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SHORT COMMUNICATION

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INTERGENERIC HYBRIDIZATION OF A VAGRANT COMMON BLACK HAWK AND A RED-SHOULDERED HAWK

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ABSTRACT.—Natural intergeneric hybridization occurs rarely in raptors. In 2012, L. Hug observed a juvenile hawk interacting with a banded adult Common Black Hawk (*Buteogallus anthracinus*) in Sonoma County, California, USA, and reported that the juvenile was a Common Black Hawk × Red-shouldered Hawk (*Buteo lineatus*) hybrid (Hug 2016; *Western Birds* 47:325–326). A disparity of opinions concerning the parentage of the juvenile prompted us to document the nesting efforts of this Common Black Hawk in 2013 and 2014. The 2013 nesting attempt failed during incubation before the identity of the mate could be confirmed. In 2014 the adult female Common Black Hawk bred with an adult male Red-shouldered Hawk (*B. l. elegans*), and this pair fledged one hybrid offspring. Evidence of this hybridization included observations of the pair engaged in courtship flights ($n = 3$), copulations ($n = 2$), and simultaneous nest attendance ($n = 2$), and the offspring's intermediate physical characters and vocalizations. Although the hybrid offspring's juvenile plumage more closely resembled a juvenile Common Black Hawk overall, the hybrid also exhibited some intermediate plumage, morphological, and vocal characteristics. This hybridization event appears to be an example of the desperation hypothesis, in which a rare vagrant, unable to secure a conspecific mate, settled on a species of raptor abundant in western California. Dietary overlap of the two parental species (e.g., crayfish, amphibians) and strong associations with aquatic habitats may also have facilitated this pairing and hybridization event.

KEY WORDS: *Common Black Hawk*; *Buteogallus anthracinus*; *Red-shouldered Hawk*; *Buteo lineatus elegans*; *desperation hypothesis*; *hybridization*; *intergeneric hybrid*.

HIBRIDACIÓN INTER-GENÉRICA DE UN INDIVIDUO VAGABUNDO DE *BUTEOGALLUS ANTHRACINUS* Y UN INDIVIDUO DE *BUTEO LINEATUS*

RESUMEN.—La hibridación natural entre diferentes géneros sucede raramente en aves rapaces. En 2012, L. Hug observó un accipítrido juvenil interactuando con un adulto anillado de *Buteogallus anthracinus* en el Condado de Sonoma, California, EEUU, e informó que el juvenil era un híbrido de *B. anthracinus* y *Buteo lineatus* (Hug 2016; *Western Birds* 47:325–326). Una disparidad de opiniones sobre la paternidad del juvenil nos alentó a documentar los esfuerzos reproductivos de este individuo de *B. anthracinus* en los años 2013 y 2014. El intento de nidificación del 2013 fracasó durante la incubación, antes que la identidad de la pareja pudiera ser confirmada. En 2014, la hembra adulta de *B. anthracinus* se reprodujo con un macho adulto de *B. l. elegans*. Esta pareja produjo un volatón híbrido. La evidencia de esta hibridación incluyó observaciones de la pareja realizando vuelos de cortejo ($n = 3$), cópulas ($n = 2$), visitas simultáneas al nido ($n = 2$), y también las características intermedias de la cría, tanto en su aspecto físico como de sus vocalizaciones. Aunque el plumaje juvenil de la cría híbrida se asemejó más en términos generales a un juvenil de *B. anthracinus*, el

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híbrido también mostró algunas características intermedias de plumaje, morfología y vocalizaciones. Este evento de hibridación parece ser un ejemplo de la hipótesis de la desesperación, en la cual un ave vagabunda y rara, incapaz de conseguir una pareja de la misma especie, se instala con un compañero disponible de otra especie abundante en el oeste de California. La superposición de la dieta de las dos especies progenitoras (e.g., cangrejos, anfibios) y las fuertes asociaciones con los hábitats acuáticos también pueden haber facilitado este evento de emparejamiento e hibridación.

[Traducción del equipo editorial]

Natural hybridization has been reported for many raptor species within Accipitriformes, Strigiformes, and Falconiformes, and varies in frequency from isolated instances to relatively commonplace occurrences in stable hybrid zones (McCarthy 2006). Natural intergeneric hybridization in raptors is exceedingly rare. Within the Order Accipitriformes, a Black Kite (*Milvus migrans*) and a Common Buzzard (*Buteo buteo*) produced two offspring (Corso and Glidi 1998); a Variable Hawk (*Geranoaetus polyosoma*), probably an escapee, and a wild Swainson's Hawk (*B. swainsoni*) produced offspring (Allen 1988, Clark et al. 2005); and an escaped Harris's Hawk (*Parabuteo unicinctus*) and a wild Common Buzzard produced three offspring (Coulson and Coulson 2012).

Hubbs' principle, or the "desperation hypothesis," describes one situation in which animals may hybridize: a rare individual fails to find a conspecific mate and settles on a mate of a common species (Hubbs 1955). In raptors, the rarity of one parent species may arise because of vagrancy, range periphery, endangerment, natural range expansion, invasive species, and escape (Newton 1979, Hamer et al. 1994, Vali et al. 2010, De Broyer 2013, Elorriaga and Munoz 2013).

The present study was prompted by a sighting report of a hybrid Common Black Hawk (*Buteogallus anthracinus*) × Red-shouldered Hawk (*Buteo lineatus*) in 2012 in Sonoma County, California, USA. Hug (2016) observed and photographed a suspected hybrid juvenile hawk following and vocalizing to an adult Common Black Hawk. S. Howell (pers. comm.), who also observed the juvenile hawk, thought it might be a hybrid Common Black Hawk × Red-shouldered Hawk or Common Black Hawk × Red-tailed Hawk (*B. jamaicensis*). SM's subsequent consultation with Common Black Hawk researchers yielded opinions that Hug's photographs were probably of a juvenile Common Black Hawk (C. Boal and J. Schnell pers. comm.) or possibly a hybrid (G. Sadoti pers. comm.). This uncertainty led SM to investigate the adult Common Black Hawk's reproductive efforts. Herein, we summarize observations of the adult Common Black Hawk prior to 2013, document breeding observations from 2013 and 2014, including the production of a single hybrid offspring, and summarize succeeding observations reported by others.

METHODS

Study Site. The Laguna de Santa Rosa Wetlands Complex (LSRWC) lies in the Russian River Valley, near

Graton, Sonoma County, California, USA (38°27'N, 122°51'W). Freshwater areas include extensive marsh, open water habitats (e.g., the Laguna), ponds, seasonally flooded shallow water areas, and canals. The climate is Mediterranean, with a rainy, cool season occurring from October through April and dry, warm conditions from May through September.

Study Species. In the southwestern US, the Common Black Hawk inhabits corridors of gallery forest along persistent, flowing streams, where it feeds mostly on fish, crayfish, and other aquatic animals (Schnell 1994). The US breeding range extends from west Texas through New Mexico, Arizona, southeastern Nevada, and southwestern Utah (Schnell 1994, Meyers 2016). The US population is largely migratory, with birds suspected of wintering in Mexico based on a single band recovery (Schnell 1994). The species is a rare vagrant in California, with only 16 accepted records, representing possibly 10–11 individuals, mostly single adults in spring, from seven counties over 33 yr (1985–2018; California Bird Records Committee 2019).

The western subspecies of Red-shouldered Hawk (*B. l. elegans*) is an abundant, year-round resident of western California, where it inhabits riparian forests, eucalyptus groves, and forested suburban areas, feeding on small mammals, frogs, snakes, birds, crayfish, and insects (Dykstra et al. 2008). It differs from its eastern counterparts in its smaller size and brighter plumages, including a juvenile plumage that closely resembles the adult.

Field Methods. SM used 10 × 50 mm binoculars to opportunistically observe a Common Black Hawk at LSRWC from 2005 to 2012. In 2009, SM captured the Common Black Hawk using a phai trap (Bloom et al. 2007) baited with a crayfish and banded her.

In 2013 and 2014, SM documented the breeding efforts of the banded Common Black Hawk, by observing the hawk and her nest weekly (and sometimes more frequently) at distances of 20–100 m. In 2014, J. Papp climbed to her nest, and P. Bloom banded and color-marked the hybrid nestling, and also collected a 0.25 ml blood sample.

RESULTS

Field Observations. An adult Common Black Hawk, first observed by SM on 14 May 2005, held a territory at the LSRWC during the spring and summer of 2005–2007 and then became a year-round resident from 14 April 2008 through at least 17 July 2014.

On 18 February 2009 SM captured the hawk and banded it on the left leg (USGS band number 1807-95757). It was an adult, with definitive basic primary feathers from three molt cycles, and was identified as a female based on its large size (389 mm wing chord, 224 mm tail length, 978 g body mass; Schnell 1994, Pyle 2008) and position during copulation.

From 2005–2012, SM occasionally observed the Common Black Hawk engaging in breeding behaviors and interacting with Red-shouldered Hawks on her territory. SM first observed her performing solo aerial courtship displays on 24 May 2005 and carrying nest material on 1 May 2006. On 24 May 2005 and 14 April 2008, a resident pair of Red-shouldered Hawks harassed the Common Black Hawk during her aerial courtship displays. On 11 February 2009, a pair of Red-shouldered Hawks chased the Common Black Hawk when she approached their nesting area. In 2005, SM once observed the Common Black Hawk and an adult female Red-shouldered Hawk perching in the same dead tree. Prey remains beneath the Common Black Hawk's perches consisted primarily of crayfish (Superfamily Astacoidea) parts.

The 2013 and 2014 nests were in nonnative blue gum eucalyptus (*Eucalyptus globulus*) trees. SM documented the 2013 breeding season over 13 observation sessions, from 2 February through mid-July. On the morning of 22 April, SM observed the banded Common Black Hawk and an adult male Red-shouldered Hawk soaring over the former's territory while both hawks vocalized frequently. On 1 June, the Common Black Hawk stood in the nest, and an adult male Red-shouldered Hawk flew to and perched in the nest tree twice. SM first observed the Common Black Hawk incubating on 6 June. On 18 June, SM and G. Sadoti observed her incubating. On 1 July, SM found the Common Black Hawk perched near her nest and presumed the nest was abandoned because no bird attended the nest during this observation period and four subsequent visits.

SM documented the 2014 breeding season over 30 observation sessions, from 4 February through 17 July. SM observed aerial courtship flights on 4 February, 22 March, and 6 April, when both birds vocalized and soared near one another with wings spread and tail fanned, sometimes with legs dangling (Fig. 1a). Paired flight was not synchronous like the soaring patterns typical of conspecifics. SM and property owner Guy Smith observed the male Red-shouldered Hawk mounting and copulating with the perched Common Black Hawk on the morning of 8 April. SM observed a second copulation that evening. The pair also vocalized frequently to one another. SM observed the Common Black Hawk collecting nest material on 18 March, and nest-building on 8 and 11 April.

During the incubation phase (four visits), the Common Black Hawk was the only parent observed on the nest. SM first observed her incubating on 11 April. On 15 May, after 34 d of incubation, the Common Black Hawk assumed a brooding posture, indicating at least one hatchling. SM first observed a nestling on 20 May.



Figure 1. Intergeneric hybridization of a female Common Black Hawk and a male Red-shouldered Hawk, near Graton, Sonoma County, California, USA, 2014: (a) Pair engaged in aerial courtship on 22 March 2014; photo by N. Dunlop; (b) Pair standing on nest containing a hatchling (not visible) on 15 May 2014; photo by S. Moore.

During the nestling phase (12 visits), SM observed both parents together on the nest on 15 May (Fig. 1b) and 5 June. The Common Black Hawk was often at the nest, and SM observed her feeding the nestling on 20 May, 29 May, and 2 June. The Red-shouldered Hawk delivered food to the nest on 20 May, 29 May, 5 June, and 20 June. SM first observed the nestling standing on 5 June at 21 d old. On 11 June, the 27-d-old nestling emitted a “nestling distress scream” (Moore 2014a) several times during banding while the mother soared overhead emitting the “common call” (alarm call; Schnell 1994); no measurements were taken during banding. On 23 June, at 39 d old, the nestling flapped its wings frequently. It fledged on 30 June at 46 d old.

By 11 July the hybrid had developed coordinated flight and food-begged often. During an 8-hr observation period, it frequented a perch within 20 m of the nest. SM observed the fledgling food-begging four times when it observed a parent flying with food. The fledgling then took flight and followed the parent to the nest where the parent transferred the food and quickly departed. The hybrid's food-begging vocalizations consisted of a recurrent, drawn out “wheel” or “whee” repeated 4–12 or more times (Fig. 2; Moore 2014b). Prolonged whee calls were sometimes broken into two syllables (whee-ee). On SM's last visit on 17 July 2014, he observed the hybrid still on its natal territory.

Subsequent observations by others of this Common Black Hawk paired with a Red-shouldered Hawk at the LSRWC include eBird (Sullivan et al. 2009) reports with notes and photographs of the pair engaged in courtship behaviors from 28 January–26 March 2015, including a food transfer, and reports from 26 March–10 April 2015 of one or both hawks perching near and on a nest. Two spring 2016 reports mention the Common Black Hawk carrying nest material. Recent eBird reports and photographs from the spring of 2019 indicated that the pair engaged in aerial courtship displays. The Common Black Hawk was most recently photographed with her band visible on 4 May 2019 (Valfer 2019).

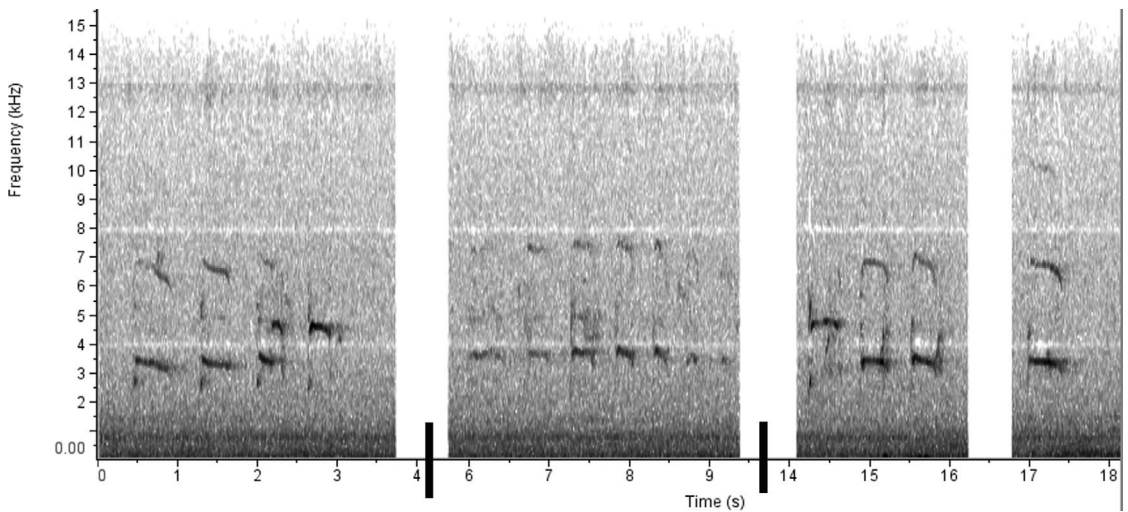


Figure 2. Sonogram of Common Black Hawk × Red-shouldered Hawk hybrid's food-begging vocalizations recorded on 11 June 2014. (Black bars on X-axis indicate time omissions when no vocalization occurred.)

Hybrid Characteristics. The hybrid's natal down at 14–18 d old was buffy with a dark eye-patch characteristic of young Common Black Hawk nestlings (Schnell 1994). By 27 d old, the dark eye-patch was replaced with grayish-white, sparsely feathered lores and emerging, brown auricular feathers. Buffy down covered the crown, sides of the neck, and furcular hollow. Elsewhere the down was whitish. The cere, scaled tarsometatarsi, and feet were yellow and irises medium brown.

The hybrid's juvenile plumage and soft parts (Fig. 3; Moore 2014c) resembled distinguishing characteristics noted for both the western Red-shouldered Hawk (*B. l. elegans*) and Common Black Hawk (Schnell 1994, Wheeler 2003, Pyle 2008). Like *B. l. elegans*, the hybrid's streaked brown crown and nape contrasted weakly with a narrow, buffy supercilium (Fig. 3a, b). Also like *B. l. elegans*, the hybrid lacked an eyeline and its mostly brown auriculars were faintly streaked with buff. Like Common Black Hawk, the hybrid exhibited wide, dark brown malar stripes which extended to the sides of the neck. The bill was blackish as in Common Black Hawk, but the pale bluish base was restricted to the areas near the gape (commissural points). The hybrid's sparsely feathered lores also resembled those of the Common Black Hawk.

With the exception of the facial pattern, the hybrid's juvenile dorsal plumage was generally dark overall, resembling a Common Black Hawk (Fig. 3a, c). The scapulars were dark brown, but edged thinly with white. The upperwing coverts were dark brown with whitish mottling and no rufous on the shoulders. Dorsally, the remiges were finely barred with at least eight dark bands, alternating with gray bands. The dorsal surface of the tail exhibited barred rectrices, with at least six charcoal-black wavy bands (Fig. 3c), with the subterminal band being

wider, alternating with gray bands, and ending in a narrow white terminal band (Fig. 3a, c). Ventrally, its buffy breast and cream-colored abdomen were heavily marked with dark brown spots and streaks (Fig. 3b, d). Its underwing coverts were cream-colored and checkered or streaked with dark brown (Fig. 3b). The undertail coverts and feathers on the legs were cream-colored and barred with dark brown. Barring on ventral surfaces of the remiges was not as fine as in the Common Black Hawk and resembled *B. l. elegans* more closely (Fig. 3d).

While the plumage mostly resembled Common Black Hawk, the hybrid's morphological characters either resembled one parent or were intermediate between the two parental species (Fig. 3). Characters resembling Common Black Hawk included the hybrid's large size, stout frame, large head, large feet, and proportionately smaller eyes. However, the overall shape of the head was rounder and more buteo-like. Some aspects of the face and bill were intermediate: the cere, lores and bill were not as elongated laterally nor compressed as vertically as in Common Black Hawk. The bill was not as strongly hooked, nor was the base of the lower mandible as wide as in Common Black Hawk. The lores were also not as sunken as in some Common Black Hawks. The tarsometatarsi were intermediate in thickness.

DISCUSSION

Our behavioral, plumage, and morphological observations confirmed the intergeneric hybridization in 2014 between a female Common Black Hawk and a male Red-shouldered Hawk, which produced a single hybrid offspring. Clark et al. (2017) caution against identifying



Figure 3. 2014 Common Black Hawk \times Red-shouldered Hawk hybrid's juvenile plumage at age 56 d old (a–c) and 46 d old (d). (a–b) Brown, streaked head and facial pattern resemble Red-shouldered Hawk except for wide, dark brown malar stripe; (a) Dark brown dorsum and absence of rufous shoulder patches resemble Common Black Hawk; (b) Buffy to cream venter heavily marked with dark brown spots and streaks; (c) Wavy lines in tail resemble Common Black Hawk; (d) Ventral barring of remiges resembles Red-shouldered Hawk. Photos by S. Moore.

hybrids based on appearance alone and recommend genetic investigation. Although we lack genetic evidence of hybridization, we provide strong behavioral evidence to corroborate the morphological and plumage-based evidence: SM observed the pair engaged in courtship displays, copulations, simultaneous nest attendance, and food provisioning of the hybrid offspring (Fig. 1).

With the exception of Hug (2016), hybridization has not been previously reported for the Common Black Hawk. Red-shouldered Hawks have engaged in other hybridization events. A male Gray Hawk (*B. plagiatas*) and a female Red-shouldered Hawk attended a nest containing a single nestling in Texas (Lasley and Sexton 1989). A Red-shouldered Hawk and a Red-tailed Hawk produced a hybrid offspring in Ohio (Clark et al. 2017). Introgression has also been observed: in 2019, a hybrid male Red-shouldered Hawk \times Red-tailed Hawk and a female Red-

tailed Hawk produced young in Maryland (Johnson 2019).

The Common Black Hawk \times Red-shouldered Hawk hybridization appears to be an example of the desperation hypothesis, for the Common Black Hawk is a rare vagrant in California (Hubbs 1955, California Bird Records Committee 2019), and the abundant Red-shouldered Hawk is in the heart of its western range (Dykstra et al. 2008). Dietary overlap (e.g., crayfish) and strong associations with aquatic habitats (Schnell 1994, Dykstra et al. 2008, Sadoti 2012, Etzel et al. 2014) may also have facilitated this pairing.

The phenotype expressed in hybrid raptors may resemble one parent species more strongly or be intermediate. Greater (*Clanga clanga*) and Lesser Spotted Eagle (*C. pomarina*) hybrids were intermediate in plumage but large in size (Vali and Lohmus 2004). Behaviorally, they migrated early like the Lesser Spotted Eagle, but their winter distributions and home range sizes were more similar to those of the Greater Spotted Eagle (Vali et al. 2018). In a study of large falcon hybrids (*Falco* spp.), the phenotype more closely resembled paternal species (Eastham and Nicholls 2005). We found that the natal down, juvenile plumage and size of the 2014 hybrid mostly resembled the Common Black Hawk although several plumage, morphological, and vocal characters were intermediate (Fig. 2, 3).

The hybrid's food-begging vocalizations (Fig. 2; Moore 2014b), although intermediate, resembled that of the Common Black Hawk more closely. The Red-shouldered Hawk's food-begging cries are a series of two-syllable (*Kea-ahh*) vocalizations (Dykstra et al. 2008), and the Common Black Hawk has a repetitive, whistling call (*whew-whew-whew*, Schnell 1994).

The developmental time frame of the hybrid was similar to that reported for both parental species. The hybrid hatched after 34 d of incubation, 1 d longer than that reported per egg for Red-shouldered Hawks (Dykstra et al. 2008) and matching that reported for Common Black Hawks. Common Black Hawk incubation is approximately 37–39 d per clutch (Schnell 1994), which probably equates to 34–36 d per egg based on an asynchronous hatch at 2-d intervals and a 2-egg clutch, such as is typical in the US. The fledging age of the hybrid (46 d) was similar to the average reported for Common Black Hawk (46.8 d), and slightly longer than that reported for Red-shouldered Hawk (6 wk) (Schnell 1994, Dykstra et al. 2008).

Based on Valfer (2019), the Common Black Hawk had survived 3727 d post-banding (10.2 yr), and based on her age at banding was at least 13 yr old in May 2019. If this was the same individual observed on 14 May 2005, then by May 2019 she had survived for 14 yr post-observation.

The blood sample from the 2014 hybrid could be used to confirm hybridization genetically. If any offspring survive, their spatial ecology, adult plumage, size, and vocalizations should be studied. If any reproduce, their mate choice, courtship behavior, clutch size, reproductive phenology, fertility and offspring viability should be noted.

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