric variation between subspecies or populations (Marsá 1988, Esteban *et al.* 2000, Villarán *et al.* 2001, Campos *et al.* 2005a). However, most of these studies focus on small populations on a relatively small geographic scale; with the exception being a study by Campos *et al.* (2005a), who analysed the biometry of four populations from Central, N and S Iberia, finding that Dippers from S Iberia (inhabiting the higher mountain ranges of Iberia) were larger than the rest. However, one of the issues unsolved in that work was the question of how the environment promoted this variation in morphology. Recently, changes in river features have been reported to affect Dippers' morphology (Moreno-Rueda & Rivas 2007), suggesting that the morphological diversification may be affected by river-specific environmental features.

Iberia is a highly mountainous region extending over an area of nearly 583 000 km^2, resulting in a high environmental diversification. Dippers, hence, occur in rivers with very different environmental conditions. In this work, we investigated whether the biometry can be predicted from population-specific environmental factors. We used data from eight populations from N and S Iberia, and made the following predictions.

(1) *Body size increases with river slope steepness*. Dippers feed on benthic insects and macroinvertebrates, captured with the bill whilst walking on the river bed (Cramp 1988). For a given river, the water speed increases as the river slope becomes steeper (Armantrout 1998). Therefore, its slope could be used as a proxy of water speed. This variable is one of the most important hydraulic factors shaping morphology of aquatic animals (Jowett & Duncan 1990). For instance, fish living in fast-flowing streams tend to be more robust (i.e. have a larger body size; Pakkasmaa & Piironen 2001) or more streamlined (i.e. have larger fins and a more hydrodynamic body; Riddell & Leggett 1981, Beacham 1985, Pakkasmaa & Piironen 2001). Similarly, Dippers inhabiting rivers with a steep slope (i.e. fast-flowing streams) should thus be expected to have a larger body size, since birds with larger body size could swim and dive more efficiently than smaller birds in such type of waters.

(2) *Body size increases with decreasing temperature*. Bergmann's rule states that body size increases with decreasing temperatures in homeothermic animals, because heat loss increases with body area (Futuyma 1998). Larger bodies have a relatively small surface which is advantageous in cold climates, whereas smaller bodies are favoured in warm climates. Mechanisms underlying such a relationship seem likely to be associated with fluctuations in over-winter survival (Marchant *et al.* 1990, Peach *et al.* 1995) in relation to body size, with larger birds being more likely to survive in harsh winters. In addition, Allen's rule posits that, in warm climates, homeothermic animals have longer, higher limbs, since this allows them to lose more heat (Futuyma 1998). A bird's wing is mainly formed by feathers, which cannot lose heat due to the absence of blood vessels. However, some wing bones have been reported to be correlated with wing length (Johnston 1969, Calmaestra & Moreno 2001), suggesting that a longer wing should be formed by both longer primaries and forelimbs. In this case, one should expect that birds inhabiting warmer climates had relatively longer wings for their body size.

(3) *Body size increases with altitude*. Altitude alone probably does not promote the morphological diversification of Dippers (Tyler & Ormerod 1994), though rivers at higher altitude tend to have steeper slopes, as well as lower temperatures during winter. Thus, birds breeding at a relatively high altitude should have a larger body size than those inhabiting lower altitudes.

(4) *Body size increases with amount of precipitation*. Precipitation could indirectly shape biometry, since rivers found in rainy areas often have relatively high water discharge, so they have more often fast-flowing waters and are deeper. Larger body size should be favoured under these conditions during foraging.

METHODS

Sampling localities and variables measured

Dippers were sampled in a total of 35 rivers of eight breeding areas in Spain, from 43°08'N to 36°56'N and 08°31'W to 00°45'E, from 50 to 1420 m above sea level (see for further details Appendix 1, Fig. 1). Each of these sampling areas included from 1 to 7 rivers (mean 4.5, SE 0.9). The sampling localities were in four basins and six mountain ranges, representative of Dipper's distribution area in Spain (López *et al.* 2003).

From September 2000 to September 2006, Dippers were caught with mist nets crossing rivers from bank to bank, in places where the species was known to breed.

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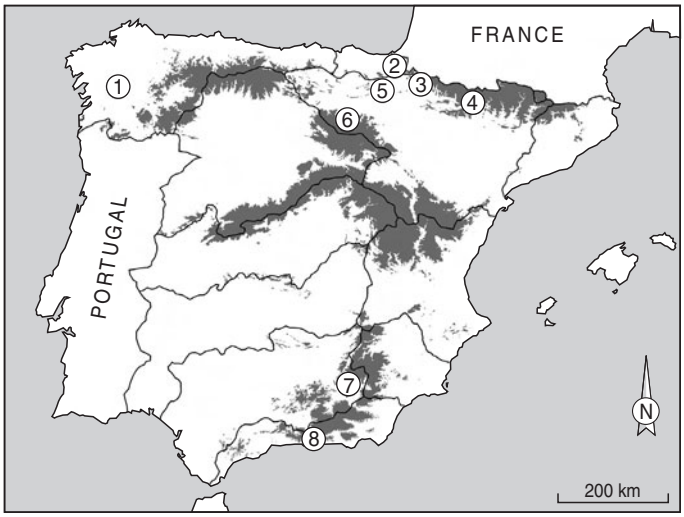


Figure 1. Sampling areas (1 to 8, as in Appendix 1) of Iberian Dippers in Spain; solid lines are river basins; shadowed areas are higher than 1000 m above sea level.

Once captured, each bird was ringed and its age determined according to the age of the primary feathers (Svensson 1996): juveniles (with juvenile primary feathers; age EURING code 3/5), and adults (birds captured after their complete moult; EURING code 4/6). Furthermore, we measured wing length (±0.5 mm; method III by Svensson 1996) and tarsus length (±0.1 mm). Before releasing, a sample of blood was taken (0.05 to 0.10 ml) from jugular vein (stored in an FTA card).

The abiotic environmental factors used in this study were: river slope (calculated in a transect of ca. 1 km, covering 0.5 km above and below the point where each bird was captured), altitude (m above sea level), mean temperatures (both annual and minimum temperature; °C), and the amount of annual precipitation (mm). We measured all variables for each capturing site. For rivers with more than a single capture an average value was given for each variable. Temperatures and precipitations were obtained from Nynyerola *et al.* (2005).

Sex determination

Sex of Dippers cannot be determined based on their colour or biometry (Campos *et al.* 2005b). Therefore, the gender was determined by means of DNA analyses (Griffiths *et al.* 1998, Gutiérrez-Corchero *et al.* 2002).

Data analyses

We excluded data of recaptures (in order to avoid pseudo-replication), and any bird with (partially) missing data for sex or age. Overall, 222 Dippers captured from 35 rivers from eight study areas were included in the analyses (Appendix 1).

Environmental variables were summarized using Principal Component Analysis (PCA) followed by varimax rotation (Tabachnick & Fidell 2001), resulting in two significant principal components (hereafter PC1 and PC2; Table 1). Prior to analyses, all the variables were confirmed to fit a normal distribution (Kruskal–Wallis test, $P > 0.05$).

We used Hierarchical Linear Mixed Models (HLMM) to test for the effect of abiotic factors (PC1 and PC2) on biometrics (wing and tarsus length, as well as wing controlling for tarsus length). We used tarsus length to assess body size (Senar & Pascual 1997). Area (1–8), as well as river (1–35) nested within each area, was fitted as a random effect in the HLMM. Age, sex and PCA components (PC1 and PC2) were fitted as fixed effects. To verify that effects of abiotic factors occurred within each zone (N and S Iberia), we also present our results whilst additionally controlling for zone fitted as an additional fixed effect. We used the χ^2-distributed Wald-statistic to evaluate significance of factors. Programs MLwinN v.2.0 (Rasbach *et al.* 2004) was used for HLMM, and SPSS v.15.0 for the PCA.

Table 1. Principal Component Analysis (PCA) on five abiotic factors used to characterize Dippers habitat. Tmin = Minimum temperature; Tmean = Mean annual temperature. We give the loadings for each emerging component.

	PC1	PC2
Slope	0.640	–0.228
Altitude	0.702	–0.545
Precipitation	–0.446	0.818
Tmin	0.657	0.670
Tmean	0.712	0.636
Eigenvalue	2.040	1.872
Explained variance (%)	40.8	37.4

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Table 2. Hierarchical Mixed Model analyses used to test for differences in wing length, tarsus length, and wing relative to tarsus length, between age and sex classes, and zones (N vs. S Iberia). For each variable we show two analyses: one controlling and one not controlling for effect of zone. We give statistics for each effect. Significant values are in bold.

Variable	Age		Sex		PC1		PC2		Zone		Tarsus	
	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*	χ^2_1	*P*
Wing	14.357	**<0.001**	513.441	**<0.001**	1.446	0.229	11.993	**<0.001**	-	-	-	-
Wing controlling for zone	13.056	**<0.001**	513.144	**<0.001**	0.002	0.964	3.017	0.082	5.207	**0.022**	-	-
Tarsus	0.708	0.400	237.228	**<0.001**	2.77	0.096	40.846	**<0.001**	-	-	-	-
Tarsus controlling for zone	0.606	0.436	238.925	**<0.001**	0.854	0.355	10.817	**0.001**	1.272	0.259	-	-
Wing controlling for tarsus	13.455	**<0.001**	166.63	**<0.001**	1.003	0.317	6.981	**0.008**	-	-	21.311	**<0.001**
Wing controlling for tarsus and zone	12.35	**<0.001**	167.966	**<0.001**	0.003	0.956	1.276	0.259	4.249	**0.039**	20.649	**<0.001**

Table 3. Parameter estimates (±SE) deducted from the Hierarchical Mixed Model analyses (Table 2).

	Age[1]	Sex[2]	PC1	PC2	Zone[3]	Tarsus
Wing	1.284±0.339	–7.139±0.315	0.422±0.351	–1.445±0.417	-	-
Wing controlling for zone	1.233±0.339	–7.123±0.314	0.014±0.363	–0.828±0.477	2.767±1.212	-
Tarsus	0.101±0.119	–1.788±0.116	0.116±0.070	–0.418±0.065	-	-
Tarsus controlling for zone	0.093±0.120	–1.787±0.116	0.074±0.080	–0.332±0.101	0.261±0.231	-
Wing controlling for tarsus	1.190±0.324	–5.667±0.439	0.336±0.336	–1.071±0.405	-	0.824±0.178
Wing controlling for tarsus and zone	1.139±0.324	–5.675±0.438	–0.020±0.353	–0.531±0.470	2.463±1.195	0.809±0.178

[1] Categorical variable (juvenile/adult); juvenile is reference category.
[2] Categorical variable (male/female); male is reference category.
[3] Categorical variable (North/South); North is reference category.

RESULTS

All biometric variables were larger for older birds and males, though tarsus length was not affected by age (Table 2 and 3). All biometric variables co-varied negatively with PC2 (Fig. 2). However, when controlling for the zone (N and S Iberia), the PC2 effect disappeared for relative and absolute wing length, but not for tarsus length (Table 2 and 3). Dippers from N Iberia were not larger than those from S Iberia, but had a longer absolute and relative wing (Table 2, Fig. 3). Furthermore, both PC1 and PC2 varied between N and S Iberia (Table 4), supporting that rivers from S Iberia differed from those from N Iberia.

Table 4. Test statistics and parameter estimates of Hierarchical Mixed Model analyses used to investigate differences between N and S Iberia (zones) in abiotic factors (Principal components PC1 and PC2; Table 1).

Y-variable	Zone χ^2_1	*P*	Parameter estimates[1]
PC1	4.116	**0.042**	0.882±0.435
PC2	7.198	**0.007**	–1.241±0.463

[1] North is reference category.

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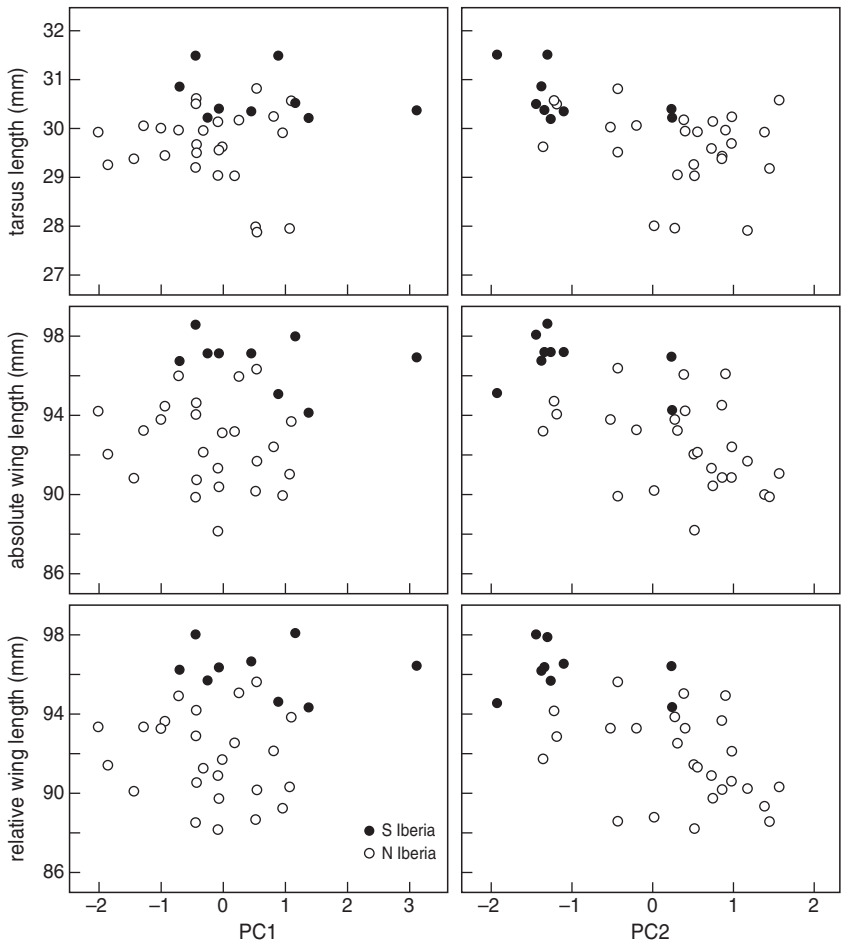


Figure 2. Tarsus length, and absolute and relative wing length, plotted against PCA components PC1 and PC2 (derived from a PCA on abiotic factors), in a total of 35 sampling rivers. All biometric variables have been controlled for age and sex effects, and in the case of relative wing length, for tarsus length as well.

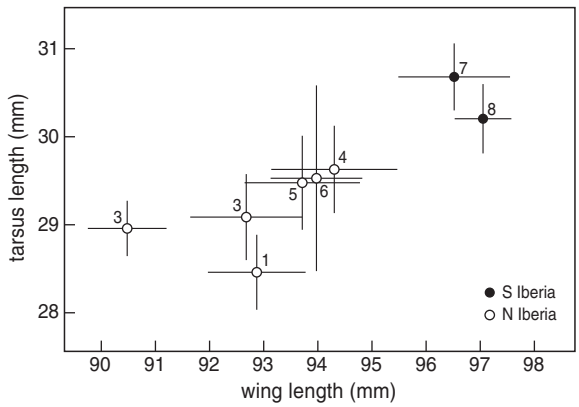


Figure 3. Wing length plotted against tarsus length (controlling for age and sex effects) for each sampling area (as indicated by numbers, see Appendix 1). Error bars represent SE.

DISCUSSION

Dippers from S and N Iberia did not differ in tarsus length, indicating that they did not differ in body size. This agrees with the data reported by Campos *et al.* (2005a) who did not find differences in female tarsus length among populations in S and N Iberia, though they did in males. In contrast, wing length did differ among zones, which is in agreement with Campos *et al.* (2005a), though this variable is a poor estimator of body size (for details see Senar & Pascual 1997). Reported long wings from birds from S Iberia (Campos *et al.* 2005a) or N Africa (*C. c. minor*; Tyler & Ormerod 1991) have been associated with the fact that they live at high altitude. However, our data may suggest that a reinterpretation of these results might be warranted, highlighting population-specific allometric patterns

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(i.e. differences in relative wing length), rather than differences in body size (see also Moreno-Rueda & Rivas 2007).

Once controlling for differences between N and S Iberia (zones), tarsus length – and not wing length – varied in relation to abiotic factors. In particular, tarsus length was negatively correlated with one of the PCA components (PC2) of abiotic factors. PC2 showed high, positive values for precipitation and temperatures, and negative values for altitude and slope. Smaller birds were found in rivers with gentle slopes, in warm places, at low altitude and with high precipitations. In this sense three of four predictions from the hypothesis that biometry can be predicted from population-specific environmental factors was met. The only exception was precipitation that we expected to have a positive effect on body size. The PCA analysis showed that slope and altitude were negatively correlated with precipitation. Despite of being in zones with high precipitation, rivers in lowlands showed less marked slopes, which would be associated to slow-flowing streams. These results suggest that water speed, rather than amount of water flown per unit time, is one of the key factors shaping Dippers morphology.

Our data support that biometric variation of Dippers is shaped by specific features of the water flows and climate, likely through natural selection (Kanuscak *et al.* 2004). Moreover, S Iberian Dippers showed a longer absolute and relative wing, supporting population-specific allometric patterns between N to S Iberia. Differences in allometric relationships have been associated with different feeding behaviour: birds inhabiting areas with rivers with less water flown per unit time seem to take advantage of their relative large wings, allowing them a higher manoeuvrability during flight, and having a diet mainly formed by aerial insects (Moreno-Rueda & Rivas 2007). Therefore, these results would support that Dippers from S Iberia are morphologically differentiated, potentially warranting the label of subspecies (see Campos *et al.* 2005a). Whether S Iberia represents an isolated population evolved independently is a question that might be solved by means of genetic studies.

This work does not reveal if the biometric variation found among Dippers is caused by phenotypic plasticity in response to environment rather than caused by spatial variation in selection acting on more rigid phenotypes. Plasticity would allow Dippers to adapt quickly to environmental changes, hence being better able to survive in year-to-year changing river environments, allowing them also to efficiently adapt to newly colonized breeding locations. Alternatively, biometry may depend on a rigid phenotype. However, most evidence suggests that Dipper biometry can change quickly in response to environmental change (Moreno-Rueda & Rivas 2007). Nevertheless, future genetic studies will be crucial to clarify how the biometric variation that we reported in this work is caused by genetic differentiation. Also, such studies could clarify if proximate mechanisms underlying phenotypic diversification constrain the adaptation to new environments and environmental change like climate warming.

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SAMENVATTING

De biometrie van Waterspreeuwen *Cinclus cinclus* in Spanje wordt veelal benaderd vanuit een geografisch perspectief, waarbij kleine lokale populaties uit het noorden en uit het zuiden van het land met elkaar worden vergeleken. Bij het onderhavige onderzoek werden de lichaamsmaten verzameld van 222 Waterspreeuwen die met mistnetten waren gevangen in 35 verschillende rivieren in acht gebieden verspreid over het land. Deze lichaamsmaten werden in verband gebracht met een aantal karakteristieken van het leefgebied van de vogels. Oude vogels bleken langere vleugels te hebben dan jonge vogels. Binnen beide leeftijdsgroepen hadden mannetjes een langere vleugel en tarsus dan vrouwtjes. Er bleken aanzienlijke verschillen tussen rivieren te bestaan in de grootte van de vogels (gemeten naar de lengte van de tarsus). De lichaamsgrootte nam toe met het verhang van de rivier en de hoogte boven zeeniveau. Daarnaast nam de grootte af met de omgevingstemperatuur en de hoeveelheid neerslag. Vogels uit het zuiden en noorden van Spanje waren even groot, maar wel waren de vleugels in het zuiden langer (dit gold zowel de absolute vleugellengte als de lengte gecorrigeerd voor de tarsuslengte). Geconcludeerd wordt dat de lichaamsbouw van Waterspreeuwen wordt beïnvloed door de leefomgeving van de vogels en dat de verhouding tussen lichaamsgrootte en vleugellengte tussen het noorden en zuiden van Spanje verschilt. (NJD)

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Appendix 1. Environmental features of the areas where the dippers were sampled. GAL = Galician, WPY = W Pyrenees, CPY = C Pyrenees, URB = Urbasa-Aralar, IBE = Iberian System, CAZ = Cazorla, SNE = Sierra Nevada; NOR = North Basin, EBR = Ebro, GUA = Guadalquivir, SOU = South Basin; Tmin = Minimum temperature; Tmean = Mean annual temperature; Precip = Annual precipitation; *n* = sample size (birds caught).

Area	Mountain range	Basin	Longitude/ Latitude	Altitude (m a.s.l.)	Slope (%)	Tmin (°C)	Tmean (°C)	Precip (mm)	*n*
1	GAL	NOR	08°31'W – 08°20'W 42°35'N – 42°08'N	200	1.2	0.1	11.2	1590	20
2	WPY	NOR	01°40'W – 01°28'W 43°04'N – 43°08'N	355	3.1	–0.1	11.8	1700	28
3	WPY	EBR	02°08'W – 00°55'W 43°01'N – 42°43'N	675	1.5	1.9	12.6	1415	60
4	CPY	EBR	00°05'E – 00°45'E 42°47'N – 42°28'N	880	1.6	0.4	13.0	1270	18
5	URB	EBR	02°07'W – 02°05'W 42°47'N – 42°43'N	540	1.9	–1.4	10.0	1145	20
6	IBE	EBR	02°46'W – 02°21'W 42°03'N – 42°28'N	955	1.7	0.0	11.0	770	17
7	CAZ	GUA	02°57'W – 02°47'W 37°54'N – 38°05'N	690	3.9	–0.4	12.0	710	16
8	SNE	SOU	03°31'W – 03°20'W 36°56'N – 37°10'N	1015	5.2	0.1	11.8	610	43

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