

THE GRAY HAWK (*BUTEO NITIDUS*) IS TWO SPECIES

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Abstract. We compared the plumage, morphology, and the alarm call of two taxa of the Gray Hawk (*Buteo nitidus*) from north and south of a distributional gap in the species' range in Costa Rica. We found all age and sex classes completely distinguishable on the basis of several discrete plumage features. Three of four age and sex classes were diagnosably distinct by measurements of external morphology alone, and the two taxa had diagnosably different alarm calls. On the basis of the level and stability of morphological differentiation, and consistent with prior work suggesting substantial genetic differentiation between the two taxa, we recommend they be recognized as full species, *B. nitidus*, the Gray-lined Hawk, south of the distributional gap in Costa Rica, and *B. plagiatus*, the Gray Hawk, north of the gap.

Key words: *Buteo nitidus*, *Buteo plagiatus*, Gray Hawk, Gray-lined Hawk, species, taxonomy.

Buteo nitidus Comprende Dos Especies

Resumen. Comparamos el plumaje, la morfología y la voz de alarma de dos taxones de *Buteo nitidus* distribuidos respectivamente al norte y al sur de un hiato en la distribución de la especie ubicado en Costa Rica. Encontramos que todas las clases de edad y sexo pueden distinguirse completamente sobre la base de varias características discretas del plumaje. Fue posible diferenciar en forma diagnóstica tres de cuatro clases de edad y sexo sobre la base de medidas de la morfología externa. Ambos taxones pudieron diferenciarse en forma diagnóstica sobre la base de sus voces de alarma. Teniendo en cuenta el nivel y la estabilidad de las diferencias morfológicas, y en concordancia con trabajos previos que sugieren una diferenciación genética sustancial entre los dos taxones, recomendamos que éstos sean reconocidos como dos especies diferentes: *B. nitidus*, distribuido al sur del hiato en Costa Rica, y *B. plagiatus*, al norte de éste.

INTRODUCTION

The Gray Hawk (*Buteo nitidus*, hereafter *B. n. nitidus*) was described by Latham (1790) as *Falco nitidus*, on the basis of a specimen from French Guiana. Subsequently, Schlegel (1862) described *Asturina plagiata* (hereafter *B. n. plagiatus*) on the basis of a specimen from Veracruz, Mexico. Schlegel considered *B. n. plagiatus* a species distinct from *B. n. nitidus* because it was larger, had more robust tarsi and feet, and had more tail bands. In their review of North American birds, Baird et al. (1874) concluded the two taxa were climatic races of the same species, and this view has largely prevailed since (Bierregaard 1994, Ferguson-Lees and Christie 2001, American Ornithologists' Union [AOU] 2008). However, not all ornithologists have agreed with this treatment. Miller and Griscom (1921), van Rossem (1930), and Sibley and Monroe (1990) treated the taxa as species. Friedmann (1950), Stresemann and Amadon (1979), and the AOU (1983) treated them as conspecific but commented that they might be full species. Johnson and Peeters (1963), in their detailed analysis of plumage variation of woodland hawks, concluded that "striking differences between the [northern and southern] races [of the Gray Hawk]

are obvious." These authors noted that the plumage discontinuity coincides with a gap in the species' distribution in Costa Rica, which is also described by Stiles and Skutch (1989). Blake (1977) presented measurement data for all recognized subspecies of the Gray Hawk, but he did not analyze the measurement differences between taxa quantitatively. He treated *B. n. nitidus* and *plagiatus* as conspecific but noted that many consider them separate species. Millsap (1986) and Riesing et al. (2003) evaluated morphological and genetic differences between the two taxa, respectively, and concluded they differ markedly.

Despite these various past treatments, there is no comprehensive published analysis of plumage, measurement, and vocal data for the Gray Hawk on which a decision regarding the species-level status of the two taxa can be based (Banks et al. 2006). In this paper we examine and compare plumages, morphology, and vocalizations of *B. n. nitidus* and *B. n. plagiatus* to address this shortcoming. Consistent with findings of previous investigators, particularly the recent mitochondrial DNA (mtDNA) work of Riesing et al. (2003), we found that the taxa are diagnosably distinct. On the basis of our review and analyses, we recommend that these taxa be treated as separate species.

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METHODS

We examined the plumages and took measurements of 405 specimens of *B. n. nitidus* and *B. n. plagiatus* in the collections of the American Museum of Natural History (AMNH), National Museum of Natural History (USNM), Museum of Comparative Zoology at Harvard (MCZ), University of Kansas Museum of Natural History (KMNH), Delaware Museum of Natural History (DMNH), and the Field Museum of Natural History (FMNH) (Appendix A). For analyses, we assigned specimens from localities south of the species' distributional gap in Costa Rica to *B. n. nitidus* ($n = 141$) and those from localities north of the gap to *B. n. plagiatus* ($n = 264$). Our sample included a full representation of described subspecies, although none of these subspecies are likely diagnosably distinct at levels that warrant such recognition (Millsap 1986). Blake (1977) recognized three subspecies across the range of what we call *B. n. nitidus*, and our sample of this taxon included 39 specimens from the range he ascribed to *B. n. blakei*, 81 from his range for *B. n. nitidus*, and 21 from the range he ascribed to *B. n. pallidus*. Blake (1977) only recognized one subspecies from the range of our *B. n. plagiatus*, but Miller and Griscom (1921) described *B. n. micrus* from Central America, and van Rossem (1930) described *B. n. maximus* from northern Mexico and the southwestern United States. Our sample included 95 individuals from the range van Rossem (1930) ascribed to *B. n. maximus* and 66 from the range Miller and Griscom (1921) ascribed to *B. n. micrus*. Locality information for two specimens was insufficient for the individuals to be assigned to a subspecies.

We did not take all measurements on every specimen, so sample sizes for the different variables and analyses vary. On adult specimens, we noted the presence or absence of distinctive barring on the crown, nape, back, scapulars, and rump; we measured the width of the second (proximal) white band across the right central rectrix (perpendicular to the shaft) and the width of the rectrix, and counted the number of rectrices on the right side of the tail (six total) with unbroken second and third white bands (bird topography follows Blake [1956] throughout). On juveniles, we recorded the general color pattern of the plumage on the crown (primarily light, streaked, or dark) and primaries (light interspaces on webs of outer primaries primarily white or primarily buff) and the pattern of markings on the breast, belly, and thighs (streaked, barred, spotted, or unmarked). Additionally, we counted the number of dark bands on the dorsal surface of the tail. We selected these plumage characters (after examination of >100 specimens) because we found them to be homogeneous within local populations but variable over the range of the species.

Measurements taken were (1) culmen length (chord from distal rim of cere to tip of bill); (2) maxilla depth (height from distal rim of cere at the culmen to the commissure); (3) wing

length (flattened); (4) tarsus length (from the posterior center of the tibiotarsal–tarsometatarsal joint to the base of the center toe at the flexion point); (5) tarsus width (anterior–posterior width at the junction of the third and fourth distal undivided scutes); (6) hind claw (chord); (7) center toe (length, excluding claw); and (8) tail (length between central rectrices from point of insertion to tip). Specimens on which all eight measurements could not be obtained were excluded from multivariate analyses. In addition, we measured the extension of the primaries beyond the secondaries on folded wings of 61 specimens in the collection of the FMNH.

We have observed both taxa in their respective ranges during >1000 hr of field work and have taken >450 photographs of both taxa. We studied these photographs and others provided to us by other photographers to develop field marks to distinguish the taxa in the field. We excerpted and include here the color illustration depicting field marks of both taxa, prepared by J. Schmitt for a projected field guide to the raptors of Mexico and Central America (Fig. 1).

Buteo n. nitidus and *B. n. plagiatus* have two primary vocalizations, a three-note call used primarily during the breeding season and a single-note alarm call (Bibles et al. 2002). There are few recorded examples of the three-note call, so we focused our analysis on the single-note alarm call. Using Raven Pro 1.3 (<http://www.birds.cornell.edu/brp/raven/ravenversions.html>) with default settings, we examined all digitized recordings of *B. n. nitidus* and *B. n. plagiatus* alarm calls available at <http://www.xeno-canto.org/> (XC; last visited 5 September 2010) and provided to us by staff at the Macaulay Library (ML) at Cornell University (<http://macaulaylibrary.org/index.do>, last visited 5 September 2010). We eliminated some calls that we suspect were misidentified, that were of poor quality, or that were obviously atypical. For the remaining 25 calls of *B. n. nitidus* and 8 of *B. n. plagiatus* (Appendix B), we selected the first typical alarm note that was suitable for numerical analysis in each recording, and we created a spectrogram for the piece of each selection that contained the full note. We created spectrograms with the short-time Fourier transformation in Raven Pro 1.3 with the time scale set to 3.05 sec, frequency position to 500 Hz, and frequency scale to 11000 Hz per line. We increased brightness and contrast to 60% to 75% to improve accuracy in identifying the start and end points of the notes. On each spectrogram we selected a rectangle containing the full length of the note and leaving out any trailing echoes, bracketing the range from 1 to 10 kHz (± 25 Hz) to limit the effect of different frequency responses from microphones of varying qualities. For each note we measured the following characteristics: (1) peak frequency, the frequency of peak power within the selection; (2) time, the duration of the audible part of the note; (3) center frequency, the frequency that divided the selection into two frequency intervals of equal energy; (4) bandwidth of the interquartile range, the difference between the frequencies of the first and



FIGURE 1. Plumage differences between *B. n. nitidus* and *B. n. plagiatus* (see Table 1 for a description of major differences) where 1 is *B. n. nitidus*; 2 is *B. n. plagiatus*; a, adult in flight, ventral view; b, adult in flight, dorsal view; c, juvenile in flight, ventral view; d, juvenile in flight, dorsal view; e, adult, perched; f, juvenile, perched.

third quartiles (the frequencies that divided the selection into two ranges containing 25% and 75%, and 75% and 25%, of the energy in the selection, respectively); (5) duration of the interquartile range, the difference between the times of the first and third quartiles (the points in time that divided the selection into two ranges containing 25% and 75%, and 75% and 25%, of the energy in the selection, respectively); and (6) pitch-drop position, the proportion of the note emitted before there was a visible, sudden drop in pitch (scored as 0 to 1.0, with 0 for notes with no sudden drop in pitch).

STATISTICAL ANALYSES

Females of *B. n. nitidus* and *B. n. plagiatus* are substantially larger than males (Snyder and Wiley 1976), so we analyzed measurements for sexes separately. Preliminary analysis indicated that tail lengths of adults and juveniles differ, therefore we treated the ages separately in analyses that included this character. We evaluated most plumage characters qualitatively but compared measured tail-pattern characters with box plots, compared means with one-way analysis of variance (ANOVA), and included them in the discriminant function analysis (DFA; see below). For all parametric statistical tests we transformed proportions with the angular transformation (Sokal and Rohlf 1981), counts with the square-root transformation, and confirmed the normality of distributions of other characters by the Kolmogorov–Smirnov test (SYSTAT 2009). On the basis of the latter tests, we log-transformed tarsus length, hind claw, and toe measurements.

We analyzed the primary-projection measurements with a three-way ANOVA, testing for taxon, age, sex, and interaction effects. We compared all measurements and metric tail characters of the two taxa by age/sex class with box plots, and we compared means with one-way ANOVA. For characters that had different means, we determined if differences were diagnosable at levels between 75% and 99% in 1% increments, following the method described in Patten and Unitt (2002). We then used DFA to find the linear combination of variables that best separated the two taxa. We examined correlation coefficients of each pairwise combination of variables to ensure no highly correlated ($r > 0.70$) pairs were included in the DFA (Green 1979, Magnusson 1983). In the DFA we used the squared Mahalanobis distances as our measure of group differences, and we used the jackknifed classification procedure on the original cases to assign specimens to taxon. We also calculated the mean and SE of posterior classification probabilities for each case to assess relative confidence in the classifications, and we evaluated the diagnosability of canonical scores as described for measurement variables. We tested the significance of discriminant functions with Wilks' λ transformed to an approximate F distribution. ANOVA and DFA were run in SYSTAT 13 (SYSTAT 2009). We calculated the sexual dimorphism index (SDI) for each character and the mean SDI over all characters by the

method described in Snyder and Wiley (1976). We calculated the SDI separately for adults and juveniles of both *B. n. nitidus* and *B. n. plagiatus*.

We compared vocalization metrics of the two taxa with box plots, and we compared means by one-way ANOVA. For characters that had different means, we determined if differences were diagnosable, and we used DFA to find the linear combination of vocalization variables that best separated the two taxa, following the approach described above for measurement data.

We considered $\alpha = 0.05$ as the critical value for significance in statistical tests. Values in text and tables are means \pm SE.

RESULTS

PLUMAGES

Plumage regions of the two taxa differed consistently in both juveniles and adults. All museum specimens from locations north of the distribution gap in Costa Rica had plumage characteristics of *B. n. plagiatus*, whereas all specimens from locations south of the gap had plumage characteristics of *B. n. nitidus* (Table 1, Figs. 1, 2). Intrataxon plumage variation was minimal relative to intertaxon differences, and almost all individuals of each taxon were as depicted in Figure 1. From the distributions of specimens, the width of the range gap appears to be no more than ~50 km (Fig. 2).

TABLE 1. Plumage differences between *B. n. nitidus* and *B. n. plagiatus* based on examination of 405 museum specimens (Appendix A). Plumage regions follow Blake (1956). The differences are shown in Fig. 1, and numerals and letters in parentheses in the table refer to illustrations in that figure.

Region	Taxon	
	<i>B. n. nitidus</i> (1)	<i>B. n. plagiatus</i> (2)
Adult		
Crown, nape, humeral, back (b, e)	Gray, narrow dark barring	Dark gray, no barring
Upper tail coverts (b)	Gray, white tips	White
Juvenile		
Crown (f)	Buff, dark streaks	Dark brown
Auricular (f)	Buff	White
Malar stripe (f)	Absent	Dark, pronounced
Breast, belly (c, f)	Buff, dark blobs	White, narrow dark streaks
Crural (c, f)	Buff, unmarked	White, narrow dark bands
Primaries, upper surface (d)	Large buff light patch	Dark brown, no patch
Rectrices, upper surface (d)	Base whitish, wide bands	Base brown, narrow bands
Upper tail coverts (d)	Buff	White, dark shaft streaks

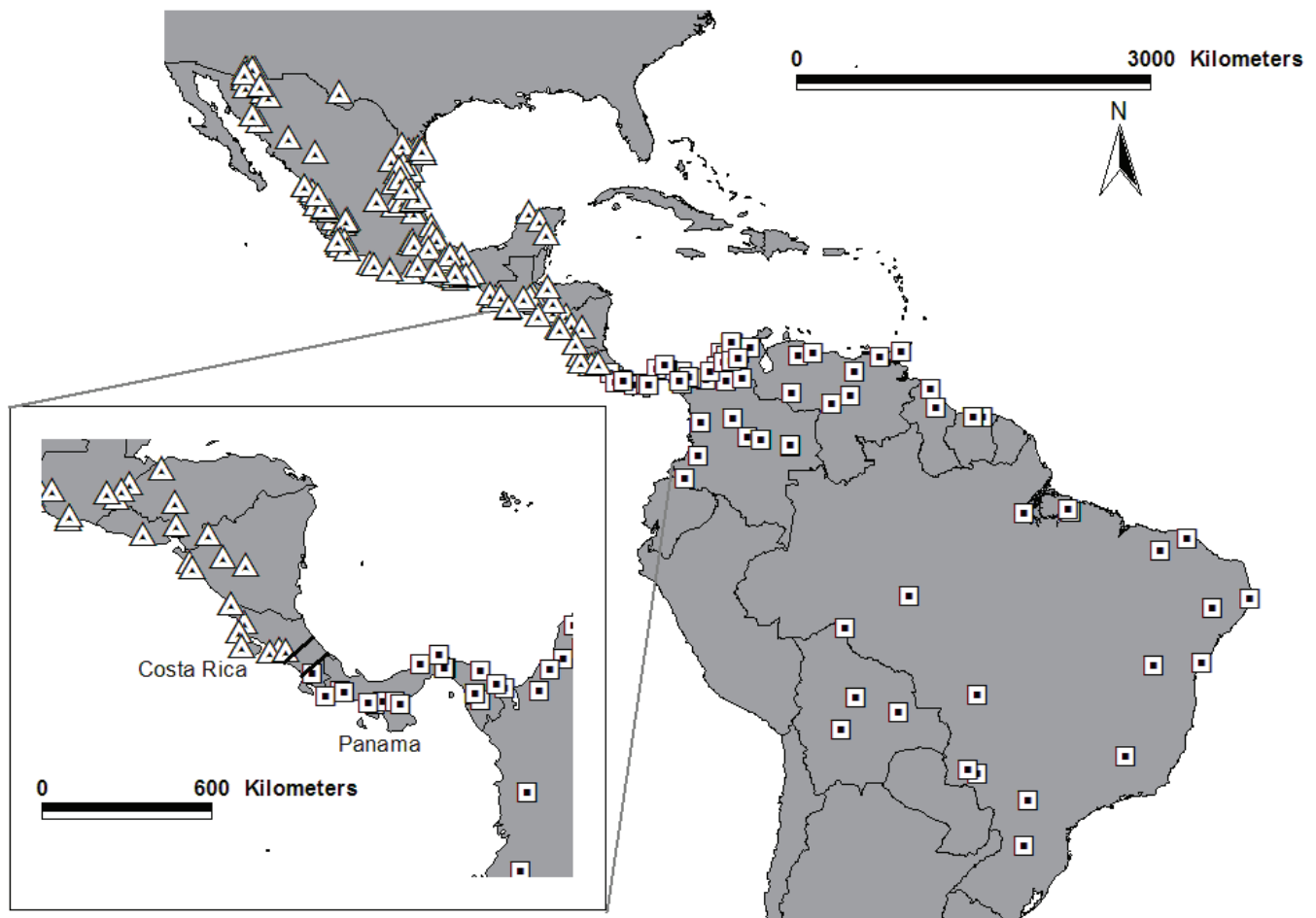


FIGURE 2. Classification of specimens of *B. nitidus* to *B. n. nitidus* or *plagiatus* on the basis of plumage characteristics in Table 1. Specimens represented by a square had characters of *B. n. nitidus*; specimens represented by a triangle had characters of *B. n. plagiatus* (see Table 1, Fig. 1). The inset shows the distribution and classification of specimens in the vicinity of the range gap in Costa Rica; see text for details.

The tail patterns of *B. n. nitidus* and *B. n. plagiatus* also differed, but in most characters, considered singly, the difference did not reach the threshold of diagnosability. Adults of both sexes of *B. n. plagiatus* had wider white second tail bands, had more rectrices with a second white tail band, and more often had evidence of a third white band than did adults of *B. n. nitidus* (Fig. 3). Adults' tail-band characters overlapped somewhat; therefore, the two taxa did not meet the criterion of diagnosability by these characters alone. Juveniles of both sexes of *B. n. plagiatus* had more dark bands in the tail than did juveniles of *B. n. nitidus*; the number of dark tail bands met the criterion of diagnosability at the 75% level for males and at the 80% level for females.

MORPHOLOGY

The two taxa overlapped somewhat in all measurements, so they did not meet the criterion of diagnosability by any single one of these characters. However, the wing and tail of *B. n.*

plagiatus were significantly longer than those of *B. n. nitidus*, and some characters associated with prey capture and handling differed for some but not all classes (Figs. 4, 5). *Buteo n. plagiatus* had a longer primary projection (59.5 ± 1.8 mm, $n = 37$) than did *B. n. nitidus* (44.0 ± 1.9 mm, $n = 27$) (three-way ANOVA; taxon-effect $F = 33.640$, $df = 1, 50$, $P < 0.001$; $P > 0.05$ for age/sex-class effects and interaction effects), but the differences did not reach the criterion of diagnosability at any level. The mean SDI was 1.7 to 2.0 times larger for *B. n. plagiatus* than for *B. n. nitidus* (Table 2). The difference was especially evident for measurements of wing length, tarsus width, and maxilla depth.

Culmen length and maxilla depth were strongly correlated with hind-claw length; we retained the hind-claw measurement for DFA because bill measurements were not available for a number of specimens on which the maxilla had been damaged. DFA resulted in correct classification of 100% of juveniles, 98% of adult males, and 88% of adult females. Mean discriminant

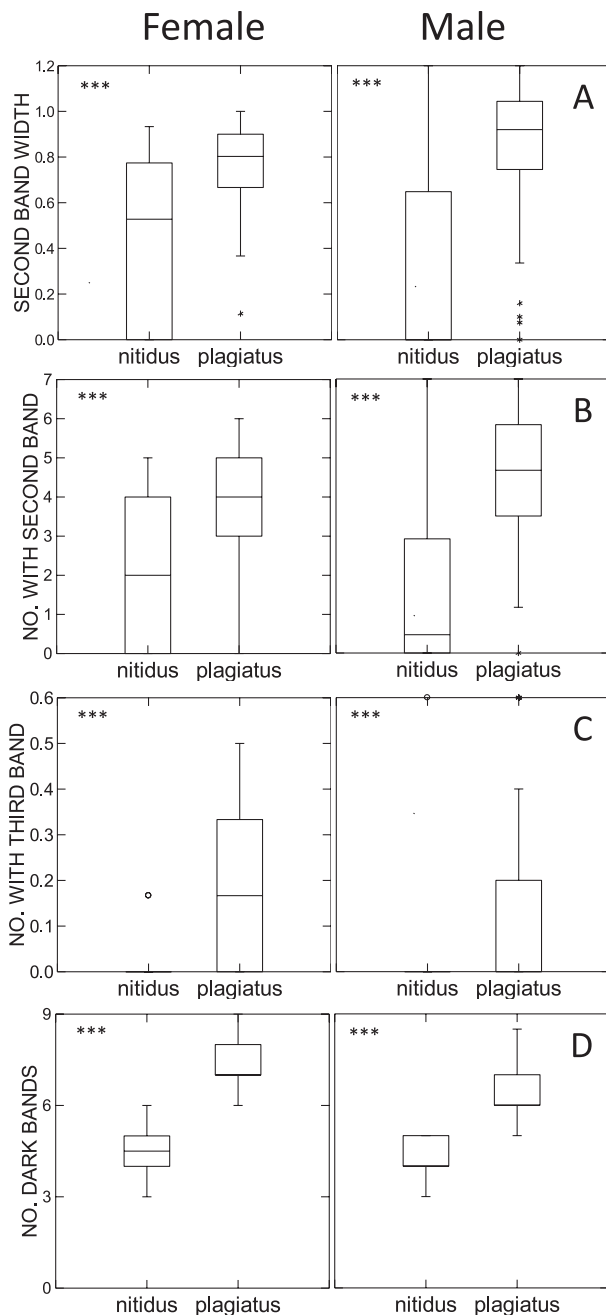


FIGURE 3. Box plots summarizing tail characters of *B. n. nitidus* and *B. n. plagiatus*. The horizontal line in the boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, and asterisks beyond whiskers are outside values. Means for each character were compared with one-way ANOVA, and asterisks or notation in the upper left corner of each graph depict results (nd, no difference; $*0.10 \geq P \geq 0.05$; $***P < 0.01$). A, B, and C are adult characters, A the proportional width of the second (proximal) white tail band relative to the width of right central rectrix, B the number of rectrices on the right side of the tail with an unbroken second white band, and C the number of rectrices on the right side of the tail with an unbroken third white band. Character D, the number of dark bands on the right side of the tail, is a juvenile character.

scores of all groups differed (Table 3). Posterior classification probabilities exceeded 95% for 95% of adult males, 66% of adult females, 96% of juvenile males, and 92% of juvenile females. Misclassified specimens were primarily from southern Central America and northern South America.

VOCALIZATIONS

Alarm calls of *B. n. nitidus* and *B. n. plagiatus* were aurally and visually different (Fig. 6). Means of all measured characteristics of the alarm notes of *B. n. nitidus* and *B. n. plagiatus* differed ($P < 0.04$ for all comparisons). Box plots showed complete separation of *B. n. nitidus* and *B. n. plagiatus* on the variables time and pitch drop, with the exception of three recordings of *B. n. nitidus* from Venezuela that had times more typical of *B. n. plagiatus* (Fig. 7). Two of these recordings were of juveniles that were or may have been dependent on their parents (ML58986, ML112269), and the third was of a bird obscured by vegetation and not observed, but the call was described as atypically protracted (ML58990). From similarities between ML58990 and calls of known juveniles of *B. n. nitidus*, we suspect this call was also from a juvenile *B. n. nitidus*. Even with the apparent complication of age-related variation in call structure, alarm calls of *B. n. nitidus* and *B. n. plagiatus* were diagnostically different at the 99% level for pitch drop, and at the 75% level for time. Time and interquartile-range duration were highly correlated ($r = 0.778$), so we retained the more direct measure, time, for DFA. Mean discriminant scores for *B. n. nitidus* and *B. n. plagiatus* differed, and 100% of individuals were classified to the correct taxon with high certainty (Table 4).

DISCUSSION

We found that allopatric *B. n. nitidus* and *B. n. plagiatus* differ diagnosably at very high probability levels in all age and sex classes across a range of plumage, measurement, and vocalization characters. The two taxa were entirely separable by plumage, even where their ranges approach one another in Costa Rica. DFA using measurements of body and tail-pattern characters resulted in correct classification of $\geq 98\%$ of juveniles and adult males and 88% of adult females, and DFA using alarm-call measurements resulted in correct classification of 100% of the vocalizations.

Riesing et al. (2003) found the mtDNA distance between *B. n. nitidus* and *B. n. plagiatus* was 9%, the same distance as between *B. n. nitidus* and *B. jamaicensis costaricensis*. In interpreting this finding, Riesing et al. (2003:340) stated "Thus, the earlier proposed species status of *plagiatus* . . . is supported by our data." There are two reasons to be cautious about interpreting the findings of Riesing et al. (2003), however. First, their sample was very small, $n = 2$ for *B. n. nitidus* and $n = 1$ for *B. n. plagiatus*. Second, the samples of *B. n. nitidus* (Ecuador and Brazil) and that of *B. n. plagiatus* (Costa Rica) came from localities far apart, leaving uncertainty whether

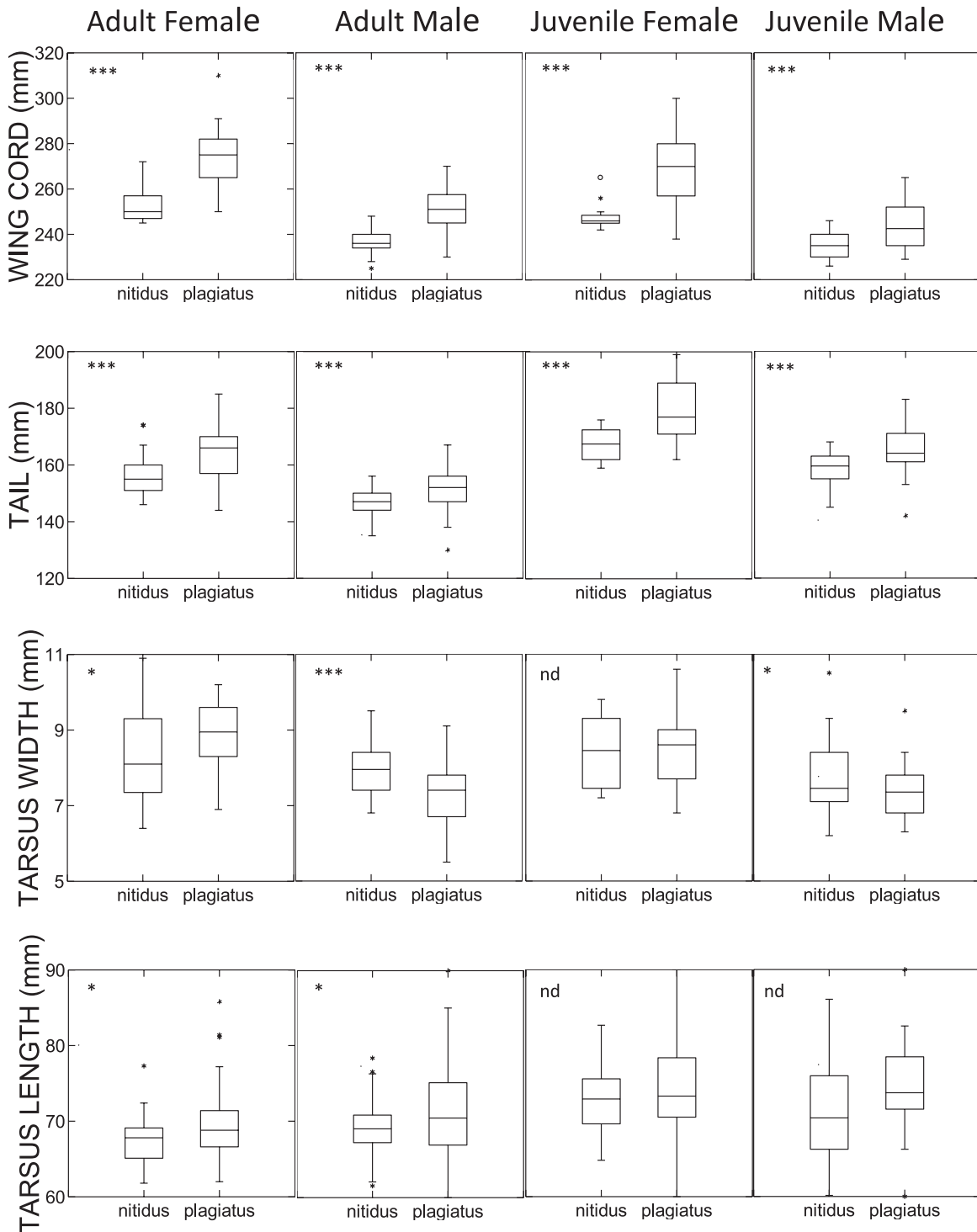


FIGURE 4. Box plots summarizing measurements of *B. n. nitidus* and *B. n. plagiatus*: wing, tail, and leg characters by taxon. The horizontal line in boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, and asterisks beyond whiskers are outside values. Means for each character were compared with one-way ANOVA, and asterisks or notation in the upper left corner of each graph depict results (nd, no difference; $0.10 \geq P \geq 0.05$; $***P < 0.01$).

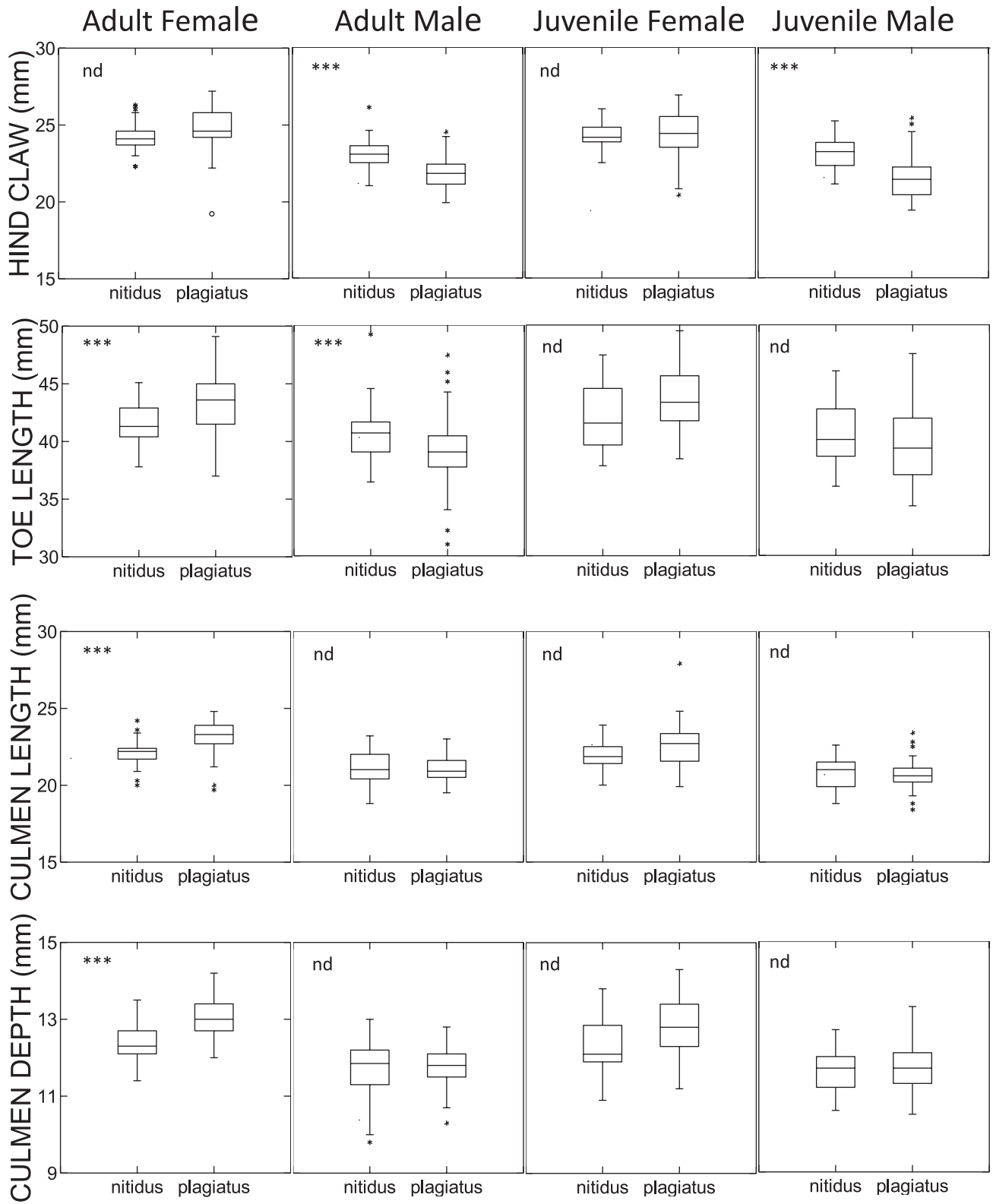


FIGURE 5. Box plots summarizing measurements of prey-handling characters of *B. n. nitidus* and *B. n. plagiatus*. The horizontal line in boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, and asterisks beyond whiskers are outside values. Means for each character were compared with one-way ANOVA, and asterisks or notation in the upper left corner of each graph depict results (nd, no difference; $0.10 \geq P \geq 0.05$; $***P < 0.01$).

TABLE 2. Sexual size dimorphism index for *B. n. nitidus* and *B. n. plagiatus*, calculated from means of measurements presented in Figs. 4 and 5 according to the method described in Snyder and Wiley (1976).

	Wing	Tail	Tarsus width	Tarsus length	Hind claw	Toe	Culmen length	Maxilla depth	Mean
Adult									
<i>B. n. nitidus</i>	0.04	0.04	0.04	0.02	0.03	0.02	0.03	0.04	0.03
<i>B. n. plagiatus</i>	0.05	0.05	0.13	0.02	0.08	0.07	0.06	0.07	0.06
Juvenile									
<i>B. n. nitidus</i>	0.06	0.06	0.08	0.02	0.05	0.03	0.06	0.06	0.05
<i>B. n. plagiatus</i>	0.09	0.08	0.14	0.02	0.12	0.10	0.09	0.08	0.09

the geographic pattern of genetic differentiation corresponds with the pattern of morphological and vocal differentiation we observed. However, the sheer magnitude of the genetic difference is noteworthy given that many pairs of good species, especially those that have recently evolved, are indistinguishable in their mtDNA (Funk and Omland 2003). We think that the best interpretation of the available information is that *B. n. nitidus* and *B. n. plagiatus* do differ genetically at a level comparable to that of other pairs of full species in the genus *Buteo* and that the mtDNA shift occurs across a zone that

includes the gap in distribution where the plumage, morphology, and alarm note change.

In addition to morphological, vocal, and genetic differences, we found that the sexual dimorphism (as well as the size of some characters related to prey capture and handling) of *B. n. nitidus* and *B. n. plagiatus* differ. Snyder and Wiley (1976) demonstrated a strong relationship between the degree of sexual size dimorphism in raptors and aspects of their diet. Therefore, the differences in dimorphism suggest the taxa may also differ in the types and relative sizes of prey the sexes capture.

TABLE 3. Results of discriminant function analysis of morphological measurements of *B. n. nitidus* and *B. n. plagiatus*. Values in table are the canonical discriminant function coefficients and constants. Classification results, Wilks' λ test of equality of group centroids, mean canonical scores for each taxon, mean (SE) posterior classification probabilities for all cases, and diagnosability levels for canonical scores are also presented.

Variable	Adult male	Adult female	Juvenile male	Juvenile female
Constant	17.12	-22.63	-3.07	-8.7
Wing	0.10	0.08	0.05	0.033
Tail	0.00	-0.01	0.01	-0.03
Tarsus width	-0.64	0.15	-0.26	-0.151
ln(tarsus length) ^a	4.56	1.64	5.49	-6.056
ln(hind claw) ^a	-15.36	-6.08	-12.03	-0.474
ln(toe) ^a	-2.27	3.74	-1.67	4.499
sqr(rectrices with second band) ^a	0.83	0.09	—	—
sqr(rectrices with third band) ^a	0.37	0.63	—	—
asn(second-band width) ^a	0.25	1.25	—	—
sqr(no. dark tail bands) ^a	—	—	5.04	6.7
Correct classification	98%	88%	100%	100%
Wilks' λ (<i>F</i>)	40.33	11.78	28.92	17.29
df	9, 114	9, 78	7, 48	7, 29
<i>P</i>	<0.001	<0.001	<0.001	<0.001
Canonical score <i>B. n. nitidus</i> group mean	-2.71	-1.53	-2.81	-2.87
Canonical score <i>B. n. plagiatus</i> group mean	1.15	0.871	1.45	1.38
Mean (SE) posterior probability <i>B. n. nitidus</i>	0.95 (0.01)	0.85 (0.08)	1.00 (0)	0.97 (0.08)
Mean (SE) posterior probability <i>B. n. plagiatus</i>	0.97 (0.03)	0.82 (0.07)	1.00 (0)	0.98 (0.04)
Diagnosability of mean canonical scores ^b	90%	<75%	95%	92%

^aIn precedes log-transformed variables, sqr precedes square-root-transformed variables, and asn precedes angular- (arcsine-) transformed variables.

^bPercentage of the population of both taxa that lies outside 99% of the range of the other taxa, as described in Patten and Unitt (2002).

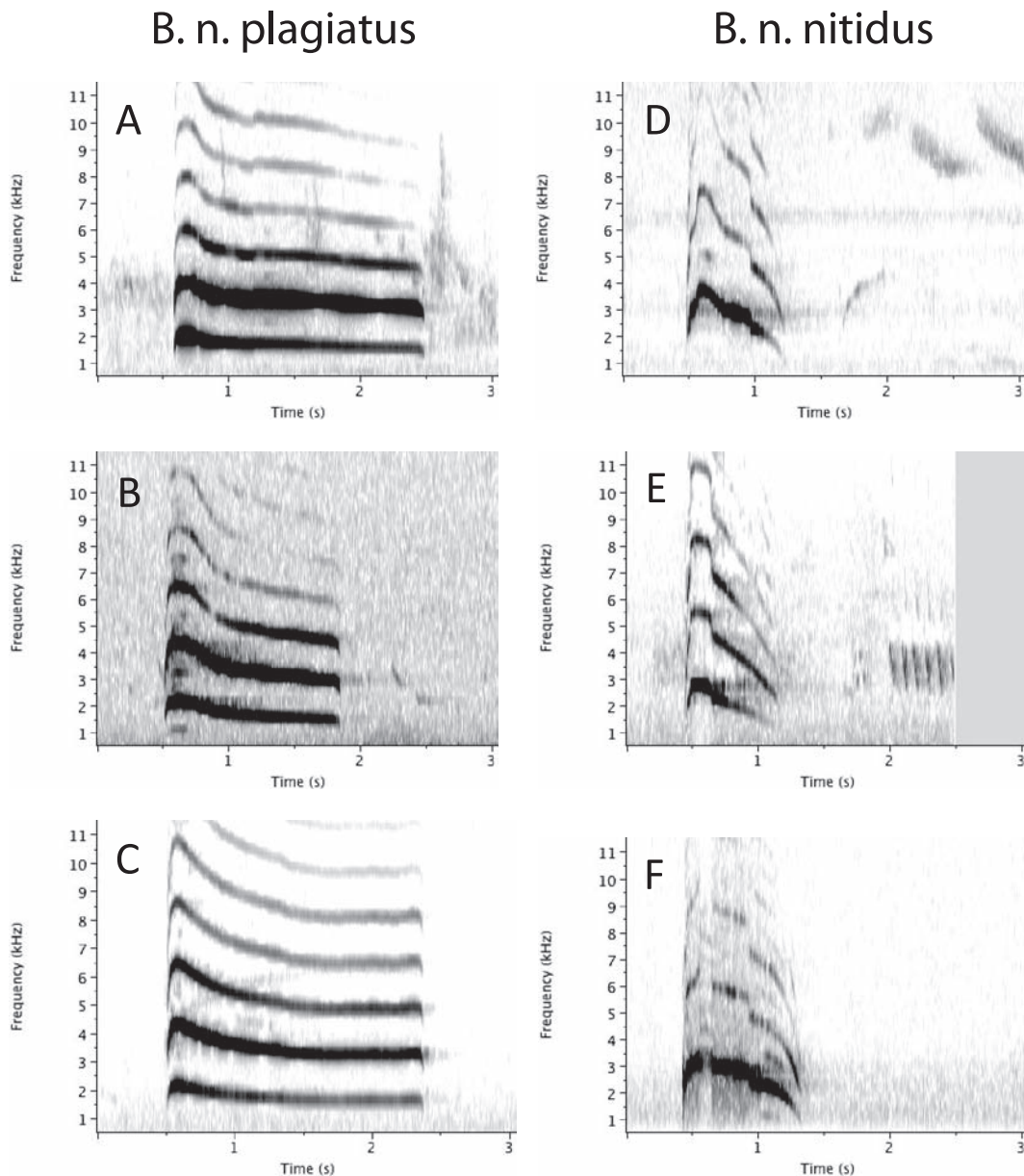


FIGURE 6. Example alarm calls of *B. n. nitidus* and *B. n. plagiatus*. Calls from *B. n. plagiatus* were longer, had more densely packed harmonics, most of the sound energy was concentrated in the second harmonic, and showed a smooth variation of the frequency along the note. Calls from *B. n. nitidus* were typically shorter, had more sparse harmonics, had sound energy concentrated in the first harmonic, and all showed a diagnostic sudden drop in pitch near the middle of the note. Call A was recorded in Arizona (ML 109002; see Appendix B), call B is from Colima, Mexico (ML 89721), call C is from El Rama, Nicaragua (XC 10888), call D is from Bolívar, Venezuela (ML 58987), call E is from Guayas, Ecuador (XC 4), and call F is from Alto Paraguay, Paraguay (XC 55595).

Slud (1964) noted that in Costa Rica *B. n. nitidus* and *B. n. plagiatus* occur almost exclusively in the tropical dry forest. The tropical dry forest is replaced immediately south of the Gulf of Nicoya on the Pacific slope by tropical moist forest, which continues southward into northern Panama (Slud 1964, Ridgely 1976, Janzen 1983).

It is this band of moist forest that currently appears to separate the ranges of *B. n. nitidus* and *B. n. plagiatus*, and by

a narrow distance of about 50 km. The moist forest in Central America has variously expanded and contracted in association with Pleistocene glaciation (Haffer 1974, van der Hammen 1974, Marshall et al. 1982, Rich and Rich 1983). Presumably, these Pleistocene events contributed to the isolation and differentiation of *B. n. nitidus* and *B. n. plagiatus*, as is the case with many other avian taxa (Avice and Walker 1998, Klicka and Zink 1999, Johnson and Cicero 2004). However,

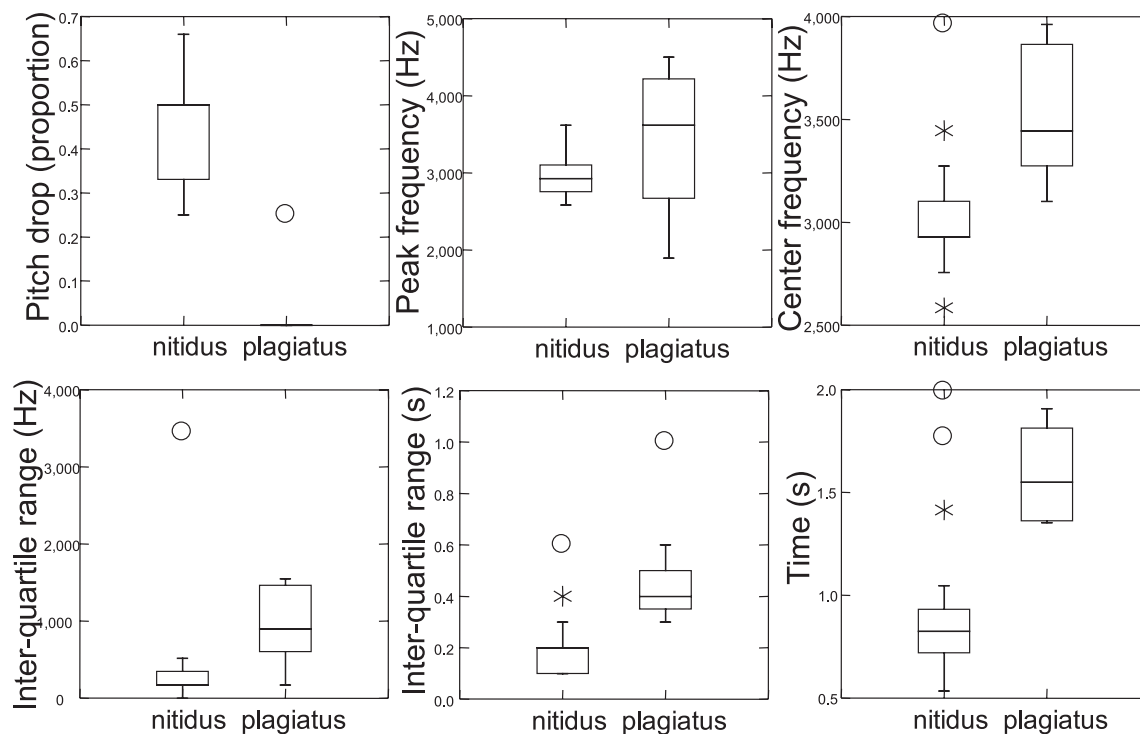


FIGURE 7. Box plots summarizing metrics of alarm notes of *B. n. nitidus* and *B. n. plagiatus*. The horizontal line in boxes is the median, boxes cover the median 50% of values (interquartile range), the whiskers extend outward from box hinges 1.5 times the interquartile range, asterisks denote outside values, and circles denote far outside values. All means were found to be different in one-way ANOVAs ($P \leq 0.035$ in all cases).

TABLE 4. Results of discriminant function analysis for alarm calls of *B. n. nitidus* and *B. n. plagiatus*. Values in table are the canonical discriminant function coefficients and constants. Classification results, Wilks' λ test of equality of group centroids, mean canonical scores for each taxon, mean (SE) posterior classification probabilities for all cases, and diagnosability levels for canonical scores are also presented.

Variable	Value
Constant	-0.905
asn(pitch drop) ^a	-7.584
Peak frequency	0
Center frequency	0.001
Interquartile-range bandwidth	0
Time	0.957
Correct classification	100%
Wilks' λ (F)	40.01
df	5, 27
P	< 0.001
Canonical score <i>nitidus</i> group mean	-1.49
Canonical score <i>plagiatus</i> group mean	4.66
Mean (SE) posterior probability <i>nitidus</i>	1.00 (0)
Mean (SE) posterior probability <i>plagiatus</i>	1.00 (0)
Diagnosability of mean canonical scores ^b	99%

^aasn precedes angular- (arcsine-) transformed variables.

^bPercentage of the population of both taxa that lies outside 99% of the range of the other taxa, as described in Patten and Unitt (2002).

if the mtDNA divergence reported by Riesing et al. (2003) is correct, and a rate of molecular divergence of 2% per million years is assumed (Johnson and Cicero 2004), the initial separation of *B. n. nitidus* and *B. n. plagiatus* must have occurred in the Pliocene Epoch, approximately 4.5 million years ago. This timing is consistent with a period of divergence in a number of other neotropical buteonine taxa coincident with the closure of the Panamanian isthmus, 15.5–2.8 million years ago (Amaral et al. 2009). Thus the divergence of *B. n. nitidus* and *B. n. plagiatus* appears to fit the pattern evident in a number of *Buteo* species, in which initial separation and divergence began in the Pliocene but were affected by, and in this case possibly maintained by, Pleistocene events (Avisé and Walker 1998, Klicka and Zink 1999, Amaral et al. 2009). Although recent clearing of the moist forest for agriculture has created patches of habitat seemingly suitable for the Gray Hawk in central and southern Costa Rica (Slud 1964), *B. n. nitidus* and *B. n. plagiatus* appear to remain geographically isolated, though the proximity of their ranges suggests some contact, if it has not already occurred, is likely in the future.

The British Ornithologists Union, which uses elements of the biological and phylogenetic species concepts in evaluating avian taxonomic rank, has adopted the following criteria for assigning species rank to allopatric taxa: "they are fully diagnosable in each of several discrete or continuously varying characters related to different functional contexts, e.g., structural

features (often related to foraging strategy), plumage colors, vocalizations (both often related to mate recognition) or DNA sequences, and the sum of the character differences corresponds to or exceeds the level of divergence seen in related species that coexist in sympatry” (Helbig et al. 2002:53). Under these criteria, we believe species rank for *B. n. nitidus* and *B. n. plagiatus* is fully supported because (1) all age and sex classes are completely distinct on the basis of several discrete plumage features; (2) three of four age and sex classes are diagnosably distinct at the $\geq 90\%$ probability level on the basis of DFA-derived canonical scores of group means, (3) the two taxa have diagnosably different alarm calls at the 99% probability level, on the basis of DFA-derived canonical scores of group means, and (4) there is evidence the taxa differ in mtDNA at a level comparable to that seen between other full species in the genus. The latter point may be of questionable significance given that the relationship between genotypic and phenotypic differentiation in birds in general (Winker 2009) and in the genus *Buteo* specifically (Kruckenhauser et al. 2004) is unclear. However, the fact that *B. n. nitidus* and *B. n. plagiatus* appear to differ in both genotype and phenotype, and that the phenotypic differences are consistent and include a broad range of characters, supports a conclusion that the taxa warrant treatment as different species. This conclusion is further supported by the fact that several other species of *Buteo* currently recognized diverge phenotypically at levels similar to what we found for *B. n. nitidus* and *B. n. plagiatus*. From our collective field and museum work with most species of *Buteo*, we would include in this group *B. brachyurus* and *B. albigula*, *B. lineatus* and *B. ridgwayi*, and *B. albicaudatus* and *B. polyosoma* (although Amaral et al. 2009 provided evidence the latter species pair may be better placed in the genus *Geranoaetus*). *Buteo jamaicensis* and *B. ventralis* provide another example, though the lack of genetic differentiation between these taxa calls into question their status as species and suggests a much more recent split than for *B. n. nitidus* and *B. n. plagiatus* (Riesing et al. 2003).

The American Ornithologists’ Union Committee on Classification and Nomenclature did not consider the findings of Riesing et al. (2003) compelling with regard to the species status of *B. n. nitidus* and *B. n. plagiatus* in the absence of additional supporting data (Banks et al. 2006). In this paper we present that supporting data for plumage, morphology, and vocalizations. Collectively, all lines of evidence strongly suggest that the current treatment of *B. n. nitidus* and *B. n. plagiatus* as conspecific does not accurately reflect the extent of differentiation between the two taxa. We recommend they be considered two species as described below:

Buteo nitidus (Latham 1790). We propose use of the name Gray-lined Hawk for this species, previously applied to it by Meyer de Schauensee (1966). The range of this species extends from southwestern Costa Rica south to eastern Peru, central Bolivia, southern Paraguay, northern Argentina, and southern Brazil.

Buteo plagiatus (Schlegel 1862). We propose retention of the common name Gray Hawk for this species, following the convention of other authors who have proposed species status for *B. nitidus* and *B. plagiatus* (Sibley and Monroe 1990). The range of this species is from southeastern Arizona, southern New Mexico, and southern and western Texas south to northwestern Costa Rica.

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APPENDIX A. Specimens of *B. n. nitidus* and *B. n. plagiatus* examined for this paper. AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; KMNH, Kansas Museum of Natural History; MCZ, Museum of Comparative Zoology; UDMNH, University of Delaware Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution.

Buteo n. nitidus ($n = 141$). **Adults** ($n = 93$). **AMNH** ($n = 38$): 12439, 471006, 470997, 798685, 470994, 471001, 4290, 804555, 71377, 130615, 99914, 97912, 804556, 471002, 288192, 241523, 34741, 471012, 471013, 136867, 471094, 186658, 183059, 44873, 471011, 44872, 73205, 471010, 471004, 177057, 44874, 470993, 277582, 131440, 97913, 71378, 30874, and 308956. **FMNH** ($n = 21$): 190720, 260977, 81434, 101362, 101543, 102458, 190719, 260979, 399311, 32164, 45003, 100816, 101359, 101361, 102459, 108036, 123846, 260978, 101597, 295951, and 190718. **MCZ** ($n = 6$): 155131, 14729, 155133, 117983, 155128, and 22987. **USNM** ($n = 28$): 425426, 448642, 454973, 372362, 384589, 388451, 90156, 512907, 386709, 400145, 400146, 409273, 409274, 409275, 457586, 532976, 383341, 372363, 410529, 107208, 401202, 391851, 369485, 368486, 368484, 410530, 470435, and 513820. **Juveniles** ($n = 48$). **AMNH** ($n = 17$): 471007, 471005, 471000, 236509, 121441, 97910, 241522, 313391, 470995, 34635, 44875, 107111, 471008, 471003, 470996, 73206, and 97911. **FMNH** ($n = 14$): 34308, 96306, 101363, 75239, 101022, 295229, 190721, 57666, 100815, 101360, 101514, 101556, 217630, and 295952. **MCZ** ($n = 1$): 155132. **USNM** ($n = 16$): 368485, 383342, 107210, 383343, 386708, 477559, 400147, 470613, 406424, 372365, 107209, 121084, 372364, 516149, 391853, and 391852.

Buteo n. plagiatus ($n = 264$). **Adults** ($n = 184$). **AMNH** ($n = 57$): 793529, illegible, 80780, 80787, 91154, 91153, 80791, 80783, 92836, 750309, 389161, 393624, 143747, 103287, 389162, 775878, 104614, 104627, 104615, 470980, 775880, 470983, 352735, 106204, 750357, 352729, 448072, 36454, 91159, 80789, 80784, 92017, 80792, 91151, 91148, 352730, 91147, 80782, 91150, 750358, 80785, 56567, 393618, 393623, 103078, 143745, 393622, 393616, 44879, 470978, 470981, 352374, 352732, 104616, 366752, 470985, and 388697. **FMNH** ($n = 34$): 183312, 130639, 156947, 21838, 111179, 111182, 124188, 126978, 126979, 126980, 126982, 126983, 370953, 100940, 102539, 124185, 124187, 183313, 96303, 100273, 100274, 100276, 156948, 95182, 100939, 124189, 124190, 126977, 96304, 120827, 183311, 208620, 96305, and 124186. **KMNH** ($n = 7$): 36053, 23711, 23209, 23709, 32629, 32630, and 23710. **MCZ** ($n = 41$): 224765, 104308, 224767, 224777, 224773, 505931, 205939, 252671, 224771, 48460, 48461, 328371, 193510, 40125, 163185, 163184, 46525, 100906, 65209, 317886, 104039, 317887, 309370, 224763, 205989, 206010, 252670, 48463, 48462, 48459, 48458, 224775, 224764, 224776, 924240, 157944, 145644, 73091, 102293, 328516, and 40124. **UDMNH** ($n = 1$): 55127. **USNM** ($n = 44$): 155624, 482018, 588468, 34002, 129321, 157371, 361432, 302647, 89770, 120287, 302646, 334764, 349524, 189117, 57869, 167724, 370556, 370559, 69072, 79803, 437507, 363451, 371343, 155623, 129322, 564795, 30538, 199376, 199368, 396524, 155625, 89769, 90002, 370553, 370554, 370557, 370558, 437506, 57868, 150646, 155626, 155627, 120286, and 189116. **Juveniles** ($n = 80$). **AMNH** ($n = 38$): 80790, 80781, 80779, 56565, 406613, 143744, 393617, 393620, 470987, 470990, 105329, 776251, 470984, 470986, 352733, 470982, 56566, 91149, 91152, 406612, 143748, 103080, 393619, 393625, 101091, 104617, 104613, 775881, 470703, 44876, 44878, 776249, 775879, 470989, 105328, 44877, 470988, and 776250. **FMNH** ($n = 17$): 100275, 22396, 102540, 102787, 120826, 208619, 22395, 111180, 111181, 111183, 124192, 126981, 22397, 110216, 189782, 370954, and 95183. **KMNH** ($n = 5$): 35611, 32631, 36417, 28908, and 40415. **MCZ** ($n = 4$): 206017, 206470, 286358, and 73092. **UDMNH** ($n = 1$): 38476. **USNM** ($n = 15$): 42775, 155632, 193864, 459493, 50772, 158530, 129323, 132138, 35060, 155628, 155633, 185338, 370555, 334763, and 57856.

APPENDIX B. Recordings of alarm calls of *Buteo n. nitidus* and *B. n. plagiatus* evaluated for this study. XC, www.xeno-canto.org; ML, Macaulay Library, Cornell Laboratory of Ornithology; Sandoval, private collection of L. Sandoval. For every record we provide collection and number, country, state/province, and locality; records are arranged alphabetically by country by taxon.

Buteo n. nitidus: XC 53323, Bolivia, Santa Cruz, Estancia Caparu; XC 1916, Bolivia, Noel Kempff-Mercado NP; XC 7052, Brazil, Pernambuco, Mata de Aldeia; XC 8755, Brazil, Ceará, Serra de Baturité; ML 32486, Brazil, Amazonas, 80.0 km N of Manaus; ML 127971, Brazil, Alagoas, Usina Serra Grande, Engenho Coimbra; ML 127606, Brazil, Amazonas, 8.0 km from ENE of Careiro do Castanho, Fazenda Toshiba; XC 12093, Brazil, Pará, Serra dos Carajás; ML 126664, Brazil, Pará, Floresta Nacional de Carajas, Salobo Road; ML 127718, Brazil, Amazonas, Projeto de Assentimento Puxurizal; ML 68076, Colombia, Magdalena, Santa Marta Mts.; XC 18189, Colombia, Antioquia, Cañón del Río Claro; XC 16312, Colombia, Antioquia, La Cueva del Cóndor; XC 4, Ecuador, Guayas, Cerro Blanco Reserve; XC 55594, Paraguay, Alto Paraguay, Kamba Aka; XC 35185, Peru, Cuesta del Pitón; XC 47556, Peru,

Madre de Dios, Oceaia; ML 58991, Venezuela, Táchira, Río Navay, San Joaquín de Navay; ML 58987, Venezuela, Bolívar, El Palmar; ML 58985, Venezuela, Aragua, Maracay, lake path, east of paved road; XC 9927, Venezuela, Bolívar, Río Caura S of Maripa; ML 58984, Venezuela, Aragua, Ocumare de la Costa; ML 58990, Venezuela, Táchira, near La Tendida (or Pozuelos); ML 58986, Venezuela, Zulia, Misión Río Tucucú; ML 112269, Venezuela, Bolívar, Campamento Río Grande.

B. n. plagiatus: Sandoval 001, Costa Rica, Heredia, Getsemani; ML 89521, Mexico, Colima, 23.0 km NW of Manzanillo; ML 4199, Mexico, Yucatán, 6.0 km E of Piste; XC 30621, Mexico, Nayarit, La Bajada; ML 4198, Mexico, Sinaloa, 116.8 km S of Culiacán; XC 10888, Nicaragua, El Rama; ML 140236, USA, Arizona, E of Harshaw Canyon, Patagonia; ML 109002, USA, Arizona, 4.0 km W of Arivaca, along Arivaca Creek.