FIRST KNOWN SPECIMEN OF A HYBRID *BUTEO*: SWAINSON’S HAWK  

(*BUTEO SWAINSONI*) X ROUGH-LEGGED HAWK (*B. LAGOPUS*) FROM LOUISIANA

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ABSTRACT.--We report a specimen that is a hybrid between Swainson’s Hawk (*Buteo swainsoni*) and Rough-legged Hawk (*B. lagopus*), which, to our knowledge, is the first hybrid specimen for the genus. Few reports of hybridization between *Buteo* species exist, most of which were observations of inter-specific pairs nesting. The specimen was collected in Louisiana and initially identified as a Rough-legged Hawk on the basis of its feathered tarsi and dark belly band and carpals. DNA sequence from the maternally inherited ND6 gene was identical to a published sequence for Swainson’s Hawk. A nuclear intron sequence of 542 bp was not sufficiently variable to eliminate any of the potential fathers. The feathered tarsi of the hybrid strongly suggested that the father was either a Rough-legged Hawk or Ferruginous Hawk (*B. regalis*). We eliminated the latter by its larger feet, gape, and beak and contrary plumage characters. Plumage and size characters of the hybrid, other than the darkly pigmented leg feathers, were intermediate between light morphs of Swainson’s Hawk and Rough-legged Hawk. The breeding range of Swainson’s Hawk extends northward well into that of the Rough-legged Hawk, albeit at a low density, which may be a factor in hybridization. The occurrence of this hybrid is evidence of the potential for interbreeding between North American members of the genus *Buteo*, most of which are genetically closely related. Such hybridization could have implications for genetic diversity, adaptation, or the evolution of reproductive barriers. In any case, such hybrids present field and museum identification problems.
Few documented cases of hybridization exist between any two of the 27 or so species in the genus *Buteo*. Hybrid combinations have been reported for Long-legged Buzzard (*B. rufinus*) and Upland Buzzard (*B. hemilasius*) in Asia (Pfander and Schmigalew, 2001), Common Buzzard (*B. buteo*) and Long-legged Buzzard (*B. rufinus*) in Europe (Dudás, *et al.*, 1999), and Red-shouldered Hawk (*B. lineatus*) and Gray Hawk (*B. nitidus*) in North America (Lasley, 1989). Additionally, an adult Swainson’s Hawk (*B. swainsoni*) was breeding for more than eight years with a presumably escaped South American Red-backed Hawk (Red-backed Buzzard) (*B. polyosoma*) in Colorado, USA, and produced offspring in some years (Wheeler 1988, Allen 1988), and an escaped falconry Red-tailed Hawk (*B. jamaicensis*) bred with a Common Buzzard in Scotland (Murray 1970).

However, to our knowledge, there are no museum specimens of the offspring of such unions. Thus, it was with great interest that we found a specimen of an apparent hybrid in the Louisiana State University Museum of Natural Science (LSUMNS). It is a juvenile male, has feathered tarsi and mostly dark carpal patches, and was collected near Baton Rouge, Louisiana as a Rough-legged Hawk (*B. lagopus*). However, it is intermediate in size and plumage between juvenile males of Rough-legged Hawk and Swainson’s Hawk, and its plumage appears almost the same as a probable hybrid between the two species first seen and photographed by Martin Reid near Ft. Worth, Texas.

Herein we present a description of the putative hybrid *Buteo* on the basis of its morphology, plumage, and mitochondrial and nuclear DNA sequences. We compare the hybrid to a set of potential parental *Buteo* taxa to conclusively identify its parents. The mother was determined to be a Swainson’s Hawk, because the mitochondrial NADH
dehydrogenase subunit 6 (ND6) sequence of the specimen is identical to sequences published for this species. Comparison of a 520 bp nuclear intron failed to exclude any of the potential father species. The father was determined by morphology and plumage to be a Rough-legged Hawk; the other possible candidates, Ferruginous Hawk (*B. regalis*) and Red-tailed Hawk (*B. jamaicensis*), could be eliminated by both plumage and larger foot and beak sizes. Swainson’s Hawks breed sparsely throughout much of the breeding range of the Rough-legged Hawk in far northern North America.

**METHODS**

The specimen, LSUMZ 159785, was collected on 4 November 1994 in East Baton Rouge Parish, Highway 30 at Burtville, Louisiana by S. W. Cardiff and D. L. Dittmann. It was sexed internally as a male, left testis 7x1.1mm, was in juvenal plumage, and had the skull 75% ossified. Its weight was 701.9g. A tissue sample was deposited in the LSUMNS Collection of Genetic Resources (catalog no. B23743).

We used a DNEasy tissue kit (Qiagen, Valencia, California) to extract DNA from frozen muscle tissue of the putative hybrid specimen, and one specimen of each of the following taxa: Rough-legged Hawk, Swainson’s Hawk, Red-tailed Hawk, “Harlan’s” Red-tailed Hawk (*B. jamaicensis harlani*), and Ferruginous Hawk. We amplified the ND6 gene for the hybrid specimen using the polymerase chain reaction (PCR) with the primers tPROfwd and tGLUrev (Haring et al. 1999). Negative control reactions were used for both extractions and PCR to insure against contamination. Standard PCR reactions were run on an MJ Research PTC-200 thermal-cycler under the following
temperature regime: initial denaturation at 96°C for 10 min; 35 cycles of 92°C for 60 s, 55°C for 60 s, 72°C for 60 s; and a final extension at 72°C for 7 min. PCR products were purified using a Qiagen Gel Extraction Kit (Qiagen). Cycle-sequencing reactions were carried out in both directions using the above primers in quarter-volume reactions with Big Dye Terminator Cycle Sequencing Kit (version 2, Applied Biosystems [ABI], Foster, California). Cycle-sequencing products were purified using Sephadex columns. Purified samples were electrophoresed on an ABI 377 automated sequencer. Sequences were assembled and edited using Sequencher 4.1 (Genecodes Corporation, Ann Arbor, Michigan) and compared with published ND6 sequences of various *Buteo* species (Riesing et al. 2003).

We amplified and sequenced the nuclear intron 5 and flanking exon regions of the cytosolic adenylate kinase (AK1) gene for each taxon using the same protocol as above, with the primers AK5b+ and AK6c- (Shapiro and Dumbacher 2001). All sequences were deposited in Genbank (accession numbers pending).

We compared the wing chord and weight of the specimen with those of juvenile male Rough-legged and Swainson’s Hawks captured for banding. We also compared the following characters on specimens of juvenile males of both species with the specimen in question: head, upperparts, breast, belly, tail, legs, and emargination of primary 7 (P7). Further, we used museum specimens and published data to compare measurements of the feet, beaks, and shape of P7 of juvenile male Rough-legged, Swainson’s, Red-tailed, and Ferruginous Hawks with the hybrid specimen. We used the “contradictory characters” approach of Rohwer (1994) to eliminate potential pairs of parental taxa for which characters of the presumed hybrid falls outside of the range of variation.
RESULTS

The mitochondrial ND6 sequence of the putative hybrid, totaling 343 bp, was an identical match to a published sequence from a Swainson’s Hawk collected in New Mexico (Table 1) (Genbank accession no. AY213028). The sequence is 0.76 % divergent from its nearest relative, the Galapagos Hawk (*B. galapagoensis*), and 3.2–3.8% divergent from the only sympatric congeners (Clark and Wheeler 2001): Red-tailed, Ferruginous, and Rough-legged Hawks (Table 1). Mitochondrial haplotypes are shared between mothers and their offspring because the mitochondrial genome is non-recombining and maternally inherited (Lansman et al. 1983). The complete mtDNA sequence identity strongly suggests that the maternal parent was a Swainson’s Hawk.

The nuclear AK1 sequence of the putative hybrid, totaling 542 bp, was identical to sequences from the Swainson’s, Rough-legged, Red-tailed, Harlan’s, and Ferruginous Hawks. The complete lack of variation at this locus prevents the elimination of any of this set of taxa as potential parents. The identification of the paternal parent was made using phenotypic characters.

Red-tailed Hawk, including Harlan’s Hawk, can be eliminated as the putative father, because it always has unfeathered tarsi. We consider it highly unlikely that two species with bare tarsi would produce a hybrid with feathered tarsi. Further, its feet and beak are much larger than those of the hybrid (Table 2). (Note that culmen and hallux measurements of juveniles average shorter than those of adults, as beaks and talons are...
Finally, juveniles of this species share few plumage characters with the hybrid (Clark and Wheeler 2001, Wheeler and Clark 1995); we would not expect, for example, a hybrid Red-tailed x Swainson’s Hawk juvenile to have the heavy dark belly band (Fig. 1) or the dark carpal patches of the hybrid.

Both Ferruginous and Rough-legged Hawks have feathered tarsi and are the most likely candidates for the father of the hybrid specimen. But Ferruginous Hawks have tremendously large gapes and large beaks (Table 2). Considering that the wing chords of juvenile male Swainson’s average 371mm, one might expect a male hybrid between these two to have a longer wing chord than the 381mm on our specimen, on the other hand, as we report below, this measure is intermediate between mean wing chords of Swainson’s and Rough-legged Hawk juvenile males. Finally, the plumage characters of both light- and dark-morph juvenile Ferruginous Hawks do not match those of the specimen (Clark and Wheeler 2001, Wheeler and Clark 1995); a hybrid Ferruginous x Swainson’s Hawk juvenile, for example, would not be expected to have the dark belly band (Fig. 1) nor the dark carpal patches of the hybrid.

Most plumage characters of the hybrid specimen are similar to juvenile male Swainson’s or juvenile male Rough-legged Hawks or intermediate between them (Figs. 1-2, Table 3). The notching of P7 is also intermediate (Fig. 3). This feather has a noticeable abrupt widening or ‘notch’ on the trailing edge for Rough-legged Hawk (same for Ferruginous and Red-tailed Hawks) but not for Swainson’s Hawk. The widening begins 93mm from the tip on a juvenile male specimen Rough-legged Hawk (Fig. 3 (A)), widening about 15mm at an angle of 70° to the feather shaft. P7 on a juvenile male Swainson’s Hawk specimen began widening gradually 47mm from the tip and lacked a
distinctive notch (Fig. 3 (B)). The hybrid’s P7 began widening 59mm from the tip with a notch and widened about 9mm at a 60° angle (Fig. 3 (C)).

The weight (702g) and wing chord (381mm) of the hybrid are intermediate between the mean weights (858g and 570g) and mean wing chords (402mm and 371mm) of juvenile males of Rough-legged and Swainson’s Hawks, respectively (Fig. 4).

DISCUSSION

Our analyses of the hybrid specimen using both morphological characters and DNA sequencing, similar to that of Marini and Hackett (2002), results, as they stated, in a more accurate identification of the parents’ species. In particular, the comparison of a single mtDNA sequence to the growing database of published sequences is an outstanding tool for identification of the maternal parent. In this case, the mtDNA sequence of the hybrid strongly suggests that its maternal parent was a Swainson’s Hawk. The mother could have been a species other than Swainson’s Hawk only if the mitochondrial identity were a mere artifact of incomplete lineage sorting. This is unlikely considering that the divergence levels between Swainson’s Hawk and each of its sympatric congeners are greater than 3%. Furthermore, the mitochondrial study of Riesing et al. (2003) demonstrated that geographically heterogeneous samples of five Rough-legged Hawks, two Ferruginous Hawks, nine Red-tailed Hawks, and three Swainson’s Hawks are each reciprocally monophyletic.

Almost all plumage and morphological characters of the hybrid specimen were intermediate between those of juvenile males of the parent species. This is consistent
with the characters of hybrids between other species of birds (e.g., Graves 1990, Marini and Hackett 2002, Rohwer 1994). However, one character, the coloration of the tarsi feathers, was not intermediate. Juvenile male Rough-legged Hawks have buffy tarsal feathers with sparse dark markings, whereas Swainson’s Hawks have bare tarsi. The specimen has tarsal feathers with heavy dark barring, clearly not intermediate. The expectation that hybrid traits fall within the range of traits expressed by the parental taxa is based on the assumption that most traits are additive and polygenic (Falconer 1989) and is implicit in most hybrid diagnoses. Nonetheless, hybrids can also express traits that are extreme relative to those of the parental taxa (Rieseberg et al. 1999). It is possible that the darkly pigmented tarsal feathers could be one such transgressive trait, caused by complementary gene action, overdominance, or epistasis. Swainson’s Hawk and Rough-legged Hawk populations are known to possess genetic variation that results in differences in the quantity and distribution of melanin-based plumage pigments (Clark and Wheeler 2001). Rohwer (1994) reported other examples of characters that were not intermediate between those of the parental species.

The Swainson’s Hawk breeds throughout much of the breeding range of the Rough-legged Hawk in far northwestern North America. This is the extreme northern periphery of their distribution, and they occur at very low densities in taiga habitat where they are sympatric with the Rough-legged Hawk (England et al., 1997; Bechard and Swem, 2002; Sinclair et al. 2003). This could increase the possibility that a female Swainson’s Hawk could fail to find a conspecific mate. Given the broad overlap in distribution between Swainson’s, Red-tailed, and Ferruginous Hawks, the lack of documented instances of hybridization or interspecific pairings between any two of these three species suggests
behavioral barriers to reproduction. Such barriers may not exist between Swainson’s and Rough-legged Hawks, which overlap only marginally, and which may have come into sympatry only recently. This hybrid pairing is compatible with the model of Short (1969), who proposed that hybridization is most likely to occur at the edges of a species’ range.

Swainson’s Hawks are rare during November in the area where the hybrid individual was found; there is only one November record for East Baton Rouge Parish, despite intensive coverage (LSUMNS data). Although Lowery (1974) indicated that Rough-legged Hawk is a regular winter visitor to Louisiana and several subsequent sight reports lacking photos have been accepted by the Louisiana Bird Records Committee, the only physical evidence substantiating the occurrence of a Rough-legged Hawk in Louisiana is a specimen collected on March 12, 1933, at Grand Isle (LSUMZ 4803). The hybrid specimen occurred at a place and time that would be unexpected for either species, because Rough-legged Hawks should occur farther north and Swainson’s Hawks farther south. This intermediate migratory behavior, as well as myriad other ecological differences between Swainson’s Hawk and Rough-legged Hawk, suggests potential sources of reduced fitness in hybrids. Hybridization can provide a mechanism for gene flow between species, particularly if hybrids are interfertile with parental species and do not suffer reduced fitness (Arnold 1992). Alternatively, hybrid unfitness can reinforce behavioral pre-mating barriers through natural selection (Saetre et al. 1997), particularly in taxa such as Swainson’s and Rough-legged Hawks that may have recently come into secondary contact.
Hybrids between raptor species are infrequently reported, most likely because they are difficult to diagnose in the field and because hybrid raptors are underrepresented in collections. Hybrids pose field and museum identification problems.

Hybrids have been reported between Red Kite (*Milvus milvus*) and Black Kite (*M. migrans*) in Sweden (Sylvén 1977), a possible hybrid Ruepell’s Vulture and Cape Vulture (*G. coprotheres*) in Botswana (Borello 2001), Brown Goshawk (*Accipiter fasciatus*) and Grey Goshawk (*A. novaehollandiae*) in Australia (Olsen 1995), Shikra (*A. badius*) and Levant Sparrowhawk (*A. brevipes*) in Israel (Yosef et al. 2001), Pallid Harrier (*Circus macrourus*) and Montagu’s Harrier (*C. pygargus*) in Finland (Forsman 1995), Western Marsh Harrier (*C. aeruginosus*) and Eastern Marsh Harrier (*C. spilonotus*) in Siberia (Fefelov 2001), Greater Spotted Eagle (*Aquila clanga*) and Lesser Spotted Eagle (*A. pomarina*) in Latvia (Bergmanis et al. 1996), and Barred Owl (*Strix varia*) and Spotted Owl (*S. occidentalis*) in Oregon and Washington (Hamer et al. 1994).

We were unable to locate a copy of Suchelet (1897), who apparently reported a hybrid between Common and Rough-legged Buzzards.

Most unusual were intergeneric hybrids reported between and Black Kite and Common Buzzard near Rome, Italy, that produced rather strange-looking offspring (Corso and Glidi 1998). Equally unusual was a mating between Gyrfalcon (*Falco rusticolus*) and Peregrine Falcon (*F. peregrinus*), in which both of the pair were females (Gjershaug et al. 1998). The hybrid Turkey x Black Vulture reported by McIlhenny (1937) was a practical joke (Jackson 1988).

Most instances of hybridization listed above were determined at the nests by observing that the adults were different species. However, one was of a hybrid raptor captured for
banding (Yosef et al. 2001) and another was identified using field observations and photographs (Corso and Glidi 1998).

This is, to our knowledge, the first specimen of a hybrid between two species of Buteo, and perhaps the first hybrid specimen for any raptor. It provides the first conclusive documentation of hybridization between two native North American members of the genus Buteo. Although the observed pairing of a Red-shouldered Hawk with a Gray Hawk (Lasley 1989) produced a downy chick, it did not fledge, and there were no photographs nor specimens from this union.

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Table 1. Uncorrected percent DNA sequence divergence between the presumed *Buteo* hybrid and potential parental *Buteo* taxa at mitochondrial (ND6) and nuclear (AK1) loci, with Genbank accession numbers.

| Species           | Source               | ND6 genbank no. | ND6 % divergence from hybrid | AK1 genbank no. | AK1 % divergence from hybrid |
|-------------------|----------------------|-----------------|------------------------------|-----------------|------------------------------|
| Hybrid            | LSUMNS B23743        | pending         | -                            | pending         | 0.00                         |
| *B. swainsoni*    | Riesing et al. 2003  | AY213028        | 0.00                         | -               | -                            |
| *B. swainsoni*    | LSUMNS B23587        | -               | -                            | pending         | 0.00                         |
| *B. swainsoni*    | Shapiro & Dumbacher 2001 | -               | -                            | AF307892        | 0.00                         |
| *B. lagopus*      | Riesing et al. 2003  | AY213017        | 3.40                         | -               | -                            |
| *B. lagopus*      | LSUMNS B8683         | -               | -                            | pending         | 0.00                         |
| *B. regalis*      | Riesing et al. 2003  | AY213018        | 3.77                         | -               | -                            |
| *B. regalis*      | LSUMNS B26245        | -               | -                            | pending         | 0.00                         |
| *B. jamaicensis*  | Riesing et al. 2003  | AY213019        | 3.21                         | -               | -                            |
| *borealis*        |                      |                 |                              |                 |                              |
| *B. jamaicensis*  | LSUMNS B33264        | -               | -                            | pending         | 0.00                         |
| *borealis*        |                      |                 |                              |                 |                              |
| *B. jamaicensis*  | LSUMNS B23470        | -               | -                            | pending         | 0.00                         |
| *harlani*         |                      |                 |                              |                 |                              |
Table 2. Comparison of measurements of the hybrid specimen with adult male Rough-legged, Red-tailed, Ferruginous, and Swainson’s Hawks (ξ in parentheses).

| Species               | Culmen (mm) | Middle toe (mm) | Wing chord (mm) |
|-----------------------|-------------|-----------------|-----------------|
| Hybrid                | 19.3        | 33.6            | 381             |
| Swainson’s Hawk       | 20.5-24.9 (22.1) | 36.7-44.4 (39.5) | 362-406 (383.6) |
| Rough-legged Hawk     | 20.8-23.0 (22.3) | 32-38.2 (35.3)  | 397-416 (407)   |
| Red-tailed Hawk       | 23.5-28.5 (25.4) | 39.8-48.5 (43.8) | 358-404 (387)   |
| Ferruginous Hawk      | 26.3-30.5 (28)  | 36-44 (38.8)    | 421-440 (431)   |

aData from Friedmann 1950.
Table 3. Comparison of plumage characters of the hybrid specimen with juvenile male Rough-legged and Swainson’s Hawks.

| Character         | Rough-legged Hawk | Swainson’s Hawk | Hybrid                          |
|-------------------|-------------------|-----------------|---------------------------------|
| Crown             | Pale              | Dark            | Dark, pale streaks              |
| Superciliary      | None              | Rufous          | Buffy                           |
| Malar             | Narrow            | Wide            | Wide                            |
| Back              | Brown, pale sides | Dark brown, pale| Dark Brown, pale tips & sides   |
| Breast            | Lightly streaked  | Heavily streaked| Heavily streaked                |
| Belly             | Solidly dark      | Buffy           | Dark with pale edges            |
| Legs              | Feathered, lightly| Bare            | Feathered, darkly marked        |
| Uppertail         | White base, dusky | Gray-brown, dark| Narrow white base, gray-brown, dark bands |
|                   | tip, no bands     | bands           | gray-brown, dark bands          |
| Primary, outer web| Grayish cast      | Dark            | Grayish cast                    |
| Primary inner web | Pale, no barring  | Darker, barring | Pale, barring                   |
FIGURE CAPTIONS

Fig. 1. Specimens showing ventral of hybrid (center), compared to juvenile male Rough-legged Hawk (top) and juvenile male Swainson’s Hawk (bottom).

Fig. 2. Specimens showing dorsal of hybrid (center), compared to juvenile male Rough-legged Hawk (top), and juvenile male Swainson’s Hawk (bottom).

Fig. 3. Notching of primary 7. (A). Rough-legged Hawk. (B). hybrid, and (C). Swainson’s Hawk. The posterior margin of each P7 is highlighted in white. (Scale is not the same on each figure.)

Fig. 4. Plot of unflattened wing chord (mm) and body mass (g) of Swainson’s Hawk (Open circles), Rough-legged Hawk (Closed circles), and the Swainson’s X Rough-legged Hawk hybrid (Closed triangle).
Clark & Witt                          Hybrid buteo specimen

Fig. 1 in

Tiff file named: HybFig1.tif
Clark & Witt                      Hybrid buteo specimen

Fig. 2 in

Tiff file named: HybFig2.tif
Clark & Witt                          Hybrid buteo specimen

Fig. 3 in

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Fig. 4.
