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Are some of the birds endemic to the Tres Marías Islands (Mexico) species?

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Summary.—The Tres Marías archipelago off western Mexico, rarely visited by ornithologists, is currently considered to have 24 endemic subspecies of landbirds. Using both new and previously overlooked information, we evaluate some of the better-marked taxa by applying recently proposed criteria for determining whether they merit recognition at species level. We propose that six of these be elevated to species (*Cynanthus lawrencei*, *Amazilia graysoni*, *Forpus insularis*, *Pheugopedius lawrencii*, *Icterus graysonii* and *Granatellus francescae*) although for some there is evidence that they occasionally interbreed with close relatives on the adjacent mainland. These taxa are threatened by introduced goats, cats and rats, and we hope that by recognising them as endemic species, greater awareness of their plight might stimulate increased conservation action to preserve them and their ecosystem.

Since taxonomy guides conservation decisions and our perception of ecological/evolutionary patterns (Hosner *et al.* 2018), it must reflect scientific findings as accurately as possible. Recognition of a taxon as a species focuses the attention and resources of conservationists, politicians, media, and the public on taxa that would have been overlooked had they been considered 'only' subspecies (Phillips 1981, Meijaard 2014). The Tres Marías archipelago off western Mexico, rarely visited by ornithologists, lies 80 km from the mainland at the closest points and is currently considered to have 24 endemic or near-endemic subspecies of landbirds (herein 'Tres Marías endemics'; Table 1). Some of these taxa are phenotypically well marked and were originally considered species in the late 19th and early 20th century.

Recently, del Hoyo & Collar (2014, 2016) attempted to apply to all the world's birds a consistent standard for deciding whether well-marked populations merit species status, namely the Tobias *et al*. (2010) criteria. Del Hoyo & Collar evaluated three of the Tres Marías endemics and decided that two deserve species rank. Apparently, these authors did not evaluate the taxonomic status of the remaining Tres Marías endemics and, perhaps more importantly, they overlooked the important taxonomic work of Grant (1965a). Grant (1965a) provided extensive comparisons between a larger number of specimens from the islands and the adjacent mainland than any other study.

Here, we evaluate some of the better-marked Tres Marías endemic taxa to test whether they deserve species rank under the Tobias *et al*. (2010) criteria, using several sources of information: data assembled by Grant (1965a), our own field observations, the ornithological literature, visual examination of study skins in the collection of the Instituto de Biología of the Universidad Nacional Autónoma de México (IBUNAM), Mexico City, photographs of specimens in the Moore Laboratory of Zoology (MLZ), Occidental College, Los Angeles, and online photographs. We present evidence suggesting that a few Tres Marias endemic

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taxa occasionally interbreed with their relatives from the adjacent mainland (this was already known for Tropical Parula *Setophaga pitiayumi* but not for other species).

Study area

The Tres Marías Islands are a linear chain of continental-shelf islands 80–110 km from the nearest mainland across a shallow sea. From north-west to south-east, the four islands are Isla San Juanito (9 km^2, highest elevation 60 m), Isla María Madre (145 km^2, 620 m), Isla María Magdalena (70 km^2, 540 m) and Isla María Cleofas (20 km^2, 380 m) (elevations taken from INEGI 1999a,b, 2003a–c). Two of the islands are practically equidistant from the mainland. Additionally, volcanic Isla Isabel (2 km^2, 190 m) potentially forms a 'stepping stone' for movement of individuals between some of these islands and the mainland, though it is much closer to the mainland (Fig. 1).

This area appears to have been united to the southern tip of the Baja California Peninsula and the Nayarit coast in the Miocene (Helenes & Carreño 2014) and was still united with the Nayarit mainland until three million years ago in the Late Pliocene (Fig. 99 and p. 206 *in* Pompa-Mera 2014). The islands were submerged until the Late Pliocene; they must have emerged above sea level well before the Late Pleistocene (*contra* Zweifel 1960, Smith *et al*. 2011, Arbeláez-Cortés *et al*. 2014, Montaño-Rendón *et al*. 2015) as there are Late Pleistocene terrace deposits in the lower-lying areas of both Isla María Madre (McCloy *et al*. 1988, Pompa-Mera *et al*. 2013, Pompa-Mera 2014) and Isla María Cleofas (Foose 1962), and hundreds of metres of uplift must have occurred for that to be the case.

Throughout the Pleistocene sea level rose and fell cyclically, repeatedly reaching 120 m below current sea level during glacial maxima (Waelbroeck *et al*. 2002, Bintanja *et al*. 2005, Rohling *et al*. 2009). Low sea levels exposed parts of the islands and the adjacent mainland that are currently under water, and reduced the isolation of the Tres Marías to just *c*.20–25 km (Ortíz-Ramírez *et al*. 2018). These changes (tectonic rifting, uplift and sea-level fluctuations) must have had a strong impact on the population dynamics of the islands' biota.

The principal vegetation on the islands is seasonally dry, medium-stature tropical forest (González-Medrano & Hernández-Mejía 2007), and is very similar to undisturbed vegetation on

TABLE 1

Bird taxa endemic or nearly endemic to the Tres Marías islands. Taxa considered herein to be species are in boldface.

Scientific name	**English name**
Patagioenas flavirostris madrensis	Red-billed Pigeon
Leptotila verreauxi capitalis	White-tipped Dove
Nyctidromus albicollis insularis	Common Pauraque
Cynanthus latirostris lawrencei	**Broad-billed Hummingbird**
Amazilia rutila graysoni	**Cinnamon Hummingbird**
Buteo jamaicensis fumosus	Red-tailed Hawk
Picoides scalaris graysoni	Ladder-backed Woodpecker
Caracara cheriway pallidus	Crested Caracara
Forpus cyanopygius insularis	**Mexican Parrotlet**
Amazona oratrix tresmariae	Yellow-headed Parrot
Myiopagis viridicata minima	Greenish Elaenia
Pachyramphus aglaiae insularis	Rose-throated Becard
Vireo hypochryseus sordidus	Golden Vireo
Vireo flavoviridis forreri	Yellow-green Vireo
Pheugopedius felix lawrencii	**Happy Wren**
Myadestes occidentalis insularis	Brown-backed Solitaire
Turdus rufopalliatus graysoni	Rufous-backed Robin
Melanotis caerulescens longirostris	Blue Mockingbird
Spinus psaltria witti	Lesser Goldfinch
Setophaga pitiayumi insularis	Tropical Parula
Piranga bidentata flammea	Flame-coloured Tanager
Cardinalis cardinalis mariae	Northern Cardinal
Granatellus venustus francescae	**Red-breasted Chat**
Icterus pustulatus graysonii	**Streak-backed Oriole**

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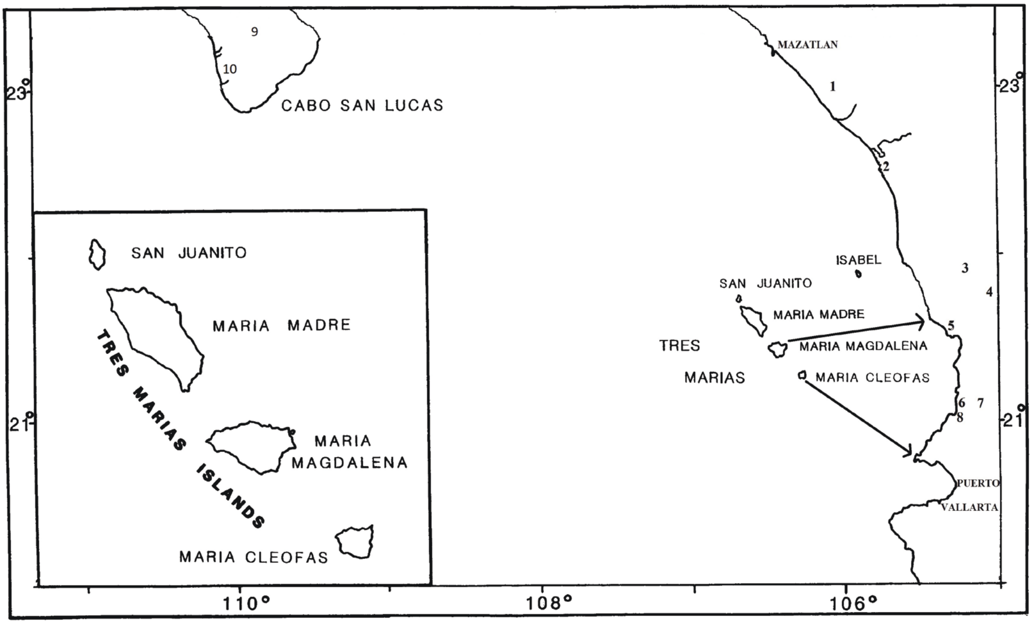

Figure 1. Map showing the location of the Tres Marías Islands with respect to the adjacent mainland (modified from Wilson 1991). The arrows show the two closest routes between the islands and the mainland. The approximate locations of the cities Mazatlán and Puerto Vallarta are indicated. Numbers indicate mainland localities mentioned in the text where Tres Marías taxa or hybrids have been recorded: 1. 'Labrados' (based on Fig. 1 in McLellan 1927), 2. 'Novilleros, west of Acaponeta' = Playa Novillero, 3. Santiago Ixcuintla, 4. Sauta, 5. San Blas and 1 3/4 km north of Singaíta, 6. Chacala, 7. Las Varas, 8. La Peñita de Jaltemba, 9. El Oro, and 10. Todos Santos.

the adjacent mainland (Grant 1965a). Rainfall patterns, mean annual rainfall and actual evapotranspiration are similar to those on the adjacent mainland (García *et al*. 1990, Maderey-Rascón 1990, Vidal-Zepeda 1990), but mean annual temperature and total annual rainfall are slightly and distinctly lower, respectively (Cuervo-Robayo *et al*. 2014, García & CONABIO 1998). Thirty-eight species of native landbirds are known or suspected to breed on the Tres Marías, of which 24 are considered endemic subspecies (Howell & Webb 1995 Appendix C, Gómez de Silva *et al*. 2017). Other endemic vertebrates include a single race of reptile (Casas-Andreu 1992) and five species and four subspecies of endemic mammals (Wilson 1991); one of the endemic mammal species is already extinct and another is on the brink (J. Cruzado Cortés pers. comm.).

Methods and taxonomic philosophy

Species are defined by their distinct evolutionary trajectory and substantial, although not necessarily complete, reproductive isolation from other species (Johnson *et al*. 1999, Coyne & Orr 2004: 30). Whereas subspecies generally differ in minor ways in one or a few characters, species usually differ more notably in a larger number of characters. These greater differences are a consequence and sometimes also a cause of reproductive isolation; the number and magnitude of phenotypic differences between two taxa therefore represent evidence of reproductive isolation. Differences between species are usually abrupt, whereas differences between subspecies often tend to be gradual. Tobias *et al*. (2010) established operational criteria to recognise whether taxa merit status as species, based largely on phenotypic and vocal differences.

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In extremely summary fashion, according to the criteria of Tobias *et al*. (2010), a taxon is treated as a species if the sum of character scores between it and the most similar taxon is 7 or more. Phenotypic differences between taxa are scored on a scale from 1 to 4, where 1 signifies a 'minor' difference and 4 an 'exceptional' difference; when characters to be scored are quantitative, the score is based on the statistical 'effect size'. Characters are selected on a case-by-case basis, concentrating on those judged to vary most significantly. For the scoring to be conservative, a max. of just three plumage, two morphometric, two acoustic and one ecological / behavioural character can be scored. In addition, when applicable, an extra score of 1 to 3 is applied based on the nature of the biogeographic contact between species, with a score of 1 for frequent hybridisation over a broad contact zone, 2 frequent hybridisation in a narrow contact zone, and 3 parapatry with little or no hybridisation. Furthermore, species status is not triggered by summing minor characters (score 1) alone.

The Tobias *et al.* (2010) criteria and del Hoyo & Collar (2014, 2016) have been praised for their consistency and transparency, and for using effect size rather than statistical significance (e.g. Winker 2010, Brooks & Helgen 2010, Patten 2015), but other aspects have been criticised (Remsen 2015, 2016, Halley *et al*. 2017; although note defence by Collar *et al*. 2015). Perhaps the most significant negative criticism by Remsen (2015, 2016) concerned the treatment of cases with extensive hybridisation along a broad hybrid zone. This criticism is not pertinent here because most of the Tres Marías endemics are not in parapatry, and there is little or no hybridisation with their mainland counterparts, with the possible exception of *Setophaga* and *Turdus*. The strongest criticism by Halley *et al*. (2017) of using a threshold of divergence to decide if a taxon deserves species status is that it can be unclear which is the relevant taxon for comparison. For the species discussed here, except perhaps Northern Cardinal *Cardinalis cardinalis*, the sister taxon is unquestionably the population on the adjacent mainland, and Grant (1965a) was careful to use that population as a basis for comparison.

There are different routes to speciation, some involving little or no phenotypic change (Winker 2009, Moyle *et al*. 2017: 12). The Tobias *et al*. (2010) criteria are conservative because they are unable to detect such 'cryptic species'. In addition, our taxonomic assessment below is conservative because: (1) for non-quantitative (subjective) characters, we have attempted to assign the lowest possible score, (2) we do not score potential vocal differences because our sample of recordings from the Tres Marías is small in the context of often large individual variation and large repertoires; and (3) like del Hoyo & Collar (2014, 2016) we have not assessed for possible colour differences in the ultraviolet spectrum. Thus we consider the character scores that we provide to be minima.

Based on the analysis of Grant (1965a), we selected for detailed analysis the species that appeared closest to reaching or exceeding the threshold of species *sensu* Tobias *et al*. (2010), except Red-tailed Hawk *Buteo jamaicensis*, where Grant's sample of adult specimens was based on too small a sample: three vs. two males and five vs. five females.

Concentrating for the most part on measurements of adult specimens, sex by sex, we calculated effect size (Cohen's *d*) of differences between Tres Marías and nearby mainland specimens by plugging in data from Grant's (1965a) Appendices A and B into an online effect size calculator (http://www.uccs.edu/~lbecker/), with standard deviation calculated by multiplying Grant's (1965a) standard error of the mean by the square root of sample size (https://explorable.com/standard-error-of-the-mean). We use the phrase 'all external measurements' for wing, tail, tarsus and bill lengths, and sometimes bill width. Grant (1971) demonstrated that tarsus length variation is independent of wing length, and that all external measurements vary independently of each other; nevertheless, we followed Tobias

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et al. (2010) and del Hoyo & Collar (2014, 2016) in scoring only up to two morphometric characters.

In the species accounts, English and scientific names follow the American Ornithologists' Union (http://checklist.aou.org/taxa/) but subspecies follow del Hoyo & Collar (2014, 2016), except for Mexican Parrotlet *Forpus cyanopygius* where we mention the sometimes recognised *F. c. pallidus*, under Happy Wren *Pheugopedius felix* we consider subspecies *magdalenae* to be a synonym of *lawrencii* (as did Grant 1965a), and under Streak-backed Oriole *Icterus pustulatus* we mention the sometimes recognised *I. p. yaegeri*. Following the scientific name of the Tres Marías taxon we name the mainland subspecies used for comparisons after 'vs.' and then we provide the total score we assigned following the criteria of Tobias *et al*. (2010). Thereafter we describe the differences and score assigned, character by character, using 'vs.' between the character description of the island taxon (mentioned first) and the mainland taxon. For quantitative characters, we provide the effect size and the number of island and mainland specimens in Table 2. Phenotypic differences follow Grant (1965a) unless otherwise noted and therefore the number of specimens used by that author in his comparisons is indicated.

Except the three Tres Marías endemics scored by del Hoyo & Collar (2014, 2016), we break down the character descriptions into categories: colour, morphometrics, evidence of hybridisation and / or additional information. Under the latter we briefly mention the results of relevant molecular studies with regard particularly to reciprocal monophyly, a criterion often considered important in deciding species limits (e.g., Hosner *et al*. 2018). We have separated species into three groups: those scored by del Hoyo & Collar (2014, 2016), those not scored by those authors but confidently scored by us, and those for which we believe there is reason to be still uncertain regarding their taxonomic status (and we do not provide a total score).

Results

Species scored by del Hoyo & Collar (2014, 2016)

BROAD-BILLED HUMMINGBIRD *Cynanthus latirostris lawrencei* (vs. *C. l. magicus* total score 8).

Scored 9 by del Hoyo & Collar (2014) based on colours of throat ('glittering turquoise-green' vs. 'sapphire-blue'), breast ('greeny-bronze' vs. 'turquoise-blue') and undertail-coverts ('whitish-edged darkish-grey' vs. 'pale grey-white'), and slightly shorter bill (most of these characters are visible in Figs. 2–4). However, the throat and breast characters, which del Hoyo & Collar (2014) scored separately, could be viewed as a single character (less blue on iridescence of throat and breast), and we could not clearly discern the difference in breast colour in IBUNAM specimens. Therefore we ignore the breast colour character (thereby 'losing' two points), but this enables a further colour character to be scored. Grant (1965a, based on 23 male and 22 female *lawrencei* vs. 41 male and 25 female *magicus*) mentioned additional colour differences, including darker grey underparts in females (score 1), and that 75% of his *lawrencei* samples of both sexes had darker green upperparts compared to 75% of his *magicus* samples (not scored). Grant (1965a) also mentioned an additional morphometric difference (slightly but significantly smaller grey tips to the rectrices, at least in females; not scored). According to Grant's (1965a) data, shorter bill length in *lawrencei* scores only 1, not 2 as in del Hoyo & Collar (2014), but wings and tail are longer (score 1).

We found that the undertail-coverts character does not distinguish 100% of one taxon from 100% of the other, as implied in the literature (Ridgway 1911, Grant 1965a, del Hoyo &

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TABLE 2

Mean (in mm), standard error, *n* (sample size), Cohen's *d* and Tobias *et al*. (2010) scores for the taxa evaluated in this paper (the first three taken from Grant 1965a). 'Island' refers to the taxon from the Tres Marías Islands and 'Mainland' to the taxon from the adjacent mainland. The symbol '—' refers to data not provided by Grant (1965a) due to small sample size or that cannot be calculated due to incomplete information.

Species	**Body part**	**Sex**	**Mainland mean / standard error (*n* of individuals)**	**Island mean / standard error (*n* of individuals)**	**Cohen's *d***	**Tobias *et al.* score**
Cynanthus latirostris	Wing	Male	52.64 / 0.39 (38)	53.23 / 0.43 (20)	0.27	low 1
	Tail	Male	31.4 /0.3 (38)	32.64 / 0.35 (19)	0.73	1
	Bill length	Male	19.58 / 0.13 (37)	18.61 / 0.15 (20)	1.32	1
	length of tip of rectrix 1	Male	3 / 0.1 (34)	1.8 / 0.14 (16)	2.10	low 2
	Wing	Female	51.96 / 0.47 (25)	52.37 / 0.22 (22)	0.23	low 1
	Tail	Female	29.72 / 0.29 (25)	30.28 / 0.21 (22)	0.45	1
	Bill length	Female	20.48 / 0.22 (24)	19.56 / 0.11 (20)	1.10	1
Amazilia rutila	Wing	Male	58.74 / 0.29 (46)	70.58 / 0.44 (27)	5.55	3
	Tail	Male	36.89 / 0.24 (41)	44.54 / 0.36 (26)	4.52	high 2
	Bill length	Male	21.44 / 0.12 (44)	23.84 / 0.14 (27)	3.15	2
	Bill width	Male	3.18 / 0.04 (41)	3.63 / 0.08 (22)	1.40	high 1
	Wing	Female	55.98 / 0.55 (13)	69.04 / 0.46 (18)	6.64	3
	Tail	Female	35.58 / 0.35 (13)	44.36 / 0.34 (16)	6.69	3
	Bill length	Female	21.51 / 0.18 (13)	24.63 / 0.17 (15)	4.77	high 2
	Bill width	Female	3.07 / 0.08 (13)	3.51 / 0.04 (16)	1.89	high 1
Granatellus venustus	Wing	Male	61.52 / (0.28) / 18	65.85 / 0.28 (21)	3.50	2
	Tail	Male	69.74 / 0.65 (16)	76.49 / 0.47 (20)	2.86	2
	Tarsus	Male	19.72 / 0.14 (18)	21.14 / 0.15 (20)	2.24	2
	Bill length	Male	8.76 / 0.09 (17)	8.96 / 0.04 (19)	0.69	1
	width of rectrix 6	male	6.19 / 0.27 (8)	7.22 / 0.17 (9)	1.59	1
	white on rectrix 6	male	28.1 / 1.08 (10)	38.38 / 0.71 (14)	3.36	2
	rectrix 6 length for same individuals as previous row	male	69.19 / 0.73 (8)	76.25 / 0.62 (14)	3.21	2
	length of white/ length of rectrix 6	male	0.405 / 0.01 (8)	0.51 / 0.01 (14)	3.17	2
	Wing	Female	59.48 / 0.33 (11)	63.35 / 0.23 (13)	3.99	2
	Tail	Female	67.83 / 0.61 (11)	74.28 / 0.37 (17)	3.60	2
	Tarsus	Female	19.52 / 0.12 (12)	21.24 / 0.08 (14)	4.75	high 2
	Bill length	Female	8.88 / 0.14 (12)	8.79 / 0.07 (13)	0.23	low 1
	white on rectrix 6	female	25 / 0.32 (5)	34.21 / 0.97 (7)	4.89	high 2
	rectrix 6 length for same individuals as previous row	female	66.6 / 1.37 (5)	73.86 / 0.57 (7)	3.01	2
	length of white/ length of rectrix 6	female	0.378 / 0.01 (5)	0.463 / 0.01 (7)	3.47	2

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Species	Body part	Sex	Mainland mean / standard error (*n* of individuals)	Island mean / standard error (*n* of individuals)	Cohen's *d*	Tobias *et al.* score
Forpus cyanopygius	Wing	Male	88.36 / 0.44 (20)	90.84 / 0.35 (21)	1.38	1
	Tail	Male	40.81 / 0.39 (20)	42.57 / 0.26 (21)	1.18	1
	Tarsus	Male	10.86 / 0.05 (20)	11.92 / 0.11 (21)	2.72	2
	Bill length	Male	13.55 / 0.1 (19)	14.05 / 0.08 (21)	1.24	1
	Wing	Female	86.98 / 0.37 (31)	90.93 / 0.57 (15)	1.85	high 1
	Tail	Female	40.9 / 0.33 (31)	43.29 / 0.33 (15)	1.51	1
	Tarsus	Female	11.06 / 0.08 (31)	12.06 / 0.14 (15)	0.82	1
	Bill length	Female	13.17 / 0.07 (30)	13.98 / 0.09 (14)	2.24	2
Vireo hypochryseus	Wing	Male	63.87 / 0.3 (40)	67.83 / 0.33 (30)	2.14	low 2
	Tail	Male	55.74 / 0.3 (41)	60.45 / 0.23 (24)	2.99	2
	Tarsus	Male	18.71 / 0.1 (43)	19.98 / 0.09 (28)	2.22	2
	Bill length	Male	8.8 / 0.08 (42)	9.1 / 0.08 (29)	0.63	1
	Coracoid	Male	13.74 / 0.09 (12)	12.5 / 0.06 (6)	5.09	low 3
	Femur	Male	14.75 / 0.08 (14)	14.76 / 0.1 (7)	0.04	0
	Wing	Female	61.58 / 0.37 (20)	65.93 / 0.23 (23)	3.09	2
	Tail	Female	53.74 / 0.43 (19)	58.85 / 0.22 (21)	3.40	2
	Tarsus	Female	18.84 / 0.14 (20)	20.06 / 0.15 (23)	1.81	high 1
	Bill length	Female	8.7 / 0.09 (20)	9.13 / 0.04 (19)	1.39	1
	Coracoid	Female	13.47 / 0.04 (9)	12.57 / — (4)	—	—
	Femur	Female	14.71 / 0.08 (10)	14.96 / 0.06 (5)	1.23	1
Pheugopedius felix	Wing	Male	56.89 / 0.25 (37)	59.41 / 0.37 (42)	1.26	1
	Tail	Male	52.49 / 0.29 (31)	56.06 / 0.33 (37)	1.96	1–2
	Tarsus	Male	21.56 / 0.13 (35)	21.93 / 0.1 (43)	0.52	1
	Bill length	Male	10.91 / 0.09 (36)	12.4 / 0.12 (41)	2.24	2
	Wing	Female	53.54 / 0.43 (18)	57.68 / 0.45 (28)	1.95	high 1
	Tail	Female	49.25 / 0.64 (17)	55.06 / 0.54 (27)	2.13	low 2
	Tarsus	Female	21.28 / 0.16 (17)	21.37 / 0.12 (29)	0.14	0
	Bill length	Female	10.54 / 0.14 (18)	12.2 / 0.09 (28)	3.08	2
Melanotis caerulescens	Wing	Male	114.17 / 0.73 (25)	109.82 / 0.57 (49)	1.14	1
	Tail	Male	123.47 / 0.92 (28)	109.46 / 0.75 (44)	2.85	2
	Tarsus	Male	29.18 / 0.18 (29)	28.46 / 0.14 (52)	0.28	low 1
	Bill length	Male	17.42 / 0.18 (28)	20.06 / 0.15 (46)	2.68	2
	Wing	Female	110.26 / 0.7 (25)	106.82 / 0.49 (24)	1.15	1
	Tail	Female	116.38 / 1.07 (25)	104.92 / 0.92 (22)	2.36	2
	Tarsus	Female	29.3 / 0.18 (31)	28.3 / 0.16 (24)	1.11	1
	Bill length	Female	17.13 / 0.21 (28)	19.72 / 0.14 (23)	2.82	2
Icterus pustulatus	Wing	Male	96.22 / 0.3 (66)	104.56 / 0.35 (42)	3.54	2
	Tail	Male	84.61 / 0.37 (61)	91.52 / 0.32 (39)	2.78	2
	Tarsus	Male	24.96 / 0.08 (66)	25.17 / 0.17 (28)	0.27	low 1

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Species	Body part	Sex	Mainland mean / standard error (*n* of individuals)	Island mean / standard error (*n* of individuals)	Cohen's *d*	Tobias *et al.* score
	Bill length	Male	14.78 / 0.78 (66)	17.35 / 0.12 (37)	0.57	1
	Bill width	Male	5.03 / 0.03 (54)	5.47 / 0.05 (23)	1.91	high 1
	Coracoid	Male	19.88 / 0.1 (42)	18.87 / 0.13 (9)	1.89	high 1
	Femur	Male	21.92 / 0.1 (43)	21.83 / 0.34 (9)	0.10	0
	Dorsal streaks	Male	30.4 / 0.69 (51)	5.4 / 0.75 (30)	5.51	3
	Wing	Female	90.82 / 0.52 (27)	97.8 / 0.42 (15)	3.13	2
	Tail	Female	81.33 / 0.68 (19)	85.67 / 0.8 (15)	1.43	1
	Tarsus	Female	24.81 / 0.13 (27)	25.87 / 0.13 (14)	1.80	high 1
	Bill length	Female	14.88 / 0.15 (26)	16.68 / 0.2 (13)	2.42	2
	Bill width	Female	4.98 / 0.04 (24)	5.44 / 0.04 (11)	2.75	2
	Coracoid	Female	19.28 / 0.11 (25)	18.23 / 0.09 (7)	2.48	2
	Femur	Female	21.92 / 0.1 (43)	21.83 / 0.34 (9)	0.10	0
	Dorsal streaks	female	28.2 / 1.35 (17)	4.4 / 1.35 (12)	4.63	2
Leptotila verreauxi	Wing	Male	143 / 0.63 (32)	152.5 / 0.6 (25)	2.73	2
	Tail	Male	109.2 / 0.69 (31)	109.5 / 0.57 (25)	0.09	0
	Tarsus	Male	29.04 / 0.25 (31)	31.58 / 0.24 (25)	1.95	high 1
	Bill length	Male	9.73 / 0.08 (31)	10.86 / 0.09 (22)	0.24	1
	Tail tip length	Male	9.8 / 0.25 (27)	8.3 / 0.3 (20)	1.14	1
	Wing	Female	140.6 / 0.77 (12)	149.8 / 0.54 (21)	3.58	2
	Tail	Female	108.8 / 1.35 (12)	106.5 / 0.43 (21)	0.64	1
	Tarsus	Female	27.69 / 0.41 (12)	30.4 / 0.24 (21)	2.13	2
	Bill length	Female	9.36 / 0.08 (11)	10.97 / 0.12 (18)	3.97	2
	Tail tip length	Female	9.1 / 0.22 (12)	7.6 / 0.33 (17)	1.36	1
Turdus rufopalliatus	Wing	Male	123.19 / 0.59 (32)	127.17 / 0.58 (22)	1.31	1
	Tail	Male	99.29 / 0.69 (32)	102.49 / 0.73 (22)	0.87	1
	Tarsus	Male	31.48 / 0.21 (32)	34.8 / 0.23 (20)	2.99	2
	Bill length	Male	13.26 / 0.08 (30)	15.18 / 0.17 (22)	2.98	2
	Wing	Female	120.42 / 0.5 (20)	124.97 / 0.52 (37)	1.66	1
	Tail	Female	95.85 / 0.68 (21)	99.6 / 0.52 (39)	1.18	1
	Tarsus	Female	31.19 / 0.17 (22)	34.67 / 0.21 (34)	3.37	2
	Bill length	Female	13.8 / 0.14 (20)	15.42 / 0.11 (35)	2.54	2
Setophaga pitiayumi	Wing	Male (excluding mainland *insularis*)	55.42 / 0.33 (21)	58.28 / 0.34 (42)	1.51	1
	Tail	Male (excluding mainland *insularis*)	42.83 / 0.48 (21)	49.14 / 0.33 (37)	3.00	2
	Tarsus	Male (excluding mainland *insularis*)	16.14 / 0.09 (22)	19.11 / 0.08 (40)	6.37	3
	Bill length	Male (excluding mainland *insularis*)	7.68 / 0.07 (22)	7.76 / 0.06 (40)	0.23	low 1
	Wing	Female (excluding mainland *insularis*)	52.22 / 0.33 (12)	56.38 / 0.28 (20)	3.47	2
	Tail	Female (excluding mainland *insularis*)	40.34 / 0.37 (11)	48.11 / 0.25 (19)	6.70	3

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Species	Body part	Sex	Mainland mean / standard error (*n* of individuals)	Island mean / standard error (*n* of individuals)	Cohen's *d*	Tobias *et al.* score
	Tarsus	Female (excluding mainland *insularis*)	16.34 / 0.19 (11)	18.84 / 0.14 (20)	5.16	low 3
	Bill length	Female (excluding mainland *insularis*)	7.78 / 0.1 (10)	7.62 / 0.06 (20)	0.55	1
Cardinalis cardinalis	Wing	Male	91.04 / 0.78 (9)	95.17 / 0.33 (38)	1.88	high 1
	Tail	Male	101.9 / — (4)	96.96 / 0.61 (28)	—	—
	Tarsus	Male	25.1 / 0.14 (8)	28.06 / 0.12 (44)	5.42	3
	Bill length	Male	13.22 / 0.29 (8)	14.17 / 0.1 (44)	1.27	1
	Bill width	Male	8.52 / 0.04 (8)	9.28 / 0.05 (27)	3.79	2
	Wing	Female	89.93 / 0.64 (6)	91.71 / 0.37 (34)	0.94	1
	Tail	Female	100.5 / 0.9 (6)	93.29 / 0.46 (21)	3.34	2
	Tarsus	Female	25.43 / 0.24 (6)	27.37 / 0.19 (32)	0.95	1
	Bill length	Female	13.47 / 0.32 (6)	13.85 / 0.08 (35)	0.59	1
	Bill width	Female	8.35 / 0.06 (6)	9.01 / 0.07 (26)	2.42	2

Collar 2014). Of 11 male specimens of *lawrencei* at IBUNAM in which it is possible to see the undertail-coverts, typical colours are present in nine specimens but P019534 has a two-toned pattern in which the anterior feathers are typical of *lawrencei* but the largest, posterior feathers are predominantly white with very pale grey central portions, very similar to *magicus* P001630 from Sinaloa (Fig. 5). Also, the usually whitish undertail-coverts of *magicus* reach their greyest extreme in P001631 and P020047 (Fig. 6), albeit a pearly grey rather than the brownish grey of *lawrencei*. We do not believe that any of these specimens are hybrids because no other character suggests this, and their geographic location is too far removed from the Tres Marías (e.g., P020047 is from too far north and inland for *lawrencei* to be a plausible parent).

Figure 2. Male Broad-billed Hummingbird *Cynanthus latirostris lawrencei*, Isla María Cleofas, May 2016 (Javier Cruz Nieto)

Occasional *Cynanthus* wander between the Tres Marías and the mainland, and apparently sometimes interbreed. A. J. Grayson (*in* Lawrence 1872: 29) reported seeing one at sea '30 miles north' of the Tres Marías Islands in May 1867, which visited his boat and flew from there toward the islands. Nelson (1899: 46) saw a male *latirostris* fly past his boat in a straight line toward the islands 'about midway' between the Tres Marías and San Blas, Nayarit. An adult male *latirostris* or *lawrencei* was observed '1 mile east' of Isla María

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Figure 3. Throat colours of Broad-billed Hummingbird *Cynanthus latirostris* specimens in the Instituto de Biología, Universidad Nacional Autónoma de México collection, on left: two *C. l. magicus*, right: two *C. l. lawrencei*; the apparently larger size and bills of the *lawrencei* specimens are an artefact of the photograph (Héctor Gómez de Silva)

Fig. 4. Typical undertail-coverts colour of male Broad-billed Hummingbird *Cynanthus latirostris magicus* (two specimens at left) and *C. l. lawrencei* (two specimens at right), from specimens in the Instituto de Biología, Universidad Nacional Autónoma de México collection (Héctor Gómez de Silva)

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Figure 5. Two specimens of male Broad-billed Hummingbirds *Cynanthus latirostris* with similarly grey anterior undertail-coverts and white or whitish posterior undertail-coverts; above *C. l. magicus*, below, *C. l. lawrencei* (Héctor Gómez de Silva)

Figure 6. Mainland specimens of male Broad-billed Hummingbird *Cynanthus latirostris magicus* with grey undertail-coverts (usually white or whitish) (Héctor Gómez de Silva)

Magdalena by Grant (1965a: 51) on 25 April 1963 flying towards the latter island; and two male *lawrencei* were collected on the mainland at Sauta, Nayarit, by C. Lamb (MLZ 28073 on 5 May 1940, and MLZ 41912 on 23 April 1946, with two male *magicus* collected there around the same date as the 1940 specimen; J. Maley pers. comm.). MLZ 28073 has the

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Figure 7. Presumed hybrid Broad-billed Hummingbird *Cynanthus lawrencei* × *magicus* specimen in the Instituto de Biología, Universidad Nacional Autónoma de México collection; note *magicus*-like blue throat and *lawrencei*-like white-edged grey undertail-coverts (Héctor Gómez de Silva)

Figure 8. Presumed hybrid Broad-billed Hummingbird *Cynanthus lawrencei* × *magicus* specimen, Isla María Cleofas, April 2016 (Héctor Gómez de Silva)

only remaining undertail-covert feather typical of *lawrencii* while, *contra* Grant (1965a), MLZ 41912 has the anterior feathers grey-brown and the posterior undertail-coverts very pale whitish grey (like the IBUNAM material in Fig. 5; MLZ specimen photos, courtesy of J. Maley).

Among mainland specimens at IBUNAM, one male (P001633 from just north-west of Las Varas, Nayarit, along the Zacualpan road) appears to be a hybrid. It has a *lawrencei*-like shorter bill and undertail-coverts colour, but a *magicus*-like blue throat (Fig. 7). This is consistent with the observation that hybrids between hummingbirds of the 'emerald' group (*sensu* McGuire *et al*. 2014) do not show mixed colours but rather a combination of characteristics of the parental species (Graves 2003a,b).

A male Broad-billed Hummingbird we photographed on Isla María Cleofas on 26 April 2016 appears to combine the plumage characters of *magicus* and *lawrencei*, namely the deep blue throat and blue-green breast / belly of the former with the undertail-coverts of the latter (Fig. 8), thus apparently representing another hybrid.

Del Hoyo & Collar (2014) used the English name Tres Marías Hummingbird, but we prefer to avoid potential confusion given that there are two species of hummingbird on the islands; consequently, we prefer the name Lawrence's Hummingbird.

CINNAMON HUMMINGBIRD *Amazilia rutila graysoni* (vs. *A. r. rutila* total score 7)
Scored 4 by del Hoyo & Collar (2014) based on larger size in all external measurements (to which they assign a score of 3) and slightly 'darker and duskier' plumage (which they score 1). Regarding colour differences, Grant (1965a, based on 27 male and 18 female *graysoni* vs. 46 male and 14 female *rutila*) stated that the underparts are uniformly dark cinnamon vs. paler cinnamon, particularly on the chin and throat. The belly of some mainland *rutila* at IBUNAM is as dark as the underparts of *graysoni*, but the chin and throat, and often asymmetrical patches on the breast, are always paler (Fig. 9). Grant (1965a) also mentioned that the upperparts are 'dark green or even red-bronze' vs. 'paler green, and in those which have a bronze colour it is always yellow-green, never red', and that the 'tips' (*sic*, actually, subterminal portions) of most, particularly the outer, rectrices are dark greenish bronze to

Figure 9. Two specimens of Cinnamon Hummingbird *Amazilia rutila graysoni* (below) compared with two specimens of *A. r. rutila* (above); note the considerable difference in size. The second specimen from the top is the darkest-throated *A. r. rutila* at Instituto de Biología, Universidad Nacional Autónoma de México; the right side of its throat is paler than the left, and thus more like the typical colour of the subspecies (Héctor Gómez de Silva)

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dull violet in 90% of *graysoni* vs. paler, bright greenish bronze in 90% of *rutila* specimens (score at least 1). The underpart colours in these taxa are based on the intensity of cinnamon pigmentation whereas the upperpart colours (as in iridescent colours of hummingbirds generally) are based on a combination of melanin and feather nanostructure; therefore we score 1 for underparts colour and 1 for upperparts colour.

Grant's (1965a) measurements reveal that the bill in *graysoni* is both relatively shorter (effect size for bill length 2 vs. effect size for most external measurements 3 [score 1]) and, especially in males, relatively narrower (effect size for bill width 1 but for bill length 2 [not scored]).

The notably larger overall size of insular *graysoni* is paralleled by Rufous-tailed Hummingbird *Amazilia tzacatl handleyi* of Isla Escudo de Veraguas, Panama (Wetmore 1959, Miller *et al*. 2011) but in the latter case, there is reportedly a narrow 'zone of morphometric intergradation' (Weller 1999), although the data on which the statement was based have not been published to date. There is no zone of intergradation between *graysoni* and mainland *rutila*.

Of the 12 specimens of *graysoni* at IBUNAM, the smallest (P019069 from Isla María Madre) has atypical upperparts, with much-reduced iridescence on the wing-coverts and back compared to either *graysoni* or *rutila*. We consider that this specimen could be a hybrid *graysoni* × *rutila*, the colour of its upperparts being heterotic (a trait of a hybrid outside the range of variation for that trait in either parental species; McCarthy 2006: 17).

RED-BREASTED CHAT *Granatellus venustus francescae* (vs. *G. v. venustus* total score 8)
Scored 7 by del Hoyo & Collar (2016) based on the lack of black breast-band of *francescae*, presence of a white hindcollar, grey of crown extending over nape, tail much longer, and a few additional characters that they did not score. Grant (1965a, based on 29 male and 18 female *francescae* vs. 24 male and 14 female *venustus*) found that the lack of breast-band differentiated 79% of his sample of *francescae* from 94% of *venustus* (Grant 1965a also observed in both taxa that, rarely, a breast-band is present but masked by overlying white feathers). Therefore, this character does not differentiate the taxa completely, and we did not score it, although we believe that it is an important character.

Del Hoyo and Collar (2016) included scores for 'white hindcollar formed by continuing white postocular stripe (at least 1), grey of crown extending over nape (1)'. We think they assigned two scores for what is essentially a single character (Fig. 10), to which we apply a score of 2.

Whereas del Hoyo & Collar (2016) mention, but did not score, 'pink of underparts generally slightly paler and less extensive', Grant (1965a) stated that 'the majority of both mainland and island samples of adult males had approximately the same amount of red ventrally. A few island specimens were observed to have less, and a few mainland specimens more, than this.' It is unclear whether this character should be scored. However, we would score the colour of the underparts of immature males; Grant (1965a), based on a sample of perhaps $n = 8$ vs. $n = 6$, reported that immature males differ in having almost no red on the underparts in *francescae* (and in his sample no trace of a black breast-band) vs. much red on the underparts and a complete breast-band (score 2). Based on Grant's (1965a) data the relative amount of white on the outermost rectrix (measured as the length of the white patch on r6 / length of r6) merits a score of 2, but we conservatively score it 1. Whereas del Hoyo & Collar (2016) afforded a score of 2 for 'tail much longer', measurements in Grant (1965a) indicate that the score of 2 applies equally to wing, tarsus and tail lengths, but bill length is shorter (score 1).

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Figure 10. Comparison of the nape and presence / absence of the white hindcollar in male Red-breasted Chat *Granatellus venustus*: above, Instituto de Biología, Universidad Nacional Autónoma de México specimen of *G. v. venustus* (Héctor Gómez de Silva); below, *G. v. francescae*, Isla María Cleofas, May 2016 (Mónica G. Pérez Villafaña)

Endemics not scored by del Hoyo & Collar (2014, 2016) but confidently scored by us

MEXICAN PARROTLET *Forpus cyanopygius insularis* (vs. *F. c. cyanopygius* / *pallidus* total score 7)

Coloration.—Males have breast, belly, neck-sides and postocular region pale malachite-green, somewhat glaucous, contrasting strongly with the yellowish-green or apple-green cheeks, throat, forehead and forecrown vs. apple-green underparts in slight contrast (if any) with the face colour (Figs. 11–12; Ridgway 1911, Grant 1965a, based on 21 male and 15 female *insularis* vs. 20 male and 31 female *cyanopygius*, www.inaturalist.org/observations/5258308, www.inaturalist.org/observations/5258315 [score 2]). This coloration is similar to male Pacific Parrotlet *F. coelestis* of western Ecuador and north-west Peru (e.g., www.hbw.com/ibc/photo/pacific-parrotlet-forpus-coelestis/close-pacific-parrotlet and www.hbw.com/ibc/photo/pacific-parrotlet-forpus-coelestis/male; the illustration of the latter species in del Hoyo & Collar 2014 is inaccurate). Rump, lower back and greater coverts of males bright cerulean blue vs. bright turquoise-blue (Ridgway 1911, Grant 1965a [score 1]). Secondaries

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Figure 11. Pair of Mexican Parrotlets *Forpus cyanopygius insularis* copulating, Isla María Cleofas, May 2016; note the male's pale malachite-green underparts, neck-sides and postocular region contrasting with the yellower green cheeks, throat, forehead and forecrown, and that the male's undertail-coverts are not concolorous with the breast and belly (*contra* Grant 1965a) (Javier Cruz Nieto)

Figure 12. Instituto de Biología, Universidad Nacional Autónoma de México specimens of Mexican Parrotlet *Forpus cyanopygius* from Nayarit; the two specimens on the right are adult male *insularis*, their malachite-green breast and belly contrasts strongly with the throat, unlike in *cyanopygius* specimens (Héctor Gómez de Silva)

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and proximal primaries darker and duller blue, edged cerulean blue vs. greenish blue (nearly cerulean blue) edged distally with pale yellowish green (Ridgway 1911 [score 2]). A. J. Grayson (*in* Lawrence 1872), Lawrence (1872), Ridgway (1888, 1911) and Grant (1965a) described the upperparts of both sexes of *insularis* as darker and more glaucous green (not scored, we are unable to discern this difference in the three *insularis* vs. six *cyanopygius* / *pallidus* specimens at IBUNAM). Grant (1965a) added that the flanks and undertail-coverts are the same colour as the breast / belly in all *insularis* males in his sample, but the detailed description of *insularis* by Ridgway (1911), the two IBUNAM specimens of adult male *insularis*, and our field photographs (e.g., Fig. 11) contradict that.

Morphometrics.—Larger in all external measurements (score 2).

Additional information.—Smith *et al*.'s (2012) molecular study found that *insularis* has diverged more from a common ancestor than *cyanopygius* / *pallidus*, consistent with a faster rate of divergence in small, isolated populations (Woolfit 2009), and the Bayesian modelling programme BP&B assigned the probability of *insularis* being a separate species as higher than 95%.

GOLDEN VIREO *Vireo hypochryseus sordidus* (vs. *V. h. hypochryseus* total score 5–6)

Coloration.—Throat, breast, flanks and upperparts duller and greener in *sordidus*, especially in fresh plumage and when specimens collected in the same season are compared (score 1 or possibly 2, Grant 1965a, based on 30 male and 23 female *sordidus* vs. 44 male and 20 female *hypochryseus*). Grant (1965a) reported that Nelson's (1898) claimed difference in bill colour is incorrect.

Morphometrics.—Larger in all external measurements, especially tail length of both sexes and wing length of females (score 2), with a significantly shorter coracoid both absolutely and relatively (effect size almost reaches the threshold for score of 3, but we assign a score of 2) and a relatively shorter femur (not significantly different between taxa, whereas all external measurements are larger [not scored]). Arbeláez-Cortés *et al*. (2014) analysed the morphometrics of ten *sordidus* and 37 specimens from the rest of the range, and confirmed the larger size of *sordidus.*

Additional information.—Arbeláez-Cortés *et al*. (2014) and Ortiz-Ramírez *et al*. (2018) reported reciprocal monophyly but shallow genetic divergence between these taxa.

HAPPY WREN *Pheugopedius felix lawrencii* (vs. *P. f. pallidus* total score 8)

Coloration.—White mid-breast and mid-belly vs. rufous breast and belly in *pallidus* (Fig. 13; Grant 1965a, based on 43 male and 30 female *lawrencii* vs. 37 male and 18 female *pallidus* [not scored]). Among 18 *lawrencii* at IBUNAM, a few are washed warm on the breast, but are still usually paler than the palest *pallidus*. Even if there is warm colour across part of the breast, there is much white on the mid-breast and mid-belly. Examination of the 'warmest' specimens of *lawrencii* (P016585) revealed a diagnostic character not previously mentioned in the literature (e.g. Nelson 1898, Ridgway 1904, Grant 1965a): the colour of the underwing-coverts. In *lawrencii*, these are white or whitish, contrasting with the warm breast-sides, whereas *pallidus* has cinnamon / rufous underwing-coverts concolorous with the breast (score 3) (Fig. 14). Ear-coverts have significantly more white than black feathers vs. black and white feathers approximately equally prominent (score 2) (Fig. 13). One or other of these differences between *lawrencii* and *pallidus* is of somewhat similar magnitude to those between certain subspecies of, e.g., Coraya *Pheugopedius coraya*, Rufous-and-white *Thryophilus rufalbus*, Buff-breasted *Cantorchilus leucotis*, Carolina *Thryothorus ludovicianus* and White-browed Wrens *T. albinucha*, but in those cases there are zones of intergradation and smooth clines, whereas between *lawrencii* and *pallidus* the differences are abrupt and

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Figure 13. Left: typical underparts colour and cheek pattern in Happy Wren *Pheugopedius felix pallidus*, Laguna El Chumbeño, Francisco Villa, Nayarit, Mexico, May 2016 (Amy McAndrews); right: *P. f. lawrencii*, Isla María Cleofas, April 2016 (Mónica G. Pérez Villafaña)

Figure 14. Cinnamon underwing-coverts of Happy Wren *Pheugopedius felix pallidus* (above) compared to the contrasting white underwing-coverts of the warmest-breasted *P. f. lawrencii* specimen in the Instituto de Biología, Universidad Nacional Autónoma de México collection (right) (Héctor Gómez de Silva)

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occur in both characters simultaneously. Grant (1965a) noted that in both plumage features, juveniles from the mainland approach those of Tres Marías birds.

Morphometrics.—Longer wing, tail and, especially in females, bill (score 2) but tarsus relatively shorter (not significantly different in female and only slightly bigger in male [score 1]).

BLUE MOCKINGBIRD *Melanotis caerulescens longirostris* (vs. *M. c. caerulescens* total score 4)

Coloration.—Based on 52 male and 24 female *longirostris* vs. 29 male and 32 female *caerulescens*, Grant (1965a) found that 'less than half' of *longirostris* were paler in the throat and crown feathers than 'most' of his *caerulescens* sample but the palest specimens of each were indistinguishable. Therefore there is large overlap (no score).

Morphometrics.—Slightly larger but has proportionately much longer bill in both sexes (score 2) whereas the tail is shorter, especially in males (score 2). Additionally, Grant (1965a) found that coracoid length may be shorter in island birds but did not provide sufficient information to calculate effect size because he considered his sample to be inadequate (three male and six female *longirostris* vs. five male and two female *caerulescens*). However, the measurement ranges have slight to no overlap, which suggest the difference is not minor (not scored).

STREAK-BACKED ORIOLE *Icterus pustulatus graysonii* (vs. *I. p. microstictus* and *I. p. yaegeri* total score 7).

Coloration.—Very few short and narrow streaks on back, usually in scapular region vs. more prominent and numerous streaks throughout back (Fig. 15; Grant 1965a, based on 39 adult male and 13 adult female *graysonii* vs. 69 adult male and 29 adult female *microstictus* / *yaegeri* [score 2]). Median coverts 'pale yellow to yellowish-white' vs. 'usually (orangey) yellow' in *yaegeri*, the geographically closest mainland taxon, and white in *microstictus*, which occurs further inland than *yaegeri* (Phillips 1995 [score 1]). Grant (1965a) mentioned but did not quantify a tendency to differ in yellow vs. orange plumage. Generally, *graysonii* is less orange overall (consistent with the median coverts character, above, and with Ridgway 1902, Jaramillo & Burke 1999) and we support this based on our field work, although one adult *graysonii* among the dozens seen was intensely orange (Fig. 16).

Morphometrics.—Larger in external measurements (score 2), but with a significantly shorter coracoid both absolutely and relatively (score 2) and a relatively shorter femur (not significantly different whereas all external measurements are significantly different [not scored]). The bill is also differently shaped ('longer in relation to width', Grant 1965a [not scored]).

Evidence of hybridisation.—Phillips (1995) collected a mainland specimen that he presumed to be a rare variant of *yaegeri* and had 'plain yellowish interscapulars, with hardly perceptible black streaking (on the back). But the middle wing-coverts are richer, and bill shorter, than *graysonii*'. This specimen is now in the IBUNAM collection (P022269). Its precise locality, according to the label, is '1¾ km N of Singaita', whereon it is also mentioned 'Apparently alone in brush, near normal-backed pair'. The bird not only resembles *graysonii* in its back pattern but also in size (Fig. 15). Therefore it combines phenotypic characters and is almost surely a hybrid. We found a second mainland specimen (P015891 from Santiago Ixcuintla) that resembles *graysonii* in its fewer and narrower back streaks, but streaks are present even on the central back (Fig. 15). In overall length this specimen is comparable to other mainland specimens, and we believe it is also a hybrid.

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Figure 15. Back pattern, size and intensity of orange in Streak-backed Oriole *Icterus pustulatus* specimens from Nayarit, from left to right: two typical *microstictus* / *yaegeri*, two presumed hybrids (with Phillips' specimen at right) and a typical *graysoni*; note the similar overall size of *graysoni* and Phillips' specimen, which is, however, more orange overall (especially the head), while the other presumed hybrid (which appears almost as long due to specimen preparation) has back streaks intermediate between *graysoni* and typical mainland Nayarit orioles (Héctor Gómez de Silva)

Figure 16. An intensely orange individual of Streak-backed Oriole *Icterus pustulatus graysoni*, Isla María Cleofas, March 2016 (Javier Cruz Nieto)

Additional information.—Cortés-Rodríguez *et al*. (2008) and Ortiz-Ramírez *et al*. (2018) found reciprocal monophyly but shallow genetic divergence between *graysonii* and mainland specimens. Shallow genetic divergence is also seen in other sister species of orioles even when they possess distinctly different plumage features (e.g. Kondo *et al*. 2004).

Tres Marías endemics that require further study

WHITE-TIPPED DOVE *Leptotila verreauxi capitalis* (vs. *L. v. angelica*)

Coloration.—Breast colour 'paler and less red' in all specimens (Grant 1965a, 25 male and 21 female *capitalis* vs. 32 male and 12 female *angelica*), although the single darkest *capitalis* was almost indistinguishable from the single palest *angelica*. Also, 50% of island specimens had more extensive white throats than in all mainland birds, 75% of island birds had fewer and paler brown feathers on the thighs and flanks than 100% of mainland birds, and in *c*.75%

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Figure 17. Above: White-tipped Dove *Leptotila verreauxi angelica*, Cruz de Huanacaxtle, Nayarit, Mexico, April 2019 (Marie O'Neill), below: *L. v. capitalis*, Isla María Cleofas, May 2016; note the contrasting white forecrown and cheeks, extensively whitish underparts, and darker brown back, wings and tail (Mónica G. Pérez Villafaña)

of island birds the vinous breast colour extended less far onto the belly than approximately 75% of mainland birds; 'hence island birds appear to have a larger, white abdomen' (Grant 1965a). The face is whiter due to the ear-coverts being white or whitish vs. usually pale pinkish grey, and because the white forehead reaches further posteriorly and contrasts

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sharply with the hindcrown / nape / postocular area (Fig. 17; Nelson 1898). The whiter face recalls Grenada Dove *L. wellsi* and both that and the more extensive white underparts resemble Caribbean Dove *L. jamaicensis*. However, unlike those species, the ear-coverts and forehead / forecrown contrast with a pink rather than blue-grey hindcrown / nape / postocular area. Half of Grant's (1965a) *capitalis* sample was darker dorsally than 100% of his *angelica* sample, consistent with Ridgway's (1916) diagnosis and Fig. 17.

Morphometrics.—Wing, tarsus and bill longer (Grant 1965a; largest effect size is for bill length of females, score 2) whereas the tail of females is shorter, and in both sexes the white on the tail tip is slightly shorter (score 1). The presence vs. absence of sexual dimorphism in tail length is a further difference between *capitalis* and *angelica*.

Reasons for uncertainty.—The whiter underparts and face of *capitalis* resemble *L. verreauxi decolor*, *L. v. decipiens* and some *L. v. verreauxi* (e.g. hbw.com/ibc/1016351 and hbw.com/ibc/996812 from Costa Rica, hbw.com/ibc/980837 from Colombia and hbw.com/ibc/1086049, hbw.com/ibc/1002421 but not darker hbw.com/ibc/1002417 from the Lesser Antilles). Occasional White-tipped Doves from scattered localities in mainland Mexico resemble *capitalis* (e.g. https://macaulaylibrary.org/asset/55312471, https://macaulaylibrary.org/asset/57930541, https://macaulaylibrary.org/asset/57744481, and https://macaulaylibrary.org/asset/39082171) at least in some features (e.g., https://macaulaylibrary.org/asset/25545561 with whitish ear-coverts but forehead / forecrown showing little contrast; or https://macaulaylibrary.org/asset/43367021 with forecrown less extensive and pinker breast, or https://macaulaylibrary.org/asset/32166601 with very whitish flanks but strongly pinkish breast, malar region and ear-coverts). We hypothesise that the mutation(s) responsible for a whitish face and underparts contrasting with the mid-crown / nape / postocular area have arisen independently several times in *Leptotila*, becoming fixed in *capitalis*, *decolor*, *decipiens*, Caribbean and Grenada Doves, but not in *L. v. verreauxi* or other races, similar to other known cases of 'parallel speciation' (e.g. Cooper & Uy 2017 and references therein). Clearly more research is needed to understand colour variation in *L. verreauxi* and relatives.

RUFOUS-BACKED ROBIN *Turdus rufopalliatus graysoni* (vs. *T. r. rufopalliatus*)

Coloration.—Underwing-coverts tawny-ochraceous contrasting with dull cinnamon sides and flanks vs. underwing-coverts concolorous or nearly so with the breast, sides and flanks (Ridgway 1907). Grey breast-band vs. grey only in the streaked feathers at the lower edge of the throat; in extreme cases this causes grey, rather than rufous, to be the dominant colour of the underparts (Grant 1965a, based on 24 male and 42 female *graysoni* vs. 32 male and 22 female *rufopalliatus*; Howell & Webb 1995 Plate 51.3b, our Fig. 18). However, a grey breast-band sometimes shows up in mainland *rufopalliatus* even well away from the Tres Marías (e.g., see Fig. 19) and while some *graysoni* have the breast-band 'faintly... tinged with dull salmon-color', in mainland *rufopalliatus* most of the breast-band is 'salmon color to almost cinnamon-rufous' (Phillips 1991). Assuming that all individuals we saw and photographed in the Tres Marías were *graysoni*, our photographs confirm the blurred distinction (e.g., Fig. 20).

'Back grayish, usually more or less tinged with brownish but hardly, if at all, contrasted to nape' vs. 'scapulars, and usually back, strongly washed with cinnamon-rufous to russet..., in strong contrast to the grayer crown and nape (if not badly worn and faded)' (Phillips 1991). Howell & Webb (1995) described the back of *graysoni* as 'greyish-rufous to olive-brown'. Our photographs from the Tres Marías show a range, from brown close to the upperparts of White-throated Thrush *T. assimilis* and showing little contrast with the nape and crown, to more rufous contrasting with the nape and crown (e.g., Figs. 18, 20 and 22). Upperwing-coverts 'dull cinnamon or duller' vs. 'salmon color to almost cinnamon-

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Figure 18. Typical Rufous-backed Robin *Turdus rufopalliatus graysoni* with broad grey breast-band concolorous with head and nape, pale salmon flanks, brown back and wing-coverts with very little back / nape contrast, and rather narrow throat streaks, Isla María Cleofas, May 2016 (Héctor Gómez de Silva)

Figure 19. Mainland Rufous-backed Robin *Turdus rufopalliatus* far from the Tres Marías, with an anomalous grey breast-band resembling *T. r. graysoni* and note the prominent throat streaks and warm-coloured back, wing-coverts and flanks, Cuernavaca, Morelos, Mexico, June 2017 (Juan Manuel Ramos Merino)

rufous' and sides and flanks dull orange-brown vs. rufous (Phillips 1991), which seem like subtle distinctions. All or most individuals we photographed on the Tres Marías had sides and flanks similar to some mainland *rufopalliatus* (e.g., Fig. 21, http://2.bp.blogspot.com/-G0D2EpXGCkI/VHzA0MTHSjI/AAAAAAAACSQ/sMP9Yby2Yic/s1600/_DSC0103.JPG). Grant (1965a) mentioned that *graysoni* 'show a tendency to possess paler and narrower chin and throat streaks than mainland birds, easily recognizable only when the extreme forms of the two samples are compared' (consistent with, e.g., Figs. 18 and 20). Phillips (1991) mentioned 'feet apparently darker' in *graysoni* but did not evidence this, and it is not supported by our field observations. In conclusion, individuals of *graysoni* representing the

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Figure 20. Presumed Rufous-backed Robin *Turdus rufopalliatus graysoni* with mainly narrow throat streaks, a strong salmon wash on the breast, and wing-coverts and back colours close to those of non-*graysoni T. rufopalliatus*, Isla María Cleofas, November 2015 (Javier Cruz Nieto)

Figure 21. Mainland Rufous-backed Robin *Turdus rufopalliatus* far from the range of *T. r. graysoni* with a salmon wash on the breast resembling some *graysoni*, Parque María Enriqueta, Mexico City, June 2017 (Héctor Gómez de Silva & Mónica G. Pérez Villafaña).

Figure 22. Rufous-backed Robin *Turdus rufopalliatus graysoni* with brown back and wing-coverts resembling the upperparts colours of White-throated Thrush *T. assimilis*, Isla María Cleofas, May 2016 (Héctor Gómez de Silva)

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extremes of plumage (e.g., with narrowly striped throats, predominantly grey underparts and / or brown backs) are easily identified, but there appears to be sufficient variance and overlap that colour differences cannot be adequately scored. The literature suggests that the main differences are duller plumage and no sexual dimorphism vs. much brighter, richer plumaged males (e.g., Grant 1965a, Phillips 1991, Howell & Webb 1995). Individuals of unknown sex and / or in faded plumage would not be identifiable.

Morphometrics.—Larger in all external measurements, especially tarsus length and bill length (score 2). Montaño-Rendón *et al*. (2015), based on 268 adult specimens from throughout the range of *T. rufopalliatus* (*sensu lato*), confirmed the existence of marked morphometric differences.

Additional information.—Montaño-Rendón *et al*. (2015) and Ortiz-Ramírez *et al*. (2018) found reciprocal monophyly and deep genetic divergence between *graysoni* and *rufopalliatus*.

Reasons for uncertainty.—Apparently, *graysoni* occurs sympatrically with *rufopalliatus* in coastal Nayarit (Grant 1965a, Phillips 1981, Howell & Webb 1995), with specimens of *graysoni* from Playa Novillero (west of Acaponeta), Santiago Ixcuintla, Sauta, San Blas, Chacala and Las Varas (most from February–April, but singles from 12 May and, especially, 20 June suggest residency and opportunities for interbreeding; Phillips 1981: 306; Table 2). The absence of clear distinctions in plumage between some *graysoni* and other races (see above) makes it particularly difficult to identify potential hybrids based on plumage, and there is slight overlap in morphometrics, especially bill length of females (Grant 1965a). Montaño-Rendón *et al*. (2015) and Ortiz-Ramírez *et al*. (2018) apparently did not include DNA of *graysoni* from the mainland, nor indeed of any *rufopalliatus* from the Nayarit coastal plain, where hybrids, if any, would be expected (all of their Nayarit *rufopalliatus* were from a single locality in the foothills). Because the extent of hybridisation, if any, is presently unknown, we recommend further studies before concluding whether *graysoni* represents a species.

TROPICAL PARULA *Setophaga pitiayumi insularis* (vs. *S. p. pulchra*)

Coloration.—Reddish-tinged vs. pale buff flanks (score at least 1), much less white on outer rectrix (score 1), no or scattered black feathers at base of culmen vs. entirely black 'culmen bridge' feathers (score 2). Additionally, only the outer pair or two of tail feathers have white in 100% of *insularis* (both sexes) vs. three outer tail feathers in 82% of male and 73% of female *pulchra* (not scored) (from Grant 1965a, based on 42 male and 20 female *insularis* from the Tres Marías, and 11 male and eight female *insularis* from the mainland vs. 23 male and 12 female *pulchra*).

Morphometrics.—Larger in all external measurements, especially the longer tarsus in males and longer tail in females (both score 3, although this seems suspiciously high because these differences are not immediately evident to the eye) but bill in females shorter (score 1).

Reasons for uncertainty.—Race *insularis* also occurs in mangroves in mainland Nayarit (Grant 1965a), and there is a specimen from Labrados, Sinaloa (McLellan 1927) and records from Todos Santos and El Oro, Baja California Sur (Iliff *et al*. 2008). Hybrid *insularis* × *pulchra* have been documented at Peñita de Jaltemba (Grant 1965a, two specimens that combine the flanks colour of *insularis* with the wing length of *pulchra* and are intermediate in tail and / or tarsus length) and San Blas (Iliff *et al*. 2008, four specimens with intermediate measurements). Also, Grant (1965a: 52) noted that his sample of mainland *insularis* somewhat approached *pulchra* in frequency of different tail patterns, and possibly also in some mensural characters, suggesting introgression. Hybridisation may be extensive where they are parapatric. Furthermore, it is also unclear if phenotypic characters differentiating

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Figure 23. Tropical Parula *Setophaga pitiayumi insularis*, Isla María Cleofas, May 2016; note the reddish-tinged flanks and lack of black feathers above the base of bill (Mónica G. Pérez Villafaña)

insularis may partially bridge the gap between *S. p. pulchra* and race *graysoni* from Socorro Island. Tail length of *insularis* is much closer to *graysoni* than *pulchra* (Ridgway 1902; under Socorro Parula, del Hoyo & Collar 2016 cite mean tail lengths for male *insularis* and *pulchra* that are too short, *cf.* Ridgway 1902).

In plumage, adult *graysoni* generally resembles juveniles of other races of *S. pitiayumi*. However, there may be a stepped cline in the percentage of adults with juvenile-like plumage; *insularis* is intermediate in proportions and especially the extent of black in the lores and orbital area (Grant 1965a: 38). Also, while black is usually thought to be completely absent in the face of *graysoni*, Baptista & Martínez-Gómez (2002: 38) found that a small percentage of individuals do show some black. There may also be a cline in the extent of white in the rectrices between *pulchra*, *insularis* and *graysoni* (Regelski & Moldenhauer 2012).

All of the above indicates that *graysoni* is perhaps not as phenotypically distinct from *pitiayumi* as scored by del Hoyo & Collar (2016) who considered *graysoni* to be a separate species, while simultaneously overlooking one important character of *graysoni* that sets it apart from the rest of *S. pitiayumi*, namely the grey of the face extends to include the malar in *graysoni* (as in Northern Parula *S. americana*) vs. the yellow of the throat extends up to include the malar in *pitiayumi* including *insularis* (Dunn & Garrett 1997, Iliff *et al*. 2008). Also, del Hoyo & Collar (2016) tentatively added a score of 2 to the diagnosis of *graysoni* based on a 'more complex voice, involving several songs, resembling those of *S. ruticilla*, *S. pensylvanica* and *S. americana*' while *insularis* apparently has a similar varied repertoire (HGdS pers. obs.). Furthermore, *S. pitiayumi* (with or without *graysoni*) may be paraphyletic with respect to *S. americana* (Lovette & Bermingham 2001, Evans *et al*. 2015). The situation is clearly very complex and requires further study, including testing the extent of introgression / hybridisation of *insularis* and *pulchra* on the Nayarit (and Sinaloa?) mainland, and a phylogeographic study of *S. pitiayumi* (*sensu lato*) with samples from throughout the species' range.

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NORTHERN CARDINAL *Cardinalis cardinalis mariae* (vs. *C. c. affinis*)

Coloration.—Based on 44 male and 35 female *mariae* vs. ten male and six female *affinis*, Grant (1965a) reported that 92% of males had a purple tinge to the plumage vs. 100% without any purple tinge (score 1), 100% of *mariae* females had cream-white abdomens vs. pale buff in 83% (score 1); and the grey chin and throat of females covered a larger area vs. more restricted white or rarely grey chin (score 2, grey is caused by 'the black basal half of the feather showing through the overlying white feather-tips, and in island specimens the extent of white in the feather tip is reduced').

Morphometrics.—Longer wing, tarsus and bill (especially bill length in males) (score 2) but shorter tail (score 2). Bill more bulging (consistent with Ridgway 1901 [not scored]).

Additional information.—Smith *et al*. (2011), Smith & Klicka (2013) and Ortiz-Ramírez *et al*. (2018) found reciprocal monophyly and deep genetic divergence between *mariae* and mainland specimens. Smith & Klicka (2013) and Ortiz-Ramírez *et al*. (2018) reported that small population size has accelerated molecular evolution in *mariae*.

Reasons for uncertainty.—Grant's (1965a) sample of *affinis* was inadequate (morphometric characters were evaluated in 4–9 males and six females, and plumage characters in ten males and six females), which is especially problematic because female plumage apparently fades considerably in specimens and males display extensive individual variation (Van Rossem 1932). Furthermore, Baja California race *igneus* is as likely to be the sister species of *mariae* as *affinis*, and it was not explicitly compared by Grant (1965a) who stated only that 'five specimens of *igneus* were available too, and it was noted that [*mariae*] differed from both subspecies (*igneus* and *affinis*) mainly in the same way.' Nelson (1898) in the original description of *mariae* described it as being closest to *igneus*, and at least in bill shape it is intermediate between *mariae* and *affinis* (Ridgway 1901: 648–649). Ortiz-Ramírez *et al*. (2018: 726) mentioned that when analysing the haplotype network, *mariae* was closer to *igneus* than *affinis*, although this apparently contradicts both their own highest-probability scenario of colonisation (in their Fig. 4) and the phylogenies of Smith *et al*. (2011) and Smith & Klicka (2013). Therefore, this case requires further study.

Discussion

Following the taxonomic ranking criteria of Tobias *et al*. (2010) we propose / endorse elevating to species six Tres Marías endemic birds (Table 1). This number of endemic species represents 16% of the islands' resident landbirds, which compares closely with the 14% of Mexican mainland species that are endemic (*sensu* Berlanga *et al*. 2015). It would be surprising for an archipelago that is 80+ km from the mainland to have no or very few endemic species. By comparison, Cozumel Island is just 19 km from the mainland and <7% of its breeding landbirds are endemic, Guadalupe Island is 240 km from the mainland and 7–8% are endemic, and the Revillagigedo archipelago is 700+ km from the mainland and 25% are endemic (following Howell & Webb 1995, Appendices C–D).

The relatively recent (Early to Mid-Pleistocene, see Study area above) emergence of the Tres Marías Islands and their proximity to the mainland might suggest that endemicity is unlikely to be a strong feature of the fauna, but Cozumel Island, which has 3–4 endemic bird species and a similar number of endemic mammals, emerged even more recently, in the Late Pleistocene, *c*.120,000 years ago (Spaw 1978).

While hybridisation between a Tres Marías endemic and its mainland relative had been documented for *Setophaga pitiayumi*, we provide evidence suggesting occasional interbreeding between Tres Marías Islands and adjacent mainland taxa in another three cases.

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While biodiversity loss is much more than the extinction of species (e.g., Ceballos & Ehrlich 2002, O'Grady *et al*. 2004), we trust that, by drawing attention to the existence of endemic birds that merit recognition as species, the uniqueness and conservation importance of the Tres Marías has been highlighted. Different species of breeding landbirds on the Tres Marías show varying degrees of distinctiveness from their nearest mainland counterparts, at both the subspecific (Grant 1965a) and the species levels (herein). Tres Marías landbirds provide a fascinating case study of speciation in process; their study contributed to the early research and understanding of evolution by the influential ecologist Peter R. Grant (e.g. Grant 1965b, 1965c).

It is well known that insular ecosystems and avian populations are seriously damaged by introduced goats, cats and rats, all of which now occur on at least the three larger Tres Marías islands (Gómez de Silva *et al*. 2017: 3). These exotic species have been successfully removed from other islands off western Mexico (Aguirre-Muñoz *et al*. 2008), but planned eradication programmes in the Tres Marías (Grupo de Conservación de Islas 2007a,b, Universidad Autónoma de Baja California 2008) have not been effected. Introduced mammals are currently the most serious threat to Tres Marías biota, and we hope that their removal can be undertaken soon.

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