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SHORT REPORT

Tawny Owls *Strix aluco* from a southern European population differ in size and degree of reverse sexual dimorphism from northern European counterparts

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ABSTRACT
Tawny Owls in southern Europe were trapped and measured. Compared to males, the females were larger, heavier, and more greyish in colour, but there was a large biometric overlap. The variable with the highest Storer's dimorphism index (SDI) was weight, though our population had one of the smallest dimorphisms observed in Europe for weight. It has been proposed that differences in diet could lead to differing behaviour and, in consequence, the observed dimorphism degree (SDI) by natural selection.

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RSD; Bergmann; Storer's dimorphism index; diet; biometrics; latitude

Most bird species show sexual dimorphism in size, with males often being larger than females. However, in some bird taxa, including most raptors (Falconiformes and Accipitriformes), and owls (Strigiformes; Newton 1979), females are usually the larger sex. This phenomenon is called reverse sexual dimorphism (RSD) (Mueller & Meyer 1985, Jehl & Murray 1986, Courter 2017, Schoenjahn *et al.* 2020). The RSD is a broadly studied phenomenon but no theory about its origin has yet been accepted, as it remains to be explained why most raptor and owl species show RSD (Schoenjahn *et al.* 2020). The RSD may be to some extent caused by a sex-dependent niche partition, which is also shaped by the availability and abundance of target prey species within given areas. This is an aspect still poorly investigated in spite of its importance to understanding the evolutionary significance of the RSD.

The Tawny Owl *Strix aluco* is a widely studied species across Europe and is also identified by the COST Action European Raptor Biomonitoring Facility as one of the most suitable candidates for pan-European biomonitoring (Ratajc *et al.* 2022). Thus, reliable information about its RSD would be very helpful in order to, for example, distinguish males from females across the latitude range, meaning that lots of conservation studies could be carried out more precisely. Insights about why RSD occur in owls would help us to understand more about the adaptations and ecology of Tawny Owls.

Our aims with this study are to: (1) describe the biometrics and degree of RSD of a Tawny Owl population from southern Europe, (2) identify which biometrical variables contribute most to the RSD, and (3) compare this population with other Tawny Owl populations in Europe.

The field work was carried out in three zones belonging to three nearby provinces in northern Iberia: Gipuzkoa, Bizkaia and Burgos. They all have an oceanic climate with mild temperatures and high precipitation rates. The landscape in Gipuzkoa and Bizkaia is mountainous with extensive urban and industrial areas. It is mostly covered by forest, especially forestry plantations such as Monterey Pine *Pinus radiata* and Eucalyptus *Eucalyptus* spp. and a few remnants of native forest (Beech *Fagus sylvatica* and Pedunculate Oak *Quercus robur*). The landscape in Burgos is also mountainous, but it is dominated by grass fields for Cattle *Bos taurus* and surrounded by large deciduous forests (mainly Sessile Oak *Q. petraea* and Portuguese Oak *Q. faginea*) in the valley, pine plantations (Monterey Pine) on the lower slopes and Beech/oak forests (*F. sylvatica* and Pyrenean Oak *Q. pyrenaica*) on the upper slopes of the mountains.

Tawny Owls were trapped from 2001 to 2021. We trapped them at night with mist-nets using playback of the calls of the two sexes as a lure. The gender identification was determined by the vocal discrimination, when the individual was answering the playback (Martínez *et al.* 2002), and the age was

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determined in the hand by observing the moult pattern (Martínez *et al.* 2002, Zuberogoitia *et al.* 2018). We also took biometric measures, and a colouration value defined by the eumelanin or phaeomelanin quantity in feathers (Karell *et al.* 2013). The biometric variables measured were: (1) BEA1: beak length, from the beginning of the cere near the skull until the tip of the beak; (2) BEA2: beak length, from the end of the cere up to the tip of the beak; (3) HEAD–BILL: length from the back of the skull until the tip of the beak; (4) TAR1: tarsus length, including the tibia-tarsus articulation; (5) TAR2: tarsus length, excluding the tibia-tarsus articulation; (6) TAR3: minimum tarsus width; (7) P7: 7th primary feather length; (8) P8: 8th primary feather length; (9) FOR: forearm length; (10) FWI: folded wing length, equivalent to method III of Svensson (1992); (11) OPW: open wing length; (12) WSP: wing span; (13) TAI: tail length; (14) LEN: body length, from the tip of the beak up to the end of the tail, measured with the bird lying on its back and stretched out as much as possible; (15) WEI: weight; and (16) COL: colour code (Karell *et al.* 2013).

For the colour code (COL) variable, higher scores would indicate a higher concentration of phaeomelanin or eumelanin, and a more reddish/brownish colour, whilst lower scores indicate less pigmented feathers and more greyish individuals. Four parts were colour scored: the facial disk, where a score of 1 = the pigmented feathers are less than 20%, 2 = 20–40% pigmented, 3 = 40% or more pigmented feathers; the ventral zone where a score of 1 = grey or dark brown feathers; 2 = reddish- or yellowish-brown feathers; dorsal zone of 1 = grey, 2 = yellowish grey, 3 = reddish brown, 4 = yellowish brown; and general appearance, where 1 = grey, 2 = yellowish grey, 3 = brown, 4 = reddish brown, 5 = red. The sum of the four colour scores varied from 4 (a grey individual) to 14 (a reddish individual).

Before any analysis, we checked all of the data in order to detect possible errors. This was done first with a visual examination of the dataset to detect obvious errors (too low or high values) and, second, by checking for the presence of extreme outliers in boxplots, which we compared with the rest of the data from the same individual. Because morphological traits can vary between age classes, we also removed from the dataset owlets and juveniles that were still growing (i.e. aged as EURING 1 and 3J).

We calculated the Storer's dimorphism index (SDI) (Storer 1966, Massemin *et al.* 2000): $SDI = 100 \times (f - m)/[0.5(f + m)]$, where f was the mean of the female metric and m was the mean of the male metric.

We tested that there was not multicollinearity between the variables (VIF < 10; Naimi *et al.* 2014). To determine which variables varied between sex classes we ran a saturated generalized linear model (GLM) with the sex (codified as a binary variable: 0 = male, 1 = female) as an object variable, with a binomial distribution of errors. Previously, we discarded some variables for the model selection (i.e. TAR1 and TAR2 are very similar, thus we only included the one that is used the most: TAR1). The variables included in the analysis were: HEAD–BILL, TAR1, TAR3, P8, FOR, OPW, WSP, TAI, LEN and WEI. Thereafter, we ran the function 'dredge' from the MuMIn package (Barton 2019) for R (R Core Team 2022) in order to select those models that had a better fit to the data. Model selection in dredge was carried out based on model Akaike values (AIC) (Burnham & Anderson 2004). Models differing by less than 2 AIC values were considered to fit the data equally well (Burnham & Anderson 2004). Thus, a model averaging was run and included all variables that differed by less than 2 AIC from the best model. Another GLM was also run with COL as the only independent variable.

We also calculated the SDI index for published data from other European populations of Tawny Owls, with the aim of obtaining a ranking to compare with our population's FWL and WEI dimorphism. All analyses were run in R (Rstudio 1.3.1073).

We trapped and measured 70 Tawny Owls (Table 1). The weight was the most dimorphic variable, with a SDI of 21.9, far beyond the other measures. In order to run the GLMs we considered only 38 individuals (15 females, 23 males) as being those where all biometric and colour variables were measured (for details see Table 1).

The top-ranked GLM model included only an effect of WEI on sex, but six additional models (including, overall, P8, FOR, TAI and OPW) were ranked at less than 2 AIC values from the top model (Table 2), indicating that such variables also contributed to sexual dimorphism. Mean beta-parameter estimates of the averaged model are shown in Table 3. Females were larger than males, being also significantly heavier (Tables 1 and 3). The GLM with COL as the only independent variable revealed a significant difference between sexes (Beta ± SE: 0.70 ± 0.34, 95% CI: 0.07-1.41), with males being on average more reddish than females.

Compared to other Tawny Owl populations, our population was observed to have the lowest body weight of all those sampled, independently of sex (Table 4). Moreover, our females had shorter wing lengths than the rest of the samples, except those from

Table 1. Descriptive statistics between sex classes for a Tawny Owl population from northern Iberia. We show for each sex the mean (± SE) and range and the SDI (Storer's dimorphism index). Variable descriptions: BEA1 = beak length including the cere; BEA2 = beak length excluding the cere; HEAD = length from back of the skull to bill tip; TAR1 = tarsus length including the tibia-tarsus articulation; TAR2 = tarsus length excluding the tibia-tarsus articulation; TAR3 = minimum tarsus width; P7 = 7th primary length; P8 = 8th primary feather; FOR = forearm length; FWI = folded wing length; OPW = open wing length; WSP = wing span; TAI = tail length; LEN = body length; WEI = weight; COL = colour code. All variables are in mm, except WEI (g) and COL (no unit). See text for further details.

	Females ($n = 34$)		Males ($n = 36$)		
Variables	Mean ± SE	Range	Mean ± SE	Range	SDI
BEA1 (mm)	30.4 ± 0.3	27.6–35.6	28.5 ± 0.2	24.3–30.8	+6.5
BEA2 (mm)	20.23 ± 0.4	16.8–25.6	18.8 ± 0.3	16.0–21.9	+7.3
HEAD (mm)	70.4 ± 0.5	66.6–76.9	68.7 ± 0.4	65.7–74.8	+2.4
TAR1 (mm)	57.8 ± 0.7	46.5–67.4	56.0 ± 0.4	51.8–60.1	+3.2
TAR2 (mm)	49.3 ± 0.5	44.0–54.8	47.7 ± 0.4	43.6–52.3	+3.3
TAR3 (mm)	6.6 ± 0.1	5.4–7.6	6.1 ± 0.1	4.9–7.0	+7.9
P7 (mm)	204.3 ± 1.5	190–228	197.5 ± 1.2	188–215	+3.4
P8 (mm)	192.8 ± 2.2	148–222	188 ± 1.0	175–197	+2.5
FOR (mm)	96.19 ± 0.6	87.1–101.6	94.4 ± 0.4	89.5–99.0	+1.9
FWI (mm)	273 ± 1.3	255–286	261.7 ± 1.4	240–275	+4.2
OPW (mm)	412.3 ± 3.5	375–452	399 ± 4.0	353–450	+3.3
WSP (mm)	915.7 ± 5.2	836–953	883.6 ± 4.6	810–934	+3.6
TAI (mm)	176.2 ± 1.6	154–191	172.6 ± 1.5	156–193	+2.1
LEN (mm)	391.2 ± 3.5	350–417	371.9 ± 3.2	322–403	+5.1
WEI (g)	475.4 ± 9.6	330–580	381.5 ± 4.2	350–455	+21.9
COL	9 ± 0.5	5–14	10.5 ± 0.5	4–14	−15.4

Britain, Denmark and one from southern Spain. In males, we found a similar pattern, although our sample was also similar to the one from Britain (Table 4).

The absolute SDI values ranged from 21.9 (WEI) or 15.4 (COL) to less than 2 (FOR). When ranking the SDI values from across Europe, our population was observed to have one of the smallest dimorphisms for both OPW and WEI, with only the Italian population having a lower weight SDI value (Figure 1). Regarding wing length, our population had bigger wing lengths than southern Iberian, Swedish and Danish populations (Figure 2). All SDI values, except COL, were positive.

Our results show that the Tawny Owl is a dimorphic species, but not as described for other populations (Sunde *et al.* 2003). Only the weight is dimorphic enough to follow the described pattern of RSD, while the other measures are barely dimorphic. Biometric differences are mostly non-significant between males and females in our study population, showing a high degree of overlap.

A bird's weight, a variable nowadays used for gender determination of Tawny Owls, was found to be the only dimorphic biometric variable. If we focus on this, only those birds with a weight greater than 455 g are females (for details see Table 1). This result agrees with Martínez *et al.* (2002), who also found that weight was a dimorphic variable, although in our case the boundary between male and female individuals was smaller than the one they obtained. In addition, Martínez *et al.* (2002) also found the bill and folded wing to be dimorphic variables. Even though these two variables were not significantly dimorphic in our study, they had a high and positive SDI value (Table 1), which means that females were larger than males. These differences could be due to the limited sample sizes used in the studies.

Our Tawny Owls also differed in coloration, with females tending to be greyer than males, which were more reddish. Tawny Owl pigmentation has been shown to be related to environmental adaptations

Table 2. Ranking of the best-ranked GLM models (the top-ranked and those differing by less than 2 AIC units), together with the saturated and the null models. Variable abbreviations: WEI = weight; P8 = P8 feather length; TAI = tail length; OPW = opened wing length; FOR = forearm length.

Model	AIC	ΔAIC	R^2	Overdispersion
WEI	24.550	0.000	0.777	0.457
P8 + WEI	25.616	1.062	0.794	0.446
TAI + WEI	25.932	1.378	0.787	0.453
OPW + WEI	26.013	1.459	0.777	0.455
FOR + WEI	26.021	1.467	0.786	0.455
Saturated	38.162	13.612	0.767	0.599
Null	52.982	28.432	0.000	1.378

Table 3. Beta-parameter estimates obtained from an averaged model from those outlined in Table 2 with less than 2 AIC units from the top-ranked model. Variable abbreviations: WEI = weight; P8 = P8 feather length; TAI = tail length; OPW = open wing length; FOR = forearm length.

Parameter	No. models included	Beta	SE (Beta)	95% CI (lower/ upper)
Integer	5	+0.70	0.61	−0.49 / +1.89
WEI	5	−4.05	1.18	−6.36 / −1.74
TAI	1	−0.46	0.59	−1.63 / +0.70
P8	1	−0.58	0.54	−1.63 / +0.47
OPW	1	−0.38	0.52	−1.40 / +0.64
FOR	1	0.66	0.93	−1.17 / +2.49

Table 4. Reference weight and folded wing length means of other Tawny Owl populations used for comparison with our sample from northern Iberia. Reference values have been compared with the mean body mass and wing length of our population, as shown in Table 1. Those marked * are data from the *Strix aluco sylvatica* subspecies, and others are *Strix aluco aluco*.

Population	Females (μ)	Males (μ)	SDI	Source
Weight (g)				
N. Iberia*	475.4	381.5	21.9	This study
W. Russia	642	472	30.5	Dement'ev *et al.* (1951)
Finland	600	420	35.3	Mikkola & Lamminmäki (2014)
Denmark	567	471	18.5	Sunde *et al.* (2003)
E. Germany	561	441	23.9	Piechocki *et al.* (1977)
Belgium	553	440	22.8	Delmée *et al.* (1978)
Italy	517	425	19.5	Moltoni (1949)
Britain	514	393	26.7	BTO Ringing Scheme
Wing length (mm)				
N. Iberia*	273	261.7	4.2	This study
Sweden	284.4	274.0	3.4	Dement'ev *et al.* (1951)
W. Russia	296.4	283.2	4.5	Dement'ev *et al.* (1951)
Denmark	273	267	2.2	Sunde *et al.* (2003)
Britain*	272.0	259.0	4.9	BTO Ringing Scheme
S. Iberia*	268.0	257.8	3.9	Martínez *et al.* (2002)

(Roulin *et al.* 2008, Piault *et al.* 2009) and different reproductive strategies (Roulin *et al.* 2003) when raising owlets. Thus, the differences between both sexes could be due to the different roles of each sex during the breeding season. As in most raptors and owls, male Tawny Owls hunt to feed their partners while the latter take care of the nest and owlets (Tapia & Zuberogoitia 2018). Nevertheless, this topic needs further research, and the colouration score is not enough to distinguish the sex of an individual, as any score may be found in either sex.

Our owls were smaller than in many other European studies, except those populations from southern areas. Tawny Owls follow Bergmann's rule (James 1970, Meiri & Dayan 2003), which states that, in general, large-bodied animal species tend to live further north than their small-bodied relatives (Blackburn *et al.* 1999). It can be observed in Table 4 how this rule is followed by Tawny Owls, with the northern birds being bigger and heavier than southern ones. However, this rule does not take RSD into account and, according with most of the RSD hypothesis, we would expect to find the same dimorphism rate (SDI) through the distribution range, but it is not true. Interestingly, the weight SDI in our population was observed to be much lower than in other populations where the biometric distance between the two sexes is significantly greater. Except for the population from Denmark, which had a lower SDI value (smaller RSD rate) than our population (Figure 1), the other populations have larger SDI values further north and further west. Thus, it can be stated that the dimorphism rate is not as conservative as Rising (1987) stated. This variation in the SDI could be due to several factors that probably need more research, though we can already advance that it is compatible with our hypothesis supporting a latitudinal effect linked to the trophic ecology. It has been demonstrated that northern Tawny Owl populations have a diet largely composed of mammals, whereas the southern ones have a wider diet spectrum (Galeotti *et al.* 1991, Grašytė *et al.* 2016, Gamero & De

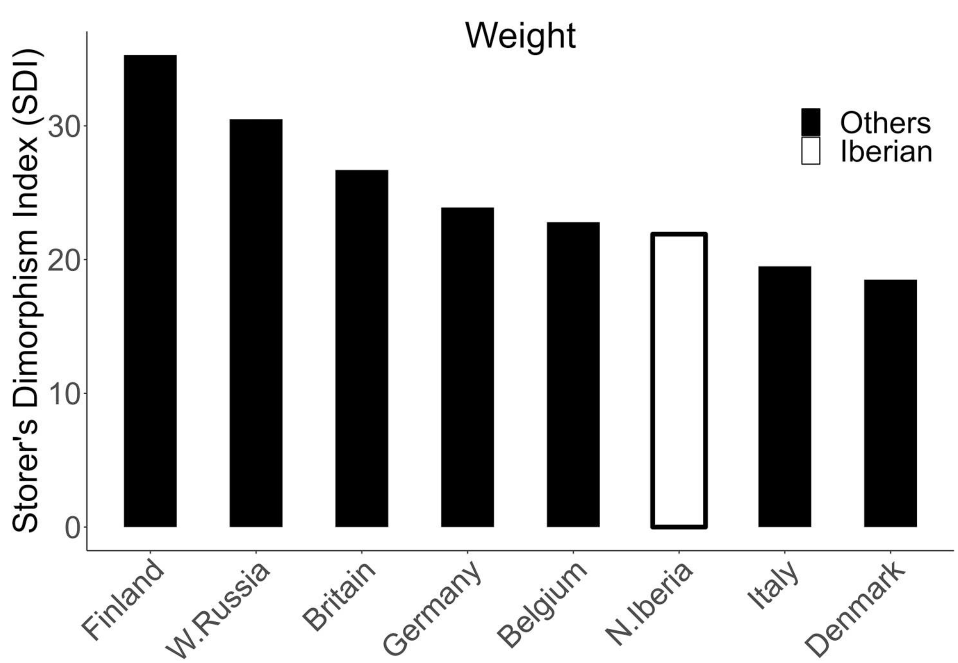

Figure 1. Comparison of the Storer's dimorphism index (SDI) for weights of Tawny Owl populations from Europe.

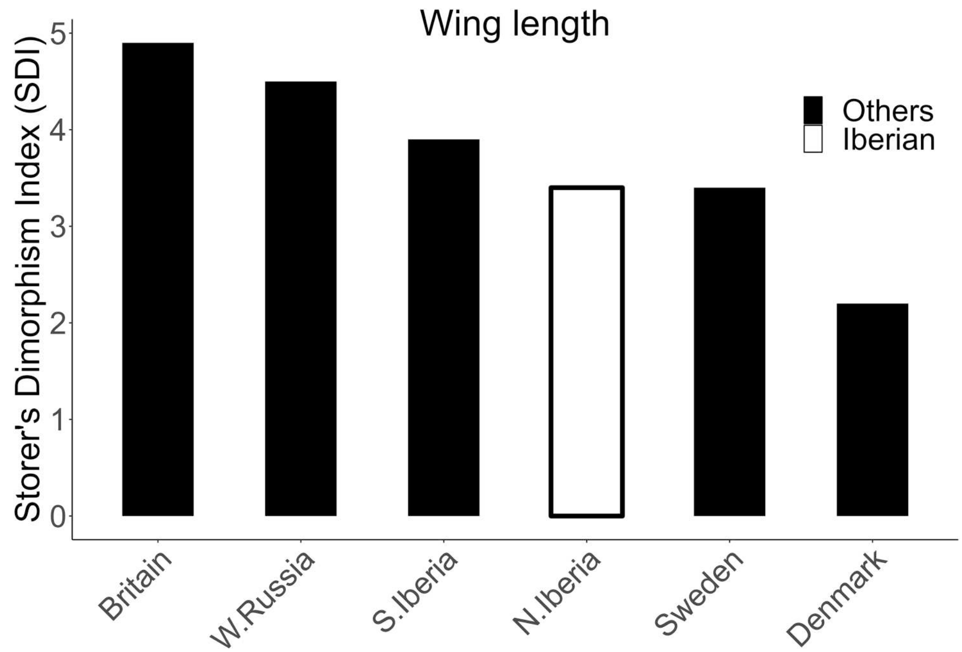

Figure 2. Comparison of the wing length Storer's dimorphism index (SDI) for Tawny Owl populations from Europe.

Miguel 2017, Solonen *et al.* 2017). According with this result, the reversed sexual dimorphism has been proposed to be related with hunting behaviours, which depend on prey groups (Pérez-Camacho *et al.* 2018). Thus, differing diet could lead to a change in hunting behaviour and end up changing the degree of dimorphism (calculated by the SDI) by natural selection. However, the wing length SDI values do not follow any latitudinal gradient, which could possibly be due to more local habitat characteristics, where each population will adapt to the accessible habitat and conditions.

In the same direction, it can be mentioned that the Tawny Owl is a ubiquitous species that has adapted very well to urban environments, which are increasing worldwide. One of the adaptations of Tawny Owls to this new environment is also related to diet, with urban individuals tending to have a broader diet than their rural counterparts (Gryz & Krauze-Gryz 2019, Palacio 2020), with the latter tending to have a more specialized diet. This change in behaviour could lead to a change in the degree of RSD in the future, and this is a topic that warrants further study.

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