Elevation of two subspecies of Dunnock Prunella modularis to species rank

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by Marco Pavia, Sergei V. Drovetski, Giovanni Boano, Kevin W. Conway, Irene Pellegrino & Gary Voelker

SUMMARY.—The Western Palearctic endemic Dunnock *Prunella modularis* was recently revealed to comprise three distinct genetic lineages, each distributed in different Pleistocene refugia. Specifically, one is isolated in the Iberian refugium, another is confined to the Caucasus refugium, and the third is distributed in both the Italian and Balkan refugia, as well as across broader Europe. There is a probable absence of gene flow between the refugia. Analysis of plumage and song characteristics reveals robust differences between the Iberian subspecies *P. m. mabbotti*, Caucasian *P. m. obscura* and nominate *P. m. modularis*. Our assessments, in conjunction with genetic isolation, support species recognition under the Phylogenetic, Biological and Comprehensive Biological Species Concepts, via qualitative and quantitative criteria, and diagnosability. We thus propose the elevation of Iberian Dunnock *P. mabbotti* and Caucasian Dunnock *P. obscura* to species level.

Dunnock *Prunella modularis* is a common songbird species that is endemic to the Western Palearctic. Some north European populations migrate short distances to winter in southern Europe, whereas populations breeding in the latter region are largely sedentary (del Hoyo & Collar 2016). No fewer than 15 subspecies have been described, with several having ranges largely circumscribed by peninsular (e.g., Iberia), insular (British Isles) or montane regions (e.g., Caucasus). Subspecific descriptions have been based on plumage differences, and in a few cases qualitative assessments of mensural characters; assessments of vocalisations have been restricted to *P. m. occidentalis* from England (e.g., Cramp 1988). Since their formal description, many Dunnock taxa have been subsumed into other races (Table 1), and recent treatments vary in recognising as many as eight (Cramp 1988, del Hoyo & Collar 2016, Gill *et al*. 2020) to just three subspecies (Dickinson & Christidis 2014, Shirihai & Svensson 2018). None of these decisions was based on genetic data.

In our recent phylogeographic study of the Dunnock (Drovetski *et al*. 2018a), sampling included individuals from the distributions of *P. m. modularis* (most of central and northern Europe), *P. m. obscura* Hablizl, 1783 (north-east Turkey, Caucasus, north Iran), *P. m. occidentalis* E. Hartert, 1910 (Britain and west France), *P. m. mabbotti* Harper, 1919 (French Pyrenees, Iberia, and possibly the Italian Apennines and Greece; recent treatments are in conflict) and *P. m. meinertzhageni* Harrison & Pateff, 1937 (former Yugoslavia and Bulgaria).

The results of the Drovetski *et al*. (2018a) study placed Dunnocks into one of three highly supported clades, each distributed in different Pleistocene refugia: a Caucasus clade, an Iberian clade, and a clade comprising all other individuals, including from the Balkans. Gene-flow analysis indicated that the Caucasus and Iberian clades were isolated from each other, as well as from the remaining clade, in which extensive gene flow was evident between Italy, the Balkans (Montenegro, Serbia and Greece) and broader Europe. Based on this genetic isolation, we suggested that Dunnock comprises three species (Drovetski

TABLE 1

The eight subspecies of *Prunella modularis* currently recognised by Gill *et al.* (2020) and their type localities, and their treatment under other modern classifications.

Taxon and authority	Type locality	Cramp (1988)	Dickinson & Christidis (2014)	del Hoyo & Collar (2016)	Shirihai & Svenson (2018)	Clements *et al.* (2019)
P. m. hebridium R. Meinertzhagen, 1934	South Uist, Outer Hebrides, Scotland	*P. m. hebridium*	*P. m. occidentalis*	*P. m. hebridium*	*P. m. occidentalis*	*P. m. hebridium*
P. m. occidentalis E. Hartert, 1910	Tring, Hertfordshire, England	*P. m. occidentalis*	*P. m. occidentalis*	*P. m. occidentalis*	*P. m. occidentalis*	*P. m. occidentalis*
P. m. modularis (Linnaeus, 1758)	Sweden	*P. m. modularis*	*P. m. modularis*	*P. m. modularis*	*P. m. modularis*	*P. m. modularis*
P. m. mabbotti Harper, 1919	3 km south of Saillagouse, Pyrénées-Orientales, France	*P. m. mabbotti*	*P. m. modularis*	*P. m. mabbotti*	*P. m. modularis*	*P. m. mabbotti*
P. m. meinertzhageni Harrison & Pateff, 1937	Beglik and Rila, Bulgaria	*P. m. meinertzhageni*	*P. m. modularis*	*P. m. meinertzhageni*	*P. m. modularis*	*P. m. meinertzhageni*
P. m. fuscata Mauersberger, 1971	Ai-Petri, Crimea, Ukraine	*P. m. fuscata*	*P. m. obscura*	*P. m. fuscata*	*P. m. obscura*	*P. m. fuscata*
P. m. euxina Watson, 1961	Uludağ, Bursa, north-west Turkey	*P. m. euxina*	*P. m. modularis*	*P. m. euxina*	*P. m. modularis*	*P. m. euxina*
P. m. obscura (Hablizl, 1783)	Gilan, Iran	*P. m. obscura*	*P. m. obscura*	*P. m. obscura*	*P. m. obscura*	*P. m. obscura*

et al. 2018a), which was supported by molecular species delimitation. Here we summarise in more detail the morphological and vocalisation data supporting the elevation of two Dunnock subspecies, corresponding to the Iberian and Caucasus clades described by Drovetski *et al.* (2018), to species status. In addition, we suggest that *P. m. meinertzhageni* of the former Yugoslavia and Bulgaria be synonymised with the nominate subspecies.

Material and Methods

Based on our genetic results (Drovetski *et al.* 2018), we compared specimens collected during the breeding season from the distributions of the three Dunnock lineages to their original descriptions (as subspecies) in order to verify the accuracy and validity of the proposed distinguishing characters. We analysed specimens held in the American Museum of Natural History, New York (AMNH), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), Biodiversity Research and Teaching Collection Texas A&M University, College Station, TX (TCWC), and Museo Civico di Storia Naturale di Carmagnola, Italy (MCCI). Specifically, we sought to assess if the plumage characters used in the original descriptions were in fact diagnostic. We analysed 50 specimens of *P. m. modularis*, 17 of *P. m. mabbotti* and 14 of *P. m. obscura* (Appendix 1). To visualise plumage variation among these taxa, we present photographs of the ventral, lateral and dorsal aspects of specimens of these lineages, including the holotype of *P. m. mabbotti* at USNM (Fig. 1). All photographed specimens were collected between late April and early June, and

Figure 1. Specimens of the three Dunnock taxa considered in this work in dorsal, ventral and lateral views. A. *Prunella* [*modularis*] *modularis*, USNM 640862 (female; left) and USNM 640847 (male; right), Greece. B. *P.* [*m.*] *mabbotti*, first pair USNM 256648 (female; left) and USNM 256755 (type specimen, male; right), French Pyrenees; second pair USNM 317499 (female; left), and USNM 317500 (male; right), Spain. C. *P.* [*m.*] *obscura*, USNM 640349 (female; left) and USNM 640358 (male; right), Greater Caucasus (S. V. Drovetski)
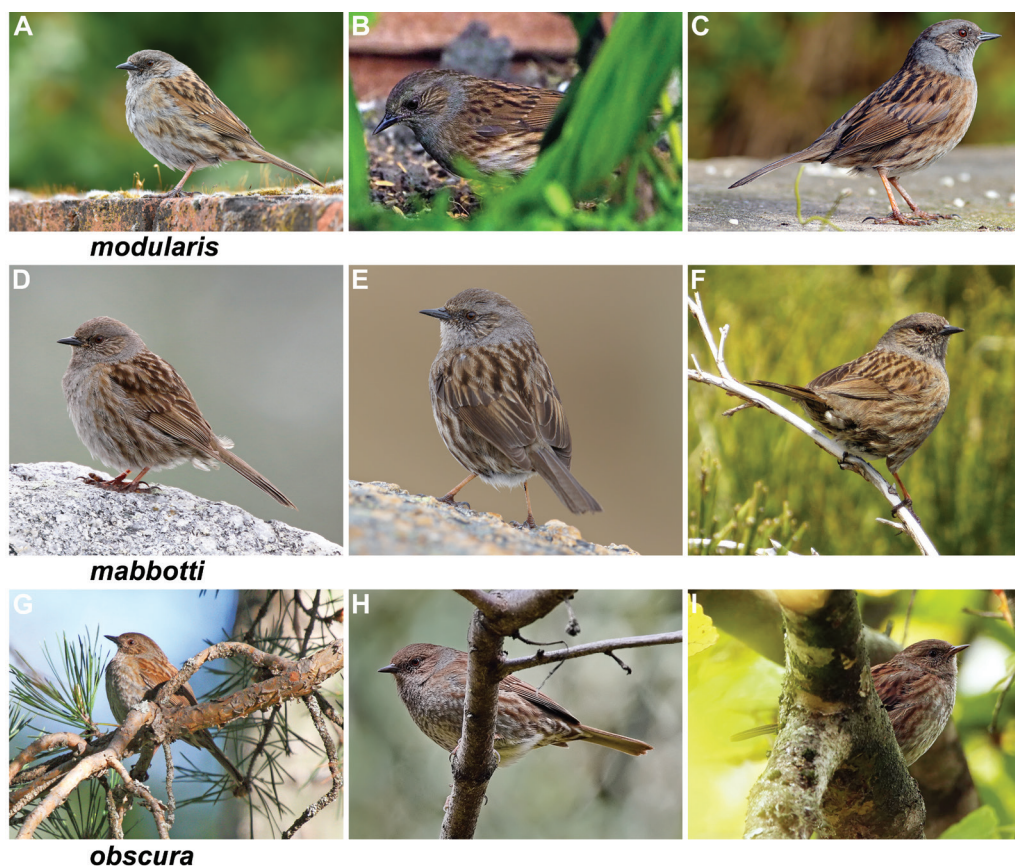
Figure 2. Individuals of the three Dunnock taxa considered herein. A. *Prunella* [*modularis*] *modularis*, UK (© L. Pulawski). B. *P.* [*m.*] *modularis*, Ireland (© B. Carruthers). C. *P.* [*m.*] *modularis*, UK (© K. Johnson). D. *P.* [*m.*] *mabbotti*, Spain (© D. Jauvin). E. *P.* [*m.*] *mabbotti*, Spain (© D. Petterson). F. *P.* [*m.*] *mabbotti*, Spain (© P. Alves). G. *P.* [*m.*] *obscura*, Armenia (© P. Adriaens). H. *P.* [*m.*] *obscura*, Georgia (© O. Nabrovenko). I. *P.* [*m.*] *obscura*, Iran (© C. Mroczko)

are therefore in breeding plumage. We also provide pictures of live individuals of the same taxa, photographed in the breeding season (Fig. 2).

We also compared songs of the three lineages, by using the Xeno-canto database (www. xenocanto.org) to select good-quality recordings made during the breeding season in the distributions of the three taxa. We analysed 125 phrases of *P. m. modularis*, 31 of *P. m. mabbotti* and 11 of *P. m. obscura* (Appendix 2). The sonograms (Figs. 3–4) and the analyses were prepared using the software Praat (Boersma & Weenink 2020). For each analysed phrase, we calculated the total length (in seconds) and the frequency range, including min. and max. (in kHz). We also evaluated whether rattles were present (Constantine & The Sound Approach 2006: 38–39) and, if so, assessed their length and frequency range. To assess if differences between taxa were significant, we calculated *p*-value and Cohen's *d* value (Table 2).

Results

Plumage characteristics.—Dunnock *P. modularis sensu lato* has a grey to brownish head with streaky ear-coverts, plain to mottled crown, a heavily streaked mantle, and grey to brown breast grading to dusky white on the central belly, with the body-sides streaked
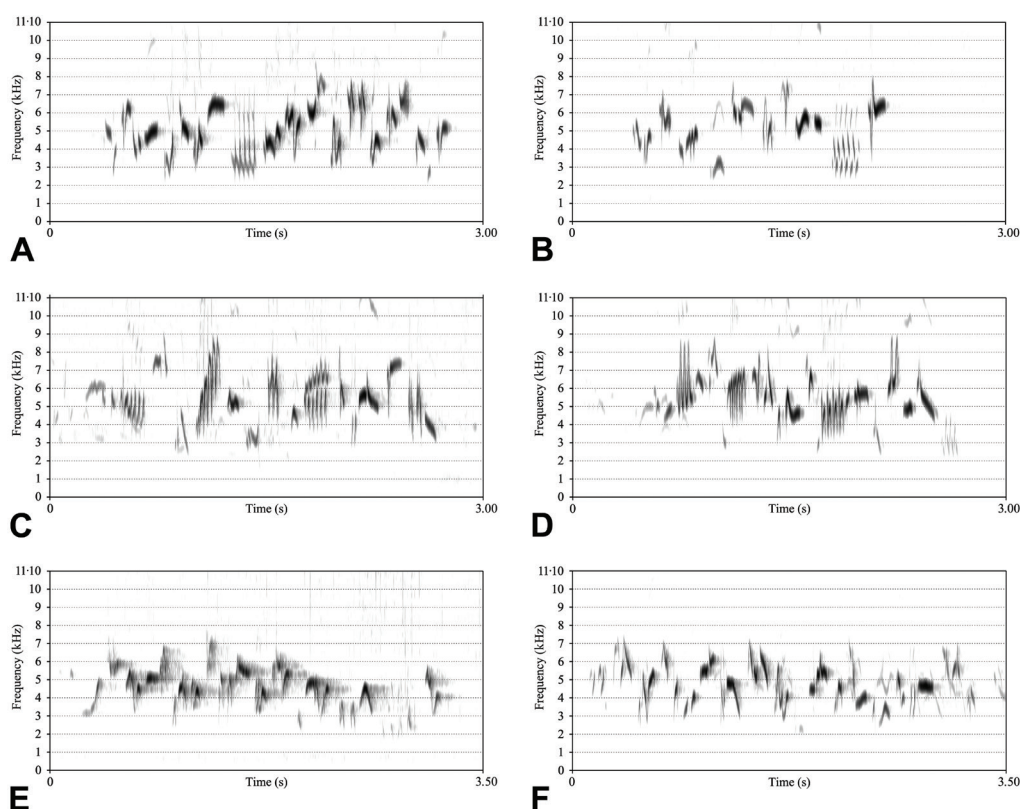
Figure 3. Sonograms of songs of Dunnock taxa considered in this work. A. *Prunella* [*modularis*] *modularis*, XC 392787 (J. Matusiak; www.xeno-canto.org/392787), Slovakia. B. *P.* [*m.*] *modularis*, XC 132703 (J. Matusiak; www.xeno-canto.org/132703), Poland. C. *P.* [*m.*] *mabbotti*, XC 342428 (A. Tomás; www.xeno-canto.org/342428), Portugal. D. *P.* [*m.*] *mabbotti*, XC 471699 (J. Calvet; www.xeno-canto.org/471699), Spain. E. *P.* [*m.*] *obscura*, XC 480650 (A. Lastukhin; www.xeno-canto.org/480650), Azerbaijan. F. *P.* [*m.*] *obscura*, XC 139532 (F. Deroussen; www.xeno-canto.org/139532), Georgia. Sonograms generated using Praat (Boersma & Weenink 2020).

buff-brown. The three subspecies assessed here (central European *P. m. modularis*, Iberian *P. m. mabbotti* and Caucasian *P. m. obscura*) show clear plumage differences relative to each other (Figs. 1–2). In particular, *P. m. mabbotti* (Figs. 1B, 2D–F) can be distinguished from other taxa of *P. modularis* by plumage differences listed in the original description (Harper 1919). Specifically, it differs from *P. m. modularis* (Figs. 1A, 2A–C) by its greyer, less rufescent back, mantle and wings, with their feather edgings buffy brown and smoke grey instead of cinnamon-brown as in *P. m. modularis* (Harper 1919), and their centres are brown instead of black as in *P. m. modularis*. Ventrally, *P. m. mabbotti* is less grey than *P. m. modularis* but closer in appearance to the latter than either is to *P. m. obscura* (Fig. 1C). Furthermore, the head of *P. m. mabbotti* is not as grey as, and lacks the brown streaking on crown and cheeks of, *P. m. modularis* and the former's ear-coverts are not as brown as those of the latter, conveying the impression of a plain face in *P. m. mabbotti*.

P. m. obscura is distinguished from the other taxa of *P. modularis* primarily by the plumage characters reported in the original description (Hablizl 1783; see also del Hoyo & Collar 2016). These differences are particularly evident on the head: buff-tinged chin, brownish nape (not grey), light brown plain supercilium (vs. pure grey in *P. m. modularis*), and light brown and finely streaked crown. Further differences include back feathers with
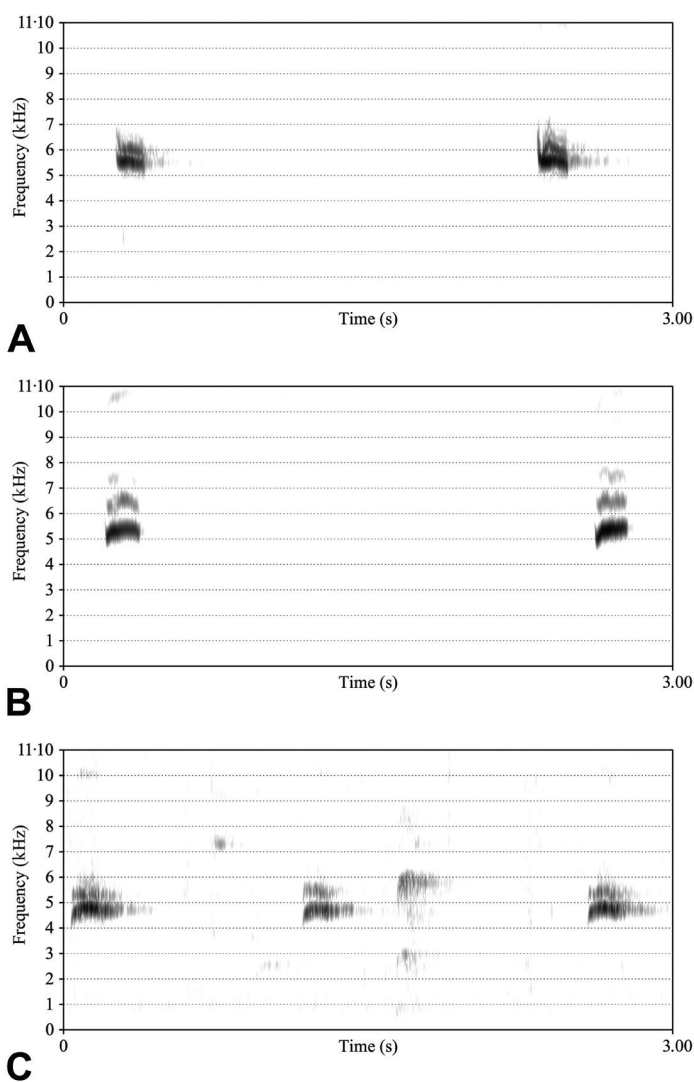
Figure 4. Sonograms of calls of Dunnock taxa considered in this work. A. *Prunella* [*modularis*] *modularis*, XC107150 (P. Åberg; www.xeno-canto.org/107150), Sweden. B. *P.* [*m.*] *mabbotti*, XC335177 (C. Mroczko; www.xeno-canto.org/335177), Spain. C. *P.* [*m.*] *obscura*, XC512728 (C. Mroczko; www.xeno-canto.org/512728), Iran. Sonograms generated using the software Praat (Boersma & Weenink 2020).

ill-defined chestnut streaks, and distinctly darker breast, compared to the other lineages, and throat to breast extensively marked with off-white or pale buff feather tips, forming a scaly pattern. Overall, *P. m. obscura* is much darker ventrally and more rufous-brown overall than the other two lineages, with less contrast between the grey and brown tones, a pattern approaching that of Japanese Accentor *P. rubida*.

Mensural data reported in the literature show great overlap between the various subspecies, with none available for breeding birds from Iberia and southern France (*P. m. mabbotti*) (Cramp 1988, Shirihai & Svensson 2018), thus we did not consider these parameters in our analysis.

Vocalisations.—The song of *P. modularis sensu lato* is a rather loud warble, usually 2.0–3.5 seconds long, and quite formless in that the notes lack a distinct structure (Fig. 3). The song of *P. modularis sensu lato* shows more prolonged units in the frequency range 4–6 kHz, and brief and sharply modulated units at 3–7 kHz with peaks up to 8 kHz. All units typically comprise different notes, apart from repetitions of a trill or rattle, usually once each phrase. Each male has repertoire of up to six (perhaps more) different songs, with each

TABLE 2

Measurements of sound parameters in *Prunella* [*modularis*] *modularis*, *P.* [*m.*] *mabbotti* and *P.* [*m.*] *obscura*. Means and standard deviations are given. s = seconds; Cohen's *d* = effect size in terms of magnitude.

TAXON		Total phrase length (s)	Max. frequency (kHz)	Min. frequency (kHz)	Frequency range (kHz)	1st rattle length (s)	1st rattle max. frequency (kHz)	1st rattle min. frequency (kHz)	1st rattle frequency range (kHz)	2nd rattle length (s)	2nd rattle max. frequency (kHz)	2nd rattle min. frequency (kHz)	2nd rattle frequency range (kHz)
P. m. modularis	Mean	2.393	8.2694	2.2029	6.0665	0.174	6.1673	2.6125	3.5548				
	SD	0.550	0.4242	0.2931	0.5423	0.039	1.1325	0.4729	1.2084				
	N	125	125	125	125	80	80	80	80				
P. m. mabbotti	Mean	2.429	8.9648	2.5530	6.4118	0.163	7.8582	3.2321	4.6261	0.169	7.5744	3.6722	3.9022
	SD	0.360	0.3666	0.3344	0.5870	0.027	1.0104	0.3904	1.0281	0.024	0.90515	0.5863	0.6914
	N	31	31	31	31	31	31	31	31	25	25	25	25
P. m. obscura	Mean	2.992	7.5911	1.9797	5.6113								
	SD	0.285	0.3358	0.3420	0.6111								
	N	11	11	11	11								
modularis / mabbotti	t-test	0.3453	8.3822	5.7861	3.1213	1.4093	7.2644	6.4842	4.3593				
	P	0.73033	0.00000	0.00000	0.00215	0.16160	0.00000	0.00000	0.00003				
	Cohen's d	0.0773	1.7735	1.1136	0.611	0.3217	1.5756	1.4290	0.9549				
modularis / obscura	t-test	3.5653	5.1584	2.3884	2.6424								
	P	0.00050	0.00000	0.01832	0.00921								
	Cohen's d	1.3692	1.8072	0.7006	0.7879								
mabbotti / obscura	t-test	4.6860	10.8999	4.8574	3.8455								
	P	0.00003	0.00000	0.00000	0.00042								
	Cohen's d	1.7367	3.9081	1.6951	1.3360								

song usually different in all units from the others; modification to an individual's song does occur between years and during counter-singing (Cramp 1988). These factors combine to render comparisons across lineages difficult, and furthermore the availability of recordings of *P. m. mabbotti* and *P. m. obscura* song during the breeding season is reduced compared to those of *P. m. modularis*.

Despite these difficulties, our comparison of songs did reveal some variation that seems to permit discrimination between *P. m. modularis*, *P. m. mabbotti* and *P. m. obscura*. Analysis demonstrates that the songs of *P. m. mabbotti* are higher pitched (with peaks up to 9 kHz) with the rattle repeated more frequently within the phrase (Fig. 3C–D). Specifically, *P. m. mabbotti* had two rattles in 81% of examined phrases and occasionally a third at the start of the phrase (Table 2), whereas in *P. m. modularis* 64% of examined songs possessed just a single rattle. On the other hand, the song of *P. m. obscura* (Fig. 3E–F) is longer and lower pitched (barely exceeding 7 kHz) than both *P. m. modularis* and *P. m. mabbotti*, and lacks the typical rattles of the other two (with one exception where a faint rattle was present). Most differences we identified are statistically significant, but effect size is relatively low based on Cohen's *d* values (Table 2).

Dunnock also produces a wide variety of calls (Cramp 1988), which makes their comparison rather complicated. Similar types of calls across the three taxa show very slight differences, with *P. m. obscura* being of lower frequency (kHz) and repeated more frequently than the other two (Fig. 4). As such, calls seem to have little bearing for distinguishing taxa.

Species concept criteria.—Diagnosability is an obvious threshold for recognising species, and diagnosable characters vary across species. In a recent study that used both morphological and genetic data to assess avian diversity, Barrowclough *et al.* (2016) postulated that recognised biological species each harbour on average 1.97 phylogenetic species based on a criterion of morphological diagnosability. Their genetic estimates found an average of 2.4 phylogenetic species per biological species. In other words, each biological species appears to include on average two phylogenetic species.

Our previous genetic results (Drovetski *et al.* 2018a), which included a species delimitation method, and Bayesian and gene-flow analyses, clearly indicated that the three lineages are reproductively isolated with no gene flow. It is highly unlikely that adding more genes (we used 11) or samples (we included 13 for Iberia, 36 for the Caucasus and 66 for the remaining clade) would alter our interpretation of reproductive isolation (see, e.g., Felsenstein 2006). Based on reproductive isolation and independent evolutionary trajectories (Drovetski *et al.* 2018a), the obvious plumage differences identified by previous works (summarised above), and song differences documented here, we suggest that *P. modularis* comprises three species under the Phylogenetic Species Concept (Cracraft 1983). Considering that an independent evolutionary history is what ultimately identifies a species (see Zachos *et al.* 2013), we consider our genetic data sufficient to also recognise the three lineages as species in accord with both the Biological Species Concept (for which reproductive isolation is the paramount issue; Mayr 1963) and the Comprehensive Biological Species Concept (Johnson *et al.* 1999). Our proposal to recognise three species is also consistent with the criteria proposed by Helbig *et al.* (2002), as all are diagnosable by plumage, mitochondrial and nuclear DNA, with differences in song.

Offering further support is that two Dunnock lineages (*P. m. modularis* and *P. m. mabbotti*) are probably parapatric (we can find no records to indicate sympatry) in south-west France, and that *P. m. obscura* is isolated from *P. m. modularis* (and other described subspecies) in the Caucasus and adjacent regions. Finally, we suggest that the length of time since lineages are estimated to have diverged should not be a factor in recognising species; to suggest otherwise seems notional rather than evidence-based. For example,

Motacilla species diverged more recently than *Prunella* species, but the former are often accepted as separate species (Drovetski *et al*. 2018b). Among the *Prunella* radiation, of the 14 recognised species, ten (including *P. modularis*) are estimated to have diverged from their closest relative within the last two million years, and the most recent divergence was just 0.13 million years ago (between Brown Accentor *P. fulvescens* and Kozlov's Accentor *P. koslowi*; Drovetski *et al*. 2013).

Taxonomic assessment

Considering the various aspects detailed above, we propose the following taxonomic arrangement for European Dunnock taxa.

Prunella modularis (Linnaeus, 1758) Common Dunnock

Remarks.—P. modularis is distributed in Europe from Scandinavia and the British Isles to France and northern Italy, and east to the eastern slope of the Ural Mountains (Cramp 1988, Shirihai & Svensson 2018). Based on our molecular work (Drovetski *et al*. 2018a), which included samples from the former Yugoslavia and Greece that were embedded within those from elsewhere in the range of the nominate subspecies, we propose that *P. m. meinertzhageni* be synonymised with *P. m. modularis*, as already suggested by Ripley (1964) and Shirihai & Svensson (2018). Placing this taxon in synonymy means that the range of *P. m. modularis* is expanded to include the Balkans and Greece. This species is polytypic and includes the following subspecies: *P. m. hebridium*, *P. m. occidentalis*, *P. m. modularis*, *P. m. fuscata*, and *P. m. euxina*.

Prunella mabbotti Harper, 1919, Iberian Dunnock, new rank

*Remarks.—*Although this taxon has been considered a synonym of *P. modularis* by some authors (e.g., Dickinson & Christidis 2014, Shirihai & Svensson 2018), our results confirm its validity. *P. mabbotti* is distributed in the Iberian Peninsula and French Pyrenees (the type locality), where it is apparently resident (Cramp 1988). Vaurie (1955: 24) noted that two birds from the Pyrenees, two from central Spain and three from Portugal were similar to each other, and distinguishable from *P. m. modularis*. However, Vaurie (1955) erroneously attributed these birds to *P. m. lusitanica* Stresemann, 1928, a substitute name introduced for *P. m. obscura* Tratz, 1914, a junior homonym of *P. obscura* (Hablizl, 1783). Vaurie (1955) synonymised *P. m. mabbotti* with *P. m. lusitanica* but following Art. 60 of the *International code of zoological nomenclature* (replacement of junior homonyms) (ICZN 1999), the species-group name *mabbotti* Harper, 1919, has priority over its synonym *lusitanica*. We elaborate on this to eliminate future confusion, because while the nomenclatural priority is widely recognised, it has not been explicitly detailed in some recent works (e.g., Ripley 1964, Cramp 1988, Hatchwell 2005).

Based on our genetic results (Drovetski *et al*. 2018a), *P. mabbotti* does not occur in either Greece or the Italian Alps. The possible presence of *P. mabbotti* in the Apennines (northern to southern Italy) requires confirmation. While some treatments suggest this distribution as possible (e.g., Cramp 1988, Hatchwell 2005), the supporting rationale is unclear and the morphology of individuals we examined (specimens and photos of live birds) from the region are attributable to *P. modularis*. In addition, a preliminary genetic analysis of a recently fledged bird sampled in Abruzzo (central Italy) revealed a relationship with *P. modularis*, not *P. mabbotti* (L. Ilahiane pers. comm. 2021). Elsewhere, *P. mabbotti* is occasionally listed for south-central France (e.g., Hatchwell 2005) which implies a distribution on the north-east slopes of the Pyrenees, which is where the type locality is situated. As such, the northern limits of *P. mabbotti* relative to south-west France populations

of *P. modularis* are not well defined, but these two forms are probably parapatric in this area, as corroborated by photographs of live birds during the breeding season. It appears that the eastern Pyrenees are occupied by Iberian Dunnocks (see, e.g., https://www.inaturalist. org/observations/39468304, https://www.inaturalist.org/observations/67241118), whereas in the western Pyrenees, where the mountains are lower, and in extreme northern Spain Common Dunnock occurs in an extension from its French distribution (see, e.g., https:// www.inaturalist.org/observations/67829328, https://macaulaylibrary.org/asset/245589781). We consider *P. mabbotti* to be monotypic.

Prunella obscura (Hablizl, 1783), Caucasian Dunnock, new rank

Remarks.—The distribution of *P. obscura* is the Caucasus region, Transcaucasia, north-east Turkey and northern Iran (type locality), where it is resident (Cramp 1988). Given this distribution, *P. obscura* is unlikely to intergrade with either *P. m. euxina* or *P. m. fuscata*, which appear to be restricted to north-west Turkey and Crimea, respectively. We consider *P. obscura* to be monotypic.

To conclude, further studies based on sampling and morphological characterisation of breeding Dunnocks in different parts of Spain, Portugal and the French Pyrenees could clarify the distribution and conservation status of *P. mabbotti* and potential contact zones with *P. modularis* in France and Iberia. Additional sampling is also needed to assess whether *P. mabbotti* is present in central Italy. Further study is necessary to confirm the relationships of *P. m. occidentalis* and other subspecies of *P. modularis* not included by Drovetski *et al.* (2018a), viz. *P. m. hebridium* Meinertzhagen, 1934 (western Scotland, Hebrides and Ireland), *P. m. euxina* Watson, 1961 (north-west Turkey) and *P. m. fuscata* Mauersberger, 1971 (Crimea), to the taxa considered herein.

References:
Barrowclough, G. F., Cracraft, J., Klicka, J. & Zink, R. M. 2016. How many kinds of birds are there and why does it matter? *PLoS ONE* 11: e0166307.
Boersma, P. & Weenink, D. 2020. Praat: doing phonetics by computer. Version 6.1.10. http://www.praat.org/ (accessed 23 March 2020).
Clements, J. F., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Sullivan, B. L. & Wood, C. L. 2019. The eBird/Clements checklist of birds of the world: v2019. https://www.birds.cornell.edu/ clementschecklist/download/ (accessed 23 March 2020).
Constantine, M. & The Sound Approach. 2006. *The Sound Approach to birding: a guide to understanding bird sound*. The Sound Approach, Poole.
Cracraft, J. 1983. Species concepts and speciation analysis. *Current Orn.* 1: 159–187.
Cramp, S. (ed.) 1988. *The birds of the Western Palearctic*, vol. 5. Oxford Univ. Press.
Dickinson, E. C. & Christidis, L. (eds.) 2014. *The Howard and Moore complete checklist of the birds of the world*, vol. 2. Fourth edn. Aves Press, Eastbourne.
Drovetski, S. V., Semenov, G., Drovetskaya, S. S., Fadeev, I. V., Red'kin, Y. A. Voelker, G. 2013. Geographic mode of speciation in a mountain specialist avian family endemic to the Palearctic. *Ecol. & Evol.* 3: 1518–1528.
Drovetski, S. V., Fadeev, I. V., Raković, M., Lopes, R. J., Boano, G., Pavia, M., Koblik, E. A., Lohman, Y. V., Red'kin, Y. A., Aghayan, S. A., Reis, S., Drovetskaya, S. S. & Voelker, G. 2018a. A test of the European

Pleistocene Refugial Paradigm, using a Western Palearctic endemic bird species. *Proc. Roy. Soc. Lond. B* 285: 2018.1606.

Drovetski, S. V., Reeves, A. B., Red'kin, Y. A., Fadeev, I. V., Koblik, E. A., Sotnikov, V. N. & Voelker, G. 2018b. Multi-locus reassessment of a striking discord between mtDNA gene trees and taxonomy across two congeneric species complexes. *Mol. Phylo. & Evol.* 120: 43–52.

Felsenstein, J. 2006. Accuracy of coalescent likelihood estimates: do we need more sites, more sequences, or more loci? *Mol. Biol. & Evol.* 23: 691–700.

Gill, F., Donsker, D. & Rasmussen, P. (eds.) 2020. IOC world bird list (v10.2). https://doi.org/10.14344/IOC. ML.10.2 (accessed 23 March 2020).

Hablizl, K. 1783. Bemerkungen in der persischen Landschaft Gilan und auf den Gilanischen Gebirgen. *Neue Nord. Beytr.* 4: 3–104.

Hatchwell, B. J. 2005. Family Prunellidae (accentors). Pp. 496–513 *in* del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) *Handbook of the birds of the world*, vol. 10. Lynx Edicions, Barcelona.

Harper, F. 1919. A new subspecies of *Prunella modularis* from the Pyrenees. *Proc. Biol. Soc. Wash.* 32: 243–244.

Helbig, A. J., Knox, A. J., Parkin, D. T., Sangster, G. & Collinson, M. 2002. Guidelines for assigning species rank. *Ibis* 144: 518–525.

del Hoyo, J. & Collar, N. J. 2016. *HBW and Birdlife International illustrated checklist of the birds of the world*, vol. 2. Lynx Edicions, Barcelona.

International Commission for Zoological Nomenclature (ICZN). 1999. *International code of zoological nomenclature*. Fourth edn. The International Trust for Zoological Nomenclature, London.

Johnson, N. K., Remsen, J. V. & Cicero, C. 1999. Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. Pp. 1470–1482 *in* Adams, N. J. & Slotow, R. H. (eds.) *Proc. 22nd Intern. Orn. Congress, Durban*. BirdLife South Africa, Johannesburg.

Mayr, E. 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge, MA.

Ripley, S. D. 1964. Family Prunellidae, accentors. Pp. 3–12 *in* Mayr, E. & Paynter, R. J. (eds.) *Checklist of birds of the world*, vol. 10. Harvard Univ. Press, Cambridge, MA.

Shirihai, H. & Svensson, L. 2018. *Handbook of Western Palearctic birds: passerines*, vol. 2. Christopher Helm, London.

Vaurie, C. 1955. Systematic notes on Palearctic birds. No. 16. Troglodytinae, Cinclidae, and Prunellidae. *Amer. Mus. Novit.* 1751: 1–25.

Zachos, F. E., Apollonio, M., Bärmann, E. V., Festa-Bianchet, M., Göhlich, U. B., Habel, J. C., Haring, E., Kruckenhauser, L., Lovari, S., McDevitt, A. D., Pertoldi, C., Rössner, G. E., Sánchez-Villagra, M. R., Scandura, M. & Suchentrunk, F. 2013. Species inflation and taxonomic artefacts – a critical comment on recent trends in mammalian classification. *Mammalian Biol.* 78: 1–6.

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Appendix 1

List of analysed specimens for each taxon. Abbreviations: AMNH: American Museum of Natural History, New York; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC; TCWC: Biodiversity Research and Teaching Collection Texas A&M University, College Station; MCCI: Museo Civico di Storia Naturale di Carmagnola.

Prunella mabbotti: AMNH 584749, July, Portugal; AMNH 584750, July, Portugal; AMNH 584752, May, France. USNM 256648, April, France; USNM 256755, April, France (type specimen); USNM 317497, May, Spain; USNM 317498, May, Spain; USNM 317499, May, Spain; USNM 317500, May, Spain; USNM 317501, May, Spain; USNM 317502, May, Spain; USNM 317503, May, Spain; USNM 317504, May, Spain; USNM 317505, May, Spain; USNM 317506, May, Spain; USNM 317508, April, Spain; USNM 317509, April, Spain.

Prunella modularis: AMNH 25035, May, England; AMNH 54484, May, England; AMNH 261763, May, Sweden; AMNH 261764, May, Sweden; AMNH 348170, April, Scotland; AMNH 348175, April, Scotland; AMNH 450916, April, England; AMNH 454255, June, England; AMNH 455661, April, Austria; AMNH 455662, April, Austria; AMNH 455665, July, Germany; AMNH 455666, July, Germany; AMNH 455667, July, Germany; AMNH 455670, July, Germany; AMNH 455671, July, Germany; AMNH 455674, April, Austria; AMNH 584699, April, England; AMNH 584702, July, England; AMNH 584713, April, England; AMNH 584723, April, England; AMNH 584768, April, Switzerland; AMNH 584769, April, Switzerland; AMNH 584773, April, Germany; AMNH 584776, April, Germany; AMNH 748654, May, Denmark; AMNH 787814,

April, Germany; AMNH 787818, April, Germany. MCCI 3684, June, Italy; MCCI 3686, July, Italy; MCCI 4301, July, Italy; MCCI 4380, June, Italy; MCCI 4386, May, Italy; MCCI 4623, June, Italy. TCWC 22939, July, Italy; TCWC 22940, July, Italy; TCWC 22941, July, Italy; TCWC 22942, July, Italy; TCWC 22943, July, Italy. USNM 111121, June, Norway; USNM 113817, April, England; USNM 113818, April, England; USNM 191639, July, Switzerland; USNM 191642, July, Switzerland; USNM 234673, April, England; USNM 256647, April, France; USNM 424650, April, Denmark; USNM 637507, May, Greece; USNM 640157, May, Greece; USNM 640847, May, Greece; USNM 640862, May, Greece.

Prunella obscura: AMNH 464668, April, Iran; AMNH 584738, March, Russia; AMNH 584741, March, Russia; AMNH 584742, March, Russia. MCCI 4095, June, Armenia; MCCI 4096, June, Armenia. TCWC 21769, June, Armenia. USNM 639814, June, Russia; USNM 639823, June, Russia; USNM 639833, June, Russia; USNM 640349, June, Russia; USNM 640358, June, Russia; USNM 640381, June, Russia; USNM 640452, June, Russia.

Appendix 2

List of analysed sound recordings for each taxon. All sounds were retrieved from Xeno-canto (www.xeno-canto.org).

Prunella mabbotti: XC 34430, Spain, Juan Malo de Molina; XC 342428, Portugal, Agostinho Tomás; XC 410813, Portugal, João Tomás; XC 421712; Portugal, Jorge Leitão; XC 443925, Portugal, Jorge Leitão; XC 468269, Spain, Marcel Gil Velasco; XC 471699, Spain, Jordi Calvet; XC 472305, Spain, Jordi Calvet; XC 477802, Portugal, Jorge Leitão; XC 502693, Portugal, Jorge Leitão; XC 560619, Portugal, Jorge Leitão.

Prunella modularis: XC 46515, France, Jacques Prevost; XC62835, Norway, Holger Schielzeth; XC 70132, England, Paul Driver; XC 77229, France, Jacques Prevost; XC 77399, Denmark, Luis A. Hansen; XC 100666, Switzerland, Bram Piot; XC 101995, Denmark, Niels Krabbe; XC 102924, Switzerland, Pascal Christe; XC 111910, Denmark, Elias A. Ryberg; XC 132703, Poland, Jarek Matusiak; XC 132705, Poland, Jarek Matusiak; XC 132707, Poland, Jarek Matusiak; XC 133850, Scotland, Mike Nelson; XC 181582, Italy, Francesco Sottile; XC 183444, England, Marc Anderson; XC 192411, Norway, Stein Ø. Nilsen; XC 193374, Norway, Stijn De Win; XC 196790, England, 'David M'; XC 243941, Switzerland, Jerome Fischer; XC 247270, Sweden, Mikael Litsgård; XC 270206, France, Peter Boesman; XC 281379, Belgium, Peter Boesman; XC 281380, Belgium, Peter Boesman; XC 325335, Lithuania, Jarek Matusiak; XC 331874, France, Cedric Mroczko; XC 335679, England, 'David M'; XC 367329, Denmark, Luis A. Hansen; XC 371122, England, David Bissett; XC 374616, France, Manuel Grosselet; XC 374617, France, Manuel Grosselet; XC 384332, Denmark, Luis A. Hansen; XC 384369, Denmark, Luis A. Hansen; XC 389110, Germany, Antonio Xeira; XC 392787, Slovakia, Jarek Matusiak; XC 415511, Norway, Stein Ø. Nilsen; XC 420704, France, Jérémy Simar; XC 420855, Italy, Giuseppe Speranza; XC 443875, Norway, Karl-Birger Strann; XC 478151, Belgium, Peter Boesman; XC 483786, France, Jérémy Simar; XC 488737, Germany, Stephan Risch; XC 602656, Finland, Alain Malengreau.

Prunella obscura: XC 138593, Georgia, Maercin Solowiej; XC 139532, Georgia, Fernand Deroussen; XC 480650, Azerbaijan, Albert Lastukhin; XC 480651, Azerbaijan, Albert Lastukhin; XC 561010, Turkey, Lider Sinav.