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Geographic variation in size and coloration in the *Turdus poliocephalus* complex: A first review of species limits

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ABSTRACT Among the most dramatically variable of bird species under the traditional polytypic 'biological' species concept is *Turdus poliocephalus* Latham 1801, which is distributed across parts of Southeast Asia and Oceania. This variation, nonetheless, has never seen comprehensive review, and particularly not in view of modern species concepts. In this study, I examined plumage coloration patterns and morphometric variables in series of specimens representing 49 of 52 described subspecies and 64 of 72 allopatric populations, and document patterns of geographic variation in plumage coloration and sexual dimorphism. Overall patterns of variation indicate 12 distinct plumage types, with 31 geographically contiguous populations that present one of the 12 plumage types. Finally, taking into account differences between populations within these contiguous sets of populations, 38 diagnosable units can be discerned. Recognition of these subunits as species is warranted: the biological species concept might recognize the 31 geographically contiguous plumage-type units, whereas the evolutionary and phylogenetic species concepts might best recognize all 38 of the distinct population units.

KEY WORDS: *Turdus poliocephalus*; geographic variation; species limits; differentiation of populations.

INTRODUCTION

Several species of birds represent traditional test cases for the study of geographic variation and decisions regarding species concepts. These 'species,' which have invariably turned out to be complexes of species, have seen detailed monographic study, illuminating patterns of variation, numbers of species taxa involved, and evolutionary processes. Examples include the landmark monographs of the genus *Aphelocoma* Cabanis 1851 (Pitelka 1951), the *Pachycephala pectoralis* (Latham 1802) complex (Galbraith 1956), and *Empidonax difficilis* Baird 1858 (Johnson 1980).

Nevertheless, one of the most complex and variable of all currently recognized bird species has yet to see monographic treatment. *Turdus poliocephalus* Latham 1801 represents a complex of >50 described subspecies occurring from Indonesia east across much of the southwestern Pacific. Indeed, the known distribution of this complex includes >70 allopatric populations, isolated either on different islands or on high mountaintops on larger islands. The complex has long been cited (Mayr 1942) as showing some of the most bizarre geographic variation in plumage coloration in the world of bird species—all black, black with a white head, all reddish brown, etc. Still, *T. poliocephalus* has yet to see a range-wide taxonomic assessment, and much of its distribution has seen no systematic attention since the original subspecies descriptions.

The purpose of this monograph is to provide the first steps toward such a base-level review of the *Turdus poliocephalus* complex. A range-wide survey of variation within and among populations in plumage and morphometric characters is provided, with the goal of understanding

overall patterns. This assessment, in a modern sense, must be considered preliminary, as no molecular analyses are yet available to complement the picture of phenotypic patterns of variation (although two partial analyses are in press). Nevertheless, as a first step, this study is intended to identify the basic units of variation within the complex, and make recommendations regarding a first pass of creating a more representative taxonomic arrangement in this clade, recognizing more than 30 species from what is presently considered a single species.

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MATERIALS AND METHODS

DATA

A first challenge was to distill the bewildering taxonomy of this complex (Appendix 1) into a workable system of operational units for analysis. Given the wild variation in the group, each allopatric population was, at least initially, considered separately. Hence, the 52 described subspecies were examined—using the ‘Peters’ check-list (Ripley 1964) as a starting point, along with subspecies described subsequently—*T. p. tolokiwae* (Diamond 1989) and *T. p. beehleri* (Ripley 1977). The existing subspecies were further subdivided into 72 operational units for analysis, with as many as 5 allopatric populations making up single subspecies, as in *T. p. vanikorensis*. For convenience and efficiency of reference, these operational units are referred to by 3-character codes—the first two (letters) indicating the subspecies, and the third (a number) indicating the particular allopatric component population (Appendix 1). To permit mapping of patterns of distribution and variation, geographic coordinates were assigned that represented the approximate geographic centroid of the population’s geographic distribution.

Working with such an extremely diverse assemblage continually emphasizes the slim sampling upon which avian systematics is based. To obtain sufficient samples for at least some quantitative analysis, it was necessary to examine specimens from 13 major natural history museums, including the American Museum of Natural History (New York, U.S.A.) (AMNH), U.S. National Museum of Natural History (Washington, D.C., U.S.A.) (USNM), Natural History Museum (London, U.K.) (BMNH), Field Museum of Natural History (Chicago, U.S.A.) (FMNH), Academy of Natural Sciences (Philadelphia, U.S.A.) (ANSP), Museum of Comparative Zoology (Cambridge, U.S.A.) (MCZ), Museum of Vertebrate Zoology (Berkeley, U.S.A.) (MVZ), Yale Peabody Museum (New Haven, U.S.A.) (YPM), Royal Ontario Museum (Toronto, Canada) (ROM), University of Kansas Natural History Museum (Lawrence, U.S.A.) (KUNHM), Museum Mensch und Natur (Munich, Germany) (ZSM), California Academy of Sciences (San Francisco, U.S.A.) (CAS), and the Russian Academy of Sciences (St. Petersburg, Russia) (ZISP). Only through inspection of all of these collections was it possible to assemble anything approaching adequate specimen representation of the complex possible; even so, some important gaps remained in the sample of specimens inspected. Digital photos kindly provided by curators of two collections that were not possible to visit

(Queensland Museum, Brisbane, Australia; Nationaal Natuurhistorisch Museum, Leiden, Netherlands) allowed some assessment of the relations of key populations.

On each specimen examined, the following measurements were made: bill length (from anterior edge of nostril to tip), wing length (chord, preserving the curvature of the primaries), tail length, and tarsus length (length of tarsometatarsus, to the lowest undivided scute on the tarsus). Colors (general only, no standards used, no lighting control) were noted for the following body regions: crown, back, throat and bib, flanks, midbelly, and undertail coverts. Bill width and depth were also measured initially, but were found to be little repeatable in general, and not measurable on many specimens, and hence were eliminated from further consideration.

ANALYSES

Specimen data were analyzed using a variety of approaches. Sexual dimorphism in morphometric characters was tested in the 9 populations for which >10 specimens were examined for each sex (note that not all measurements could be taken from all specimens, so actual sample sizes were somewhat lower than numbers of specimens examined). Two-tailed *t*-tests assuming uneven variances were used to test for significance of differences between the sexes.

Sexual dimorphism in plumage coloration was evaluated based on color notations for each of the body regions listed above. If male and female descriptions were equivalent for all of the regions, that population was scored as not showing dimorphism. If sexual differences were subtle (e.g., ‘black’ versus ‘black edged brown’), the population was scored as showing weak dimorphism. If differences were marked in one or more body regions, the population was scored as strongly dimorphic.

Differences among populations in morphometric characters were tested only for males, given greater sample sizes for males than females. Population differences were tested using only those populations and characters for which measurements of >4 individuals were available. Various statistical tests were used to test for significance of differences among populations.

Geographic phenomena were mapped based on island central points for populations on small islands, or approximate centroids of mountain ranges for populations on large islands. All geographic manipulations and analyses were developed in ArcView, version 3.2.

RESULTS

In all, 750 specimens of *Turdus poliocephalus* that were (1) apparently adult, and (2) with an identifiable locality (i.e., not just a subspecific identification) were examined. Of these specimens, 296 were females, 425 were males, and 29 were unsexed. Specimens of 49 of 52 subspecies—all except *T. p. biesenbachi* of Mt. Papandajan, Java; *T. p. canescens* of Goodenough Island, D'Entrecasteaux Archipelago; and *T. p. stresemanni*, Mount Lawoe, Java—were inspected personally, representing 64 of 72 allopatric populations—all except the three subspecies listed above, plus *T. p. efatensis* from Nguna Island, *T. p. malekulae* from Pentecost Island, *T. p. niveiceps* from Botel Tobago, and *T. p. vanikorensis* from Santa Cruz and Vanikoro islands—that make up the complex. For 42 allopatric populations, >5 males were inspected and measured.

VARIATION WITHIN POPULATIONS

Differences in coloration between the sexes were variable, with some populations having sexes identical, and others showing marked sexual dimorphism (Appendix 2; Figure 1). Most populations for which data were available showed no apparent plumage dimorphism (26 populations) or subtle differences (20 populations); 2 populations, however, showed strong dimorphism: *T. p. niveiceps* of Taiwan (NV2), and *T. p. carbonarius* of central Papua New Guinea (CR1). Such a mosaic distribution of dimorphic and non-dimorphic forms is suggestive of multiple independent evolutionary derivations of dimorphism or non-dimorphism in this complex (Peterson 1996).

Sexual dimorphism was clear in all 3 measurements that were components of overall body size (wing length, tail length, tarsus length; Table 1) in the 9 populations for which tests were possible. Indeed, males were significantly or near-significantly larger than females in 8 of 9 populations in wing and tail measurements, and in 5 of 9 populations in tarsus length. Curiously, females had longer bills than males on average in all 9 populations (significantly so in TH1).

VARIATION AMONG ALLOPATRIC POPULATIONS WITHIN SUBSPECIES

An important question was that of whether the existing described subspecies constitute homogeneous units, or whether they include heterogeneous sets of populations. In coloration characters, no clear or qualitative differences among allopatric populations within single subspecies were found in any of the 6 body regions examined (Table 1). This result placed a first level of confidence on the presently-defined limits among subspecies—indeed, I saw no reason for doubting the correctness of the synonyms listed in Ripley (1964)—*Turdus poliocephalus laro-chensis* as a synonym of *T. p. marensis*, and *T. p. bicolor* as a

synonym of *T. p. ruficeps*; I did not have access to the type material of *T. p. hoogerwerfi*, which Ripley synonymized with *T. p. loeseri*.

In morphometric characters, however, the situation was different, with significant statistical differences among several suites of consubspecific populations (Table 2). Sample sizes were sufficient for tests for 5 currently recognized subspecies that occurred on multiple islands or mountaintops; of these subspecies, 2 showed no significant differences among disjunct populations in any of the characters analyzed (*T. p. becki*, *T. p. samoensis*). The remaining three subspecies, however, held disjunct populations significantly different from one another in at least one of the morphometric characters examined. For *T. p. malekulae*, comparisons of bill length, wing length, and tail length indicated significant differences ($P < 0.05$) between MA1 and MA2; comparisons of tarsus length indicated no significant differences ($P > 0.05$). For *T. p. vanikorensis*, of the 4 morphometric characters, only bill length showed significant differences ($P < 0.05$) among VA1, VA2, and VA3. Finally, for *T. p. layardi*, the only morphometric character for which a test was possible (bill length) showed significant differences between LA1 and LA3 ($P < 0.01$).

ODD DISTRIBUTIONAL SITUATIONS

Looking at the basic distribution of populations and subspecies limits across the range of the species (Figure 2), several oddities stand out, and beg detailed analysis. For example, *T. p. pritzbueri* is distributed on Lifu Island (PR1) and Tanna Island (PR2). PR1, however, is located much closer to Mare Island, where *T. p. marensis* (MR1) occurs, and PR2 much closer to Erromanga Island and Futuna Island, where *T. p. albifrons* populations AL1 and AL2 occur, respectively. Here, whereas sample sizes were insufficient for morphometric comparisons for several of the populations, a clear answer is available based on plumage—*T. p. albifrons* and *T. p. pritzbueri* are black with white heads, whereas MR is all over dusky blackish brown. Hence, rather than one or the other of the PR populations being the oddity, upon closer inspection, the oddity is MR1, which is an all-over blackish population located between a suite of white-and-black populations (AL and PR) and the unique red-olive population *T. p. xanthopus* of New Caledonia.

A second distributional oddity is the population (MY2) on Sibuyan Island in the central Philippines. Quite intriguing is that, whereas *T. poliocephalus* has not been found on any of the other islands of the central Philippines (e.g., Tablas, Romblon, Masbate), two specimens have recently been collected from a previously unknown

Table 1. Summary of tests for sexual dimorphism in four morphometric measurements in *Turdus poliocephalus* populations for which >10 specimens were examined for each sex. *P*-values are based on two-tailed t-tests assuming unequal variances. Statistical significance is shown as * indicates $P < 0.05$, + indicates $0.1 < P < 0.05$, and – indicates $P > 0.1$. Note that significances in wing chord, tail length, and tarsus length involve males being larger than females, but the single significant comparison for bill length is for females being larger than males.

Population	Bill length			Wing chord			Tail length			Tarsus length		
	Female (f)	Male (m)	P	Female (f)	Male (m)	P	Female (f)	Male (m)	P	Female (f)	Male (m)	P
ER1	14.9±0.5	14.6±0.6	–	105.8±3.8	110.2±4.4	*	77.7±3.3	82.2±6.3	–	30.7±0.9	31.8±0.6	*
FU1	13.2±0.5	12.8±0.5	–	115.9±5.5	122.0±4.0	*	91.1±2.8	94.1±2.2	*	31.8±1.3	32.9±0.5	*
KE1	13.6±0.8	13.1±0.4	–	113.9±2.3	119.7±6.9	+	86.9±4.4	93.2±4.9	*	32.2±1.0	33.2±1.1	+
MI1	13.6±0.6	13.4±0.4	–	106.8±4.2	110.1±3.2	+	80.4±1.6	84.0±2.5	*	30.0±1.0	31.1±3.1	–
ML1	13.9±0.9	13.7±0.5	–	120.5±3.7	124.8±3.8	*	89.9±5.1	96.4±5.3	*	34.0±1.6	34.3±0.7	–
NI1	14.4±0.4	14.0±0.6	–	119.4±3.5	122.0±3.4	+	89.9±3.1	93.5±3.4	*	32.4±1.3	33.4±1.2	*
SE1	14.3±0.8	14.0±0.5	–	126.0±3.4	131.4±3.2	*	100.7±3.3	104.0±3.1	*	34.6±1.0	34.7±1.3	–
TH1	14.8±0.8	13.9±1.1	*	118.4±3.9	122.7±3.3	*	89.8±4.0	92.6±3.0	+	32.4±1.0	33.2±1.5	+
VA1	13.2±0.7	13.0±0.5	–	102.7±2.1	104.6±4.8	–	67.0±2.0	69.5±3.4	+	31.3±1.6	32.3±1.3	–

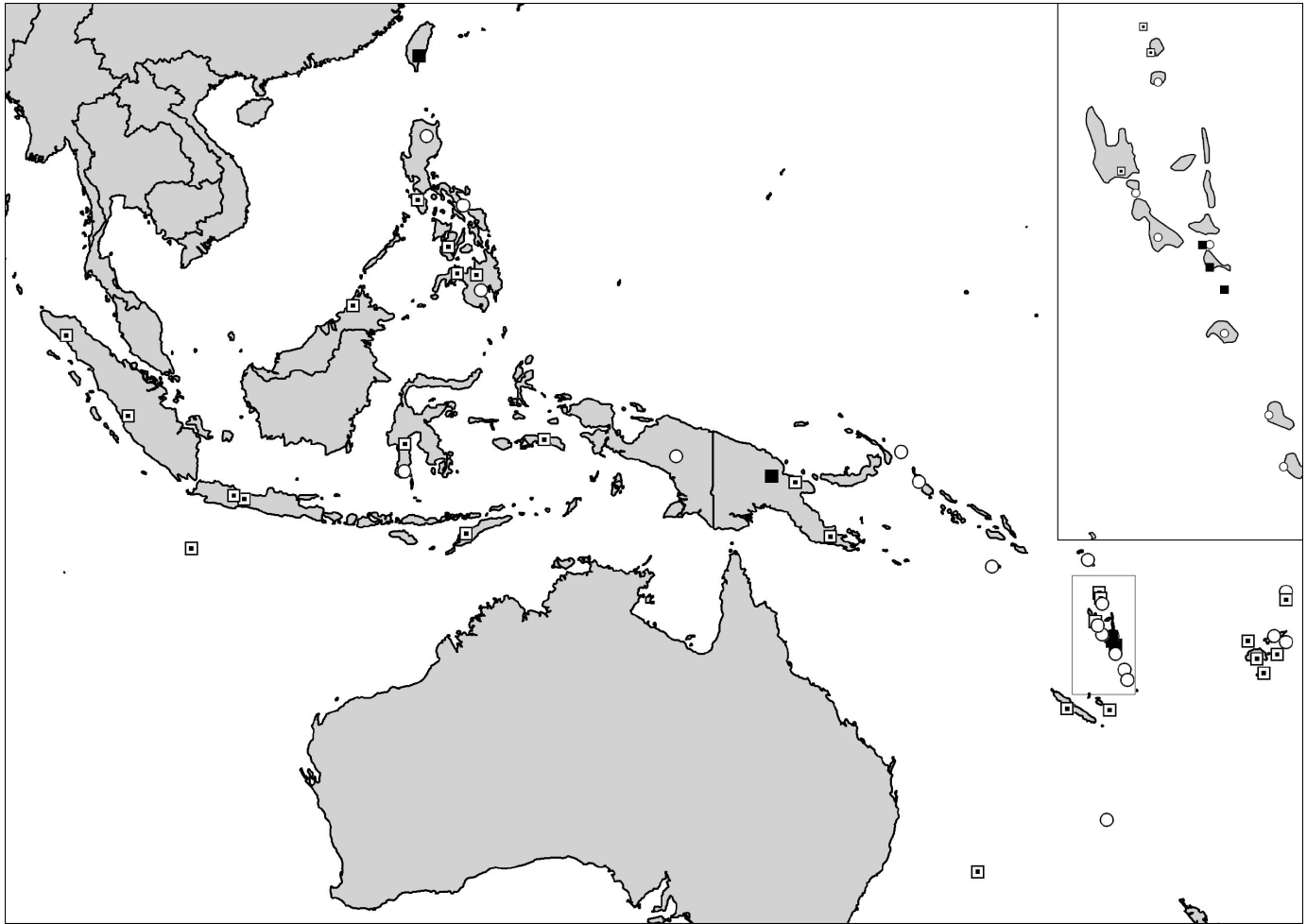


Fig. 1. Map summarizing geographic patterns in sexual dimorphism in plumage coloration among populations of *Turdus poliocephalus*. White circles = no dimorphism, dotted squares = subtle sexual differences, and black squares = strong sexual differences.

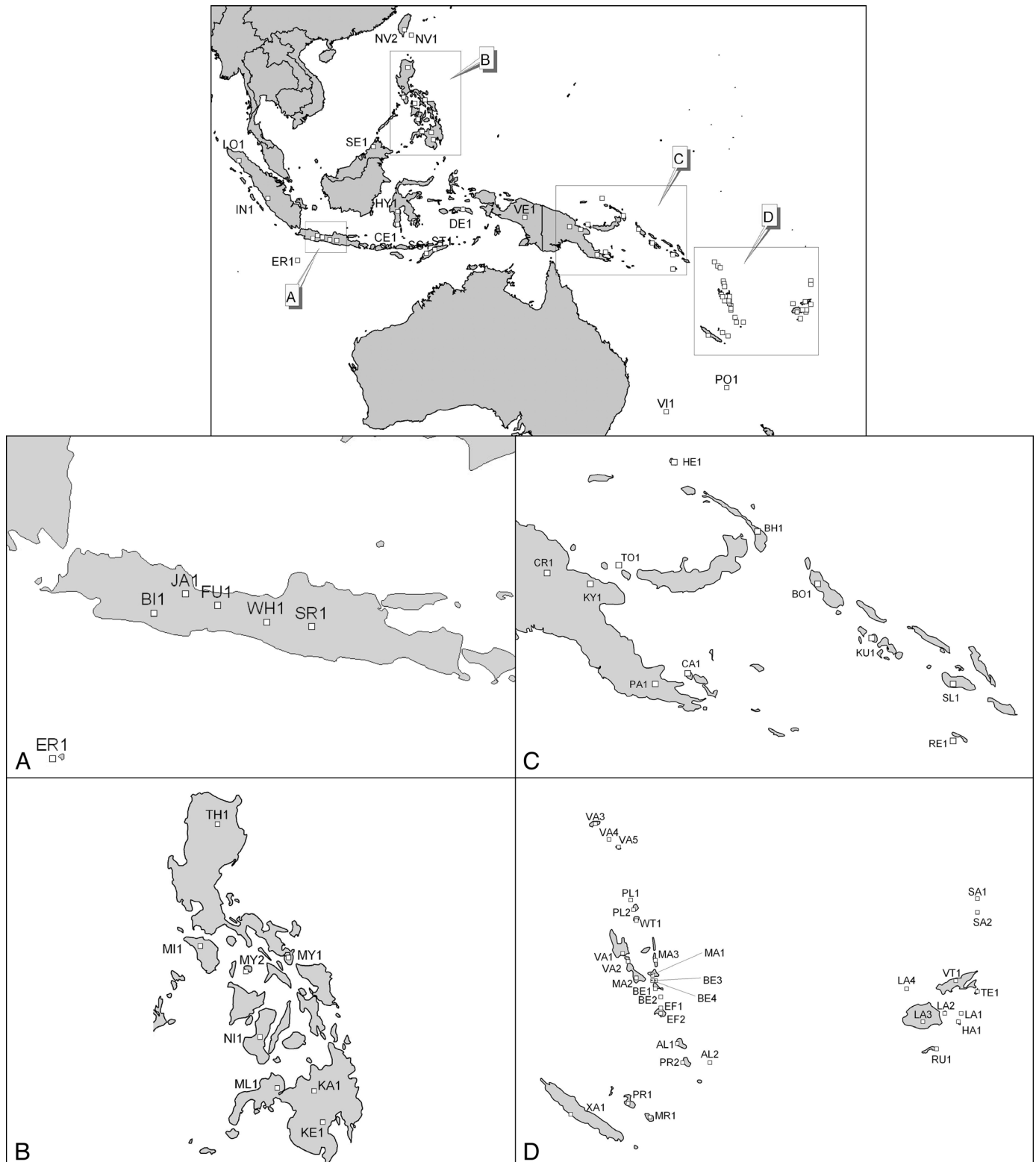


Fig. 2. Map summarizing the geographic distribution of allopatric populations of subspecies of *Turdus poliocephalus*.

Table 2. Summary of tests for differences among populations within presently recognized subspecies of *Turdus poliocephalus*. Statistical comparisons are based on Mann-Whitney *U*-tests when pairs of populations are compared, and a *z* value (standard normal variate) is reported; *H* statistics are provided where >2 populations were available, based on a Kruskal-Wallis Test.

Population	Bill length			Wing length			Tail length			Tarsus length		
	Average (range)	Test statistics	<i>P</i>	Average (range)	Test statistics	<i>P</i>	Average (range)	Test statistics	<i>P</i>	Average (range)	Test statistics	<i>P</i>
BE1	-			105 (102-107)			68 (65-75)			32.4 (31.7-33.2)		
BE2	13.1 (12.1-14.6)	<i>z</i> =-0.53	-	104 (99-106)	<i>H</i> =4.54, df=2	-	67 (62-71)	<i>H</i> =2.72, df=2	-	32.2 (31.3-33.0)	<i>H</i> =0.91, df=2	-
BE3	12.6 (12.2-13.0)			100 (96-102)			64 (62-67)			32.5 (32.1-33.2)		
LA1	33.2 (32.0-33.9)	<i>z</i> =-2.72	<0.01	-			-			-		
LA3	36.7 (35.9-37.7)			-			-			-		
MA1	12.9 (12.7-13.2)	<i>z</i> =-2.53	<0.05	101 (99-103)	<i>z</i> =-2.50	<0.05	66 (64-70)	<i>z</i> =-2.03	<0.05	32.4 (32.0-33.0)	<i>z</i> =-1.47	-
MA2	13.9 (13.2-14.5)			107 (105-110)			71 (66-74)			32.0 (31.4-32.7)		
SA1	13.6 (13.2-14.1)	<i>z</i> =-1.36	-	108 (107-111)	<i>z</i> =-1.08	-	71 (67-75)	<i>z</i> =0.37	-	34.2 (33.0-35.7)	<i>z</i> =-1.78	<0.10
SA2	14.0 (13.5-14.6)			107 (104-109)			70 (67-74)			33.2 (32.6-34.4)		
VA1	13.0 (12.2-14.0)	<i>H</i> =8.47, df=2	<0.05	106 (101-110)	<i>H</i> =0.25, df=2	-	70 (66-77)	<i>H</i> =0.02, df=2	-	32.3 (30.2-35.5)	<i>H</i> =3.98, df=2	-
VA2	13.8 (13.1-14.3)			107 (102-117)			70 (66-74)			31.3 (30.7-32.2)		
VA3	12.9 (12.1-13.6)			107 (104-115)			69 (66-72)			31.9 (30.9-32.7)		

population in the highlands of Sibuyan Island (FMNH 358378-9) (Goodman et al. 1995). This island is surrounded by islands inhabited by three very distinct subspecies: the blackish *T. p. mayonensis* of Luzon (MY1), the gray *T. p. nigrorum* of Negros (NI1), and the striking red-and-white *T. p. mindorensis* of Mindoro (MI1). On the basis of plumage, the Sibuyan specimens are clearly allied with the Luzon populations (MY1), being overall blackish in coloration and not easily separable from Luzon series. In morphometric characters, measurements of the two Sibuyan specimens fell within the observed range in a bigger sample ($N = 13$) of MY1, indicating that no significant differentiation is likely to exist. The lack of differentiation of this population, although on a different 'Pleistocene island' (Heaney et al. 2005) from the remainder of *T. p. mayonensis* populations, is intriguing.

Third, the distributions of the populations of *T. p. vanikorensis* show odd spatial relations with populations of *T. p. placens* and *T. p. whitneyi*. Three populations of *T. p. vanikorensis* are located north of the latter populations, whereas two populations are to the south. All five *T. p. vanikorensis* populations show the same general plumage

characteristics—blackish olive back and blackish brown belly—and all 5 lack sexual plumage dimorphism. Hence, the questions are (1) whether meaningful variation exists among islands in this region, and (2) whether the two disjunct sets of *T. p. vanikorensis* populations show any integrity with respect to the other two subspecies.

In terms of plumage coloration, no differences were apparent either between the northern and southern *T. p. vanikorensis* populations, or between *T. p. vanikorensis* and *T. p. whitneyi*—for each body region, the most common color description in notes was coincident among these three groups of populations. *Turdus p. placens* differs in having a rustier and grayer bib, flank, and belly than other populations, but these differences are not particularly striking. In terms of morphometric characters, no significant differences were detected between northern and southern *T. p. vanikorensis*, or between *T. p. vanikorensis* and the combination of *T. p. placens* and *T. p. whitneyi* ($P \gg 0.05$). Hence, no morphometric differences were apparent among any of the various populations in this region.

Finally, several interesting gaps are present in the known distribution of the species complex. For example, no specimens yet document its presence on Palawan, in spite of populations in the Philippines and in Borneo, to the north and the south of the island in question. Similarly, *T. poliocephalus* is not known to occur on New Britain, in spite of being known from Papua New Guinea, New Ireland, and Bougainville Island. Finally, the two specimens recently obtained from Sibuyan Island suggest that the species could be present on a number of other small-to-medium islands in the region. Indeed, a recent specimen record places the species on Panay (Kennedy et al. 2000), from where it was not previously known. Elsewhere, just in the Philippines, intriguing possibilities include Leyte, Camiguin Sur, Basilan, and the Sulu Islands.

LOCAL COMPLEXES OF DIFFERENTIATED FORMS

The *T. poliocephalus* complex presents several clusters of populations that are strikingly differentiated from one island or group of islands to the next. The Philippines holds an impressively diverse suite of *T. poliocephalus* populations, with at least six distinguishable subunits. Negros, Luzon, and Mindoro each hold distinctive populations of the species; Mindanao holds a remarkable three differentiated populations, one on the Zamboanga Peninsula (*T. p. malindangensis*), one in the mountains of northern Mindanao (*T. p. katanglad*), and one in the mountains in southern Mindanao (*T. p. kelleri*). This within-island differentiation of species is not unprecedented in the Philippines (Kennedy et al. 1997), but is nevertheless impressive. No significant morphometric differentiation was observed between the two subspecies on Luzon (*T. p. mayonensis* and *T. p. thomassoni*, $P \gg 0.05$), although subtle plumage differences exist. Interestingly, *T. p. mayonensis* is the only Philippine subspecies to be found on more than a single island (see discussion of Sibuyan Island populations above), and its presence on Sibuyan Island—a distinct Pleistocene island—is particularly intriguing given the degree to which *Pleistocene* patterns of connection and isolation have served to structure genetic variation and species' distributions in the archipelago (Peterson and Heaney 1993, Peterson et al. 2000, Heaney 2001, Heaney et al. 2002, Heaney et al. 2005). Regardless, though, the situation of *T. poliocephalus* in the Philippines is extremely complex, with at least six clearly diagnosable forms represented.

A second complex is that of the populations of Fiji and Samoa. Here, six subspecies have been described, and each is diagnosable from all others and particularly from adjacent populations. Northernmost in this group are the populations of Samoa (*T. p. samoensis*), which are all-over black; then, among Fijian populations (roughly in north-to-south order, *T. p. vitiensis* is all-over dark gray; *T.*

p. tempesti is black with a white head; *T. p. layardi* is olive, brick, and white; *T. p. hades* is all-over blackish; and *T. p. ruficeps* is black with a red head. The two populations of offering greatest possibilities of confusion in terms of coloration (*T. p. samoensis* and *T. p. hades*) are separated by three clearly differentiable intervening populations.

Finally, worthy of mention are the many populations of the Banks, New Hebrides, and Loyalty archipelagoes. Here, the populations are all-black or blackish (*T. p. vanikorensis*, *T. p. placens*, *T. p. becki*, *T. p. malekulae*, and *T. p. efatensis*), but populations continuing to the south are black with a white head (*T. p. albifrons*, *T. p. pritzbueri*), again all-over blackish (*T. p. marensis*), and then all-over reddish-olive (*T. p. xanthopus*). This complex is thus divisible into 3-4 clearly diagnosable subunits, with the blackish southern *T. p. marensis* separated from other (northern) all-black populations by intervening white-headed populations.

GEOGRAPHIC VARIATION IN SIZE AND RELATIONSHIP WITH ISLAND AREA

The body size of populations of the *Turdus poliocephalus* complex shows an odd relationship with island area (Figure 3). Populations of the smallest islands have uniformly small body size (maximum 120 mm wing chord in males, most populations <113 mm); on moderate-to-large islands, body size increases considerably with island size, reaching a maximum of 140+ mm (*T. p. versteegi*, New Guinea). This relationship is linear when viewed on a semilogarithmic scale (simple linear regression, $P < 0.05$).

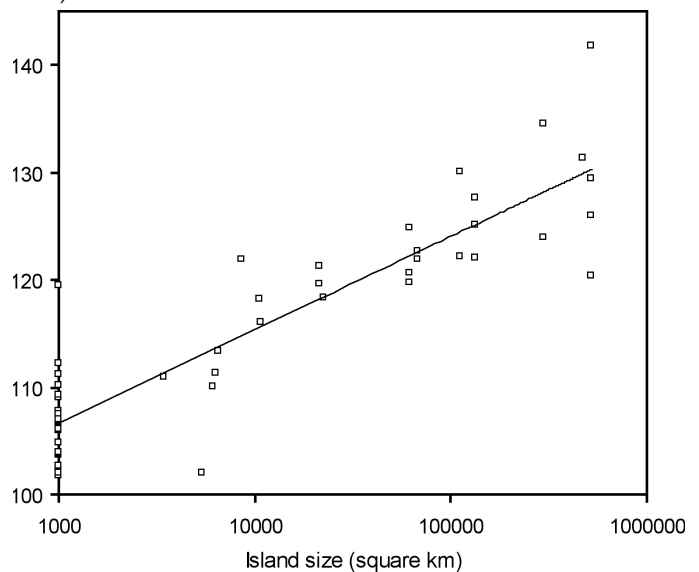


Fig. 3. Relationship between island area (in km², shown on log₁₀ scale) and body size in populations of the *Turdus poliocephalus* complex (shown as male wing chord, in mm). Note that the smaller islands (i.e., <4000 km²) are all set at an area of 1000 km² for lack of precise areas for several islands.

MAJOR AND MINOR SUBUNITS WITHIN *T. p. POLIOCEPHALUS*

The species complex can be divided into a number of plumage types, each of which is clearly and easily distinguishable from each other. Twelve major types and subspecies showing the different phenotypes are summarized in Table 3. Several of these plumage types are represented by single subspecies or populations, whereas several others are represented by numerous subspecies and populations. (Subspecies *T. p. biesenbachii*, *T. p. canescens*, and *T. p. stresemanni* are here treated based on inspection of digital photos, and hence their placement and status are provisional.)

When account is taken of geographic contiguity, the number of distinct forms rises considerably. For instance, among forms that are black with white heads, *T. p. deningeri* is present on Ceram in central Indonesia, whereas the other two forms are much farther to the east (in the New Hebrides islands) and south (on Goodenough Island). Taking such discontinuities into account, in general, the number of distinct forms within the 'species' rises to 31 (Table 3). Finally, even among contiguous forms of the same general plumage type, some populations can be distinguished on the basis of more subtle plumage differences—at least another seven forms would be distinguishable (Table 3).

DISCUSSION

The *Turdus poliocephalus* complex is enormously variable across its extensive geographic distribution. In fact, variation is so extreme that a total of 12 major plumage types, 31 geographically contiguous diagnosable units, and 38 distinct diagnosable forms with continuous geographic ranges can be distinguished. This variation is so dramatic as to make one incredulous that the complex can still be considered as a single species, with not even a single form split off as a distinct species under recent taxonomic treatments (Sibley and Monroe 1990). Even the *Pachycephala pectoralis* complex, with its own multitude of forms over much the same geographic region (Galbraith 1956), has had three forms 'removed' (*P. schlegelii*, *P. flavifrons*, and *P. soror*), now considered separate species. Hence, the case of *T. poliocephalus* is certainly among the most extreme cases of lumping in all birds.

SPECIES LIMITS

The fact that *Turdus poliocephalus* remains considered as a single biological entity, in spite of such dramatic differences from population to population, begs the question of why it has not been subdivided into several distinct species. The answer of why *as of yet* it has not been split up lies in the history of the development of the taxonomy of the birds of the southwest Pacific islands. This region saw its most dramatic exploration during the famous Whitney South Sea Expeditions, and exploration of the region ornithologically largely ceased with the initiation of conflicts in the Pacific theater of World War II. Moreover, the ornithological leader of the Whitney expeditions was Ernst Mayr, a long-time champion of the biological species concept (BSC).

The BSC emphasizes that species are 'groups of actually or potentially interbreeding populations' (italics mine) (Mayr 1942). As such, insular populations present a particular problem for the concept—the idea of establishing the potential for interbreeding will always re-

main a matter of conjecture. Can we, for example, decide whether the *Turdus poliocephalus* populations of Mindoro would interbreed freely with those of Samoa were they to come into contact? For this reason, many taxa remained 'overlumped' under the BSC, particularly given the interpretations from Mayr and colleagues that dominated the period of exploration of the southwestern Pacific.

More recent interpretations of the BSC have become increasingly liberal regarding assumptions of reproductive isolation among disjunct populations. Compare, for example, the decisions of the American Ornithologists' Union check-list committee over a 15 yr span in the latter twentieth century (AOU 1983, 1998)—disjunct forms such as *Aphelocoma coerulescens* versus *A. californica* have now been split up into smaller species units. Other treatments under the BSC have been even more liberal in decisions regarding splitting up such complexes (Sibley and Monroe 1990). Hence, the BSC has clearly shifted towards recognizing more, and more finely subdivided, species units, in many cases through decisions involving disjunct differentiated populations.

Alternative species concepts have been debated hotly in ornithology (McKittrick and Zink 1988, Amadon and Short 1992), perhaps more acrimoniously than for other taxonomic groups (Wiley 1978, De Queiroz and Donoghue 1988). These alternative concepts—the Phylogenetic Species Concept (PSC) and Evolutionary Species Concept (ESC) being the principal players—have the advantage of not requiring conjecture regarding what populations *might* do were they to come into contact. Whereas they have several other features that can be debated (not herein, though), and that may indeed represent failings (at least to some), the point is that these concepts offer a useful alternative.

Considering the results of this study in the context of the BSC, the traditional ('Mayrian') view of the BSC would assume universal reproductive potential and retain *Turdus*

Table 3. Summary of distinct forms within the presently recognized *Turdus poliocephalus*, including distinct phenotypes and geographically contiguous sets of populations showing them. Parentheses indicate sets of geographically contiguous populations sharing the same major plumage phenotype that are distinguishable consistently on the basis of plumage characters. Numbers, letters, and symbols refer to map in Figure 4. Populations not inspected in person, and here classified only provisionally include those named as *T. p. biesenbachi* (% in Figure 4), *T. p. canescens* (& in Figure 4), and *T. p. stresemanni* (# in Figure 4).

Phenotype	Subspecies presenting phenotype	Geographically contiguous sets of subspecies
Gray overall	<i>nigrorum</i>	- 1 <i>nigrorum</i>
Black or blackish overall	<i>becki</i> , <i>beehleri</i> , <i>bougainvillei</i> , <i>erebus</i> , <i>efatensis</i> , <i>hades</i> , <i>heinrothi</i> , <i>kulambangrae</i> , <i>keysseri</i> , <i>malekulae</i> , <i>mareensis</i> , <i>rennellianus</i> , <i>samoensis</i> , <i>tolokiwae</i> , <i>vanikorensis</i> , <i>versteegi</i> , <i>vitiensis</i> , <i>whitneyi</i> , <i>sladeni</i> , <i>thomassoni</i> , <i>mayonensis</i> , <i>papuensis</i> , <i>kelleri</i>	- (2 <i>efatensis</i>), (3 <i>becki</i> , <i>malekulae</i> , <i>vanikorensis</i> , <i>whitneyi</i>) - (4 <i>beehleri</i> , <i>bougainvillei</i> , <i>erebus</i> , <i>heinrothi</i> , <i>keysseri</i> , <i>rennellianus</i> , <i>tolokiwae</i> , <i>sladeni</i>), (5 <i>versteegi</i>), (6 <i>papuensis</i>), (7 <i>kulambangrae</i>) - 8 <i>hades</i> - 9 <i>mareensis</i> - (A <i>samoensis</i>), (B <i>vitiensis</i>) - (C <i>thomassoni</i> , <i>mayonensis</i>) - D <i>kelleri</i>
Pallid olive-red overall	<i>erythropleurus</i>	- E <i>erythropleurus</i>
All-over reddish-olive	<i>xanthopus</i>	- F <i>xanthopus</i>
Olive back, wine-red below	<i>vinitinctus</i>	- G <i>vinitinctus</i>
Black with white head	<i>albifrons</i> , <i>canescens</i> , <i>deningeri</i> , <i>pritzbueri</i>	- H <i>deningeri</i> - (I <i>albifrons</i> , <i>pritzbueri</i>) - & <i>canescens</i>
Black with white head, orange border	<i>niveiceps</i>	- J <i>niveiceps</i>
Black with gray head	<i>poliocephalus</i> , <i>tempesti</i>	- K <i>poliocephalus</i> - L <i>tempesti</i>
Black with orange head	<i>ruficeps</i>	- M <i>ruficeps</i>
Blackish above, orange below	<i>loeseri</i>	- N <i>loeseri</i>
Blackish above, brick red below	<i>placens</i> , <i>schlegelii</i> , <i>seebohmi</i> , <i>hygroscopus</i> , <i>indrapurae</i> , <i>javanicus</i> , <i>whiteheadi</i> , <i>sterlingi</i> , <i>biesenbachi</i> , <i>stresemanni</i>	- O <i>placens</i> - (P <i>schlegelii</i>), (Q <i>sterlingi</i>) - R <i>seebohmi</i> - S <i>hygroscopus</i> - T <i>indrapurae</i> - U <i>javanicus</i> , <i>biesenbachi</i> (provisional placement only) - V <i>whiteheadi</i> , <i>stresemanni</i> (provisional placement only)
Blackish or olive above, brick red and white below	<i>celebensis</i> , <i>layardi</i> , <i>fumidus</i> , <i>katanglad</i> , <i>mindorensis</i> , <i>malindangensis</i>	- W <i>celebensis</i> - X <i>layardi</i> - Y <i>fumidus</i> - Z <i>mindorensis</i> - (\$ <i>katanglad</i>), (¥ <i>malindangensis</i>)

poliocephalus as an all-inclusive species. When, however, recent shifts in interpretation of the BSC are taken into account, variation within the present *T. poliocephalus* can be interpreted differently—if disjunct, dramatically differentiated populations are interpreted as potentially *not* interbreeding, then subdivision of *T. poliocephalus* is indicated, particularly given the discrete population-to-population variation that characterizes the complex. However, recognizing the 12 major plumage types would not be acceptable, given their often-broadly-disjunct distributions; rather, attention would best focus on the 31 geographically contiguous manifestations of plumage types. Variation within these units (Table 3) could be interpreted as more minor, ‘subspecific’ differences. Under the PSC and ESC, the full suite of 38 distinguishable forms would be recognized as diagnosable evolutionary units worthy of the label ‘species.’

NEXT STEPS

In spite of the extensive museum survey that was key to this study, three forms were nonetheless not inspected. Of these, the populations described as *T. p. biesenbachi* have been reviewed critically (Mees 1996), with the conclusion that they are best submerged in *T. p. fumidus*; as such, distinguishing characteristics are assumed to be subtle at best. The other two subspecies (*T. p. canescens* and *T. p. stresemanni*) are likely to be better-marked, and therefore warrant careful attention in future studies in museum and laboratory to establish their likely status in the breakdown outlined herein. My inspection of digital photos of the types of these subspecies—kindly provided by the curators of the relevant collections (see Methods)—fits well with these expectations: *T. p. canescens* is another white-headed black form that is disjunct from the others, whereas *T. p. biesenbachi* and *T. p. stresemanni* are at

least not markedly distinct from adjacent populations—detailed comparisons of specimen series may nonetheless reveal differences.

As was warned in the Introduction, this contribution is intended as a first step in understanding one of the most complex of bird ‘species.’ Many questions, however, remain unresolved—vocal characters, for instance, remain completely unexplored for this group, given the near-complete absence of vouchered recordings. Ecological variation clearly also is marked within this group—populations range from sea level to above treeline, depending on the island. These suites of characters would be key in further elucidating the details of species limits in such a complex group.

Similarly, molecular variation within *Turdus poliocephalus* remains unassessed, as frozen tissue samples exist for only a few of the subunits. Molecular studies would provide several critical pieces of information—is the complex

a monophyletic unit, or has it resulted from several invasions of the Pacific by multiple mainland thrush species? A first answer comes from a recent publication (Voelker et al. 2007), which shows that 4 geographically disparate *T. poliocephalus* races are monophyletic with respect to a thorough sampling of the rest of *Turdus*, but much more sampling is needed to make this picture clear. More extensive phylogenetic studies based on DNA sequence variation could provide a clear and unequivocal answer to this question, as well as illustrate levels of genetic differentiation separating the different forms and populations.

Systematics aside, several additional important points remain to be clarified. The ecology and elevational distributions of different island forms are dramatically variable, with some populations restricted to the very highest mountains (e.g., populations of New Guinea), whereas others range broadly into mid-elevation cloud forests (e.g., populations of Mindanao, pers. obs.), and still oth-

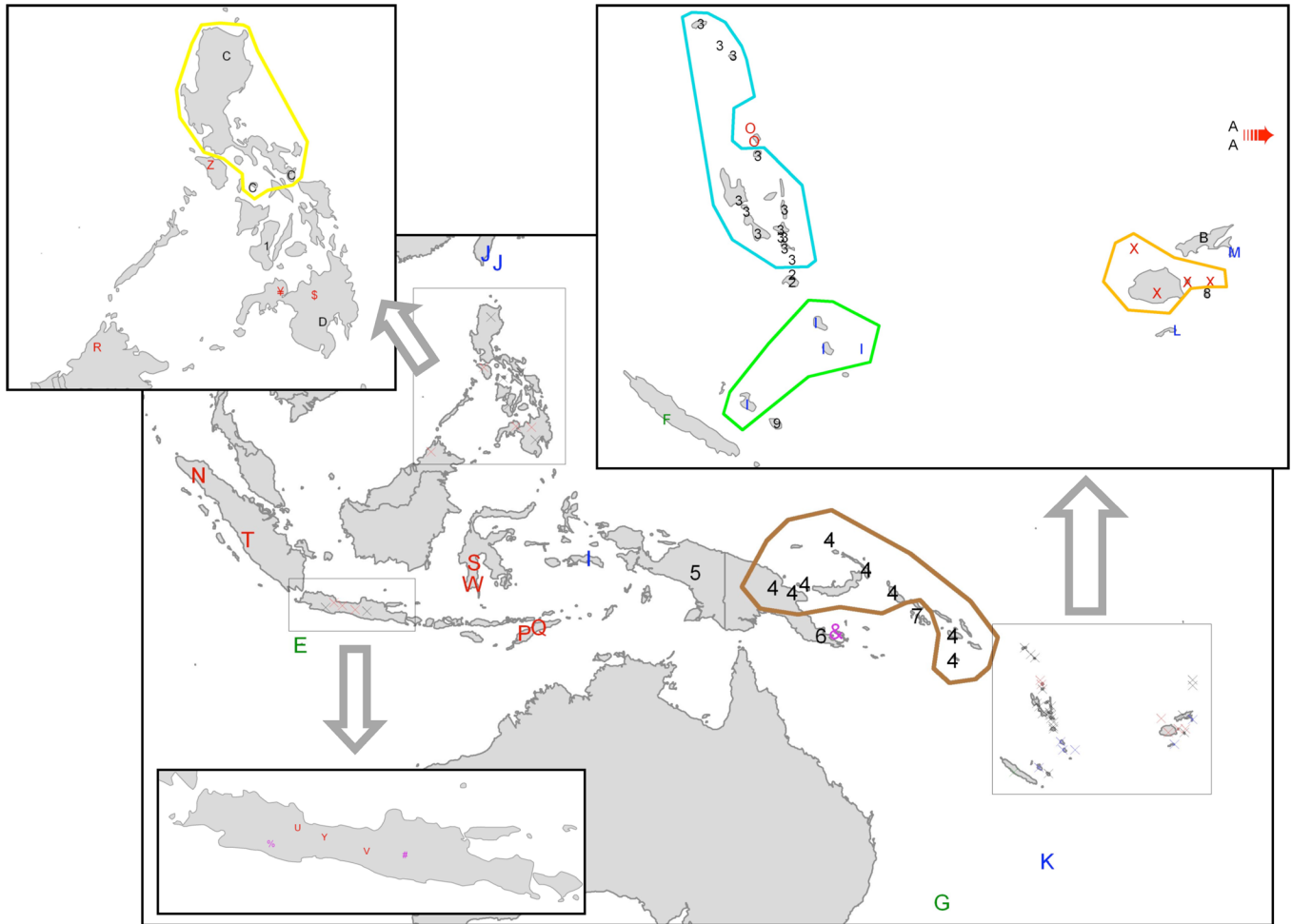


Fig. 4. Summary of species-level breaks proposed in this study, with forms keyed to labels provided in Table 5. Forms that are predominantly black or blackish are shown with black symbols; forms that are black with a light head are shown in blue; forms that are dark above and reddish below are shown in red; forms that are reddish-olive are shown in green; and forms that were not inspected in this study are shown in pink. Polygons of different colors are provided to link the different island populations of broadly-distributed species.

ers are found in lowland forests near sea level (based on tag annotations on numerous specimens). These details of the ecology of this 'species' further emphasize the dramatic differentiation that exists from one population to the next in the complex.

Apparent absences on several islands are yet more intriguing. Populations in the *Turdus poliocephalus* complex occur on the tiniest of islands (e.g., Lord Howe Island, ~10 km²), and yet many much-larger islands remain without known populations. Of particular note in this respect is the Philippines, where populations are known only from Luzon, Mindoro, Sibuyan, Negros, Panay, and Mindanao. Numerous islands (e.g., Leyte, Samar, Siquijor, Dinagat, Tablas, Romblon, etc.) apparently lack populations—if such were to exist (see the recent discovery of populations on Sibuyan and Panay islands), many of them may prove to represent distinct species-level forms, given the rampant and dramatic interpopulation differentiation in the Philippines.

GENERAL COMMENT

The development of this study further emphasized two points. First, even though birds represent one of the best-sampled and best-studied major taxonomic groups (Peterson 1998), the specimen record for birds around the world remains woefully incomplete, and a considerable amount of scientific collecting is still called for to enable detailed study (Remsen 1995, Winker 1996)—witness the inability to examine series of all of the named subspecies in the particular complex under study herein. Second, the current state of avian taxonomy begs broad and sweeping reassessments in order to achieve a representative and balanced taxonomic view of the group (Peterson and Navarro-Siguenza 1999). A complete generation of alpha-taxonomic studies could focus simply on reassessing and reworking the taxonomy, even of a group as well-studied as birds.

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APPENDICES

Appendix 1. Summary of populations and subspecies sampled, islands, geographic coordinates, approximate island area (with areas <4000 km² indicated as 'small,' given problems with obtaining area estimates for all small islands), and numbers of adult males and adult females examined. Authorities are provided after first mention of each subspecies—full bibliographic references are available in Ripley (1964). Museums with major holdings are listed in the last column (see Materials and Methods for a list of abbreviations for museums).

OTUnit	Subspecies	Island	Latitude	Longitude	Approx. area (km ²)	Male	Female	Museums
AL1	<i>albifrons</i> (Ramsay 1879)	Erromanga Island	-18.8	169.0	small	5	1	AMNH
AL2	<i>albifrons</i>	Futuna Island	-19.5	170.2	small	1		AMNH
BE1	<i>becki</i> Mayr 1941	Emae Island	-17.1	168.4	small	4		AMNH
BE2	<i>becki</i>	Epi Island	-16.8	168.2	small	5		AMNH
BE3	<i>becki</i>	Lopevi Island	-16.5	168.2	small	5	5	AMNH
BE4	<i>becki</i>	Paama Island	-16.5	168.1	small		1	AMNH
BH1	<i>beehleri</i> Ripley, 1977	New Ireland	-4.0	153.8	5,406	1	1	USNM
BI1	<i>biesenbachi</i> Stresemann 1930	Java	-7.3	107.7	132,656			Leiden
BO1	<i>bougainvillei</i> Mayr 1941	Bougainville Island	-6.0	155.0	6,280	5	5	AMNH
CA1	<i>canescens</i> (De Vis 1894)	Goodenough Island	-9.3	150.2	.			Queensland Museum
CE1	<i>celebensis</i> (Büttikofer 1893)	Celebes	-5.3	120.0	112,087	9	9	AMNH
CR1	<i>carbonarius</i> Mayr and Gilliard 1951	New Guinea	-5.6	145.0	517,443	4	3	AMNH
DE1	<i>deningeri</i> Stresemann 1912	Ceram	-3.1	129.5	10,716	3	3	AMNH
EF1	<i>efatensis</i> Mayr 1941	Efate / Vate Island	-17.7	168.4	small	7	2	AMNH
EF2	<i>efatensis</i>	Nguna Island	-17.5	168.4	small			--
ER1	<i>erythropleurus</i> Sharpe 1887	Christmas Island	-10.5	105.5	small	14	11	AMNH
FU1	<i>fumidus</i> Müller 1843	Java	-7.15	109.1	132,656	11	12	MCZ
HA1	<i>hades</i> Mayr 1941	Ngau Island	-18.0	179.3	small	6	1	AMNH
HE1	<i>heinrothi</i> Rothschild and Hartert 1924	St. Matthias Island	-1.5	149.7	small	1		AMNH
HY1	<i>hygroscopus</i> Streseman 1931	Celebes	-3.4	120.0	112,087	8	7	AMNH
IN1	<i>indrapuræ</i> Robinson and Kloss 1916	Sumatra	-1.5	101.2	295,468	4	4	AMNH
JA1	<i>javanicus</i> Horsfield 1821	Java	-6.9	108.4	132,656	11	4	AMNH
KA1	<i>katanglad</i> Salomonsen 1953	Mindanao	8.1	124.9	61,913	10	8	FMNH
KE1	<i>kelleri</i> (Mearns 1905)	Mindanao	7.0	125.2	61,913	11	11	FMNH
KU1	<i>kulambangrae</i> Mayr 1941	Kulambangra Island	-8.0	157.0	small	1		AMNH
KY1	<i>keysseri</i> Mayr 1931	New Guinea	-6.0	146.6	517,443	3	1	AMNH
LA1	<i>layardi</i> (Seebohm 1890)	Koro Island	-17.7	179.4	small	4	5	AMNH
LA2	<i>layardi</i>	Ovalau Island	-17.7	178.8	small	1		AMNH
LA3	<i>layardi</i>	Viti Levu Island	-18.0	178.0	6,490	8	7	AMNH
LA4	<i>layardi</i>	Yasawa Island	-16.8	177.4	small	5	4	AMNH
LO1	<i>loeseri</i> de Schauensee 1939	Sumatra	4.0	97.0	295,468	11	7	ANSP
MA1	<i>malekulæ</i> Mayr 1941	Ambrim Island	-16.3	168.1	small	6		AMNH
MA2	<i>malekulæ</i>	Malekula Island	-16.4	167.5	small	5	6	AMNH
MA3	<i>malekulæ</i>	Pentecost Island	-15.8	168.2	small			--
MI1	<i>mindorensis</i> Ogilvie-Grant 1896	Mindoro	13.2	120.9	6,084	11	11	YPM
ML1	<i>malindangensis</i> (Mearns 1907)	Mindanao	8.2	123.6	61,913	18	11	FMNH
MR1	<i>mareensis</i> Layard and Tristram 1879	Mare Island	-21.5	168.0	small	6	7	AMNH
MY1	<i>mayonensis</i> (Mearns 1907)	Luzon	12.8	124.0	67,595	11	5	FMNH
MY2	<i>mayonensis</i>	Sibuyan	12.3	122.5	small	2		FMNH
NI1	<i>nigrorum</i> Ogilvie-Grant 1896	Negros	10.0	123.0	8,542	21	14	FMNH, YPM
NV1	<i>niveiceps</i> (Hellmayr 1919)	Botel Tobago	22.2	122.0	small			--
NV2	<i>niveiceps</i>	Taiwan	23.0	121.0	22,346	17	6	AMNH
PA1	<i>papuensis</i> (De Vis 1890)	New Guinea	-9.7	149.0	517,443	9	7	AMNH
PL1	<i>placens</i> Mayr 1941	Ureparapara / Bligh Island	-13.6	167.3	small	1	1	AMNH
PL2	<i>placens</i>	Vanua Lava Island	-13.9	167.4	small	3	2	AMNH

PO1	<i>poliocephalus</i> Latham 1801	Norfolk Island	-29.0	167.8	small	9	9	AMNH
PR1	<i>pritzbueri</i> Layard 1878	Lifu Island	-21.0	167.2	small		1	MCZ
PR2	<i>pritzbueri</i>	Tanna Island	-19.5	169.2	small	7	4	AMNH
RE1	<i>rennellianus</i> Mayr 1931	Rennell Island	-11.8	160.0	small	6	5	AMNH
RU1	<i>ruficeps</i> (Ramsay 1876)	Kandavu Island	-19.0	178.5	small	7	5	AMNH
SA1	<i>samoensis</i> Tristram 1879	Savali Island	-13.5	180.0	small	5	3	AMNH
SA2	<i>samoensis</i>	Upolu Island	-14.0	180.0	small	5	4	AMNH
SC1	<i>schlegelii</i> Sclater 1861	Timor	-9.5	124.2	21,192	12	5	AMNH
SE1	<i>seebohmi</i> (Sharpe 1888)	Borneo	6.0	116.5	469,872	17	15	MCZ
SL1	<i>sladeni</i> Cain and Galbraith 1955	Guadalcanal Island	-9.7	160.0	small	2		FMNH
SR1	<i>stresemanni</i> Bartels 1938	Java	-7.6	111.2	132,656			AMNH
ST1	<i>sterlingi</i> Mayr 1944	Timor	-8.9	125.4	21,192	3		AMNH
TE1	<i>tempesti</i> Layard 1876	Taveuni Island	-16.9	180.0	small	6	2	AMNH
TH1	<i>thomassoni</i> (Seebohm 1894)	Luzon	17.5	121.5	67,595	15	16	FMNH
TO1	<i>tolokiwae</i> Diamond 1989	New Guinea	-5.3	147.7	small	1		AMNH
VA1	<i>vanikorensis</i> Quoy and Gaimard 1830	Espiritu Santo	-15.5	167.0	small	13	11	AMNH, FMNH
VA2	<i>vanikorensis</i>	Malo Island	-15.8	167.2	small	6	2	AMNH
VA3	<i>vanikorensis</i>	Santa Cruz Island	-10.8	166.0	small			--
VA4	<i>vanikorensis</i>	Utubua Island	-11.3	166.5	small	5	2	AMNH
VA5	<i>vanikorensis</i>	Vanikoro Island	-11.6	166.9	small			--
VE1	<i>versteegi</i> Junge 1939	New Guinea	-4.3	138.5	517,443	5	3	AMNH
VI1	<i>vinitinctus</i> (Gould 1855)	Lord Howe Island	-32.5	159.0	small	11	9	AMNH
VT1	<i>vitiensis</i> Layard 1876	Vanua Levu Island	-16.5	179.2	3,459	4	4	AMNH
WH1	<i>whiteheadi</i> (Seebohm 1893)	Eastern Java	-7.5	110.2	132,656	5	2	AMNH
WT1	<i>whitneyi</i> Mayr 1941	Gaua / Santa Maria Island	-14.3	167.5	small	2	3	AMNH
XA1	<i>xanthopus</i> Forster 1844	New Caledonia	-21.4	165.1	10,570	6	5	AMNH

Appendix 2: Summary of plumage coloration for selected body regions in males and females of subspecies of *Turdus poliocephalus*.

Subspecies	Crown m	Crown f	Back m	Back f	Bib m	Bib f	Flanks m	Flanks f	Midbelly m	Midbelly f	Undertail coverts m	Undertail coverts f	Dimorphism
<i>albifrons</i>	white	whitish gray	black	black	white	whitish gray	black	black and brick	black	white and brick	black white terminal spot	black white shaft streak	Light
<i>becki</i>	blackish olive	blackish olive	blackish olive	blackish olive	gray	gray	gray edged brown	gray edged brown	gray edged brown	gray edged broadly brown	blackish olive with terminal white spot	blackish olive with terminal white spot	Light
<i>bechleri</i>	dusky blackish	dusky blackish	dusky blackish	dusky blackish	dusky blackish	dusky blackish	dusky blackish	dusky blackish, edged brown	dusky blackish	dusky blackish, edged brown	dusky blackish	dusky blackish	Light
<i>bougainvillei</i>	blackish olive	blackish olive	blackish olive	blackish olive	blackish olive	blackish olive	blackish olive	blackish olive edged brown	blackish olive	blackish olive	blackish olive	blackish olive	Light
<i>celebensis</i>	gray olive	gray olive	gray olive	gray olive	gray	gray, brown edged	brick	.	brick with white	brick with white	black with white shaft streaks	black with white shaft streaks	Light
<i>deningeri</i>	white	white	black	black	whitish gray	whitish gray	dark gray	dark gray	dark gray	dark gray	dark gray	dark gray	None
<i>efitensis</i>	black	black	black	black	black	blackish gray	black	dusky brown	dusky brown	black (not totally diff from female)	black (sometimes with white tip)	black white midstripe	Light
<i>erebus</i>	blackish	blackish olive	blackish olive	blackish olive	blackish	olive brown	blackish	olive edged brick	blackish	olive edged brick	black with tiny terminal spot	dusky with terminal spot	Strong
<i>erythropleurus</i>	light olive	light olive	light olive	light olive	light yellow gray	light yellow gray	light brick	light brick	white	white	white edged light brick	white edged light brick	None
<i>fumidus</i>	blackish gray	blackish gray	blackish gray	blackish gray	dark gray	dark gray	brick	brick	brick and white	brick and white	black, white midstripe	black, white midstripe	None
<i>hades</i>	black	.	black	black	.	.	black	.	black	.	black	.	.
<i>heinrothi</i>	dusky gray-black	.	dusky blackish	dusky blackish	dusky gray	.	dusky gray-black	.	dusky gray-black	.	black with tiny terminal spot	.	.
<i>hygroscopus</i>	gray	gray	dark gray	dark gray	gray	gray	brick	brick	brick	brick	black	black	None
<i>indrapurae</i>	frosted black	frosted black	black	black	dark gray	very dark gray	brick	brick	brick	brick	black	black	None
<i>javanicus</i>	gray	gray	gray	gray	gray	gray	gray	gray	brick	brick	gray, white shaft streaks	gray, white shaft streaks	None
<i>katanglad</i>	dark gray	dark gray	blackish gray	blackish gray	gray-brown, darker brown caudal border	gray-brown, darker brown caudal border	brick red	brick red	white	white	black white midstripe	black white midstripe	None

<i>kelleri</i>	dark brown	dark brown	dark brown	dark brown	light brown	medium brown, barely distinguishable from flanks and midbelly	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	dark brown	Light
<i>keyseri</i>	blackish olive	blackish olive	blackish olive	blackish olive	dark gray	dark gray	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive edged brick	dusky olive	dusky olive	None
<i>kulambarangae</i>	black olive	black olive	black olive	black olive	black gray	gray	black brick	black brick	black brick	black brick	black brick	black brick	black brick	black brick	black brick	black brick	black brick	black brick	.
<i>layardi</i>	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	None
<i>loeseri</i>	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	blackish gray	None
<i>malekulae</i>	blackish olive	blackish olive	blackish olive	blackish olive	gray olive	gray olive	blackish olive edged brown	blackish olive edged brown	blackish olive edged brown	gray olive	gray olive	gray olive	gray olive	gray olive	gray olive	gray olive	blackish olive, white shaft streak	blackish olive, white shaft streak	Light
<i>malindangensis</i>	dark brown	dark brown	dark brown	dark brown	light gray-brown	light gray-brown	dull chocolate brown	dull chocolate brown	dull chocolate brown	white with chocolate-brown crescent	white with chocolate-brown crescent	white with chocolate-brown crescent	white with chocolate-brown crescent	white with chocolate-brown crescent	white with chocolate-brown crescent	white with chocolate-brown crescent	black white midstripe	black white midstripe	None
<i>marensis</i>	dusky black brown	dusky black brown	dusky black brown	dusky black brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	dusky gray brown	black, white terminal spot	black, white terminal spot	None
<i>mayonensis</i>	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	blackish brown	black with white streak on shaft	black with white streak on shaft	Light
<i>mindorensis</i>	medium gray	medium gray	medium gray	medium gray	light gray	light gray	brick	brick	brick	white	white	white	white	white	white	white	black white midstripe	black white midstripe	None
<i>nigrorum</i>	blackish gray	blackish gray	blackish gray	blackish gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	medium gray	blackish gray tipped buff	blackish gray tipped buff	None
<i>niveiceps</i>	white	olive, faintly streaked white	black	olive	white, bordered black, then dark orange-brown	white, streaked olive, then dark orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	light orange-brown	black, white shaft streaks	black, white shaft streaks	Strong
<i>papuensis</i>	blackish olive	blackish olive	blackish olive	blackish olive	dark gray	dark gray	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black edged brick	black	black	None
<i>placens</i>	blackish olive	blackish olive	blackish olive	blackish olive	gray olive	gray olive	olive brick	olive brick	olive brick	olive brick	olive brick	olive brick	olive brick	olive brick	olive brick	olive brick	blackish olive with terminal white spot	blackish olive with terminal white spot	None

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