Why the taxonomy of francolins and spurfowls (Galliformes, Phasianidae) needs revision: responses to Hustler (2021) and Hunter et al. (2021a,b)

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Introduction

The tortuous taxonomic history of ‘francolins’

Until well into the 20th Century, Afro-Asiatic perdicine, phasianid galliform taxa, referred to commonly as francolins, spurfowls and partridges, had both enigmatic and contentious taxonomic and phylogenetic histories (Mandiwana-Neudani 2013; Mandiwana-Neudani et al. 2019a,b). The genus Francolinus Stephens (1819) had been inconsistently sundered and repeatedly lumped into multiple genera, variable numbers of species and a plethora of subspecies. For example, Roberts (1924) recognised 2 genera, using Francolinus for the bulk of species that have feathered throats and single, short and blunt tarsal spurs, which they called ‘francolins’; they restricted Pternistis to those that have unfeathered throats with brightly coloured skin and long and multiple spurs, distinguishing them with the common name ‘spurfowls’. Alternatively, Wolters (1975–82) recognised 6 genera, using some to group smaller, short-single-spurred taxa with quail-like dorsal plumage, and Pternistis more ‘generously’ to incorporate larger, long-multiple-spurred taxa with streaked and/or vermiculated back parts, irrespective of throat plumage versus bare skin. As a further complication, geographically variable Afro-Asian francolins/spurfowls/partridges were split into more than 160 often clinal and/or morphologically idiosyncratic subspecies (Peters 1934). Finally, all these taxa were embedded within the highly polyphyletic subfamily Perdicinae (Horsfield 1821) within the Phasianidae (Kimball et al. 1999; Crowe et al. 2006; Wang et al. 2017). The even more controversial and contentious history of the use of common names for these taxa is outlined in detail in Crowe and Little (2004).

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Taxonomic resolution

In an innovative and ground-breaking monograph titled The francolins, a study in speciation, Hall (1963) employed the biological species and superspecies concepts (Mayr 1963) and used morphological, eco-behavioural, palaeo-climatic and vegetational evidence to investigate francolin morpho-ecological geographic variation, speciation, taxonomy, phylogenetics and biogeography. Assuming that the "degree of [morphological] divergence can be correlated with the length of isolation", Hall (1963) consequently –

• recognised a single, basally diphyletic genus Francolinus within the Perdicinae;

• recognised 8 taxonomically unnamed, putative monophyletic superspecies/Groups, 41 species, and 117 subspecies within two, also unnamed, basal clades;

• attempted to "reconstruct the climate changes, with the resultant isolating and re-joining of populations, which could have formed this pattern"; and

• gave "some tentative datings to various steps in speciation".

Hall’s (1963) taxonomy and phylogeny remained widely accepted for more than three decades (Crowe et al. 1986; Johnsgard 1988; Sibley and Monroe 1990; del Hoyo et al. 1994). Francolinus sensu lato became the most speciose genus within the Galliformes and one of the largest genera in the class Aves (Bock and Farrand 1980).

Taxonomic challenges

During the 1980s, reassessments of Hall’s taxonomy and phylogeny questioned the monophyly of Francolinus as well as Hall’s major clades and groups, and synonymised many of her recognised subspecies (Crowe and Crowe 1985; Crowe et al. 1986; Milstein and Wolff 1987).

Crowe and Crowe (1985) identified 25 informative morpho-behavioural characters and recognised two unnamed, major basal clades: quail-like francolins including the nominate
genus, and the partridge-like spurfowls. Analyses of these characters did not corroborate monophyly of *Francolinus* sensu Hall (1963) yet did not suggest a viable alternative. The analyses did support the monophyly of at least four of Hall's groups, whereas the other groups appeared to be paraphyletic or polyphyletic.

Crowe et al. (1986: 24–75) summarised and further revised the findings to date for African taxa. They provisionally accepted francolin monophyly, since the Crested Francolin *Francolinus sephaena* sensu lato morpho-behaviourally 'links' francolins and spurfowls because it has attributes of both 'francolins' and 'spurfowls'. Crowe et al. (1986) retained Hall's (1963) Groups/superspecies and species, except for shifting *streptophorus* from the Striated to the Red-winged Group, and they investigated the 100+ subspecies recognised by Peters (1934) and Hall (1963) as taxonomic starting points; in the end, they reduced the number to 86 taxa.

By the 1990s, analyses of DNA restriction fragment length polymorphisms (RFLPs) combined with morphological and behavioural characters (Crowe et al. 1992) rejected the monophyly of *Francolinus* sensu Hall (1963). These analyses recognised at least four major assemblages: the five Asiatic species, two groups of African quail-like francolins, and the African spurfowls which linked with the Japanese Quail *Coturnix japonica*. Within these assemblages, the monophyly of six of Hall's eight species groups was supported.

In 1991, author TMC reported on this progress to Pat Hall at her home in England and he illustrated his Consilience Species Concept (eventually published in Crowe et al. [1994]) vis-à-vis her Red-necked Francolin *Francolinus afer* sensu lato. DNA sequence-based molecular evolutionary research decisively refuted the monophyly of the subfamily Perdicinae and *Francolinus* sensu Hall (Randi et al. 1991; Crowe et al. 1992; Bloomer and Crowe 1998; Kimball et al. 1999).

More recent research (e.g. Crowe and Little 2004; Crowe et al. 2006; Crowe 2010; Mandiwana-Neudani et al. 2011; Cohen et al. 2012; Bowie et al. 2013; Mandiwana-Neudani 2013; Mandiwana-Neudani et al. 2014; van Niekerk and Mandiwana-Neudani 2015; Crowe et al. 2019; 2020; Hunter et al. 2019; Mandiwana-Neudani et al. 2019a,b [hereafter M-N+]) recommended radical changes to the phylogeny and taxonomy of *Francolinus* sensu Hall (1963). *Francolinus* is now split into two distinctly related monophyletic clades: "True" quail-like 'francolins' (including the nominate genus) and partridge-like African spurfowls (Crowe et al. 2006).

Francolins are relatively small and have at most one (generally short) tarsal spur, more musical and whistling calls, generally roost on the ground, and have striped and barred rufous dorsal plumage resembling that of quails. Taxonomically, they are partitioned among the genera *Francolinus*, *Ortygornis*, *Peliperdix*, *Campeolophus* and *Scleroptila* spp., which respectively conform to Hall's Spotted, Striated, Red-tailed and Red-winged Groups (Mandiwana-Neudani 2019a). Phylogenetically, these genera link with jungle fowls (*Gallus* spp.) and bamboo partridges (*Bambusicola* spp.) within the subfamily Gallininae (Crowe 2006).

Sparrowfowl are relatively large, have two (generally long) tarsal spurs, emit raucous, grating or cackling advertisement calls (given mainly at dawn/dusk), and they perch in trees and have dark dorsal plumage vermiculated with grey, white and/or buff. Taxonomically, they form a single genus, *Pternisits*, within the subfamily Coturnicinae, linking with quails (*Coturnix* spp.), *Alectrois* partridges and the Madagascar Partridge (*Margaroperdix*, confirming Frost's [1975] research based on chick plumage) (Crowe et al. 2006). Within the cladistically pectinate *Pternisits*, all of Hall's (1963) Groups are paraphyletic (evolutionarily reticulate?) except for the 'Bare-throated' species (Mandiwana-Neudani 2019b) (Figure 1).

M-N+ emulated Hall (1963) and dealt with geographical variation, speciation, phylogeny and the biogeography of francolins and spurfowls throughout their Afro-Asian ranges. Using independent morpho-behavioural and DNA sequence-based evidence, M-N+ re-interpreted francolin and spurfowl taxonomy in light of modern concepts of species and subspecies based on refutable character-based versus trait-based evidence.

M-N+ phylogenetically placed all of Hall's (1963) 'unplaced' species. Three species were assigned to francolin genera. One species, *nahani* (placed in the monotypic genus *Acenterortyx* by Chapin [1926]), was shifted along with the also evolutionarily enigmatic African Stone Partridge *Ptilopachus petrosus* from the Phasianidae to the New World Quails, family Odontophoridae (Cohen et al. 2012; Bowie et al. 2013). The most unexpected result was the resolution of the phylogenetic position of *Xenoperdix* (nomenclaturally literally 'strange' 'partridges' (originally described in an early manuscript as "francolins") from the Eastern Arc mountains in Tanzania (Dinesen et al. 1994; Bowie and Fjeldså 2005); they join Asian Hill Partridges (*Arborphila* spp.) and the Crested Wood-partridge *Rollulus rouloul* to form the subfamily Arborophilinae, the sister-clade to all remaining phasianids (Crowe et al. 2006). All these findings have been confirmed by subsequent molecular phylogenetic research using extensive genomic datasets (Wang et al. 2013; Kimball et al. 2021).

**Taxonomy**

At the levels of species and subspecies, M-N+ employed the holistic Consilience Species Concept of Crowe et al. (1994, 2016) and used congruent variation in independent morpho-behavioural characters and measures of molecular genetic divergence to delineate the taxa. They further reduced the number of francolin and spurfowl subspecies, in part by elevating some to full species status. Here, we address objections raised in commentaries that argue against implementation of some of these taxonomic changes.

**Taxonomic ‘reflections’**

In his *Taxonomic revision of francolins – reflections from a central African perspective*, Hustler (2021 [hereafter Hustler]) follows on from other taxonomic reflection pieces on spurfowls and francolins (Hunter et al. 2021a,b [hereafter Hunter+]). Collectively, those authors criticise M-N+’s research design, analytics, and the status and ranking of some francolin and spurfowl terminal taxa. Mandiwana-Neudani et al. (2021) and Crowe et al. (2021) attempted to address concerns raised by Hunter+, but apparently not sufficiently.
In brief, largely based on biological information summarised in standard nation-delimited works — for example, Irwin (1981), Dowsett-Lemaire and Dowsett (2006, 2014) and Dowsett et al. (2008) — and information extracted from GenBank and the specimen databases of the American Museum of Natural History (AMNH) and the British Museums of Natural History (BM), respectively, Hustler and Hunter+ opine that because of concerns in relation to:

1. the taxa and type specimens examined;
2. unacceptably small taxon sample sizes;
3. confusion, subjectivity, and errors vis-à-vis characters employed;
4. sources and representativeness of specimens (outlined in Hustler—Table 1);
5. uncertainty about vocalisation “scores”;
6. selected taxonomic concerns;
7. key deficiencies and inadequate explanations concerning the taxonomic changes; and
8. errors in distribution maps,

M-N’s work is a taxonomic “missed opportunity” and “poorer for these omissions”; hence, they recommended that “the taxonomic changes proposed be postponed until more accountable data become available”. Here, we address and clarify these concerns and challenge Hunter+ and Hustler’s recommendation.

Research programme history, taxa examined and sample sizes

The M-N+ research programme on francolins and spurfowls originated in 1976 as a result of TMC reading Hall (1963) and through discussions with Pat Hall during the 4th Pan-African Ornithological Congress, at which he presented his research on geographical variation, taxonomy, speciation, phylogeny and the biogeography of African endemic guineafowls, family Numididae (Crowe 1978).

During the 1980s, TMC visited all 13 museums mentioned in the acknowledgements of M-N+, some of them multiple times. His early morpho-behavioural research was conducted before the DNA-sequencing and Microsoft Excel spreadsheet eras. He captured information on 3×5-inch cards, all of which were discarded in 2018 when the M-N+ manuscripts were essentially completed.

TMC reviewed published information on the biology of francolins and spurfowls and examined the morphology of all francolin and spurfowl holdings in the collections at museums visited. He normally stopped sampling a putative subspecies taxon once 10 specimens had been assessed. In total, he examined nearly 2 000 specimens representing all species and virtually all subspecies recognised by Peters (1934) and Hall (1963). In brief, his goals in the 1980s were to:

1. re-investigate and possibly supplement Hall’s (1963) morphological characters (versus traits) as outlined in her Table 1;
2. identify aspects of vocalisation and ecology that could also be used as characters or supplementary taxonomic information;
3. investigate the species and subspecies recognised by Peters (1934) and Hall (1963);
4. determine the extent to which the status of these was supported by consilient characters (sensu Ruse 1975, 1979); and
5. produce a cladistic phylogeny to test Hall’s (1963) cladogram.

The taxonomic utility of characters was determined by comparing variation within versus between collection sites. The distinction between characters and traits is discussed in detail below.

During the period 2003–2008, authors TGM-N and/or TMC re-examined 1 094 representative francolin/spurfowl specimens (480 francolins covering 59 putative terminal taxa, and 614 spurfowls covering 68 putative terminal taxa) housed at the AMNH (New York), the Natural History Museum at Tring (UK), and the Transvaal Museum (now the Ditsong National Museum of Natural History, Pretoria, South Africa), and they sampled specimens from 71 putative terminal taxa for molecular genetic analysis.

In morphological research, the sample sizes per putative terminal-taxon ranged from 1 to 64, with a modal value of 7. Information about the specimens examined was compiled in Excel spreadsheets, and individuals representing the terminal taxa recognised were photographed. All specimens that were assessed morphologically and sampled genetically corresponded phenotypically to either types, holotypes and/or paratypes considered, synonymised and/or taxonomically recognised by Hall (1963) and eventually studied by TMC during the 1980s.

Like Hunter+, Hustler erroneously points out that: “There does not appear to be a single taxon that is represented by more than one genetic sample”. Mandiwana-Neudani et al. (2021) and Crowe et al. (2021) have already addressed this concern. Because of unavoidable sampling constraints stemming from limited historical collecting, rigid museum policies relating to destructive sampling and the costs related to relatively expensive Sanger sequencing, TGM-N and TMC chose specimens for genetic study in a complementary fashion that maximised coverage of geographical variation within Hall-recognised polytypic species.

Moreover, if one considers species recognised by Hall (1963) as “single taxa”, M-N+ took and analysed multiple genetic samples for many species. For example, M-N+ morphologically examined 112 specimens of Hall’s

Figure 1: The strict consensus parsimony cladogram of Mandiwana-Neudani (2019a,b: cited in the text as M-N+) for ‘Bare-throated’ Spurfowls. Note the much lower nodal support value for that embedding *Pternistis rufopictus* within the *P. cranchii/afer* clade.
Francolinus coqui, including 12 putative subspecies, all of which were sampled for genetic analysis; they also examined 46 specimens of Hall’s Francolinus afer, including 11 putative subspecies, all of which were sampled for genetic analysis. All specimens that were assessed morphologically and sampled genetically corresponded to phenotypes otherwise assessed and recognised by Hall (1963) and confirmed by TMC during the 1980s.

**Type specimens and taxonomy**

Hustler incorrectly infers that M-N+ “do not appear to have consulted the type specimens”. In fact, TMC and/or TGM-N examined all accessible type specimens. Also, contra Hustler, M-N+ had no “preconceived opinions of [francolin/spurfowl] taxonomic relationships”, but attempted to test the taxonomic hypotheses of Hall and others, and while doing so proposed changes and identified taxa that may warrant full species status and presented falsifiable evidence to support their hypotheses.

Hustler is further incorrect in citing Frankham et al. (2012) as supporting his statement that “the lowest denominator of conservation is the type specimen, the originally described specimen of the taxon”. In Frankham et al. (2012), there is no mention of, or reference to, the words type specimen. In fact, these authors focus on discussing the utility of the vast array of species concepts in conservation in general, and criticising the patterned-based phylogenetic species concept (Crowe 1987; Cracraft 1997) in particular.

Hunter+ still further suggest that M-N+’s “organismal approach seems to concentrate on a pattern-based species concept, using a pattern partitioning and score allocation system”. This is incorrect: M-N+ employed the holistic consilience species concept (Crowe et al. 1994, 2016, 2021; Mandiwa-Neudani et al. 2021) and used congruent evidence from independent morpho-behavioural characters and measures of molecular genetic divergence to delineate species and subspecies. Thus, there was no ‘pattern-partitioning’ or ‘score allocation’.

In modern evolutionary, comparative and conservation biology, the currency of taxonomy, cladistics and conservation is a viable, morpho-behaviourally and, ideally, genetically qualitatively diagnosable population or groups of populations linked to a vouchered type/holotype. Many conservation biologists (including us) use the term evolutionarily significant unit (ESU) (Mortz 1994) to describe such phylogeographic entities. Type specimens and topotypes are irreplaceable, highly valuable reference specimens necessary for historical comparative taxonomic analyses. They do not embody or represent an idealised, essentialist, typological entity that represents a character or suite of characters that unambiguously differentiates a taxon from all other individuals and populations (Zelnio 2012).

We further disagree with Hustler on the paramount importance the topotype (i.e. a specimen from the type series or another obtained at the type locality or as close as possible to it) in taxonomic, organismal, conservation and/or genetic analyses—although such material is preferable. It is acceptable, and indeed common taxonomic practice, to study and comparatively analyse vouchered specimens from throughout the geographical range of terminal taxa that exhibit characters shared with the type specimen.

**Taxonomic characters**

Hustler questions M-N+’s “confidence in their organismal matrix as a taxonomically useful set of attributes”, stating that “type specimens set this baseline, and without reference to these any comparisons are subjective”. We disagree since avian type specimens are often opportunistically collected study skins (or descriptions thereof) which may be hundreds of years old and may not exhibit or convey all the taxonomically useful character information critical to a terminal taxon’s unambiguous diagnosis.

The organismal matrix employed by M-N+ largely incorporates long-employed, homologous, morphological characters possessed by ‘types’ of all description and outlined in detail by Hall (1963: 116–117, Table 1) and confirmed and/or extended by TMC during the 1980s (Crowe and Crowe 1985; Crowe et al. 1986).

The main difference between a taxonomic character and a trait is that a trait is a feature that varies within populations (e.g. eye colour in humans) or geographically continuously (clinally) between populations (e.g. size and colouration). Characters are features that are effectively qualitatively distinct attributes that diagnostically discriminate clusters of populations into potential taxa.

Hunter+ also state that there is “no explanation with regard to why the plumage patterning was given such an emphasis in the matrix variables, thereby giving it some primacy in the two papers’ determination of species”. Taxonomists analyse characters wherever they find them. Since much of traditional avian taxonomy is based on study skins in museum cupboards, it is not surprising that many characters relate to the integument. Hall (1963) showed that she was aware of this, as follows:

- Pages 153, 155–156: “I cannot agree with and of the classifications made for this Group [Red-winged, Sclopetilia spp.] which seems to place too great a reliance on minor morphological characters...without regard to the ecology of the forms or their likely evolution.” Hence, she lumps northern forms (gutturalis, lorti, archeri) with southern forms (levallantoides and jugularis) within a single species taxon, levallantoides.
- Page 133: Despite the fact that its plumage is “quite unlike” that of close relatives, she ranked the Montane Group spurfowl (Ptternistis castaneicollis atrifrons) as a subspecies because “Benson (1945: 393) found it was similar in habits, environment and voice to other forms of F. castaneicollis”. M-N+ do not support Hall’s (1963) treatment of Sclopetilia spp. (Mandiwa-Neudani et al. 2019b: 214); instead, they recognise gutturalis as a full species linked to Francolinus shelleyi uluensis. This finding is supported by recent ecological evidence (Turner and Crowe 2022).

Regarding atrifrons, M-N+ side with Hall (1963), since Töpfer et al. (2014) confirmed Benson’s (1945) findings and found that atrifrons is only ~1.2% genetically divergent from Pternistis castaneicollis castaneicollis.

Finally, Hustler and Hunter+ repeatedly refer to characters being scored and state that “there is no explanation of the scientific basis used for the scoring characteristics and the scores allocated”. The ‘scores’ employed are not quantitative assessments; rather, the numbers are alternative character states that were never
treated in taxonomic and phylogenetic analyses in an ordered or additive fashion, since they could have been treated as ‘a, b, c,’ etc.

**Hustler’s Table 1**

Hustler mentions “multiple inconsistencies” for GenBank DNA sequences and francolin and spurfowl species listed in databases of the BNHM and AMNH. Based on re-visiting Hall (1963), re-examination of original notes, and unpublished information from TGM-N’s dissertation (Mandiwana-Neudani 2013) and early drafts thereof, we clarify and provide additional information regarding these alleged inconsistencies, point by point, in Supplementary Table S1.

In summary, we trust that our clarifications remove any deficiencies or inconsistencies vis-à-vis the identity, collection localities, and representativeness of the specimens and sequences concerned.

**‘Uncertain’ vocal characters**

With regards to vocalisation characters, like Hunter+, Hustler asserts that there is “much uncertainty” about the vocalisation research by M-N+ in general and the “morpho-vocalisation scores” in particular. Hunter+ also suggest that the research involved “subjective, rather than objective consideration, particularly because the scoring does not appear to be supported by any comparative sonograms”. On the contrary, vocalisations were neither “considered subjectively” nor scored. Instead, they were characterised qualitatively in a taxonomically/cladistically unordered fashion by examining previously published quantified sonograms of homologous advertisement calls (i.e. Mandiwana-Neudani et al. 2014). More on this concern is presented in our discussions of contentious taxa.

**Hustler’s selected taxonomic concerns: Stuhlmann’s Francolin**

Hustler is correct in asserting: “The defining phenotypic identification criterion used [to diagnose *Campocolinus stuhlmanni*] by Mandiwana-Neudani et al. (2019a) is the reduction in breast [sic actually abdominal] patterning [sic more specifically, barring], but this is not mentioned in the type description, which states that it is very similar to nominate *Pe. coqui* (Reichenow 1889).”

The relevant part of Reichenow’s original description translated is: “This new species [F. *stuhlmanni*] is very close to *F. subtorquatus* [coqui] and differs from the latter in its uniform rusty and not banded lower tail coverts; in addition, it differs in a somewhat larger size. It substitutes *F. subtorquatus* in East Africa. A specimen belonging to the latter species was collected by Dr. Böhm in Kakoma”.

M-N+ concur and expand: “Stuhlmann’s Francolin *C. stuhlmanni* resembles [nominate] *coqui* except that the extent of barring on the abdomen is much reduced, but not virtually absent as in *hubbardi*”. One other diagnostic character is that the *stuhlmanni* crown is greyish mottled with chestnut, whereas that of *coqui* is dark rufous.

M-N+ chose to apply the specific epithet *stuhlmanni* to this ‘Red-tailed’ francolin (*Campocolinus* spp.) because it had been employed by Constantine Walter ‘Con’ Benson — taxonomic doyen of East-Central African birds (cf. Benson et al. 1971, 1977) — for *coqui* specimens he collected in Malawi. Also, according to Peters (1934: 72), this terminal epithet was available for coqui-like francolins from Portuguese East Africa (Mozambique) and Nyasaland (Malawi).

As for the *stuhlmanni* material examined by M-N+, there were four specimens. All are adults that were collected in today’s Malawi by Benson during the 1930s and identified as ‘*Ortygornis coqui stuhlmanni*’; they are housed at the Ditsong Museums of South Africa:

- TM 23150: male, Ntwaro’s Village Kasitor, Mzisuba, Nyasaland
- TM 23158: male, Mzimba, Nyasaland, 1934; the cytochrome b (CYTB) sequence (GenBank FR694152) was obtained from a toe pad taken from it
- TM 23159: female, Msukuwoodland, Dowa District, Nyasaland
- TM 23160: female, 10 miles north of Emgeni, Mzimba District, Nyasaland.

All four specimens resemble nominate *coqui* adults except for the much-reduced barring on the abdomen and having greyish mottled crowns.

Hustler states that there is a Coqui Francolin specimen identified as *Pe. c. stuhlmanni*, collected by CW Benson 120 km north of the specimens examined by M-N+ in Malawi, housed in the Zimbabwe Museum of Natural History, and that has coqui-like breast barring. Hustler does not provide a fuller description of the specimen, a collection locality or a museum specimen number.

With regard to the similar taxonomic coding for the advertisement calls of *stuhlmanni* and *coqui*, because no publication covering francolins from East and Central Africa and dating back to CW Benson indicates any geographical variation in advertisement calls of coqui-like francolin subspecies, Mandiwana-Neudani et al. (2014) assumed no geographic variation was evident in phylogenetic but not in taxonomic analyses.

In short, Hustler is incorrect in suggesting that relevant specimens and information in relation to the taxa in question appear to have been “overlooked” and/or “mixed up”. There are phenotypically-*stuhlmanni* specimens housed in an African museum that were collected by a highly knowledgeable Central African avian taxonomist and then analysed and diagnosed morphologically and genetically by M-N+.

Hustler is correct when he states that “Mandiwana-Neudani et al. (2021) reported that the American Ornithological Society’s North American Classification Committee did not pass a single proposal to split species based on molecular data alone (Cicero et al. 2021)”. However, Hustler misleads when he claims that M-N+ recommend elevating *stuhlmanni* to species based on molecular data alone. Its diagnosis is based on both morphological and molecular evidence. Indeed, TMC has long taken the position that neither DNA nor morphology should be accorded dominant status in taxonomic and phylogenetic research (Crowe 1988).

Finally, the large CYTB distance of 5.5% sequence divergence between *stuhlmanni* and *coqui* is comparable in magnitude to values found between uncontested *Campocolinus* species, and up to five times that for subspecies (Mandiwana-Neudani et al. 2019a: Table 7).
Using another mitochondrial marker, cytochrome c oxidase 1 (CO1), the probability of con specificity drops to 1% above a level of 2% CO1 divergence in birds (Ward 2009). Regarding reliable CYTB divergence values based on long sequences between Hall’s Red-tailed Francolins, genera differ at >9%, species at 5–9% and conspecifics at <2%:

- Campocolinus vs Peliperdix lathamii: 9.7–10.9% 
- coqui vs schlegelli: 8.5% 
- coqui vs albogularis: 7.7–8.1% 
- coqui vs stuhlmanni: 5.7% vs maharaeo 5.9%, spinetorum 8.0%, thikae 5.5% 
- coqui vs ‘campbelli': 1.9% 
- coqui vs ‘lynesi’: 0.5% 
- coqui vs ‘angolensis’: 0.2% 
- coqui SA vs coqui Zambia: 0.4% 
- albogularis vs dewittei/meinertzhageni: 5.3% 
- dewittei vs buckleyi: 5.5% 
- albogularis vs buckleyi: 0.9% 
- buckleyi vs ‘gambagae’: 0.4%

**The utility of advertisement calls in the taxonomy of ‘Red-tailed’ (Campocolinus) francolins**

The major diagnostic difference among the strophes of *Campocolinus* spp. advertisement calls is in their duration (Mandiwana-Neudani et al. 2014). There appear to be three main types of high-pitched, harsh and tinny advertisement calls. All have an introductory element followed by a pause, and then another five to seven elements that trail away in volume and have tonal and trilling parts. The global structure of the sonograms remains similar except for differences in strophe duration, number and structure of elements, and the amplitude that is apparent in sonograms.

More specifically, the duration for *albogularis* is short (1.0 s) and consists of six tonal elements with relatively stable harmonics, with some parts of the elements trilled. That of *schlegelli* is much longer (1.89 s) and consists of seven elements, in which case the first element (E1) is more tonal and has clearly defined rising harmonics; E2 is fully trilled; and the last four elements (E3–7) start with an overslurred component followed by trilling parts. The strophe of *coqui* is 1.95 s and has eight elements, which generally have two components: the first component has stable harmonics, followed by the second component with trilling and descending harmonics.

**Campocolinus albogularis, dewittei and meinertzhageni**

M-N+ did not mix and match material from “different” subspecies, namely *dewittei* and *meinertzhageni*. They only physically and genetically examined *meinertzhageni*, which was synonymised within *dewittei* which had nomenclatural priority. Hustler implies that there are *dewittei* specimens held by the Royal Museum for Central Africa (Tervuren, Belgium). If so, TMC would have morphologically examined them during the 1980s. At that time, Crowe et al. (1986) also synonymized *dewittei* and *meinertzhageni*.

This lumping strategy was followed because Hall (1963: 162) stated that they differ only by traits, quantitatively and clinically in “patterning of females” and “darkness.” More specifically: “Birds of both sexes from south of the Congo Forest are slightly larger and more richly coloured than those from West Africa; and in the females of the south-east Congo (*dewittei*) the barring is heavier but no more extensive than in *buckleyi*. The darkest birds (*‘meinertzhageni’*) are from eastern Angola and possibly the Balovale District of Zambia.

Hustler misquotes Hall (1963) when he asserts that she “recommend[ed] that the names be kept separate for the populations in the Democratic Republic of the Congo (*dewittei*) and Zambia/Angola (*meinertzhageni*), respectively, until more specimens were available”—a recommendation he claims that M-N+ ignored.

What Hall (1963) actually wrote tentatively about these taxa was that “it seems best to use [them]”. Therefore, following criteria advocated by Hustler, M-N+ chose to recognise only one taxon, *dewittei* sensu lato, because of a lack of marked “consistent phenotypic” differentiation between the putative subspecies. Any confusion regarding the sources of data and names used in Tables 3 and 6 of Mandiwana-Neudani (2019b) is a result of misunderstanding. It is true that “the CYTB data were collected from *P. a. meinertzhageni* [=Francolinus *albogularis meinertzhageni*, BM 1957 35 13, Luvacano, Angola, 1957] as indicated in Table 3 of Mandiwana-Neudani (2019b). M-N+ neither morphologically examined nor genetically sampled *dewittei*. The morpho-vocalisation scores were not from *dewittei*; the morphological information was from *meinertzhageni*. The earlier-described taxon *dewittei* in Table 6 of Mandiwana-Neudani (2019b) reflects the decision to lump the two. With regard to vocalisation entries in that table, since there is no qualitative morphological difference between *meinertzhageni* and *dewittei* (lumped ‘dewittei’), and no reports of any differences in vocalisations, its advertisement call was coded as identical to *albogularis* for phylogenetic but not for taxonomic evaluation.

Pertaining to CYTB distance evidence, we can also understand why Hustler may be confused. The value used for M-N+’s ‘dewittei’ sensu lato in taxonomic deliberations is that for a synonymised Angolan specimen labelled *meinertzhageni*, presented in Table 7 of Mandiwana-Neudani (2019b).

Hustler suggests that M-N+ may also have “lumped species” and asks for an “explanation of how any variation in the CYTB data between these lumped taxa was dealt with”. M-N+ lumped some of Hall’s (1963) subspecies but they did not lump any of her recognised species. Variation among DNA sequences for all putative taxa examined was expressed as uncorrected pairwise genetic distances between representatives of putative species and subspecies.

Finally, M-N+ recognise *dewittei* sensu lato as a quasi-cryptic ESU species taxon, namely the Chestnut-breasted Francolin. This decision was made because of the large CYTB distance of ‘meinertzhageni’ from *albogularis* (5.3%) and *buckleyi* (5.5%), which differ from one another by only 0.9%. Furthermore, the putative *albogularis* subspecies *gambagae* which was synonymised with *buckleyi* differs from it by only 0.4% (see above under the discussion of *stuhlmanni*).
‘Red-necked’ spurfowls: Hall’s (1963) Francolinus afer complex

Following the taxonomic practice at the time, Hall (1963) recognised one species, *afer*, based on the biological species concept, because of evidence of inter-taxon admixing. Despite this, she partitioned intraspecific populations into two largely allopatric, well-marked, taxonomically unnamed, reproductively compatible assemblages, comprising 12 subspecies:

- black-and-white ‘afer-types’ (i.e. *afer, castaneiventer, notatus, lehmanni, swynnertoni, humboldtii, melanogaster, loangwae and leucoparaeus*), and
- vermiculated ‘cranchii-types’ (i.e. *cranchii, intercedens and harterti*).

The ‘cranchii-types’ are relatively continuously and contiguously distributed, and they comprise geographically variable populations ranging from southern Democratic Republic of the Congo to northern Angola and northern Zambia. They have heavily black and grey vermiculated underparts, with the lower breast feathers widely edged with chestnut (*cranchii*).

Some specimens confined to the Rusisi Valley at the north end of Lake Tanganyika (*harterti*: type from Usumbura) are much darker and have wide, blackish or reddish black, instead of chestnut, edges to the breast feathers. Specimens from elsewhere in Tanzania (*intercedens*: type locality Lake Rukwa, Tanganyika Territory) are transitional forms between *P. cranchii* and *böhmi*. They differ from *cranchii* in that the black shaft stripes on the upper breast are heavier, and those lower down are largely white and almost without vermiculations.

In specimens attributed to *böhmi* (Reichenow: type locality Igonda, Tanganyika Territory), the feathers of the breast and belly are not heavily vermiculated, and those of the forehead, chest, breast and belly have wide, black shaft stripes. The breast and belly are white, practically without vermiculation, with broad chestnut edges separated from the white by a definite black streak; this gives the breast the appearance of being made up of streaks of black, white and chestnut. In this respect it resembles the breast of *Pternistis rufopictus*.

Some specimens with slightly darker and more brownish upperparts (*nyanzae*: type from Fort Ternan, Nyando Valley, Kisumu, Kenya Colony) from the west, east and south shores of Lake Victoria Nyanza, have narrow black shaft stripes extending onto the feathers of the forehead, chest and upper breast. (This taxonomy of *nyanzae* has been discussed under matters raised in the section Hustler–Table 1, above.)

The ‘afer-types’ have no vermiculated plumage, and their faces and underparts are strongly patterned with black, white and grey. Specimens from one geographically isolated cluster of ‘afer-types’ populations in southwestern Angola (*afer sensu stricto*) have an all-white face and the underparts are broadly streaked with black and white.

The remaining ‘afer-type’ subspecies are confined to eastern and southern Africa, split into northern and southern assemblages by the Limpopo River. The more northerly forms are more contiguously distributed and have grey breast plumage with black streaking, a black abdomen, and black and white streaked flanks. Specimens from coastal Kenya (*leucoparaeus*) have a black and white eye-stripe and white faces; specimens from northern Tanzania south to southern Malawi and southeastern Zambia (*melanogaster* and *loangwae*) have black faces; birds from eastern Zimbabwe and southern Mozambique (*swynnertoni*) have white faces and a white necklace above the breast. Finally, some birds from the Malawi/Mozambique border (*humboldtii*) have faces with varying amounts of black and white. Hall (1963) considered *humboldtii* to be a taxonomically “unsatisfactory” and “unstable population”. Clancey (1967: 143) characterised *humboldtii* as “an unsatisfactory intermediate” between *swynnertoni* and *loangwae*.

South of the Limpopo River, *castaneiventer* (including *nudicollias, krebsei* and *notatus*) has black facial plumage, and the geographically variable underparts are streaked with black, white and/or maroon. Specimens from an isolated population *lehmanni* in southwestern Transvaal (now Mpumalanga Province), South Africa, are intermediate between *castaneiventer* and the black-and-white *swynnertoni* (see below): the face is black and the abdomen streaked white as in *castaneiventer*, but the breast is grey with black shaft streaks as in *swynnertoni*.

We have already addressed and clarified Hustler’s inconsistencies as outlined in his Table 1. However, beyond this, he asserts that M-N+’s “taxonomic treatment of the *Pternistis afer* subspecies, which occurs east of the rift valley into central and southern Africa and along the coast, is unproven and very incomplete”. This is because M-N+ “inexplicably lump all the forms east of the rift valley into *Pt. a. humboldtii* which was “apparently misidentified”. He further incorrectly states: To add to the confusion, the CTYB data allocated to *Pt. cranchii intercedens* were collected from a *Pt. a. swynnertoni* specimen (Table 1)’.

In fact, M-N+ were aware that the CTYB sequence they attributed to *Pt. a. humboldtii* was obtained from a topotypical *Pt. a. swynnertoni* specimen. This is acknowledged in Mandiwana-Neudani et al. (2019b: Table 3). Indeed, it was the only specimen of Hall’s (1963) north of the Limpopo ‘afer-types’ for which a tissue sample for genetic analysis was obtained. M-N+ only had access to photographs of *melanogaster* and *leucoparaeus* specimens, and no access to *loangwae*.

The subspecies epithet *humboldtii* (Peters 1854) was used to designate these northern ‘afer-types’ subspecies collectively because it has taxonomic priority over *leucoparaeus* (1884), *melanogaster* (1898), *swynnertoni* (1921) and *loangwae* (1934).

The CYTB sequence attributed to *Pt. cranchii‘intercedens’* was not collected from a *Pt. a. swynnertoni* specimen. It was obtained from a phenotypically *intercedens* specimen (AM416180 from the AMNH collection) from Tukuyu, Rungwe District, southwestern Tanzania.

M-N+ recognise two well-marked species of Red-necked Spurfowl, *afer* and *cranchii*, that largely conform to Hall’s (1963) ‘afer-types’ and ‘cranchii-types’.

In terms of genetic evidence, within Cranch’s Spurfowl, *cranchii*, the ‘nyanzae’ specimen has an identical CYTB DNA sequence, and the darker populations from the Ruzizi Valley, north of Lake Tanganyika (*harterti*) and the white-bellied ‘intercedens’ are, respectively, only 0.6% and 0.8% CYTB divergent from *cranchii*. Hence, no subspecies are warranted.
In terms of genetic distance: *swynnertoni* (representing *humboldtii* sensu lato) is 2.6% from *cranchii*, 3.5% from *afer*, and 3.6% from *castaneiventer*. *Pt. cranchii* is 1.6% from *afer*, and 3.6% from *castaneiventer*. Subject to examining a range of representative specimens and obtaining sequences for *humboldtii*, *melanogaster*, *loangwae* and *leucoparaeus*, if their morphology is uniform across their range and if the respective genetic distances from *afer*, *cranchii* and *castaneiventer* are found to be ≥3.0%, we argue that there are at least four species of Red-necked Spurfowl: *cranchii*, *afer*, *castaneiventer* sensu lato, and *humboldtii* sensu lato. However, given the information currently available, M-N+ recognise three well-marked ESU subspecies within their *afer* sensu lato: the isolated and well-marked Angolan *afer* sensu stricto, southern African *castaneiventer*, and *humboldtii* sensu lato from central and eastern Africa north of the Limpopo River. Although it is variably divergent (1.6–3.5%) from forms of *cranchii*, Angolan *afer* is 2.8% CYTB divergent from *castaneiventer* and 3.5% divergent from *humboldtii*; *Pt. a. castaneiventer* is 3.6% divergent from both *cranchii* and *humboldtii*.

**'Hybridisation'**

There are two zones of admixture between the qualitatively morphologically and markedly genetically distinct *cranchii* and *afer*. The eastern one stretches from Kondoa Dodoma in central Tanzania through central Malawi into the Luangwa Valley; the other traverses northern and central Angola. Admixed birds from Tanzania and Malawi have well-defined streaks on the abdomen, with variable amounts of chestnut and black and white. Those from Angola have less regular and defined streaking. All 'hybrids' are characterised by morphologically less well-structured intermediate populations (Hall 1963) and hence do not warrant taxonomic recognition.

In terms of genetic distance, all admixed birds, eastern 'litigi' and 'böhmi' and western 'benguellensis' and 'cunenensis', are genetically very close (0.4–0.9% divergent) to *cranchii*. To put these distance values into perspective, the distance between the generally accepted 'Hall Bare-throated' species, the Grey-breasted Spurfowl *P. rufopictus*, is 1.7–2.2% from *cranchii*/admixed forms, and 2.3–3.2% from *afer* sensu lato:

- *cranchii* vs conspecifics: 0%, 0.6%, 0.8%
- *cranchii* vs 'hybrids': 0.8%, 0.5%, 0.8%, 0.4%, 0.5%
- *cranchii* vs *afer*: 1.6%
- *cranchii* vs *swynnertoni*: 2.6%
- *cranchii* vs *castaneiventer*: 3.6%
- *cranchii* vs *rufopictus*: 1.8%

To summarise, Hall’s (1963) ‘*Franolinus afer*’ is a complex of ESUs comprising two species that have diverged in isolation and reconnected episodically. During periods of reconnection with one another, and possibly even with *P. rufopictus*, there may have been significant genetic admixture of the sort found in multispecies syngeneons (Buck and Flores-Renteria 2022)—groupings of genetically related taxa that frequently engage in natural ‘hybridisation’ caused by a lack of strong reproductive barriers to interbreeding. This genetic exchange between ESUs may not be realistically represented in a bifurcating cladogram.

Nearly 60 years ago, Hall (1963: 129) concurred that “the diverse characters of the *afer* subspecies point to a lengthy period in which the two blocks of vermiculated *cranchii* and black-and-white *afer* subspecies were isolated from each other”. “Similarly, the variation between many of the black-and-white populations *leucoparaeus*, *melanogaster*, *swynnertoni* points to periods in which they have been isolated.”

The unexamined *loangwae* differs from *cranchii* in having a black abdomen with white streaking rather than with chestnut-brown streaks. Dowsett-Lemaire and Dowsett (2006) and Dowsett et al. (2008) treat its taxonomy ‘nationally’. In *Birds of Zambia*, *loangwae* is accorded full ‘racial’ status, replacing *cranchii* in eastern Zambia and admixing with it at Mafingas in the northeast. In *The Birds of Malawi*, it is “sometimes known” as *Franolinus afer humbletii* which “hybridises in the Lower Shire valley with *F. a. swynnertoni*, and with *F. a. melanogaster* around [Lake] Chilwa”.

**Errors in distribution maps**

From the onset of their research in the 1980s, M-N+ chose to rely on maps from *An Atlas of Speciation in African Non-Passerine Birds* (Snow 1978) as a fair representation of taxon geographical ranges. This was because it presented the most comprehensive and comparative distribution range maps of taxa generated by the point localities of collected, identified and vouched specimens. Subsequently, they used *The Atlas of Southern African Birds* (Harrison et al. 1997) to fill in some of distributional gaps for southern African taxa. Still, when deemed necessary for biogeographical purposes, M-N+ used Hall’s (1963) inferred distributions, based on proximate specimen collecting localities, and her interpretation of the distribution of vegetation types, total rainfall isohyets and inferred long-term climate change, to ‘complete’ the ranges of species and subspecies recognised in order to consider possible past dispersal and vicariance events.

Unlike Hunter+, we do not regard Hall’s (1963) and Snow’s (1978) maps as archaic. They are based on vouched, physically examinable specimens, and the maps were prepared by experienced, museum-based avian taxonomists. Distributional information from atlases is provided largely by birders and is normally vetted by citizen scientists and not experienced practising taxonomists. Nevertheless, atlas data are potentially valuable in filling gaps from poorly collected areas.

Subsequent to the publication of M-N+, in response to comments from experienced field ornithologist Don Turner (one of the authors of Hunter+), Crowe et al. (2019) clarified taxonomic, distributional and genetic information relating to subspecies of Hildebrandt’s Spurfowl *Pternistis hildebrandti* and the Yellow-necked Spurfowl *P. leucoscepus*. Later, in direct response to Hunter+, Mandiwana-Neudani et al. (2021) confirmed that the latest distribution maps in Little (2021) incorporate information from citizen science atlas projects. Even so, Hustler still asserts that “rather than clarifying the situation, these maps and associated taxonomic information add to the confusion and there are additional distribution errors and the lack of attention to detail remains. It is disappointing that these important maps are presented in a coffee-table
book and not in the major, peer-reviewed contributions to francolin taxonomy, which should contain all of the latest information in one place. This perpetuates the torturous trail that has plagued the African avian taxonomy literature and should have been avoided”.

Given this allegation, we urge Hustler, Hunter+ and interested and affected citizen scientists/atlas participants to collaborate to produce improved maps, perhaps using the Cornell Lab of Ornithology *Birds of the World* as base maps. In the meantime, we feel that the current M-N+ maps convey useful information for further taxonomic, phylogenetic and biogeographical research as well as for conservation planning, complemented by atlas information for fine-scale action. For example, the M-N+ map for *Pternistis afer/crantchi* (Figure 7) is remarkably similar to that for the same forms in *Birds of the World* (McGowan and Kirwan 2020), which presumably incorporates more up-to-date information in sources alluded to by Hustler and Hunter+, but depicts much more useful information, such as ESUs and zones of admixture.

**Conclusions**

We agree with Hustler and Hunter+ that the recommendations in M-N+ are by no means exhaustively proven. However, based on the specimen, character and molecular evidence, and analyses thereof in M-N+, which is reiterated, clarified and presented here within a clear conceptual context, we maintain that the data and methods employed by and the conclusions of M-N+ are valid and that their findings are a significant advance on Hall (1963). The concerns, criticisms and inconsistencies of Hustler and Hunter+ are largely a result of their varied continued support for Hall’s (1963) long-outdated taxonomy, misunderstandings or overstatement. Therefore, their conclusion that M-N+ is not a “significant contribution” to taxonomy is unwarranted.

**A way forward**

Hustler calls for taking a “clean slate” approach which requires “sequencing all [>100] currently recognised francolin and spurfowl subspecies accurately and accountably”. Even given the current, somewhat more lenient, limitations set by museums on destructive sampling and the improved and less-expensive costs of sequencing, such as multi-sampling strategy is implausible. Even if this approach were possible, setting reproductive isolation (the primary criterion of the biological species concept) as the sole or primary standard for justifying species rank would necessitate continued recognition of about 100 traditional subspecies and ‘races’ poorly suited for meaningful taxonomic and/or evolutionary research (Wilson and Brown 1953), let alone for effective conservation action (Crowe and Bloomer 2017).

Inter-terminal hybridisation/admixture in nature is not uncommon among francolins and spurfowls. Using Hall’s Red-necked ‘Francolin’ *Pternistis afer* sensu lato as an example, in Zimbabwe, Cooper’s Spurfowl *Pternistis cooperi* (Roberts 1947) “occur[s] with some frequency from the Mashonaland Plateau at Rusape, Headlands and from near Salisbury [now Harare]” (Irwin 1981). It is a natural ‘hybrid’ between *P. afer swynnertoni* and *P. swainsonii*, probably due to range expansion by *swainsonii* into ‘afer’ habitat that had been transformed by agriculture (Little and Crowe 2011). “All the hybrids are very similar and combine the characters of the parent species” (Irwin 1981).

Given that *swainsonii* and *swynnertoni* are 4.9% CYTB divergent, it is likely that there may be admixture and outright hybridisation between other forms of galliform (Ottenburghs 2019) spurfowls and francolins. So far, this has been reported (www.bird-hybrids.com):

- within *Pternistis: afer/leucoccephus, rufopictus/leucocephus, castaneicollis/erckelli, erckelli/bicalcaratus, hildebrandti/natalensis, clappertoni/icterorhynchus* and *natalensis/swainsonii*
- within *Campocolinus: albogularis/coqui*
- within *Francolinus: francolinus/pictus*
- within *Scleropitila: levallantii/psilolaema and levallantoides/shelleyi*
- within *Ortygornis: sephaena/rovuma*
- between francoins and spurfowls: *Ortygornis sephaenai* *Pternistis swainsonii.*

This is one reason why M-N+ employed the consilience species concept.

From a molecular genetic perspective, a more-realistic strategy is embodied in an ongoing project by one of us (RCKB). He and his team are employing a DNA probe-capture-set that allows genomic investigation of ~10 million nuclear and mitochondrial DNA base pairs from a broad range of phasianoids. This powerful genomic tool used within the context of a more modern, holistic and integrative species concept should allow him and his students/collaborators to generate the desired “more accountable data” and then to produce the robust terminal taxa required by Hustler and Hunter+. One potential project this might consider could involve investigation along a ‘transect’ beginning with central African *cranchii* and moving northeast through *rufopictus* into *leucocephus.*

From an organismal perspective, there is also a need to sample/collect specimens and obtain genetic samples, such as for *Campocolinus stuhlmanni, C. dewittei, meinertzhageni,* and a range of *Pternistis afer* subspecies and synonymised forms from southern *castaneiventer* and ‘*melanogaster’, *loangwae* and *leucoparaeus*’ north of the Limpopo, to better determine patterns of morphological and genetic variation.

Citizen scientists could also play key roles in projects led by scientists discovering intraspecific and interspecific variation in vocalisations (Hunter et al. 2019; van Niekerk et al. 2021) and in ecology (Turner and Crowe 2022).

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