

Integrative systematics at the species level: plumage, songs and molecular phylogeny of quailfinches *Ortygospiza*

by Robert B. Payne & Michael D. Sorenson

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Species delimitations in birds generally are readily discerned and find a consensus among ornithologists, and this happy circumstance follows from the mutually consistent evidence that is typically derived from application of different species concepts to the same set of birds. First, under a ‘biological species concept’, populations that share unique behaviours and interbreed where their ranges meet are considered the same species. Breeding in sympatry without interbreeding provides evidence of reproductive isolation of two populations and thus of species, whereas the occurrence of birds of intermediate morphology suggests recent or current gene flow and indicates a single species is involved (Mayr 1963, 2000, de Queiroz 2005). Second, a ‘phylogenetic species concept’ uses the presence of exclusive sets of characters of birds (Cracraft 1983, Sites & Marshall 2004). Operationally, under this concept species have been recognised based on morphological characters, much as in Linnaeus (1758), without any phylogenetic analysis having been performed (Wheeler & Platnick 2000). Finally, molecular data have been analysed in a phylogenetic perspective, with the ideal of genetically exclusive lineages as a criterion for recognising species; that is, the historical isolation and independent evolution of populations, in the current version of a lineage or ‘evolutionary species concept’. We now know, however, that gene trees do not always coincide with species trees, owing to incomplete lineage sorting of genes (de Queiroz 1998, 2005, Arbogast *et al.* 2002, Avise 2004), and species can be delimited without reciprocally monophyletic gene trees (Knowles & Carstens in press).

An ‘integrative species concept’ combines these views of species in the past and present. A complementation of independent lines of evidence is very important for diagnosing biological species. We consider both the geographical patterns of morphological differences between populations and the phylogeny of genetic lineages. In addition to morphological variation and genetic lineages, we note that songs are important to the birds: experimental evidence points to songs as a major behavioural cue in mate recognition by breeding females (Searcy & Yasukawa 1996, Payne *et al.* 2000, Sorenson *et al.* 2003). In consequence we interpret song differences between morphologically recognised taxa as evidence that more than one species may be present, and the lack of song differences as an argument that populations are conspecific (e.g. Alström & Ranft 2003). In addition, an integrative species concept offers a response to claims that species are best recognised simply in terms of genetic distances between populations, insofar as rates of genetic divergence differ between lineages, and as gene trees may coalesce only after a

speciation event (Moritz & Cicero 2004, Dayrat 2005, Will *et al.* 2005). Integrative systematics proposes that taxa should be compared within an estimated phylogeny, rather than simply in character lists of taxa. The integration recognises that genetic sequence data viewed in a phylogeny is part of a comprehensive view in which geographic variation, morphology and behaviour provide equally useful information at the species level.

African quailfinch *Ortygospiza* are small terrestrial finches that occur in short-grass and seasonally flooded riverine plains of open country in sub-Saharan Africa. They are inconspicuous, staying on the ground, then rising on whirring wings and with rattling flight-calls. Adults are sexually dimorphic in plumage, and they vary in bill and plumage colour and the intensity of plumage markings, especially in males. As evidenced by plumage and by molecular data, *Ortygospiza* are most closely related to the African estrildid genera *Amadina*, *Amandava* and perhaps *Paludipasser* (Sorenson & Payne in Fry 2004, Sorenson *et al.* 2004). The number of quailfinch species has been less certain. Here we describe the adult plumage and bill colour of quailfinch taxa, and the evidence of breeding sympatry. We compare songs and nestling mouth colours and patterns to evaluate any behavioural differences between populations, both as traits that may be important in successful reproduction and as markers of gene flow. Finally, we use molecular genetics to determine the phylogenetic relationships among geographic populations across Africa. We consider these criteria together to assess whether previously described taxa represent species. Using these criteria we reason that quailfinch are best recognised as a single species, *Ortygospiza atricollis*.

Systematic history and plumage variation in *Ortygospiza*

Based on geographic variation in plumage, previous authors have recognised one, two or three quailfinch species. Sclater (1930a) and Chapin (1954) recognised a single species, and Wolters (1975, 1985) recognised one species with three groups: a west African 'black-faced quailfinch' *O. atricollis* (Vieillot, 1817), a central African 'black-chinned quailfinch' *O. gabonensis* Lynes, 1914, and an eastern and southern 'African quailfinch' *O. fuscocrissa* Heuglin, 1863. More recently, Fry (2004) recognised these 'racial groups' as three species and reported areas of geographic overlap between them.

Most earlier and some recent accounts recognised two quailfinch species, with the taxa combined in different ways. Over much of Africa, white-chinned quailfinch, described from Senegal (*O. atricollis*), have some white around the eye, whereas black-chinned birds (*O. gabonensis*) lack this. Immelmann *et al.* (1965, 1977a), Mayr *et al.* (1968), Benson *et al.* (1971), Goodwin (1982) and Dickinson (2003) recognised these as two species. In another representation of two species, Sharpe (1890) and Shelley (1905) recognised one species with white on the throat and around the eye, '*O. polyzona*' (Temminck, 1823), and a second species without white except 'a few whitish plumelets round the eye', *O. atricollis*. In a third model, White (1963) recognised *O. fuscocrissa* for the distinctly spectacled forms of

eastern and southern Africa, and *O. atricollis* for the west African birds and the black-chinned birds from central Africa.

Differences in delimiting quailfinch species stem from inaccuracies in plumage descriptions, puzzling original descriptions, and questionable records of breeding sympatry of populations. First, the quailfinch with white around the eye have an incomplete eye-ring, the posterior part of the ring is variably complete and the anterior ends of the broken ring extend from the eye to the bill as white lines above and below the lores (which vary from grey to black). These white markings are most prominent in birds from east and southern Africa, which have a distinctive spectacled appearance, more so than birds in west Africa. Descriptions of black- and white-chinned quailfinch in Sharpe (1890) overlooked the presence of a small white chin patch in the western birds. Vieillot (1817) described the small white chin patch in his species *Fringilla atricollis* from Senegal, as mentioned also by Cassin (1860). Confusion more importantly traces to Temminck's description of *Fringilla polyzona* with two specimens, a female and a male, apparently from two geographic sources. (Temminck, 1823: col. 221, fig. 3) illustrated a pale female, and his text described a female with the chin white and the underparts pale with the dark bars on the flanks broadly separated by the belly. Temminck's text description of a male, however, was of a dark bird with a black throat. Sclater (1930a) recognised one species of quailfinch, *O. atricollis*, with seven subspecies, one being *O. a. polyzona* (Temminck, 1823) which Sclater (1930a: 784) recognised as being like the pale birds in South Africa; his footnote remarked that Temminck's description of the male involved the Gambian form. Temminck reported the birds as from 'les provinces de royaume de Gambie sur les côte d'occidentales d'Afrique'. His illustration depicts a female with a white streak above the eye; syntype RMNH 90327 has the face nearly all white and unfeathered, apparently due to feather loss post-collection and to application of a white substance, perhaps a preservative (for museum acronyms see Acknowledgements). No other syntypes of *polyzona* have been traced; either in RMNH or in MNHN (RBP; J.-F. Voisin *in litt.* 2006). Roberts (1930) declared *polyzona* to be a synonym of *O. a. atricollis*, on the grounds that the description of the male must have priority. Grant & Mackworth-Præd (1956) concurred and emphasised that Vieillot designated the birds as being from The Gambia, making *O. polyzona* (Temminck, 1823) a synonym of *O. atricollis* (Vieillot, 1817), and recent accounts have followed this reasoning (e.g., Mayr *et al.* 1968). Temminck's illustration resembles both the female syntype of *polyzona* (incorrectly labeled as from Senegal), and a female quailfinch (UMMZ 211483) from the Save River near Beira, southern Mozambique.

In the dark-plumaged quailfinches, *O. gabonensis* Lynes, 1914, was described from Gabon and diagnosed by the back-feathers being streaked (not uniform), the absence of white on the chin and around the eye, and the white bars of the underparts being broader than in other quailfinch (the 'female' in his description was a juvenile: Cowles 1957). Lynes subsequently collected another new quailfinch at Kawambwa, north-east Zambia, *O. a. fuscata* Sclater, 1930, the plumage nearly

black above, dark cinnamon on the belly and narrower white bars on the underparts than the most similar form, the dark-plumaged, black-faced *O. a. ansorgei*. *O. a. fuscata* had the bill orange with sepia on the tip and around the nostrils (Sclater 1930b). Sclater (1930a) recognised *gabonensis* as a subspecies of *O. atricollis*, as did Bannerman (1949). The other black-chinned taxon was *O. a. dorsostrata*, described by van Someren (1921a) from western Uganda as being like *gabonensis*, but ‘richer rufous on the breast; moreover, the male has a small white chin-spot, the female not. There is no white ring round the eye.’ These dark-plumaged quailfinch occur in central Africa, mainly at the fringes of the rainforest zone.

In the quailfinches with little white on the face and chin, other taxa have been described in addition to nominate *O. a. atricollis*. *O. a. ansorgei* Ogilvie-Grant, 1910, from Guinea-Bissau, was described on the basis of the black chin and throat extending onto the chestnut breast, the white bars below fewer, the upperparts darker; one of two males had a small white patch on the chin, and in both specimens of the type series the bill was dark red-brown above and crimson-lake below. *O. a. ansorgei* in The Gambia, Guinea-Bissau, Guinea, Sierra Leone to Liberia and Côte d’Ivoire in the far west, have a small white line on the chin (sometimes lacking; Gatter 1997: 280 in Liberia; MCZ 153629 from Guinea-Bissau), and a black face with little or no white around the eye and lores. Elsewhere in west Africa, from Senegal and Mali to Nigeria and Cameroon, *O. a. atricollis* has white feathers above and below the eye and lores. Although colour plates in regional field guides and other works illustrate west African birds as lacking white around the eye and lores (Serle & Morel 1977, Clement 1993, Barlow & Wacher 1997, Borrow & Demey 2001, Fry 2004), and Bates (1930) mentioned no white around the eye and lores, nominate *O. atricollis* does have some white in these areas, but this is not obvious in poorly prepared specimens. In Nigeria, eight of ten males photographed by RBP at Bukuru, Nigeria, in September–October 1995, had a few white feathers below the eye and on the lores (Fig. 1); five of six adult females also had some white in these areas (mainly on the lower branch of the lores) and a partial ring below the eye. These ‘white-chinned’ *ansorgei* and *atricollis* are otherwise dark, more like *fuscata* in northern Zambia than the paler quailfinch of east and southern Africa.

O. a. ugandae van Someren, 1921, in Uganda and the North Kavirondo region of western Kenya, was described as similar to *O. a. ansorgei* but uniformly grey-brown above. Later, van Someren (1922) noted *ugandae* to have ‘uniform grey-brown mantles, black foreheads, extensive black throats, and small white chin-spots, with a white ring round the eyes; breasts pale brownish’; and *dorsostrata* to be like *gabonensis* but ‘richer rufous below and the flanks darker. The female has no white chin-spot. The male has a small indication of white on the chin, but no white round the eye.’ Birds in Uganda and Sudan are intermediate between *O. a. atricollis* and *O. a. muelleri* (*ugandae* are darker chestnut below than *muelleri*); Sudan birds (SMNS series) have more white on the face than *O. a. atricollis*, in contrast to the evaluation by Nikolaus (1987). In fact, the plumage of *ugandae* is barely separable from the plumage of *muelleri* except for the narrower white eye-



Figure 1. Plumage variation in west African quailfinch. All are males, except f = female. (a–f) Jos, Nigeria, October–November 1995 (a, -/y; b, UMMZ 233845; c, -/o; d, UMMZ 233846; e, -/r; f, -/G); (g) captive UMMZ 232576 (the specimen in Groth 1998); (h) Marakissa, The Gambia, September 1996; (i) Ngaoundere, Cameroon, male taken with four fledglings, UMMZ 232472.

ring in *ugandae*, though the white eye-ring is distinct in the holotype, FMNH 257709, taken near *O. a. muelleri* in southern Kenya. The dry woodland and steppe region of sub-Saharan Africa between Senegal and Sudan and into northern Uganda and western Kenya is a nearly continuous vegetation zone (Keay 1959, Moreau 1966). This region is separated by drier country from other vegetation zones where quailfinch occur, and we refer to the region where *atricollis*, *ansorgei* and *ugandae* occur as west Africa.

O. a. fuscocrissa Heuglin, 1863, in Ethiopia, north-east Africa, has broad white spectacles, the white lines conspicuously broader than in west African quailfinch. In *O. a. fuscocrissa* the median breast and flanks have black bars broader than the white bars, and the back is brown, more distinctly streaked blackish than in *O. a. atricollis*.

Next, *O. a. muelleri* Zedlitz, 1911, in east Africa is similar to *fuscocrissa* but the upperparts are nearly uniform with darker, indistinct streaks. The widespread *O. a.*

muelleri occurs from east to southern Africa. In specimens we find little difference between plumage in east Africa (Tanzania) and southern Africa (southern Zambia, Zimbabwe and South Africa). *O. a. bradfieldi* Roberts, 1929, in Namibia, 'grayer and less brown' than South African quailfinch, does not consistently differ between these regions, and as in White (1963) and Immelmann *et al.* (1965, 1977a), *bradfieldi* is considered a synonym of *O. a. muelleri*. In South Africa, *O. a. digressa* Clancey, 1958, specimens are mostly darker than *O. a. muelleri* from south-central Zambia and east Africa, as in Clancey (1977). Nevertheless, not all South African specimens are darker than *O. a. muelleri* from south-central Zambia and east Africa; the dark specimens from Transvaal are worn and soiled (MCZ) when compared with birds in fresh plumage from the same areas (USNM), and these fresh series are not distinguishable from most *O. a. muelleri*. In north-west Zambia, *O. a. minuscula* White, 1946, was described as similar to '*polyzona*', but smaller, the centre of the breast deep rufous (like *fuscata*) and the belly very pale, almost whitish (White 1946). White (1963) later listed *minuscula* as a synonym of *mulleri* [*sic*]. In semi-arid northern Botswana and the Hwange area of western Zimbabwe, *O. a. pallida* are 'paler above and below than *O. a. bradfieldi* Roberts [1929]' (Roberts 1932).

At Lake Bangweulu, Mweru Marsh, Lake Kako and Abercorn (Mbala) in the floodplain region of north-east Zambia, Benson (1955) described *O. a. smithersi* as dark above, almost like *fuscata*. *O. a. smithersi* has broad white spectacles and a white chin like *muelleri*, with rich rufous underparts and mostly black upperparts, with broad black streaks and the grey streaks less extensive than in *fuscata* which it most closely resembles in size. The bill of *O. a. smithersi* is 'mainly sepia' rather than red in the dry season (July–August), perhaps non-breeders; in this region the only breeding record of quailfinch is during the rains in February (Benson 1955).

Other plumage traits that differ between geographic populations of *Ortygospiza* include the intensity of the underparts coloration, and the width of barring on the breast and flanks. None of these traits varies distinctly between taxa (Table 1), except for the darker and more boldly barred *O. a. fuscocrissa* in Ethiopia, compared with quailfinch in adjacent regions. Size does not differ significantly in the samples available, except that *O. a. fuscocrissa* has longer wings and black-chinned *O. a. gabonensis* has shorter wings than the other measured quailfinch (Fry 2004; RBP unpubl.).

Bill colour

Bill colour was formerly reported to differ between black-chinned and white-chinned populations of *Ortygospiza* (Traylor 1963, White 1963). Benson (1955) proposed that this feature could be used to distinguish two species, red-billed *O. gabonensis* and dark-billed *O. atricollis*. In fact, during the breeding season all adult quailfinch photographed or with annotated specimens have red not dark bills, regardless of taxon and geographic location.

Bill colour changes with season; breeding-season males have the upper mandible bright red like the lower mandible (Immelmann *et al.* 1965, 1977a,

Traylor & Parelius 1967). Ten breeding males photographed or collected by RBP in 1995 in northern Nigeria (Jos, Bukuru), and a male in 1999 in The Gambia (Marakissa) and another in Dalaba, Guinea (*O. a. atricollis* and *O. a. ansorgei*, respectively) had bills ranging from partly red to uniformly red (Fig. 1). In Ethiopia, specimens of *O. a. fuscocrissa* have the bill red in November (FMNH 83878) and black in February (FMNH 83874); in birds taken in May, Heuglin (1863) described the bill as blackish above ('rostrum nigricante'). In Kenya, van Someren collected two *O. a. muelleri* at Lake Nakuru with a large white chin spot, white eye-ring, large testes (one bird), and uniformly 'coral red' bill (FMNH 203787 in October, FMNH 257714 in December). In Tanzania the holotype of *O. a. muelleri* was a male with a bright red bill ('leuchtend rot'; Zedlitz 1911). In aviaries, male *O. a. muelleri* observed as long as eight years had red bills in each breeding season (RBP); and Ruschin (1972) observed red bills year-round in east African *O. a. muelleri*. In the field, breeding-season birds in Natal, Zambia, Zimbabwe and Botswana also have red bills (Clancey 1965; M. P. S. Irwin *in litt.* 2000), as they do in other regions of Africa.

Juvenile quailfinch have dark bills. As the birds mature, the bills turn reddish, first on the lower mandible (*O. a. atricollis*, Garoua and Ngaoundéré, Cameroon, UMMZ 202407, 232473–75; *O. a. fuscata*, Angola, FMNH 84299, 84300; *O. a. gabonensis*, Congo-Brazzaville, FMNH 213747; observations of non-breeding and breeding *O. a. muelleri* in aviaries: RBP unpubl.).

Allopatry or sympatry of quailfinch taxa

Taxa of quailfinch are mainly allopatric. Near-sympatry between white-chinned ('*Ortygospiza atricollis*') and black-chinned ('*O. gabonensis*') quailfinch has been reported in four regions, yet none of these published reports involved known breeding sympatry. Quailfinch in some regions are seasonal in their local occurrence on floodplains and grasslands, and in the dry season they appear in areas where they are not known to breed. As a result of their seasonal movements, different taxa sometimes occur together.

Chapin (1954) reported two taxa in eastern Ituri, DR Congo, but he recognised only one species, *O. atricollis*. Chapin's report served as the recent basis for concluding that quailfinch comprise two sympatric species (Traylor 1963, 1968, Dickinson 2003). In fact, the birds were taken at different localities. On the Albertine escarpment near Bogoro the birds (*dorsostriata*) lacked white on the face and had the back more streaked black than birds at lower altitudes at Kasenyi (*ugandae*), as at Kasindi and elsewhere west of the Rift and south of Lake Edward. Birds at Bogoro were breeding in September; birds at Kasenyi and west of Lake Albert and Lake Edward were not breeding in January and May (AMNH, BMNH, FMNH). Bogoro specimens include one with ten feathers white at the base of the chin (AMNH 264434); in plumage intermediate between *dorsostriata* and *ugandae*.

The taxon *ugandae* has been considered a synonym of *dorsostriata* (Sclater 1930a, Friedmann & Loveridge 1937). The holotype of *ugandae* (FMNH 257709)

TABLE 1
Plumage and bill characters of quailfinch taxa (male)¹.

Subspecies	Region	Chin white	Throat white	Eye-ring white	Lores white	Back colour	Back streaked	Flanks colour	Belly colour	Bill colour ²
<i>ansorgei</i>	West	+,(0)	0	0,(+)	0	dark	no	chestnut	chestnut	red
<i>atricollis</i>	West-Central	+	+	0,+	0,(+)	brown	slight	chestnut	chestnut	red
<i>ugandae</i>	upper Nile, E	+	+	(0),+	0,+	brown	slight	tawny	tawny	-
<i>dorsostriata</i>	upper Nile, W	0,(+)	0,(+)	0,(+)	0	brown	some	tawny	tawny	-
<i>gabonensis</i>	W equatorial	0	0	0	0	dark	yes	whitish	whitish	red
<i>fuscata</i>	S-WC	0	0	0	0	blackish	yes	tawny	chestnut	red
<i>smithersi</i>	N Zambia	++	++	++	++	blackish	yes	tawny	chestnut	-
<i>fuscocrissa</i>	Ethiopia	++	++	++	++	brown	some	tawny	tawny	red
<i>muelleri</i>	S to EC	++	++	+,++	+,++	brown	slight	buff	buff	red
<i>pallida</i>	SC	++	++	++	++	pale	slight	buff	pale buff	red
<i>digressa</i>	SE	++	++	++	++	brown-grey dark	slight	buff	buff	red

¹In some taxa characters vary within a region; in Table 1 this variation is represented by two symbols, separated by a comma; that in parentheses is the less common; ²during breeding season.

from North Kavirondo has a small white chin spot and an incomplete, narrow white eye-ring, which extends around the lores to the bill. It otherwise is nearly identical to a bird with no white on the face (FMNH 118268) from Entebbe, identified as *dorsostriata*; its plumage is intermediate but more like *dorsostriata* than *O. a. muelleri* from southern Kenya (FMNH 257714). Van Someren (1922) noted that *ugandae* has white around the eye and on the chin, whereas *dorsostriata* does not; but male *dorsostriata* sometimes has a little white on the chin, and the back is more distinctly streaked. Finally, on the north shore of Lake Victoria near Entebbe some are intermediate in colour and pattern to the described taxa. Most specimens of quailfinch in Uganda have no notation of large gonads on their labels; and there is no evidence from either field observations or specimens that two taxa breed assortatively in sympatry (Chapin 1954: 500; AMNH, FMNH, BMNH).

In Uganda both *O. gabonensis* and *O. atricollis* were reported at Semliki Wildlife Reserve in a birding guide (Rossouw & Sacchi 1998), but not in the Uganda bird atlas (Carswell *et al.* 2005), which remarked on the difficulty of distinguishing these two forms. M. Wilson (Semliki contributor to Rossouw & Sacchi 1998) has seen only black-chinned birds there; and when he and RBP observed birds in August 2006, only black-chinned birds were seen on Semliki Flats. Semliki is west of the eastern escarpment of Lake Albert; Murchison National Park is east of the same escarpment. These observations do not support the occurrence of two taxa at the same locality. In Uganda one series of reports appears to refer to a single population with continuous plumage variation (van Someren

1921a,b, 1922). In Uganda no seasonal breeding records are known for black-chinned quailfinch, and only one record (June) for white-chinned quailfinch (Brown & Britton 1980, Carswell *et al.* 2005).

Other published reports of sympatric quailfinch are from Zambia, but none involved documented breeding or local sympatry in the breeding season. In north-east Zambia, Benson (1955) noted two taxa of quailfinch, but not at the same locality during the breeding season. *O. a. smithersi* was breeding in the south Bangweulu region in February; both *O. a. smithersi* and *O. a. fuscata* were taken at Abercorn (Mbala), the former on seasonal drying floodplains and the latter on permanently wet grasslands or sponge dambos, and Benson suggested the birds have different habitat preferences.

Second, in north-central Zambia near Ndola and the North Kafue basin, both black-chinned and white-chinned birds have been reported, but the identifications of white-chinned birds are in question. In this region, black-chinned quailfinch are common, and all birds observed in the field and aviaries in this region were black-chinned (Benson & Irwin 1967). At Itawa, Ndola, District Commissioner and resident collector E. L. Button noted for *fuscata*, on the label of specimen FMNH 206576 taken on 3 September 1944, they have 'been in just over a week, now plentiful, found nest with incubated eggs in February and in March'. Penry (1986) found only *O. a. fuscata* breeding at Chingola near Ndola.

Third, in north-west Zambia both white-chinned *muelleri* [*'polyzona'*] and black-chinned *fuscata* occur in November (Benson 1960), but quailfinch do not breed there until the rains in January (White 1946, Benson *et al.* 1971). In the same region Traylor (1963) reported black-chinned and white-chinned birds, but they were in moult and not breeding at this time, November, and were taken in different areas; *fuscata* on the damp floodplain of the perennial South Lueti River, *muelleri* on the Liuwa Plain with only scattered surface water at the end of the dry season (Traylor 1965; FMNH).

Other evidence of movements by quailfinch populations in certain areas is their seasonal occurrence and absence. Quailfinch are regarded as local residents in some areas, near permanent water at the edge of the Kafue Flats, Lochinvar National Park, southern Zambia (Dowsett 1966), but at Mazabuka, within 10 km of the Kafue Flats and 50 km of Lochinvar, they are seasonal visitors during the rains (Winterbottom 1959). They are absent near Choma, southern Zambia, in June–October (Aspinwall 1980). White-chinned quailfinch in Zambia are more widespread and liable to 'considerable local movements depending on habitat conditions' than black-chinned quailfinch, though for the latter too 'some minor seasonal movement remains probable' (Benson *et al.* 1971). In Malawi they undertake local movements and in some areas are seen only in flocks (Benson 1953, Dowsett-Lemaire & Dowsett 2006). In parts of Zimbabwe they undergo 'seasonal wandering' (Irwin 1981), and they are absent in some seasons in the highlands of south-east South Africa (Clancey 1996). In Kenya they are either resident or seasonal, as they appear in some areas

during or after a wet season (both flocks and possible breeders) (Lewis & Pomeroy 1989).

In Zambia and east Africa, the plumages of male quailfinch taken in regions between white-chinned and black-chinned populations are intermediate. (1) In north-west Zambia (Barotseland) on the Liuwa Plain, birds taken by Traylor (1965; FMNH) and first reported as *minuscule* are intermediate between the paler-backed, less streaked *muelleri* of southern Zambia and northern Botswana, and the darker, more streaked *fuscata* in north-west Zambia. Traylor's birds have the white chin of *muelleri* but the white eye-ring is narrower. (2) As in Benson (1955), *smithersi* of north-east Zambia is a mosaic intermediate between the white-chinned '*polyzona*' [= *muelleri*] to the south and the black-chinned *fuscata* to the north. (3) The indistinctly streaked back and the incomplete and narrow white eye-ring of *ugandae* in Uganda are intermediate between traits of *dorsostriata* in the west and *muelleri* in the east. A few recognised as *dorsostriata* in Uganda at Mpumu and Kigambo have some white on the chin (Cowles 1957; BMNH). Sclater (1930a) considered *ugandae* a synonym of *dorsostriata*, whereas Cowles (1957) and Rand *et al.* (1959) suggested that *dorsostriata* is a synonym of *gabonensis*. (4) In the north-west Congo and Gabon, birds identified as *gabonensis* include one specimen with white on the chin (Cowles 1957). More field work may reveal additional information about movements and local variation of quailfinch populations.

In summary, of the records of two taxa of quailfinch in sympatry, in neither Ituri or in Uganda were they in local breeding sympatry. In north-west Zambia they were not in local sympatry and were not seen together in the breeding season, and in north-east Zambia birds were taken in different habitats and not during the breeding season (mainly January–March: Benson *et al.* 1971, Fry 2004), and some may have been seasonal non-breeding visitors. Quailfinch are mainly allopatric, and only in parts of Zambia were they said to 'occur on the same ground' (Britton 1980), but not in the breeding season. There is no direct information that the white-chinned and black-chinned quailfinch of east, central and southern Africa co-occur without interbreeding. Quailfinch are seasonal in occurrence in some areas, absent until the rains, then appear and breed; they are locally migratory, and sometimes occur outside their breeding area. Furthermore, those in both north-east and north-west Zambia (*smithersi* and '*minuscule*') are intermediate between the nearest other populations to the north and south.

mtDNA phylogeny

We obtained sequences of the mitochondrial ND2 gene for 12 specimens representing nearly all recognised taxa across the geographic range of the species (Table 2). We used the following criteria to select specimens for genetic information: 1) the most recent specimens that were available for molecular sampling; mtDNA deteriorates with age and the more recent specimens can be amplified and sequenced with greater accuracy (Payne & Sorenson 2003, Sefc *et al.*

2003, 2006); 2) in North American museums; and 3) voucher specimens were compared with other series to validate the identification.

Laboratory methods were identical to previous studies (Sorenson *et al.* 2004, Sorenson & Payne 2005) except that estrildid-specific internal primers were used to permit the amplification and sequencing of smaller DNA fragments from older specimens. Primer pairs for tissue samples were L5216rv and H5766rv (Sefc *et al.* 2003), and L5758rv (5'-GGNGGNTGAATRGGNYTNAAYCARAC-3') and H6313rv (5'-ACTCTTRTTTAAGGCTTTGAAGGC-3'). Additional internal primers included L5476.E (TTYKCYAGYATRAYYAAYGCATG), H5481 (TGNGTRATRTCAYTGDCGNT), L6007.E (TCHCTNGCAGGNYTNCNC), and H6022.E (GTHAGTTCTTGGATGATNAGTCATTTTGG); primer names refer to the strand and position of the 3' base in the *Gallus gallus* mtDNA sequence (Desjardins & Morais 1990). ND2 sequences for the three *Amandava* species and two *Amadina* species were used as the outgroup. Phylogenetic analysis based on parsimony and maximum likelihood (ML) produced identical results. The latter analysis used a general time-reversible model of nucleotide substitution with an estimated proportion of invariant sites; model chosen based on AIC value as calculated in MODELTEST (Posada & Crandall 1998) using parameters estimated from the data. Genetic distances reported below are ML estimates based on the same model and parameter values.

These data produced a single well-supported monophyletic tree (Fig. 2) with three distinct and genetically divergent clades. (1) A clade including west African

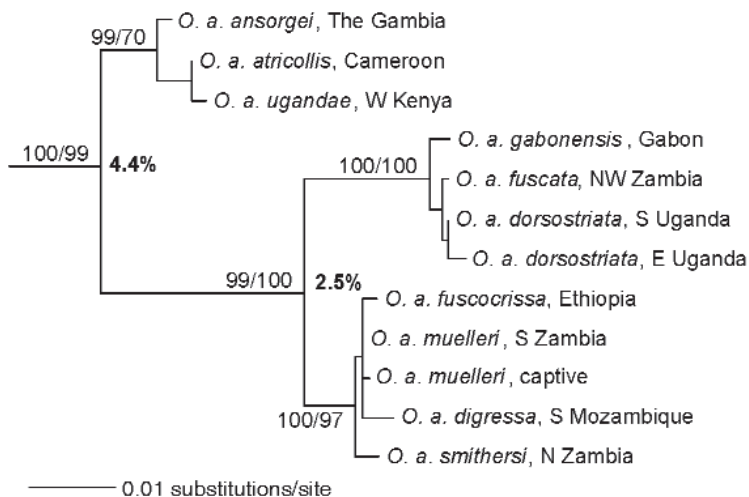


Figure 2. Phylogeny of quailfinch mitochondrial DNA lineages based on complete sequences of the ND2 gene (outgroup taxa not shown). Branch lengths are proportional to maximum likelihood (ML) estimates of number of substitutions per nucleotide. The mean ML genetic distance across the two basal nodes is shown. Parsimony and ML bootstrap values are shown for the primary groups on the tree.

TABLE 2
Sources and voucher specimens of genetic samples.

Taxon	Locality	Year	Tissue ^a	Voucher specimen
<i>ansorgei</i>	Marakissa, The Gambia	1996	1	UMMZ 234175
<i>atricollis</i>	Ngaoundere, Cameroon	1992	1	UMMZ 232472
<i>ugandae</i>	Mumias, North Kavirondo, western Kenya	1917	2	FMNH 257709
<i>muelleri</i>	captive (parents known)	1993	1	UMMZ 233156
<i>muelleri</i>	Lochinvar National Park, southern Zambia	1972	2	UMMZ 219735
<i>digressa</i>	Beira, Mozambique	1965	2	UMMZ 211483
<i>fuscocrissa</i>	Gojam, Ethiopia	1927	2	FMNH 83874
<i>dorsostriata</i>	Entebbe, eastern Uganda	1915	2	UMMZ 94816
<i>dorsostriata</i>	Masaka, southern Uganda	1916	2	FMNH 91697
<i>fuscata</i>	Kawambwa, northern Zambia	1953	2	UMMZ 222394
<i>gabonensis</i>	Ogooué-Maritime, Gabon	1951	2	FMNH 210584
<i>smithersi</i>	Abercorn, northern Zambia	1954	3	AMNH 648202

^a Tissue used for genetic analysis. 1: muscle tissue; 2: single feather from specimen; 3: toe pad tissue from specimen.

ansorgei, *atricollis* and *ugandae* is basal to the other two. (2) Black-chinned taxa in central Africa, *gabonensis*, *fuscata* and *dorsostriata*, form a second clade, and (3) the white-chinned taxa occurring from eastern to southern Africa (*fuscocrissa*, *muelleri*, *smithersi* and *digressa*) form a third clade. Relatively large genetic distances between clades (2.5–4.4%) combined with limited intra-clade differentiation suggest long-term historical isolation of quailfinch populations in different regions, dating perhaps a million years or more (e.g. Fleischer *et al.* 1998, Arbogast *et al.* 2002, 2006).

The results on the basis of genetic monophyly are consistent with the possibility of one, two or three species of quailfinch. However, if two species were recognised, these would be west African *O. atricollis* (Vieillot, 1817) (clade 1 in the gene tree) and central and east African *O. fuscocrissa* Heuglin, 1863 (the oldest-named taxon in clades 2 and 3 in Fig. 2), and this clade would include black-chinned *gabonensis*. These two clades do not correspond to any previously suggested arrangement for quailfinches. The main conclusion from the genetic data is that we reject the recognition of two species, one with a white chin and one with a black chin. The three clades are consistent with the three *Rassengruppen* of a single species of quailfinch as described by Wolters (1975) and recently recognised as three species (Fry 2004). The mostly ‘white-chinned’ quailfinch of west Africa are basal to a clade comprising black-chinned quailfinch of central Africa and spectacled quailfinch of eastern and southern Africa. In conclusion, the genetic data are consistent both with one species (*O. atricollis*) and with three species (*O. atricollis*, *O. fuscocrissa*, *O. gabonensis*), and do not support the hypothesis of two species (*O. atricollis* and *O. gabonensis*).

Song

Vocalisations of quailfinch include a short contact-call, a harsh *klek* that rises quickly to 3–4 kHz and persists for *c.*0.07–1.0 sec, and a song (here, ‘loudsong’) characterised by a harsh pattern of irregularly alternating notes given in phrases that repeat with some variation, as *klik klak kloik kluk klek* (Immelmann *et al.* 1965, Goodwin 1982, Nuttall 1993, Payne & Payne 1994). The loudsongs continue for up to several seconds. The loud *klek* contact-calls and *klik klak kloik* loudsongs develop from modulated calls given by young after they fledge and are heard in flocks with juvenile quailfinch (Payne & Payne 1994). Female loudsongs are short and discrete (Nuttall 1993; RBP unpubl.), whereas male loudsong phrases repeat over time with minor variations of the sequence of notes in the *klik klak kloik* motifs (Fig. 3; compare with Nuttall 1993, Fig. 5, where labeled as ‘contact phrase’ rather than ‘song’). These same elements of loudsong are also given as contact-calls and rattling flight-calls. Loudsongs are usually given on the ground. In RBP’s aviaries, the birds began loudsong well before bright lights-on or sunrise. Shorter versions of loudsong also are given on the ground in the field and in the flight aviaries where the birds bred successfully. In Fig. 3, according to the field recordists’ notes (<http://www.bl.uk/collections/sound-archive/cat.html>, viewed 9 November 2006), songs a, b, d, e, f and j were of perched birds, as probably was song k (the recordist ‘saw it well’). Songs c, g, h and i lack data on context. In both form and context, most vocalisations in Fig. 3 are loudsongs, either complete or incomplete (*contra* Nuttall 1993, 2005, who did not recognise these as ‘song’); the other vocalisations consist of the same kinds of shorter calls. Calls and songs have the same acoustic elements in several other estrildids as well (e.g., Immelmann 1969, Nicolai 1964, Güttinger 1970, Zann 1975, 1976, Payne & Payne 1994).

Loudsongs of quailfinch are similar throughout their distribution. The *klik klak kloik...* songs of ‘white-chinned’ birds in The Gambia, Nigeria and Cameroon (Barlow *et al.* 2002; British Library Natural Sound Archive [NSA]; RBP), Murchison National Park, Uganda (RBP), southern Zambia (Stjernstedt 1993; NSA) and South Africa (Nuttall 1993; NSA), and in ‘black-chinned’ birds in northern Zambia (Stjernstedt 1994; NSA) are all similar. The loudsongs have hoarse notes given in irregular sequence, sometimes the first higher and the last lower; one long, the second mid length, and the third short (Fig. 3). Penry’s (1986) *take it away* and *drink* descriptions of flight-calls of black-chinned birds in northern Zambia apply equally to white-chinned *O. a. muelleri* elsewhere in Zambia and to white-chinned *O. a. atricollis* in Cameroon and Nigeria (Payne & Payne 1994; Fig. 3). *Take it away* is also a motif in the loudsong *klik klak kloik*. In Ethiopia, the songs of white-chinned *O. a. fuscocrissa* were described in similar terms, ‘... die Stimme ist ein ziemlich unmelodisches Pipen, das oft schnarrend klingt und weit weniger fein, als bei den vorhergehenden’ (Heuglin 1863). In north-west Zambia, when a black-chinned male quailfinch ‘*O. gabonensis*’ was collected, ‘the call did not differ in any way from that of *atricollis*’ (S. Keith *in* Benson & Irwin 1965). Quailfinch in the



Figure 3. Loudsongs of quailfinch *Ortygospiza atricollis*. (a) *O. a. ansorgei*, captive (UMMZ 232576); (b) *O. a. atricollis* <> *ansorgei*, Sifoe, The Gambia (Barlow *et al.* 2002; UMMZ 234175); (c–d) *O. a. atricollis*, c, Zaria, Nigeria (NSA 3635); d, Rayfield, Nigeria, 3 November 1995 (RBP 49A); (e–g) *O. a. muelleri*, e, male b/b, captive (RBP 1996 tape 70b, UMMZ 236155); f, female r/r, captive (RBP 1991 tape 20b, UMMZ 234138); g, South Africa, Kruger National Park (Gillard 1987); (h–j) *O. a. fuscata*, Itawa, Ndola region, northern Zambia (h, NSA 26681; i, NSA 26692; j, NSA 81087; k, NSA 25769).

Ndola region of northern Zambia (including Chingola and Itawa Swamp) were identified as black-chinned *fuscata*. Recordings of these birds were examined (NSA 34109, 34110, 25769, 26681, 26692, 81085, 81087). A bird recorded at Itawa Swamp on 4 May 1991 was 're-identified' as (white-chinned) '*O. atricollis*' on an edited copy of NSA 25769; and this edited copy is suspect, both for acoustic parameters and for the re-identification. Chappuis (2000) reported that calls of black-chinned birds at Itawa, near Ndola, Zambia, were more shrill than white-chinned birds, but no difference is evident in the unedited NSA recording or in published cassettes (Stjernstedt 1993, 1994). The modulated 'shrill' sounds in certain recordings (not all calls are shown in Fig. 3) appear to be calls of juveniles (Payne & Payne 1994).

The pitch of calls may vary with excitement level. Penry's (1986) idea of species-distinctive pitch and modulation in calls of black-chinned and white-chinned quailfinch is not supported by his audiospectrograms, nor do differences appear in larger series of recordings, where both black-chinned and white-chinned birds give loudsongs either over or under 4 kHz (Fig. 3). Song recordings of quailfinch vary in the presence and loudness of an undertone of the loud trace at 4 kHz. The occurrence of sounds above and below the fundamental frequency (the loudest trace on the audiospectrogram) appear to vary with loudness of the call, the excitement of the bird, and the recording conditions (overtone often occur in 'over-recorded' samples with settings of recorder sensitivity producing artefacts, and undertones are not prominent in birds recorded at close range in captivity). Additionally, the undertones appear more often in notes of 4 kHz or higher than in lower notes. The overtone and undertone amplitudes at different frequencies are easily distorted, and the relative amplitudes may vary with recording conditions (Wickstrom 1982). Acoustic harmonics vary with a male's distance to his mate not only in quailfinch (Nuttall 1993) but also in another estrildid, *Poephila acuticauda* (Zann 1975). This modulation of song overtones may be effected by active neural control of resonance filtering (Beckers *et al.* 2003). In consequence, we do not emphasise the acoustic overtones and undertones; we merely point to their occurrence and prominence in the quailfinch.

A third vocalisation is a soft 'burbling' song of irregularly repeated downslurred notes of short (<0.05 s) duration. This soft 'burbling' or 'scissors-grinding' song is used in sexual behaviour at close range and at the nest. Soft song is delivered at an amplitude *c.* 10–15 dB lower than loudsongs (Payne & Payne 1994). Soft songs are similar in west African and southern African quailfinch (*O. a. ansorgei* and *O. a. atricollis*, and *O. a. muelleri*) (Nuttall 1993, Payne & Payne 1994); no recordings of soft songs are available for black-chinned quailfinch.

Nestling mouth pattern and colour

Nestling mouth markings have been used to diagnose closely related estrildid finches (Nicolai 1987). Nestlings and fledglings have distinctive mouth patterns and colours they display to the adult when begging for food. These may offer visual

signals that aid in behavioural recognition and parental care. In some estrildids, young with atypical mouths receive less food and survive less well than young with the species-typical mouth patterns and colours (Immelmann *et al.* 1977b, Payne *et al.* 2001). For this reason, nestlings with different mouth patterns and colours might not have the visual signals necessary for parental care. If nestling mouth patterns and colours differed between birds, lower fitness of ‘hybrid’ offspring might present a barrier to successful interbreeding (Payne 2005).

In nestling and fledgling quailfinch the mouth has three greenish-blue balls each side of the gape, a black gape between them, and a yellowish palate with six black spots, a pattern of colours and spots that differs from all other estrildids (Payne 2005). Recently fledged young in a family group of *O. a. atricollis* photographed in Cameroon at Ngaoundere in 1992 (UMMZ) have the same mouth colours and patterns as nestlings throughout the range of white-chinned quailfinch in Nigeria (*O. a. atricollis*), Kenya and South Africa (*O. a. muelleri*) (Serle 1938, van Someren 1956, Schifter 1964, Kunkel 1966, Nuttall 1992, Payne & Payne 1994, Payne 2005). Mouths and palates of young *O. a. fuscata* of the black-chinned *gabonensis* complex are apparently the same as in the other known quailfinch (Chapin 1954, Payne 2005). There is no evidence of different nestling begging signals and mouth colours between quailfinch taxa that would affect whether a brood is reared successfully.

Discussion

To assess systematic status of quailfinch taxa, we combine information on morphology, distribution, behaviour and molecular genetics as analysed in a phylogenetic context. The uniformity across quailfinch taxa in song and bill colour of adults, and in the mouth colours and patterns of nestlings, indicates a single species, *Ortygospiza atricollis*. In addition, no geographically neighbouring taxa of quailfinch are known to breed assortatively in sympatry, whereas in many cases they intergrade morphologically: *atricollis* with *ansorgei* and *ugandae*; *ugandae* with *dorsostriata*; *smithersi* with *fuscata* and *muelleri*; and *fuscata* with ‘*minuscula*’ and *muelleri*. The migratory behaviour of some populations may lead them to co-occur in the non-breeding season, but reported cases of sympatry involve birds that breed in different localities; for example, in Ituri, breeding populations of *ugandae* and *dorsostriata* are 50 km apart (Chapin 1954). Plumage variation in *Ortygospiza* (Table 1) indicates only one or two character differences between neighbouring taxa in most instances. The gradation of plumage between taxa, the lack of known local breeding sympatry, and the consistency of songs across taxa are consistent with previous conclusions of a single species (Friedmann & Loveridge 1937, Chapin 1954, Benson 1955, Traylor & Parelius 1967). These reports, like those of museum workers (Sclater 1930a, Wolters 1975, 1985), recognised quailfinch as a single species because the variation in plumage pattern and colour between the black- and white-chinned forms is no greater than variation between subspecies.

With genetic data, one approach to the recognition of species is the genetic distance between clades: the percentage of nucleotide sites that differ between

sequences, sometimes based on a single gene and on an arbitrary ratio of the variation within and between nominal species (Hebert *et al.* 2004). However, there is no agreement in genetic distance across sister species of birds. For example, the arbitrary threshold noted above is poor in predicting species status in other estrildids, in which family we find numerous examples of both small genetic distances between sister species (e.g., <1.0%) and deep genetic distances within a species (up to 6%; Sorenson *et al.* unpubl.). Genetic distances vary greatly among different lineages and the level of difference between species in one lineage does not predict the difference in other lineages (DeSalle *et al.* 2005). In other animals, the error rate of recognising or not recognising known species on the basis of genetic distance is as great as 30% (Meyer & Paulay 2005, Hickerson *et al.* 2006, Meier *et al.* 2006).

A phylogenetic analysis of genetic data in quailfinch suggests the recognition of either one or three clades as species. In general, though many clades are species, not all are so (i.e., some clades distinguish families and genera, e.g. Sorenson & Payne 2005, whereas at the other end of the scale, some mitochondrial lineages simply trace maternal kinship, e.g. Avise 2004, Payne *et al.* 2002). Furthermore, not all genes differ between related species (Avise 2004). For example, in *Vidua* finches, several species share the same mitochondrial gene sequences, due to incomplete lineage sorting between species that derived from a polymorphic ancestor, and to hybridisation (Sorenson *et al.* 2003). In *Poephila* finches, different nuclear genes provide discordant estimates of phylogenetic relationships between species. Nevertheless, mitochondrial gene trees are concordant with a majority of nuclear gene trees from the same birds (Jennings & Edwards 2005). In addition, although ND2 is slightly more variable than ND3 and *Cyt-b*, their nucleotide sequences give nearly identical phylogenetic results in other songbirds (Zink & Weckstein 2003). These observations support the use of mtDNA at the species level in the finches, with one variable sequence (ND2) being representative of other such sequences (Jennings & Edwards 2005, Edwards *et al.* 2005).

Within the framework of an integrative species concept, the more important question is whether genetic differences are congruent with morphological and/or behavioural differences between taxa. Additional information is necessary before we can determine the biological and evolutionary significance of a clade (Avise 2004). For example, does a clade correspond to birds with the same morphology, the same songs, and a geographic distribution that overlaps that of a closely related population—three criteria that are necessary to consider in determining at which level a clade corresponds to a species. Because collectively the quailfinch are monophyletic, they form a pattern of ancestry and descent, a generally necessary condition but not a sufficient condition for recognising a species. Certain clades are recognisable within the collective clade, yet the lack of a mutually exclusive and morphologically diagnosable set of morphological characters (Table 1) suggests it is inappropriate to recognise any one included clade as a species. The idea of two quailfinch species is unsupported by the genetic data, because the lineages in

'white-chinned' taxa are paraphyletic, as are the taxa in '*atricollis*' as recognised by White (1963). Based on his interpretation of our genetic phylogeny, Fry (2004) divided quailfinch into three species diagnosable by the presence or absence of a few key plumage characters; conspicuous white spectacles ('*O. fusco-crissa*'), a lack of white on the chin and face ('*O. gabonensis*'), and presence of a white chin but no prominent white on the face ('*O. atricollis*'). However, these characters vary both within and between the three lineages recovered in a phylogenetic analysis of mtDNA nucleotide sequences (Table 1, Fig. 2), and there is morphological evidence of gene flow in regions where the different plumage taxa almost meet. Although the genetic data suggest that quailfinch populations were isolated in three different regions for a significant part of their history, the contact in current distributions and observations of birds intermediate in plumage do not support a conclusion that the three clades correspond to species-level lineages that are on independent evolutionary trajectories. Of course the tree topology also suggests distinct genetic lineages or independent evolutionary pathways, but we cannot know the future or whether the lineages will combine again before they become extinct; we can only interpret the past from data that link the birds at the present time (de Queiroz & Donoghue 1988, O'Hara 1994, de Queiroz 1998).

When results from single genes yield unresolved phylogenetic trees, it is desirable to determine the phylogenies of multiple genes. In the present case, the gene tree based on ND2 gene sequences is well supported, and adding more mtDNA data is unlikely to change our inferences. It might be of interest to recover genetic sequence data within a large sample; that is, to test the robustness of the two most basal branching points in the phylogenetic estimate in Fig. 2. And data from nuclear loci would be of interest, but many specimens in our study range in age up to 90 years. Obtaining nuclear sequence data from these older specimens would require a great deal of additional effort and expense; and, given the relatively limited sampling in the field, particularly from regions of contact between subspecies, it is not clear to us that these data would add much to the present analysis. More extensive and intensive sampling in zones of overlap would be helpful, as with *O. a. ugandae* to test its association with *O. a. atricollis*, *O. a. dorsostrata* and *O. a. muelleri*: recently collected specimens are simply unavailable. Additional geographic sampling and analysis of nuclear loci also would provide a better understanding of the historical structure and current extent of genetic exchange between populations, and a large sample would be necessary to distinguish between variation within and between taxa. Presumably, geographic isolation of quailfinch populations in the past explains the three divergent genetic clades. Though subsequent expansion and shifts in distribution have probably brought them back into contact in certain areas, their contemporary distributions are largely non-overlapping.

The morphological variation within and among quailfinch taxa, the absence of documented breeding sympatry, the seasonal movements of birds between breeding and non-breeding areas, and the similarity in songs all suggest gene flow between

adjacent populations and the lack of divergence in signaling systems that would occur in speciation. Together with the molecular phylogeny these observations lead us to conclude that quailfinch are best recognised as a single, geographically variable species, *O. atricollis*.

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Addresses: Prof. Robert B. Payne, Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109–1079, USA. Prof. Michael D. Sorenson, Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts 02215, USA.