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Species rank for *Rheinardia ocellata nigrescens* (Phasianidae)

by G. W. H. Davison, Peter Boesman, N. J. Collar & C. L. Puan

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SUMMARY.—Crested Argus *Rheinardia ocellata* has two highly disjunct populations in Vietnam and Lao PDR (nominate *ocellata*) and Malaysia (subspecies *nigrescens*). When evidence from the small sample of museum specimens is supplemented by novel photographic and acoustic evidence, Malaysian *nigrescens* proves to be distinct on a suite of characters: yellower bill with blackish nares, buffier supercilium, throat and breast, different-coloured and -structured crest, different-patterned upperparts and tail, a purer, more fluent, longer, lower Short Call (used by advertising males), markedly divergent from the explosive, nasal, double-noted equivalent in nominate *ocellata*, and a higher number of loud notes in the Long Call including an unexplained bimodal vs. unimodal pattern (hence either average 8.6 or 14.5 vs. 7.1 loud notes per call). In combination these characters indicate a level of differentiation compatible with species rank for *nigrescens*, and this is strongly reflected in Tobias criteria scoring. The conservation of the two forms requires urgent reconsideration.

Crested Argus *Rheinardia ocellata* is a spectacular but reclusive species of pheasant with two subspecies in widely separated, highly restricted ranges in Vietnam and Lao PDR (nominate *ocellata*) and peninsular Malaysia (subspecies *nigrescens*), and largely owing to the trapping of birds in Vietnam, compounded by forest clearance, it is listed as Endangered on the IUCN Red List (BirdLife International 2020). Differences between the two taxa have never been considered particularly strong, but mentioned as a topic that needs examining (Liang *et al.* 2018), and the only close comparison between them was made at the time of the description of *nigrescens* nearly 120 years ago. However, as the conservation status of the species appears to be increasingly precarious (classified as Near Threatened in the years 2005–16), its taxonomic status has also become a matter worthy of further investigation.

The name *Argus ocellatus* was published by Elliot (1871) in reference to several very large pheasant feathers of unknown origin held in the Paris museum. These had been studied by Verreaux in the period 1835–59, who gave them the same name *Argus ocellatus* but only in manuscript (Delacour 1951). It was not until two skins were obtained during 1879–81, one from Commandant Rheinart and the other from the Governor General of Cochin China, that their origin was determined as present-day Vietnam and the genus name *Rheinardia* was published by Maingonnat (1882).

A similar taxon from the Malay Peninsula collected by Waterstradt (1902), although probably not quite on the mountain he assumed (Barlow 1969), was described by Rothschild (1902) as *Rheinardius ocellatus nigrescens*. All subsequent authorities (e.g. Peters 1934, Delacour 1951, McGowan 1994, Johnsgard 1999, Hennache & Ottaviani 2005) down to the four current world lists (del Hoyo & Collar 2014, Christidis *et al.* 2018, Clements *et al.* 2019, Gill *et al.* 2020) have followed Rothschild in treating *nigrescens* as a subspecies of *R. ocellata*. Nevertheless, the two taxa are disjunct by more than 1,000 km in a direct line (1,800 km by the shortest present-day land route), and they lie in two biogeographically

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distinct provinces within the Oriental region, in mainland Indochina and on the Sunda Shelf (Whitmore 1984, Sterling & Hurley 2008, Corlett 2014).

In the original description of *nigrescens*, Rothschild (1902) distinguished nine characters in the male: (1) mantle and wings darker, brownish black, with chestnut-rufous mottling instead of dark brown; (2) spots of the upper surface mostly quite round and pure white, instead of more or less buff and irregular or elongated; (3) markings on the rump less numerous but larger and with more white; (4) white spots on the outer secondaries mostly quite round, instead of taking the form of irregular oblique lines; (5) upper crest feathers black, instead of dark brown, the white feathers of the crest apparently more numerous; (6) outer webs of the enormously elongated rectrices deeper in colour, more of a blackish brown, and at the same time more uniform; (7) broad superciliary stripe not greyish white, but strongly tinged rufous; (8) bill somewhat stouter; and (9) tail perhaps less elongated. The female is not appreciably different from her counterpart, but 'is somewhat brighter and more rufous, but this may be due to the freshness of the plumage'.

Nine points of distinction is a relatively large number for a taxon being described as a subspecies, and certainly suggests a level of divergence worthy of reassessment in the light of modern taxonomic trends. We do so here, based on re-examination of museum material, and on sound recordings as well as newly available information from observations on live individuals of both taxa.

Methods

Morphological study.—We inspected specimen material of both taxa at the American Museum of Natural History (AMNH), New York, USA, and the Natural History Museum (NHMUK), Tring, UK, made plumage comparisons between them and took biometrics. Material measured involved six full-tailed adult male *nigrescens* (three in AMNH, including the type, 544050; three in NHMUK) and nine full-tailed adult male *ocellata* (five in AMNH, four in NHMUK); registration numbers are given in Table 1. Mensural data were taken from males in millimetres using tape measures, long rulers and digital callipers accurate to two decimal places, for bill (skull to tip), crest (base to tip of longest straightened filoplume), tarsus (tarsometatarsus from back of 'ankle' to distal side of the joint-covering scute at the base of the longest toe), wing (curved) and tail (from point of insertion to tip, shafts as straight as possible). We also examined colour photographs of captive birds of both taxa on the internet and in our own and others' private collections, and, through the courtesy of J. Corder, World Pheasant Association, we examined footage of a series of videos he made of wild and captive male *nigrescens* several decades ago (no captive population of *nigrescens* currently exists).

Vocal study.—To evaluate possible vocal differences, we gathered as many sound-recordings as possible (Appendix). The established bird sound archives (Macaulay Library, Xeno-canto, AVoCet, BLNS) proved to have very few recordings, none of them involving *nigrescens*. However, between 2015 and 2019 we made our own digital recordings of more than 20 captive birds of nominate *ocellata* in Saigon Zoo, Ho Chi Minh City, Vietnam, predominantly in April–May and November, and of wild *nigrescens* at Gunung Rabong Forest Reserve, Kelantan, Malaysia, over the same period, using a Sony™ ICD-PX470 hand-held recorder without an external microphone. These recordings were saved as MP3 files and archived online in bird sound databases (see Appendix). Sonograms were derived from these recordings using CoolEdit Pro software and Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA). Sound parameters were measured manually on these sonograms.

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In addition, descriptions of calls of *nigrescens* are based on fieldwork at Gunung Rabong in 1976, 1977 and 2015–2019, and at an unnamed mountain just south of Gunung Rabong in 1984. Counts of the number of loud notes per Long Call and Sharp Call were made of more than ten captive males and seven females of *ocellata* while under direct visual observation in Saigon Zoo, and of possibly ten wild unsexed individuals of *nigrescens* not under visual observation in Malaysia. We considered a 'note' to be any continuous line on a sonogram prior to a pause. Within a note, 'syllables' are distinct parts of a note which typically are audible and on a sonogram usually can be seen as changes in the continuous line (e.g. from falling to rising, etc.). We defined separate calling bouts as vocalisations from a given individual separated by more than 60 seconds.

To gauge the degree of difference between taxa in plumage, dimensions and voice we made use of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2 is minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character (allowed 1) may be counted. The notation 'ns' ('no score') with a value in square brackets is to indicate the degree of difference but, because of the restriction on the number of characters, the score is disallowed.

Results

Morphological evidence.—Our review of specimen material confirms the diagnosis of *nigrescens* by Rothschild (1902), with the exceptions that in his first character (darker wings and tail) we could not see 'chestnut-rufous mottlings instead of dark brown' and in his eighth (stouter bill) we could detect no obvious distinction (Table 1). Below we condense the differences into six plumage/bare-part characters, using 'vs.' to indicate comparison with nominate *ocellata*, and with Tobias criteria scores in brackets at the end of the description of each character (scores, as opposed to no scores [ns], allocated to the differences we judge most prominent):

1. supercilium buff vs. stony white, usually broader and stronger, and contrasting more strongly with the blacker crown and 'face' (area around eye and on ear-coverts) (Fig.1a,b; score at least 2);
2. nareal area blackish, adjacent area of bill (distal to nares) rosy (as noted in Ogilvie-Grant 1908), rest of bill yellowish horn with a paler tip and cutting edge vs. bill including all

TABLE 1

Means and ranges of five variables in fully adult male specimens of *Rheinardia* held in the American Museum of Natural History, New York (AMNH), and Natural History Museum, Tring (NHMUK). Sample sizes are nine for *ocellata* (eight for bill) and six for *nigrescens*. Specimens contributing data are: (*ocellata*) AMNH 258935, 259081, 544045–047, NHMUK 1907.12.13.1, 1927.6.5.25, 1928.6.26.98 (bill unmeasurable), 'H.1888' (unregistered); (*nigrescens*) AMNH 544049–51, NHMUK 1903.5.1.1, 1906.7.23.384, 'Mus. FMS' (unregistered).

	bill	crest	tarsus	wing	tail
ocellata	41.1 (37.2–44.3)	79 (62–92)	88 (86–91)	339 (333–350)	1,369 (985–1,494)
nigrescens	41.7 (40.7–42.3)	100 (89–110)	96 (92–100)	366 (355–377)	1,278 (930–1,642)

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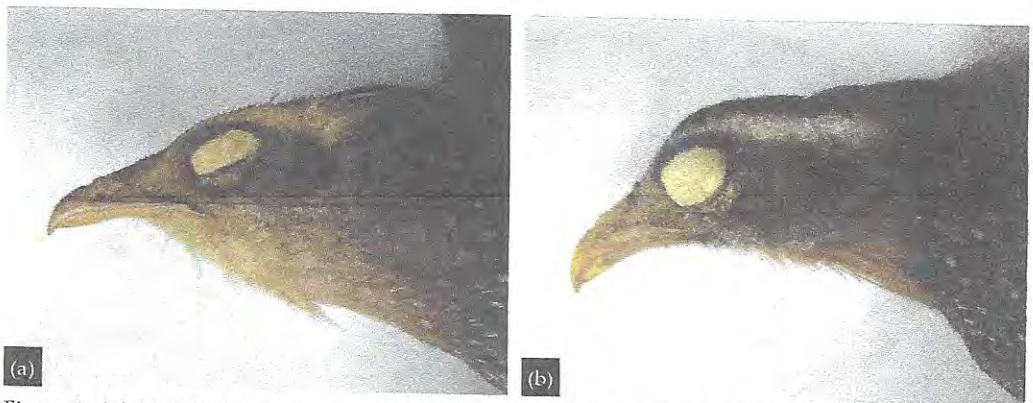

Figure 1. Adult male (a) *nigrescens* and (b) *ocellata* to show supercilium and bill (N. J. Collar, © Natural History Museum, London)

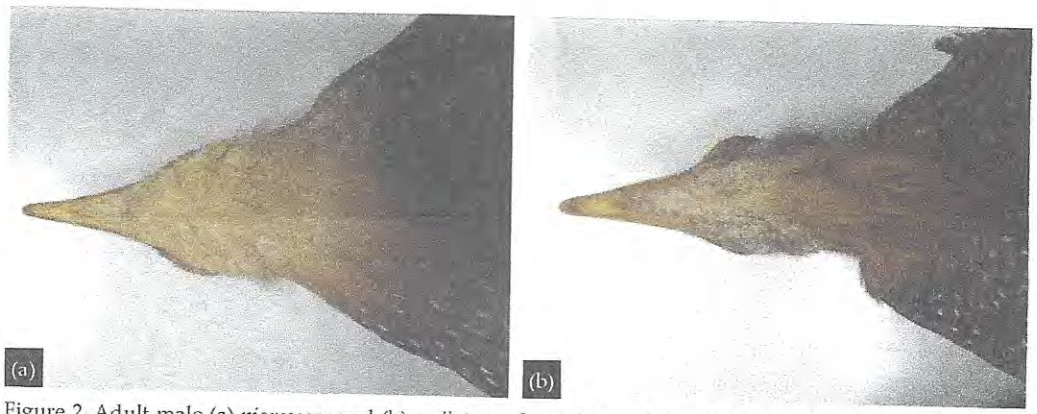

Figure 2. Adult male (a) *nigrescens* and (b) *ocellata* to show chin and throat (N. J. Collar, © Natural History Museum, London)

but the base of the nareal area rosy pink, slightly paler at the tip, deeper pink above and behind the nostril, as noted by Delacour (1951) and apparent in many photographs of *c.*15 live individuals in Saigon Zoo (Figs.1a,b, 4a,b; score 3);

3. white of throat more contrasting, buffier (in an echo of the supercilium differences) and more extensive, vs. a less striking greyish white shading quickly into a dull rufous-brown lower neck (present in *nigrescens* as a very narrow zone where the white lower throat grades into the spotted body) (Fig.2a,b; ns[2]), in both taxa the throat feathers forming a little forward-projecting beard when the crest, head and neck feathers are all erected;
4. occipital crest pointing directly backwards rather than tending to spread laterally, in museum skins, with much longer and coarser filoplumes (lacking the fluffiness of the nominate), and consisting of two colours in different proportions, namely a relatively sparse number of elongate black feathers positioned above 5–10 times as many much longer white feathers, vs. soft, decurving sooty-brown feathers shading first to slightly rufous-tinged brown and then creamy white, producing an obviously different profile in display (discussed below; Figs. 3a,b, 4a,b; score 3);
5. white spots on the blacker body and wings much more distinct, being smaller and fewer (hence more widely spaced) and more linearly arranged compared to the dense buffy-white speckling of the nominate (Fig.5a,b; ns[2]);

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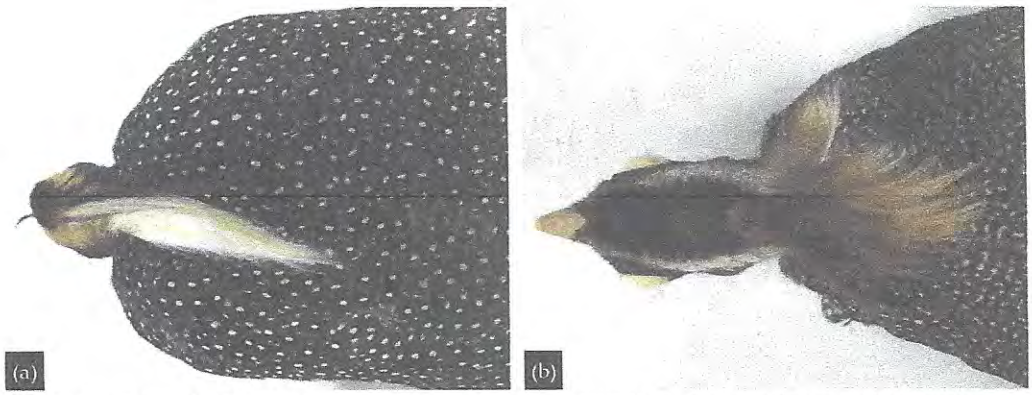

Figure 3. Adult male (a) *nigrescens* and (b) *ocellata* to show crest (N. J. Collar, © Natural History Museum, London)

Figure 4. Adult male (a) *nigrescens* and (b) *ocellata* to show different crest structure in display (also bill colour): (a) still from J. Corder video (made at Sungkai Wildlife Conservation Centre, Malaysia); (b) photograph by J. Bordonné, www.zoospassion.com (in Saigon Zoo, Vietnam)

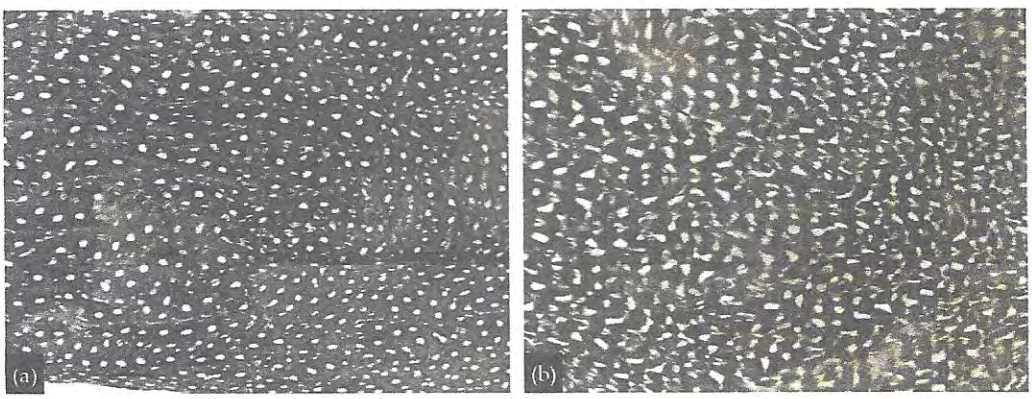

Figure 5. Adult male (a) *nigrescens* and (b) *ocellata* to show dorsal spotting (N. J. Collar, © Natural History Museum, London)

6. inner vanes of the largest rectrices with dull matt rufous-orange background on which white spots are inset in broad grey rings, vs. with grey background, the dull matt rufous-orange contracting to islands between the white spots (Fig.6a,b; ns[2]).

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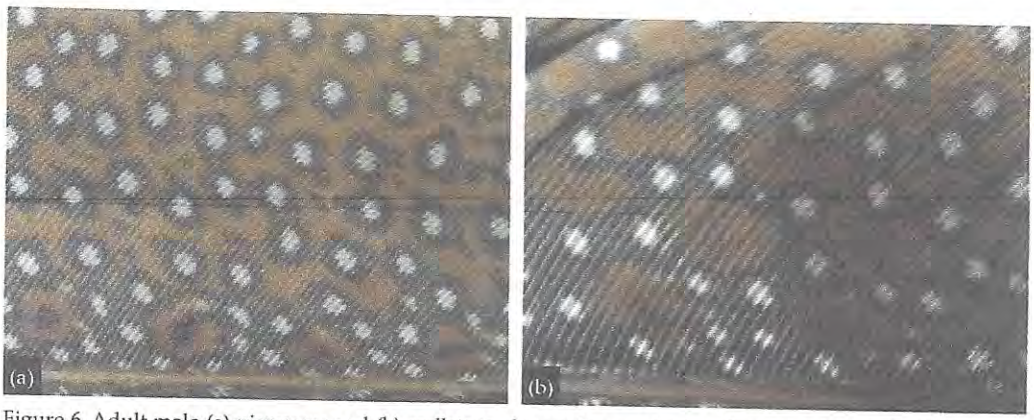

Figure 6. Adult male (a) *nigrescens* and (b) *ocellata* to show colour pattern on largest rectrices (N. J. Collar, © Natural History Museum, London)

In morphometrics *nigrescens* emerges slightly larger overall, with no overlap in tarsus or wing (Table 1). There is also very little overlap in length of crest, which shows much the greatest degree of difference between means (Table 1); we do not emphasise this as it is correlated with body size, but the crest is proportionately longer in *nigrescens* and the colour and shape differences are evident in display (next paragraph). The tail of *nigrescens* averages slightly shorter, but this is almost certainly an effect of sample size: tails in *Rheinardia* possibly increase in length with age (McGowan 1994), and in fact one *nigrescens* (NHMUK 1903.5.1.1) has a tail of 1,642 mm, far longer than the next longest, an *ocellata* (NHMUK 1928.6.26.98) at 1,494 mm. The sample sizes are too small to subject to statistical analysis, but the evidence suggests that the longer tarsus of *nigrescens* might involve a score of 2.

When erected, the crest of male *nigrescens* forms a very spiky pure white radiating mass of untidy feathers, while the long black feathers that lie over the white ones when at rest are projected far forward, overhanging the forehead and bill, apparently straightening under their own weight (Fig. 4a). Contrastingly, the crest of male *ocellata* forms a fluffy, bouffant powderpuff of golden-buff feathers, while the short brown feathers project above the forehead and in profile view form a short rounded curl (Fig. 4b; also Seth-Smith 1932, Huxley 1941). The difference in crest colour and length is striking when the crest is being raised, as their movement causes the long spiky feathers of *nigrescens* to scatter outwards (J. Corder, video).

Vocal evidence.—From the recorded and published material available to us we find both taxa possess three loud call types, which we term Short Call, Long Call and Sharp Call. In nominate *ocellata* all three calls have been sound-recorded; in *nigrescens* only the Short Call has been digitally recorded while the other two have written descriptions based on experience in the field. The Short Call is given by males at or near display sites, apparently in advertisement, and as far as is known it is not given by females. The Long Call and Sharp Call are given by both sexes.

Short Call.—In nominate *ocellata* (Fig.7a,b) this call is a loud, explosive, slightly nasal *wooOh-WAWh* delivered as two clearly separated and equally accentuated notes (structurally similar to the homologous vocalisation of Great Argus *Argusianus argus*; as in that species the separation of the notes is not always as clearly defined on sonograms as appreciated by ear, owing to reflections and reverberation). The first note is slightly rising, the second overslurred and reaches a higher maximum pitch. It has been heard given once (rarely twice) per calling bout (by captive males) but few of these calls were heard during the observation periods, which were seasonally limited, and the regional literature indicates the

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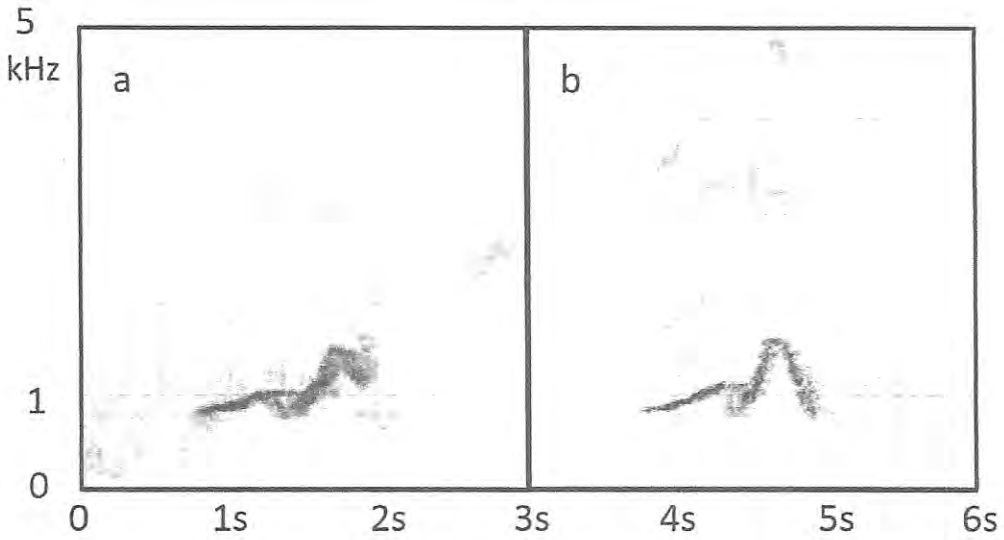

Figure 7. Short Call of *Rheinardia ocellata*: (a) in captivity (ML273908: male, Saigon Zoo, Ho Chi Minh City, Vietnam, 18 April 2019, GWHD); (b) in the wild (AV7666: Bach Ma National Park, Vietnam, 10 February 2003, P. Verbelen).

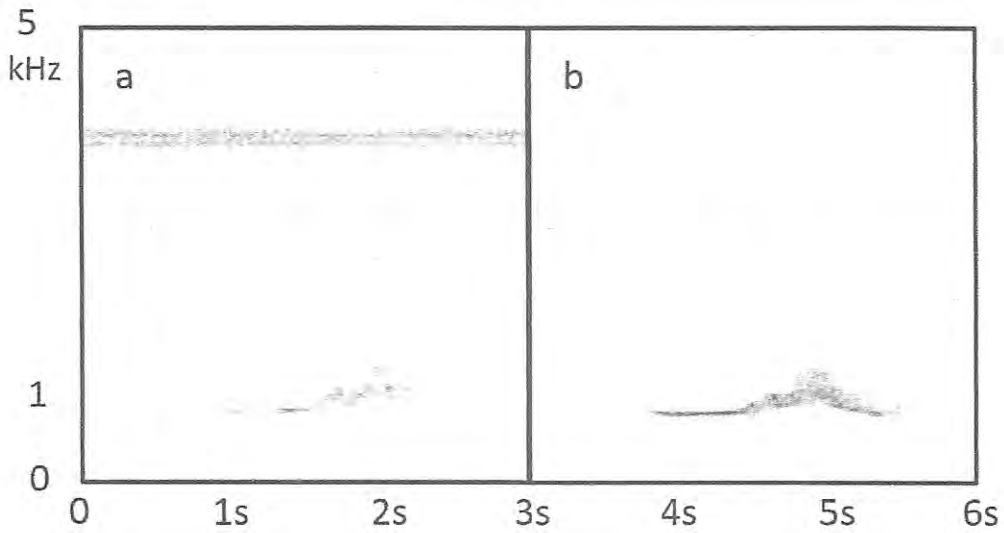

Figure 8. Short Call of *Rheinardia nigrescens* in the wild: (a) Gunung Rabong, Malaysia, 4 April 2018, GWHD (ML273906); (b) Gunung Rabong, Malaysia, 23 April 2019, GWHD (ML273907).

call can be repeated multiple times (see Discussion). In *nigrescens* (Fig.8a,b) the Short Call is a rather pure whistled *whuuhuhHUhuuu*, sounding less forceful and delivered fluently in one breath at fairly consistent amplitude, hence resembling a protracted single note with different internal emphases. The whistled note starts on a flat pitch, followed by a quavering middle part and ends again at about stable pitch. It is typically given once per calling bout, but has been heard repeated up to eight times in succession. When repeated, which is often when responding to extraneous sounds such as gibbons, hornbills, thunder or tree-falls, it can be with a distinct interval of a few seconds between calls, or as a rolling uninterrupted sequence.

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TABLE 2
Measured sound parameters of the Short Call in males of the two taxa.

	ocellata		*nigrescens*	
Recording no. (see Appendix)	ML273908	AV7666	ML273907	ML273906
Total duration of call	1.34 s	1.19 s	1.64 s	1.60 s
Start frequency	780 Hz	800 Hz	780 Hz	760 Hz
Max. frequency	1,600 Hz	1,650 Hz	1,225 Hz	1,250 Hz
Number of notes	2	2	1	1
Number of oscillations	2	2	3–4	3–4
Max. time at stable frequency	<0.2 s	<0.2 s	0.64 s	0.75 s
Clear harmonics?	yes	yes	no	no

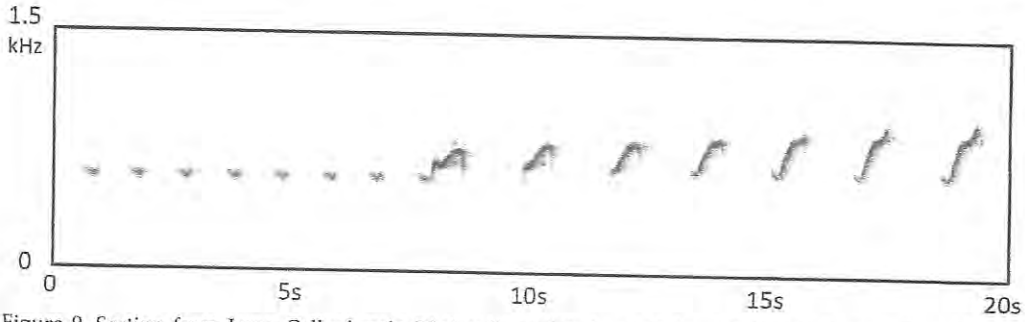

Figure 9. Section from Long Call of male *Rheinardia ocellata* in captivity (ML273918: Saigon Zoo, Ho Chi Minh City, Vietnam, 22 November 2019, GWHD) showing seven of the soft preliminary notes, and an eighth preliminary transitioning into all of the complete seven very loud rising disyllabic notes.

Sonograms were made of these calls and measurements of them reveal that male *nigrescens* has a longer (mean 1.62 vs. 1.27 seconds) but lower-pitched call (mean max. frequency 1,238 Hz vs. 1,625 Hz; Table 2) consisting of a diagnostic single continuous whistle on level pitch followed by quavering modulations, vs. two emphasised overslurred notes. The three recordings are too few to calculate effect sizes; for example, the methodology of Isler *et al.* (1998) requires calculation of percentiles in the *t*-distribution of measurements drawn from a sample of vocalisations. Donegan (2018) assessed strengths and weaknesses of the method. However, given this is a very stereotypic call (heard >100 times in various field situations but not recorded, and immediately recognisable), we can confidently estimate Tobias scores for the three differences to reach respectively 2 (for length), [ns]2 (for pitch) and 4 (for 1 vs. 2 notes), resulting in a total score for this vocal character of 6. Isler *et al.* (1998) also used three differences between pairs of taxa, in their case for suboscine Thamnophilidae.

Long Call.—This call is given by both sexes of nominate *ocellata* (Fig. 9). It starts with a series, often prolonged over several minutes, of up to several hundred very soft notes that can be heard only from a few metres away and detected visually by slight throat movements, before suddenly transitioning into very loud disyllabic notes, usually *c.*5–9 in a series delivered with wide open bill and straining hyoids. This series of rising whistles, each of which lasts *c.*1 second, often gradually increases in pitch, every whistle reaching a slightly higher frequency than the previous one. The very soft preliminary notes are delivered at a rate of *c.*1 per second, and each lasts approximately 0.4 seconds. In *nigrescens* soft preliminary notes have not been heard, but if present they would not have been detected because of distance in the field. The known part of the call is a single introductory

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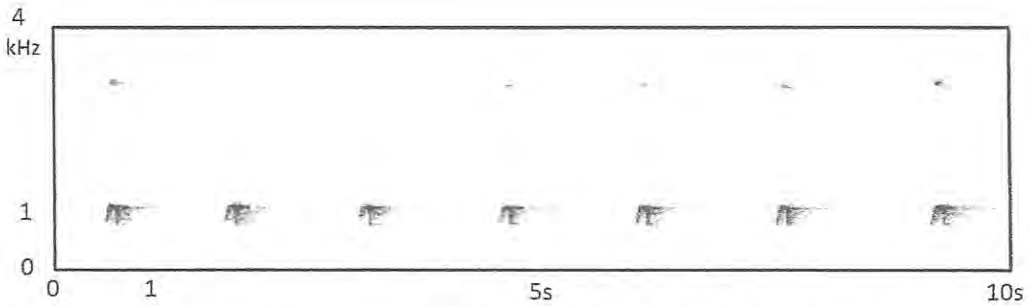

Figure 10. Seven notes from a prolonged Sharp Call of a male *R. ocellata* in captivity (ML273916: Saigon Zoo, Ho Chi Minh City, Vietnam, 22 November 2019, GWHD).

whistled note that morphs into a series of 8–17 very loud inflected disyllabic notes. It is uncertain whether both sexes of *nigrescens* give this call, as no direct observations have ever been made.

The Long Call of nominate *ocellata* could be transcribed as *...u, u, u, uKIAU; KIAU; KIAU;* ... (here, the last four of the very soft preliminary notes followed by three very loud notes). The Long Call of *nigrescens* could be transcribed as *woooKI-IAU; KI-IAU; KI-IAU;* ... (here, the introductory whistle morphs into three of the subsequent very loud inflected notes). The introductory whistle is similar to that which introduces each Short Call in *nigrescens*. Once a Long Call was ended as well as begun by a whistled *wooo*.

Long Calls by captive male *ocellata* involved 4–11 loud notes per call (preliminary soft notes not counted) with a mean of 7.12 (n = 109 calls). They had a unimodal distribution, with 74% of calls containing 6–8 loud notes. Long Calls by captive female *ocellata* ranged from three to 12 loud notes per call with a mean of 6.74 (n = 42 calls). They almost had a unimodal distribution, with 81% of calls containing 5–9 loud notes (slightly fewer calls with six than with five or seven loud notes). Long Calls by unsexed wild *nigrescens* ranged from seven to 17 loud notes per call, with a mean of 11.6 (n = 22 calls), and were therefore longer on average than Long Calls of *ocellata*, with nine (41%) of the *nigrescens* calls containing more loud notes (13–17) than any *ocellata* Long Call (max. 12 loud notes, from a female). A Kruskal-Wallis test revealed that there was a highly significant difference between the three groups (χ^2 = 37.889, p<0.001), with number of notes from *nigrescens* significantly different from those of *ocellata* females (Dunn's pairwise test; Bonferroni corrected p<0.001) and *ocellata* males (p<0.001). However, the distribution of loud notes in *nigrescens* was arguably bimodal, with 11 calls containing 7–10 loud notes, and 11 containing 12–17 loud notes. These are based on field notes from a broad area of forest covering at least three separate mountain flanks, and therefore unlikely to reflect individual call differences between two birds. If these are treated as two non-overlapping classes (e.g., females vs. males, or perhaps non-court-holding vs. court-holding males), their means are (*nigrescens*-1) 8.6 (n = 11) vs. (*nigrescens*-2) 14.5 (n = 11) loud notes per call. A Kruskal-Wallis test revealed a highly significant difference between all four groups (χ^2 = 41.976, p<0.001), with the numbers of notes from *nigrescens*-1 and *nigrescens*-2 significantly different from those of *ocellata* females and *ocellata* males (Dunn's pairwise tests; Bonferroni corrected p<0.05). A biological difference is evident between *ocellata* (difference between males and females of only 0.38 in mean number of notes per Long Call, and unimodal distribution of call notes within a large sample of males) vs. unsexed *nigrescens* (two non-overlapping categories of Long Call, and more notes on average in both these categories than in male and female *ocellata*). Accepting that further additions for vocal differences are ineligible under the Tobias criteria, if we assess the difference between these calls in terms of their constituent elements, we might

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allow a score of 1 for the more inflected loud note in *nigrescens*, 1 for the introductory *wooo*, and 2 for the greater number and bimodal nature of the loud notes per call, yielding a score for this vocal character of [ns]4).

As a non-parametric test Kruskal-Wallis is not powerful, which is why we also applied Dunn's pairwise test and Bonferroni correction, considering these a reasonable option given the non-normal distribution and different sizes of samples. Larger sample sizes could provide a basis for improved statistical treatment.

Sharp Call.—A Sharp Call is given by both sexes of *ocellata* (Fig. 10). Based on the absence of fear behaviour among all birds before and during the call, it is not necessarily an alarm call. It is similar to the Long Call only in that it consists of a series of notes, but it is quieter and higher pitched, and consists of more notes (but a more variable number, from 12 up to 191 heard), and these are delivered at less regularly spaced intervals than notes in the Long Call. The notes are each much shorter than those of the Long Call, and appear on a sonogram as an inverted U shape. Each note lasts less than 0.5 seconds and is delivered at roughly 1.5–2.0 second-intervals, sometimes with pauses. Although the volume of the individual notes can increase over the series, there are no distinct soft preliminary notes, and no sudden transition to very loud notes. A seemingly identical Sharp Call has been heard only once in the wild from *nigrescens*, but at a distance and was not attributable to sex.

Discussion

Using the Tobias *et al.* (2010) criteria, museum skins alone provide a sufficiently high score (8) to indicate that *R. nigrescens* and *R. ocellata* merit species status. To that we are able to add the distinctive appearance and deportment of the crest, a significant display feature, and considerable differences in advertising calls (totalling 6).

The Short Call and Long Call of the Malaysian taxon were described by Wells (1975, 1999), Medway & Wells (1976), Davison (1978) and Jeyarajasingam & Pearson (1999), all based on fieldwork by D. R. Wells in 1972 and by Wells and GWHD in 1976. Three calls of nominate *ocellata* were described by Robson (2008), apparently corresponding to the Short Call and Long Call described above, as well as an alarm call. That alarm call may correspond to what we term the Sharp Call, although our observations of captive birds suggested it was not (or not necessarily) delivered in an alarm situation. Craik & Lê (2018) also described two loud calls, but possibly conflated descriptions of the two taxa, by incorporating details of Wells' (1999) account of the Short Call of extralimital *nigrescens* ('trisyllabic "WOO KIA'WAU" ... in series of up to 12', although correctly noting that it is usually uttered singly), followed by a correct description of the Long Call of *ocellata* ('6–8 far-carrying "oowaaa" calls'), the latter similar to the description by Robson (2008).

Our observations demonstrate that the Short Call, delivered by males at their display sites (Davison 1978), differs in structure between *R. nigrescens* and *R. ocellata*. As its function appears to be in mate attraction, any vocal differentiation in this call must be considered important. It is interesting to note that the Short Call of *ocellata* is very similar to allopatric *Argusianus argus*, while the Short Call in *nigrescens* (sympatric with *A. argus* but separated by elevation) is quite different, suggesting that the voice of *nigrescens* evolved to differentiate it from *A. argus*, while *ocellata* retained more ancestral features. Their respective Long Calls also differ in structure, in number of notes, and probably in the degree of difference between males and females.

The calls of *R. ocellata* analysed here were mainly from captive individuals, and those of *R. nigrescens* were made by wild birds. In general non-passerine vocalisations are not learnt. Forebrain areas that are similar in morphological appearance, location and connectivity to the song control areas of oscine passerines (songbirds), some parrots and hummingbirds are

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lacking in various suboscine passerines, owls, doves, gulls and gallinaceous species (Gahr 2000) that do not learn vocalisations. These are reasons to suppose that the forms and types of calls of *R. ocellata* were not, or not greatly, affected by captive conditions; the validity of this assumption was further affirmed by comparing our recordings with the few available of *ocellata* in the wild (AV7666, XC69377, BLNS46837).

The total Tobias score for *R. nigrescens* reaches a relatively high 14 (double the threshold the criteria set for species rank), which ostensibly exaggerates its distinctiveness but underlines the value of assessing all aspects of phenotypic divergence. Outside the Galliformes an interesting parallel exists in the case of African Houbara *Chlamydotis undulata* and Asian Houbara *C. macqueenii*, two species that look extremely similar at rest but which differ significantly in feather deportment and pattern in display, including the crest, as well as in the number of call notes (Collar & Combreau 2017). Among Galliformes, several splits made employing the Tobias criteria have been validated by various parallel or follow-up studies and observations, e.g. Hainan Peacock-pheasant *Polyplectron katsumatae* (Davison *et al.* 2012), Elgon Francolin *Scleroptila elgonensis* (Hunter *et al.* 2019, Turner *et al.* 2020) and Taiwan Hill-partridge *Bambusicola sonorivox* (Hung *et al.* 2014), all involving considerably lower scores. We predict that if future molecular work becomes possible it will confirm species rank for *R. nigrescens* and *R. ocellata*. We prefer use of Tobias criteria rather than simple comparison with other pairwise cases in the family, but if the latter method is employed our findings indicate that phenotypic differences between *R. nigrescens* and *R. ocellata* outlined above are greater in number and larger in degree that those that separate, e.g., Rock Partridge *Alectoris graeca* from Chukar *A. chukar* and Gunnison Grouse *Centrocercus minimus* from Sage Grouse *C. urophasianus*.

Our recognition of what we propose to call Malaysian Crested Argus *R. nigrescens* as a species distinct from Vietnamese Crested Argus *R. ocellata* is likely to have several conservation implications. First, for planning purposes, the IUCN conservation status of the two resulting species-level taxa will require re-assessment, and is likely to result in heightened concern for both. Second, for the conservation of wild populations, awareness of species status might place them at heightened risk of poaching for trade. In Vietnam *R. ocellata* occurs in several protected and proposed protected areas such as Bach Ma National Park, Ngoc Linh Nature Reserve and Song Thanh Nature Reserve, all in Quang Nam province, and Khe Nuoc Trong Proposed Nature Reserve, Quang Binh province (Gray *et al.* 2014, Vũ *et al.* 2017a,b, Vu & Tran 2020), but a sharp decline in advertisement calls in some former strongholds including both Laos (Brickle *et al.* 2008) and Vietnam (Gray *et al.* 2014) indicates the need for a new full assessment of its status and needs (Le Trong Trai pers. comm. 2019; BirdLife International 2020). Fortunately, in Malaysia the bulk of the *R. nigrescens* population lies within the boundaries of Taman Negara National Park (Mamat & Yasak 1998, Liang *et al.* 2018), but no uninhabited area with a long boundary that is difficult to patrol can be considered totally secure. However, there are in principle multiple levels of protection, with permits being required to enter forest (National Forestry Act, most recent major revision 2010), total protection of all species of plants and animals within Taman Negara, and total protection for the species anywhere, under the Protection of Wild Life Act (most recent major revision 2010). Third, improved knowledge of the calls of both species (including whether they are delivered by males or females) should improve the interpretation of survey and census results which, for these elusive birds, are largely based on sound records.

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Appendix: sources of calls used in the analyses in this paper

AV = AVoCet (Avian Vocalization Center)
BLNS = British Library (Wildlife and Environmental Sounds)
ML = Macaulay Library, Cornell Laboratory of Ornithology
XC = Xeno-canto, Naturalis Biodiversity Center

Rheinardia ocellata nigrescens
Short Call: ML273906 and ML273907 (Gunung Rabong Forest Reserve, Kelantan, Malaysia, G. W. H. Davison)

Rheinardia o. ocellata
Short Call: ML273908 (Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), AV7666 (Bach Ma NP, Vietnam, P. Verbelen)
Long Call: ML273909–273915 and ML273918 (all Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), AV5578/XC69377 (Ho Ke Go, Vietnam, F. R. Lambert), BLNS46837 (Vu Quang Nature Reserve, Vietnam, J. C. Eames)
Sharp Call: ML273916–273918 (all Saigon Zoo, Ho Chi Minh City, Vietnam [in captivity], G. W. H. Davison), BLNS46837 (Vu Quang Nature Reserve, Vietnam, J. C. Eames).

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