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STABLE ISOTOPE ANALYSIS REVEALS BIASES IN THE PERFORMANCE OF A MORPHOLOGICAL METHOD TO DISTINGUISH THE MIGRATORY BEHAVIOUR OF EUROPEAN ROBINS ERITHACUS RUBECULA

EL ANÁLISIS DE ISÓTOPOS ESTABLES REVELA SESGOS EN EL FUNCIONAMIENTO DE UN MÉTODO MORFOLÓGICO PARA DIFERENCIAR EL COMPORTAMIENTO MIGRATORIO DE LOS PETIRROJOS ERITHACUS RUBECULA

Iván de la Hera1,2, Guillermo Fandos1, Javier Fernández-López1,3, Alejandro Onrubia4, Antón Pérez-Rodríguez1,5, Javier Pérez-Tris1 and José Luis Tellería1

1 Departamento de Zoología y Antropología Física, Universidad Complutense de Madrid, E-28040 Madrid, Spain.
2 School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland.
4 Fundación Migres, E-11380 Tarifa, Spain.
5 UMR 6282 ‘Biogéosciences’, CNRS - Univ. Bourgogne Franche-Comté, F-21000 Dijon, France.

* Corresponding author: ivan.delahera@ucc.ie

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SUMMARY.- Morphological methods to distinguish avian groups of research interest (e.g. sex, population or cryptic species distinction) need to be externally validated to ensure a reliable performance across situations. In this study, we used hydrogen stable isotope ratios of feathers ($\delta^{2}H_f$) to test the validity of morphological classification functions (MCFs) previously designed to assess the migratory behaviour of European Robins *Erithacus rubecula* wintering in southern Iberia. Our results showed that a great number of migrants (mostly females and juveniles) were erroneously assigned as sedentary, which could compromise the reliability of previous ecological studies that made use of these MCFs. The development of improved MCFs or the use of alternative differentiation methods ($\delta^{2}H_f$) could help us to gain a more realistic insight into the habitat distribution and ecological interactions of sympatric migratory and sedentary robins overwintering in southern Iberia.

RESUMEN.- Los métodos morfológicos para distinguir grupos de aves con interés de investigación (e.g. distinción de sexos, poblaciones o especies crípticas) requieren de validación independiente para asegurar su funcionamiento adecuado de forma consistente. En este estudio, usamos la relación de isótopos estables del hidrógeno en las plumas ($\delta^{2}H_f$) para comprobar la validez de las funciones de clasificación morfológicas (MCFs) diseñadas con anterioridad para identificar el comportamiento migratorio de los petirrojos *Erithacus rubecula* invernantes en el sur ibérico. Los resultados revelaron que un gran número de migrantes (sobre todo hembras y jóvenes) fueron clasificados erróneamente como sedentarios, lo que podría comprometer la fiabilidad de los estudios ecológicos previos que han hecho uso de estas MCFs. El desarrollo de MCFs mejoradas o el uso de métodos de diferenciación alternativos ($\delta^{2}H_f$) podrían ayudarnos a obtener una idea más realista acerca de la distribución entre hábitats e interacciones ecológicas de los petirrojos migratorios y sedentarios que invernan en simpatría en el sur ibérico.
Discriminant function analyses (DFA) and other similar statistical approaches based on avian morphological traits are a readily accessible method to separate morphologically discrete groups of birds (Ellrich et al., 2010; Tellería et al., 2013). They are particularly useful to identify males and females in monochromatic but still morphologically dimorphic species (Arizaga et al., 2008; Bertolero et al., 2016). With mixed success, they have also been implemented in the identification of cryptic species (Wilson et al., 2012; Gordo et al., 2017), as well as to identify populations within the same species differing in morphological traits (Wennerberg et al., 2002; Maggini et al., 2016). In many cases, morphology is now clearly outweighed by more novel techniques (Webster et al., 2002). For example, molecular genetics can provide unambiguous sex and species identifications (Griffiths et al., 1998; Bensch et al., 2002), while methods based on bird morphology are normally subject to variable degree of uncertainty in their assignments. In any case, under budget constraints, logistical limitations (e.g. permits for biological samples collection) and/or when these alternative techniques do not substantially improve the classification potential of morphology, the latter still can be the most cost-effective way to satisfactorily differentiate among avian groups of research interest (De la Hera et al., 2012). In any case, given the potential uncertainty associated with the use of morphology, it is essential to validate the reliability of morphological methods using independent approaches, which can be very useful to reveal previously unnoticed flaws in their performance.

The study of the sympatric interactions between local sedentary birds and overwintering conspecific migrants in southern Iberia has greatly benefitted from the use of morphological classification functions (MCFs) that are one of the outcomes of DFA (StatSoft, 2004). It is well known that natural selection favours longer and more pointed wings in migrants compared to sedentary counterparts (Piersma et al., 2005), and this variation is sometimes large enough for developing effective MCFs to distinguish each other. For instance, MCFs built from Iberian breeding populations of known migratory behaviour provided a 90 and an 80 percent of correct assignments of the migratory behaviour for the Eurasian Blackcap (Sylvia atricapilla) and European Robin (Erithacus rubecula), respectively (Pérez-Tris et al., 1999; Pérez-Tris et al., 2000). However, these MCFs have only been optimized for distinguishing among a few Iberian breeding populations, and these constitute only a small fraction of the wintering population occurring in Southern Iberia. Consequently, whether these MCFs can successfully be applied to distinguish among wintering birds of unknown origin needs to be explicitly corroborated (Ellrich et al., 2010).
Most of the migratory blackcaps and robins wintering in Iberia originate from further Northeast in Europe, so they would have a more migratory-like morphology than any Iberian counterpart (Cramp, 1992; Korner-Nievergelt et al., 2014). This should ensure an even better performance of these MCFs for the migratory group when they are applied to seasonally sympatric populations wintering in Southern Iberia. This has been confirmed for blackcaps (De la Hera et al., 2007) and validated using a well-known pattern of stable isotope variation for the Palaearctic region (De la Hera et al., 2012). However, the validity of the MCFs designed for distinguishing between migratory and sedentary robins remains to be tested using an independent control. Unlike blackcaps, robins show a great within-population variation in wing morphology, with male and adult robins having on average longer wings than females and juveniles, respectively (Ellrich et al., 2010; De la Hera et al., 2014). In this respect, there are two main concerns that could affect the performance of MCFs during winter. First, female and juvenile robins are more prone to migrate (Adriaensen & Dhondt, 1990) and hence more likely to reach southern Iberia for overwintering, where their short wings might overlap in size with those of local sedentary robins, particularly with males (Ellrich et al., 2010). On the other hand, juveniles were overrepresented in the Iberian robin sample used to develop these MCFs, and the sex ratio of the sample was unknown (Pérez-Tris et al., 2000), which raises the possibility that the error rate would change if testing a wintering population with a different population composition.

To clarify the accuracy of the MCFs proposed by Pérez-Tris et al. (2000) for distinguishing between sedentary and migratory robins during the wintering period in southern Iberia, we took advantage of the predicted geographic variation in the hydrogen stable isotope signals of robin feathers ($\delta^{2}H_f$; Catry et al., 2016). We first characterized isotopically the sedentary robin population of research interest in southern Iberia, as well as one migratory population in northern Iberia. We then made predictions on how the $\delta^{2}H_f$ of wintering robins, classified as migratory or sedentary by the MCFs, should vary in relation to the values of these two breeding populations of known migratory behaviour if the MCFs worked well (see premises 1 and 2 below).

We determined the $\delta^{2}H_f$ signature of the sedentary population occurring in the Campo de Gibraltar (Cádiz, South Spain) by sampling one tail feather (one rectrix number 5; Jenni & Winkler, 1994) from robins captured during August 2006 (after moulting period) and May 2014 (before moulting period). Robins were trapped in two woodland sites (36°09'48"N, 5°34'56"W and 36°09'54"N, 5°34'55"W) located in ‘Los Alcornocales’ Natural Park. In parallel, we also sampled feathers from robins breeding in Álava (Northern Spain...
42°54′02″N, 2°32′07″W), where the robin population is considered migratory (De la Hera et al., 2014).

On the other hand, wintering robins in Gibraltar were trapped between mid-November and mid-February during two different winters (2006-07 and 2013-14). Winter sampling took place in the two abovementioned woodland localities, as well as in two nearby shrubland areas (36°09′03″N, 5°37′54″W and 36°05′11″N, 5°42′09″W) that host robins only during the winter period (Tellería et al., 2001). Each trapped robin was aged as adult or juvenile using plumage characteristics (Jenni & Winkler, 1994). We also recorded the eighth primary (P8) length (being P1 the innermost primary) and the so-called wing formula (Svensson, 1992): the primary distances of the 9 longest primaries (excluding the vestigial outermost primary: P10). ‘Primary distance’ was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, with a value of zero for the primary (or primaries) constituting the wingtip. All morphological measurements were taken by two standardized ringers in 2006-07 (IdH, JP-T) and only by one of these in 2013-14 (IdH). Additionally, we used a syringe to extract a sample of blood from the jugular vein that was used for molecular sexing (Griffiths et al., 1998), and collected one rectrix number 5. Note that feathers of both breeding and wintering sampled birds had grown in the same season: the previous summer (either 2006 or 2013), providing thus comparable feather samples with their corresponding winter.

Feather samples were sent to the Colorado Plateau Stable Isotope Laboratory (http://www.isotope.nau.edu/), where their hydrogen isotopic ratios were measured by coupled pyrolysis/isotope-ratio mass spectrometry. $\delta^2$H values were expressed in units per mil (%), and normalized according to the VSMOW-SLAP scale using the values obtained for three keratin standards (Keratin-SC Lot SJ, Caribou hoof and Kudo horn). The $\delta^2$H values of 20 individuals were measured a second time to estimate analytical repeatability (Lessells & Boag, 1987), which was highly significant ($r = 0.98$; $F_{19,20} = 130.9$; $P < 0.001$) supporting the reliability of obtained $\delta^2$H measurements.

We used the same DFA that gave rise to the MCFs detailed in Pérez-Tris et al. (2000) to classify as either migratory or sedentary the 149 robins captured during winters 2006-07 and 2013-14. From this DFA, we obtained, for each wintering individual, the probability of being migratory ($P_{\text{mig}}$) or sedentary ($P_{\text{sed}}$) according to its morphology (StatSoft, 2004). The sum of $P_{\text{mig}}$ plus $P_{\text{sed}}$ equals 1, so that the migratory behaviour assigned to each particular robin will be that for which the $P$ is higher, which accurately matches with the outcome of MCFs assignations (Pérez-Tris et al., 2000). We then tested the reliability of
these MCFs by comparing the δ²Hf values of the wintering robins assigned as migratory
(P_{cmig} > 0.5) or sedentary (P_{cmig} < 0.5) with the δ²Hf values of robins captured in Álava
(migratory) and Gibraltar (sedentary) during the breeding period. Given the lack of
homogeneity of variances between the four groups of birds, we used Welch t-tests with
separate variance estimates to make comparisons among them (Fig. 1). We predicted that a
good performance of the MCFs will be supported by the fulfilment of two premises: 1) wintering robins assigned as sedentary by the MCFs and breeders captured in Gibraltar would
have similar δ²Hf scores; and 2) the δ²Hf values of wintering robins assigned as migratory
should be at least similar to Álava breeders or smaller (reflecting a more Northern origin;
Hobson et al., 2004). This last assumption is based on the observation that most of the
migratory robins wintering in Gibraltar should come from farther North-Northeast than Álava
(Bueno, 1998; Korner-Nievergelt, et al. 2014), since the breeding densities of the species
south of Álava are relatively low compared to North and Central European migratory
populations, and sedentariness is to be expected in many Iberian populations (Purroy, 2003;
Telleria, 2012).

δ²Hf values greatly varied among the four groups of robins compared , (Fig. 1). Thus,
robins captured in Gibraltar during the breeding period showed higher δ²Hf scores than
conspecifics captured in Álava (t_{40} = -8.64, P < 0.001; Fig. 1), with their ranges of values
overlapping only very marginally (δ²Hf range for Gibraltar: [-40.4, -16.3]; δ²Hf range for
Álava: [-82.5, -40.3]). Out of the 149 wintering robins captured in Gibraltar region, 53 were
assigned as migratory and 96 as sedentary by the MCFs. Wintering robins assigned as
migratory by the MCFs showed the most negative δ²Hf scores of the four groups for
comparison (Fig. 1). These values were significantly lower than those displayed by the
wintering robins assigned as sedentary (t_{147} = -2.76, P = 0.006), Gibraltar breeders (t_{55} =
10.26, P < 0.001) or Álava breeders (t_{69} = 2.54, P = 0.013; Fig. 1). However, birds classified
as sedentary by the MCFs also differed markedly in their δ²Hf values from the local birds
captured during summer in Gibraltar (t_{118} = 5.42, P < 0.001), contrary to what would be
expected if the MCFs were operating correctly. In contrast, their δ²Hf values were similar to
the ones displayed by the robins breeding in Álava (t_{112} = 0.15, P = 0.877; Fig. 1).

Given the marginal overlap in the δ²Hf values between robins breeding in Álava and
Gibraltar, we decided to use -40‰ as an arbitrary δ²Hf threshold to separate sedentary from
migratory robins in our study site during winter and to analyse in further detail the
performance of the MCFs. This -40‰ threshold should tell apart most of the sedentary
population in our study site (mean ± SD for Gibraltar breeders, -27.59 ± 6.62, N = 24), but it
is likely to assign erroneously to the sedentary group some North and Central Iberian
migrants that would show similar or less negative values than Álava breeders (mean ± SD for
Álava breeders, -53.75 ± 12.75, N = 18). According to the probability density functions of
Álava and Gibraltar breeders, we would expect that 14 of the wintering robins with less
negative values than -40‰ were actually migrants. Accordingly, the analyses shown below
should be taken with caution.

Using abovementioned criteria, we estimated that the rate of correct classifications of
the MCFs was 92% for sedentary birds (3 erroneous assignations out of 38 birds with $\delta^2Hf > -$
40‰; see right quadrant in Fig. 2) and a 45% for migrants (61 errors out of 111 birds with
$\delta^2Hf < -40‰$; left quadrant in Fig. 2), with significant differences in the error rate between
populations (Chi-squared: $\chi^2 = 25.6, P < 0.001$). Thus, the MCFs worked better than random
detecting sedentary birds (Chi-squared: $\chi^2 = 26.95, P < 0.001$), but did not perform
differently from chance for migrants (Chi-squared: $\chi^2 = 1.09, P = 0.296$). Our data also
revealed clear age and sex-related biases in the distribution of the MCFs errors. The three
sedentary birds classified erroneously as migrants were all males (two adults and one
juvenile; Fig. 2), while the 61 migrants incorrectly assigned to the sedentary group were all
females or juveniles (only 7 males within the 40 errors made on juveniles, and none of the 17
migratory adult males was misclassified; see Fig. 2). Among the migrants wrongly assigned
as sedentary (n = 61) errors were not homogeneously distributed between sex and age
categories (Chi-squared: $\chi^2 = 17.11, P < 0.001$).

Our results showed that the mean $\delta^2Hf$ values of wintering robins assigned as
sedentary by the MCFs were lower than those shown by Gibraltar breeders (Fig. 1), which
refuted one of the main assumptions that supported the validity of these MCFs. In general,
this classification method worked well to identify sedentary robins (92% of correct
assignations), but its performance was virtually random on migrants (55% of them were
incorrectly classified as sedentary). MCFs are based on the existing differences in wing size
and shape between migratory and sedentary robins (Pérez-Tris et al., 2000), but both
populations show marked sex and age-related variation in these characteristics that caused a
relatively large morphological overlap between populations. This situation was
further aggravated by the fact that the migratory population occurring during winter in
Campo de Gibraltar region is overrepresented by juveniles (Chi-squared: $\chi^2 = 6.19, P =
0.013$) and females (Chi-squared: $\chi^2 = 5.23, P = 0.022$) when compared to the sedentary
fraction, and these two population groups have more chances of being misclassified as
sedentary according to their wing morphology (Fig. 2). Such circumstance, in combination
with a potential bias in the representation of the different age and sex categories in the sample of Iberian breeders used to develop the MCFs, might have led to an unrealistic 80% of correct assignations (Pérez-Tris et al., 2000) that is effectively less when applied to the wintering population. New MCFs that incorporated the sex of the individuals in their construction—something initially overlooked in the development of the original MCFs—would significantly increase their ability to distinguish migratory and sedentary robins in their sympatric wintering grounds.

Supporting this idea, updated MCFs obtained from a new DFA that considered the sex of the individuals and was developed using the -supposedly- 111 migratory and 38 sedentary robins from our winter sample (Table 1), assigned correctly over 93% of individuals to their respective groups (Wilks' Lambda: 0.39; F11,137 = 19.7, P < 0.001). This result supports the view that morphological characterisation can still be a useful tool for discriminating between migratory and sedentary robins, under the condition that individuals need to be sexed first. However, we discourage a broad use of these newly proposed MCFs before their performance is properly tested using independent samples. Likewise, we acknowledge that our MCFs are based on the study of only two breeding populations, so that a more extensive sampling of Iberian Robins would be necessary to extrapolate the classification method to other wintering areas of Robin sympatric occurrence and to have a better characterization of the isotopic signals of Iberian migrants.

Our study is another good example of the potential problems that researchers can find when applying morphology-based differentiation methods on populations different from the ones used to develop the technique (Ellrich et al., 2010). Isotopic signatures revealed that the MCFs available to distinguish migratory and sedentary robins in sympatric wintering grounds of southern Iberia did not work properly, but overestimated the number of local sedentary birds. This suggests that previously described between-habitat patterns of sedentary robins in Gibraltar region might be biased by the misclassification of many migratory females and juveniles as sedentary, providing a misleading picture of how these birds are spatially distributed during winter in southern Iberia (Pérez-Tris et al., 2000). Values of δ²Hf seem to be a more reliable method than morphology to assess the migratory behaviour of robins (although this is not the case in other species; De la Hera et al., 2012), and could be used to re-assess whether sedentary robins are really outcompeted from woodlands during winter by arriving migratory counterparts (as MCFs initially suggested; Tellería et al., 2001; Tellería & Pérez-Tris, 2004) or, alternatively, they are able to remain in their breeding habitats year-round as it is the case for other species (i.e. Blackcaps; Pérez-Tris & Tellería, 2002). This is
an important question in areas where individuals with different migratory behaviour occur in
sympatry during winter, since it can help us to assess the vulnerability of some of these
wintering populations that are currently facing a drastic decline as a consequence of global
warming and other anthropogenic alterations (Herrero & Zavala, 2015; Tellería, 2015).

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Table 1. Classification functions obtained from a Discriminant Function Analysis that considered the 149 wintering robins whose migratory behaviour was estimated using $\delta^{2}H_f$ values. New individuals will be assigned to the group (migratory or sedentary) for which the corresponding function provides the highest value. For each individual, equations are solved by adding the value of the constant to the sum of products of each coefficient multiplied by its morphological trait. Males and females were coded as 1 and 2, respectively.

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Figure legends.

Figure 1. Variation in δ²Hf values between robins captured during breeding in Álava and Gibraltar that are known to be migratory and sedentary (left quadrant), respectively; and values for the wintering robins assigned as migratory (Pc\textsubscript{mig} > 0.5) or sedentary (Pc\textsubscript{mig} < 0.5) by their morphology (right quadrant). Graph shows medians (black dots), percentiles 25-75 (boxes) and percentiles 1-99 (whiskers).

Figura 1. Variación en los valores de δ²Hf entre petirrojos capturados durante la reproducción en Álava y Gibraltar para los que se sabe que son migratorios y sedentarios (cuadrante izquierdo), respectivamente; y valores para los petirrojos invernantes asignados como migratorios (Pc\textsubscript{mig} > 0.5) y sedentarios (Pc\textsubscript{mig} < 0.5) a partir de su morfología (cuadrante derecho). La gráfica muestra medianas (puntos negros), percentiles 25-75 (rectángulos) y percentiles 1-99 (segmento de líneas).

Figure 2. Variation in the posterior classification probabilities of being migratory (Pc\textsubscript{mig}) between different age and sex categories of wintering robins assigned as migratory or sedentary according to their δ²Hf values. Individuals above the dashed line (Pc\textsubscript{mig} > 0.5) were assigned as migratory by the MCFs, while individuals below it (Pc\textsubscript{mig} < 0.5) were classified as sedentary.

Figura 2. Variación en las probabilidades posteriores de clasificación de ser migratorio (Pc\textsubscript{mig}) entre diferentes categorías de edad y sexo de los petirrojos invernantes asignados como migratorios o sedentarios de acuerdo a sus valores de δ²Hf. Los individuos sobre la línea discontinua (Pc\textsubscript{mig} > 0.5) fueron asignados como migradores por las MCFs, mientras que los individuos bajo esa misma línea (Pc\textsubscript{mig} < 0.5) fueron clasificados como sedentarios.
De la Hera et al. Figure 1. $\delta^{2}H$/ values and the migratory behaviour of robins.
De la Hera et al. Figure 2. $\delta^2$H$_f$ values and the migratory behaviour of robins.