ORNITOLOGIA NEOTROPICAL 17: 105–146, 2006 © The Neotropical Ornithological Society

THE ECOLOGY, BEHAVIOR, AND CONSERVATION OF A WEST INDIAN CORVID, THE WHITE-NECKED CROW (CORVUS LEUCOGNAPHALUS)

James W. Wiley

U. S. Geological Survey, Reston, Virginia, USA. Email: jwwiley@mail.umes.edu1

Resumen. – Ecología y conservación del Cao (Corvus leucognaphalus). – El Cao anteriormente habitaba en St. Croix, Puerto Rico y Hispaniola. Ahora sobrevive sólo en Hispaniola, donde las poblaciones declinan por algunas de las mismas razones responsables de su extirpación en Puerto Rico: fragmentación y pérdida del hábitat, y tiroteo. La depredación de los huevos y pichones por el Zorzal Pardo (Margarops fuscatus) también fue una razón importante en la extirpación del Cao en Puerto Rico. Estudié el Cao en la República Dominicana intermitentemente entre 1974 y 2004. La especie ocupa una gama amplia de hábitat, incluyendo costas húmedas y bosque montano, bosque de pino, bosque de cactus, manglar pantanoso y sabana de palmeras. Su conducta vocal es compleja y diversa, al igual que la de otros cuervos. El Cao se alimenta de una amplia variedad de plantas y presas animales. Durante los periodos de alimentación, los Caos seleccionaron plantas en 76,4% de las observaciones, mientras que del total de presas ofrecidas a los pichones 51,6% fueron animales. Las áreas centrales de actividad de tres parejas reproductoras promediaron 9,8 \pm 3,7 ha, considerando que el tamaño de su territorio promedio era de 5,5 \pm 5,2 ha. La construcción de los nidos comenzó a finales de Enero. Los nidos fueron estructuras voluminosas construidas en lo alto de los árboles. El período de incubación fue de aproximadamente 18-22 días y el período de anidación de 35-44 días. El tamaño de la nidada fue de cuatro huevos en seis nidos y tres huevos en un nido que inspeccioné hasta el término de la anidación. De 27 huevos en esos siete nidos, 25 pichones eclosionaron y 22 volaron de los mismos. La atención al nido fue más alta durante la incubación, y fue disminuyendo durante el período de anidación de los pichones. No se observó ningún tipo de depredación y sólo hubo una incidencia de ectoparasitismo en pichones. Se recomienda un programa de reintroducción del Cao a Puerto Rico como viable e importante para la supervivencia de la especie.

Abstract. – The White-necked Crow (*Corrus leucognaphalus*) formerly inhabited St. Croix, Puerto Rico, and Hispaniola. It survives only in Hispaniola, where populations are declining for some of the same reasons primarily responsible for its extirpation from Puerto Rico: habitat fragmentation and loss, and shooting. Egg and chick depredation by the Pearly-eyed Thrasher (*Margarops fuscatus*) was also important in the extirpation of the Puerto Rico population. I studied the crow in the Dominican Republic intermittently from 1974 to 2004. The species occupies a wide range of habitats, including wet coastal and montane forest, pine forest, cactus forest, mangrove swamp, and palm savanna. Its vocal behavior is complex and diverse, more like that of ravens than of crows. White-necked Crows fed on a wide variety of plant and animal matter. Foraging crows selected plant materials in 76.4% of my observations, whereas animals made up 51.6% of the food items delivered to nestlings. Core activity areas of three breeding pairs averaged 9.8 ± 3.7 ha, whereas their average territory size was 5.5 ± 5.2 ha. Nest building began in late January. Nests were bulky structures placed high in trees. Eggs were incubated 18–22 days and the nestling period was 35–44 days.

¹*Mailing address:* Maryland Cooperative Fish and Wildlife Research Unit, 1120 Trigg Hall, University of Maryland Eastern Shore, Princess Anne, Maryland 21853, USA. *E-mail:* jwwiley@mail.umes.edu

Clutch size was four eggs at six nests and three eggs at one nest I inspected at clutch completion. Twentyfive chicks hatched from 27 eggs at those nests, and a total of 22 fledged. Adult nest attendance was highest during incubation, then declined through the nestling period. I observed no predation and only a moderate incidence of ectoparasitism of chicks. A program of reintroducing the White-necked Crow to Puerto Rico is recommended as feasible and important to the survival of the species. *Accepted 8 December 2005*.

Key words: Behavior, breeding, conservation, corvid, *Corvus leucognaphalus*, Dominican Republic, ecology, extinction, extirpation, Haiti, Hispaniola, Puerto Rico, vocalization, White-necked Crow.

INTRODUCTION

STUDY AREAS

The four species of West Indian corvids, all in the genus Corvus, with their raucous calls and flocking behavior, are prominent members of avian communities in the Antilles. Resident and visiting naturalists have accumulated considerable anecdotal information through incidental observations of these birds, yet the basic natural history of West Indian corvids is poorly known (Johnston 1961, Cruz 1972, Goodwin 1976). With the rampant habitat alteration occurring throughout most of the West Indies, several corvid populations have declined or disappeared (Barbour 1943, Greenway 1958, Bond 1973, Goodwin 1976). The White-necked Crow (Corvus leucognaphalus; Fig. 1) formerly occurred in Hispaniola, Puerto Rico, and St. Croix (Fig. 2), but today survives only in Hispaniola, including Île de la Gonäve and Isla Saona. Because of its decreasing range and extirpation from entire landmasses, a main objective of my study was to determine why the crow disappeared from parts of its former range. Resolution of the question of the crow's decline required a basic knowledge of its life history and behavioral ecology. Thus, my objectives included determining the crow's general ecology and behavior. Finally, my objectives included providing managers with information to allow them to make biologically sound decisions for the conservation of the Whitenecked Crow.

I conducted fieldwork in the Dominican Republic in October 1974, December 1975 to July 1976, July and August 1978, July to September 1982, August 1989, March to April 1996, May to June 2000, June and December 2001, January, March to May, and August 2002, and December 2004. I watched crows in several locations, but my major study area was in Los Haitises, north-central Dominican Republic, and Pedernales, southwestern Dominican Republic (Fig. 3). The Haitises region is rugged limestone karst ("mogotes") of Miocene origin, with narrow valleys having deep soils, and extensive natural hardwood forests (Zanoni et al. 1990). Elevations at Los Haitises ranged from 250 to 360 m. The area is west of the village of Pilancón, and approximately 20 km northeast of Bayaguana (i.e., study area centered at 18°5576"N, 069°36'11"W). The nearest weather stations to the Haitises study area, Bayaguana and Sabana de la Mar (35 km northeast), reported mean annual rainfalls of 181 cm and 212 cm, and mean annual temperatures of 24.5°C and 25.2°C, respectively. The rainfall and temperatures in my Los Haitises study area probably fall between those given for the two stations. Maximum rainfall occurs from May to October. The karst is quite permeable, and standing water is rare.

The plant community in Los Haitises is classified as a subtropical wet forest (Holdridge Classification; OAS Ecological Map, Washington, DC, 1967). Characteristic trees

WHITE-NECKED CROW ECOLOGY AND CONSERVATION



FIG. 1. Adult White-necked Crow at nest with late-stage chicks, Los Haitises, Dominican Republic.

include cupey (*Clusia rosea*), fourleaf buchenavia (*Buchenavia capitata*), West Indian mahogany (*Swietenia mahagoni*), kapoktree ((*Ceiba* pentandra), masa (Tetragastris balsamifera), American muskwood (Guarea guidonia), Spanish cedar (Cedrela odorata), bullwood (Sloanea

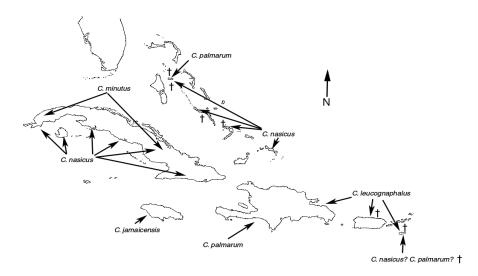


FIG. 2. Recent and present distribution of the genus *Corrus* in the West Indies (After Olson & Hilgartner 1982). \dagger = extirpated or extinct population.

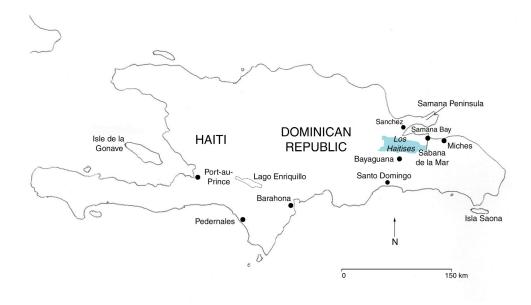


FIG. 3. Hispaniola (Haiti and Dominican Republic), showing study areas and other sites mentioned in text.

berteriana), and corcho bobo (Pisonia albida); plant names follow Little & Wadsworth 1964), Little et al. (1974), Zanoni et al. 1990, and USDA, NRCS (2004). The study area consisted of virgin forest, as well as active and abandoned small farms. Although the region was declared a national park (Parque Nacional Los Haitises) in 1976, clear-cutting and burning for farming accelerated through 2004. Subsistence crops are mixtures of several fruits and vegetables. Abandoned farms are quickly invaded by higuillo de hoja menuda (Piper aduncum), matchwood (Didymopanax morototoni), monkey's hand (Lepianthes peltata), and sword fern (Nephrolepsis multiflora). Further descriptive information on the study area is presented by Wiley & Wiley (1981), Snyder et al. (1987), and Zanoni et al. (1990).

The Pedernales study area included the coastal plain and low foothills east of the town of Pedernales. The area is eroded limestone within the subtropical thorn woodland life zone. The plant community of the area is highly disturbed and represents a secondary replacement of more diverse past communities. Porknut (Acacia macracantha) comprises about 50% of the cover, with Hispaniolan royal palm (Roystonea hispaniolana), coconut palm (Cocos nucifera), and mango (Mangifera indica) also abundant. Other important trees and shrubs included Capparis ferruginea, Jamaican caper (C. cynophallophora), tuna (Opuntia moniliformis), lignum-vitae (Guajacum officinale), baitoa (Phyllostylon brasiliense), Gouane palm (Coccothrinax ekmanii), and chechen (Metopium brownei) (Fisher-Meerow 1983, Fisher-Meerow & Judd 1989). Annual rainfall at Pedernales averages 47.1 cm, with two main rainfall periods, May and June, and September and October. Annual temperature averages 27.9°C.

I examined crow nests in the wet degraded forest in the coastal foothills south of Barahona (mean annual temperature 26.7°C; mean annual rainfall 101.9 cm; wet-

WILEY

test months May and June, and September and October). The area has calcareous soils and is within the subtropical humid forest zone, with characteristic tree species including West Indian mahogany, Haitian catalpa (*Catalpa longissima*), caracolí (*Pithecellobium glaucum*), and Hispaniolan royal palm.

METHODS

I collected behavioral and ecological data by watching crows from lookouts in tops of emergent trees, from hilltops that offered overviews of crow ranges, and from blinds placed in trees 3-12 m from five nests. To avoid disturbing nesting crows and ensure normal behavior at nests, I entered blinds before first light. If an entire day was not spent in the blind, I exited the area when crows were known to be distant. I gathered data on the interactions of crows and other avian species opportunistically from lookouts and blinds. Distances of crow and other species' activities were estimated at 10-m increments from 0-150 m, and at 25 m increments beyond 150 m. Activities of crows and other species were plotted on field maps of the study sites. Some distances were measured (e.g., particularly between nests and sites often visited by crows), but most were estimated. I characterized crow core activity areas as that portion of the total activity area where 80% (n = 3 pairs, 1649 activity points) of activities (foraging, loafing, pair interactions, local movement, roosting) were observed. Sex determination was possible from behavior at the three nests where most intensive observations were made. Although no crows were marked, I could often identify individuals through unique behavior and plumage characteristics.

To examine White-necked Crow population changes over a protracted period, I surveyed bird populations along trails through representative habitats in the Haitises (4 routes) study areas from 1974 to 2004. Three survey routes were 1-km long, whereas one route (LH # 3) was 1.4-km in length. I sampled bird populations in March and April, with surveys conducted during the first two hours of daylight on two consecutive days for each route per month. I surveyed each 100 m transect section within a 6-min sampling period, recording all observations per section. Surveys were suspended during rain or when wind speed reached Beaufort 4. If rainsqualls were short, a disrupted survey was continued when the squall passed and leaf drip subsided. I recorded all birds seen or heard, with no attempt to record detection distances to individuals or to species under varying sampling conditions. Thus, the counts provide rough indices of abundance, but cannot be used to provide absolute area-density figures.

To examine nest-building behavior and role of mates in nest construction, I watched three crow pairs from lookouts placed in emergent trees and from blinds situated in trees adjacent to nests at Los Haitises. Observations were made in full-day bouts from before first light through last light. Determination of gender of individuals was sometimes possible based on courtship and copulation behavior. More often, however, I was not able to determine sex of pair members and characterized the individuals as "A" and "B" during interactions. Quantification of building behavior (e.g., material delivery rates, source distance from nest) was based on bouts when the subjects were visible for the entire behavioral sequence.

Crow vocalizations were recorded on a Uher 4000 IC Report tape recorder with a parabolic reflector microphone and analyzed using Raven (ver. 1.0) sound analysis software.

I collected descriptive data on crow eggs and nestlings, using vernier calipers and spring scales to measure eggs and chicks. Few measurements were taken of chicks because I avoided disturbing nesting pairs to ensure their normal behavior during my observations. The day of hatching could not be determined for all chicks I examined; in those cases, I estimated the chicks' ages based on known ages of nestmates and behavioral observations made from blinds. I divided the nesting period into four stages for analyses of breeding behavior: incubation, and early (first third of nestling period), mid- (middle third), and late-nestling stages.

I evaluated diet choices of White-necked Crows by observing food items delivered to nests, as well as observing foraging and transfers of food between mates. Biomass estimates, particularly for plant matter, are crude because the amount of material delivered to nests could not always be accurately determined; e.g., especially regurgitated fruit pulp and smaller seeds. Because crows typically carried small food items to the nest in their sublingual pouch, identification of foods was infrequent and then possible only when passed between adults or to the chicks, or when dropped to the ground or on the nest rim. Although not always clearly visible, certain plant foods (e.g., Clusia rosea pulp) could be determined from the distinctive color or consistency. I was also able to make identifications by inspecting cached items or remains at and below nests. Weights of food items are mostly best estimates, based on approximate amounts delivered. Many plant parts were weighed, but the mass of others was estimated from weights taken of comparably sized, similar items. I weighed representatives of most animal species delivered to nests by crows.

Interviews of older woodsmen were conducted in Puerto Rico from 1973 to 1986. Individuals were asked about their recollections of crows, their past numbers and distribution, and natural history as part of a broader effort to determine past wildlife and habitat characteristics in Puerto Rico.

Statistical analyses follow procedures in

Zar (1975). Standard deviations are used as the measure of variance about the mean. Significance level was set at 0.05.

I present my results in the context of a review of reported observations pertinent to my observations of White-necked Crows.

RELATIONSHIPS AND DESCRIPTION

The White-necked Crow is the largest of the four corvids in the West Indies, including the Cuban Crow (Corvus nasicus) of Cuba, Isla de Juventud (formerly Isle of Pines), and the southern-most Bahama Islands, the endemic Jamaican Crow (C. jamaicensis), and the Palm Crow (C. palmarum) of Hispaniola, with scattered, relict populations in Cuba (Fig. 2). Based on differences in voices, plumages and tarsus and bill sizes, Garrido et al. (1997) split C. palmarum into two species: C. minutus, restricted to Cuba, where it is rare and local, and C. palmarum, endemic to Hispaniola, where it is common. Wetmore (1920, 1937) reported that Corvus pumilis, an extinct species intermediate in size between leucognaphalus and palmarum, formerly inhabited Puerto Rico and the Virgin Islands. Olson & Hillgarner (1982), however, suggested that C. pumilis could be added under C. nasicus, although it might be a larger representative of C. palma-rum. If C. nasicus formerly occurred in Puerto Rico and the Virgin Islands, it was presumably sympatric with C. leucognaphalus, thereby dispelling any consideration that C. nasicus and C. leucognaphalus are conspecific (see below). Brodkorb (1959) proposed a new species, C. wetmorei, based on fossils from New Providence, but Olson & Hilgartner (1982) considered C. wetmorei as a junior synonym of C. nasicus.

The White-necked Crow is a large corvid (about 50 cm in length), completely black, with a blue-purplish gloss, especially on the upper parts. Long, soft semiplume-like feathers cover the throat. Rictal bristles cover the

WHITE-NECKED CROW ECOLOGY AND CONSERVATION

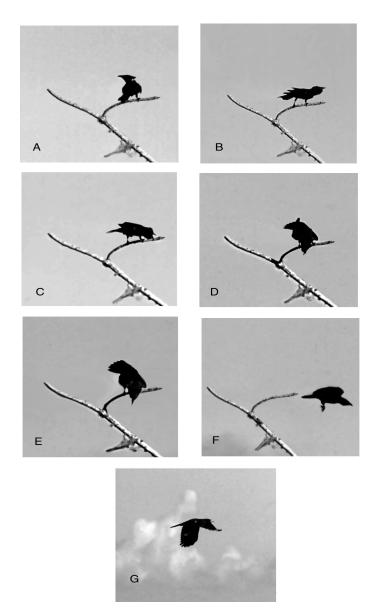


FIG. 4. Anxiety display of White-necked Crow, Miches, Dominican Republic, 1976. A: Perched crow, showing white bases of neck feathers. B & C: Calling with *high-can*'s, and throat feathers splayed. D & E: Head down, tail splayed and flipped, and wings out from body. F & G: Leaving perch in direction of intruder, giving *high-can*'s.

nostrils and are directed forward and up, as in ravens (Fig. 1). Gundlach (1874) noted these forward-directed bristles and remarked on the similarity between *Corvus nasicus* and *C. leucognaphalus* in the structure of the nasal bristles. The adults have bright orange-red irides,

which Württemberg (1835) characterized as fire-red eyes. The crow's common name is derived from the snowy-white bases of the neck feathers, visible only during displays (Fig. 4). Although *C. leucognaphalus* shares this plumage characteristic with the Chihuahuan Raven (*C. cryptoleucus*) of southwestern North America and Mexico, Jollie (1978) considered this similarity as meaningless parallelism. Baumel (1953) reported a White-necked Crow with vestigial claws on the wings, the first such report for the family Corvidae.

The White-necked Crow shows moderate sexual dimorphism in size but none in plumage. This is similar to several corvid species (e.g., Carrion Crow Corvus corone corone and Hooded Crow C. c. corniz; Saino & De Bernardi 1994). The average sexual size dimorphism index (D.I.; Storer 1966) of Whitenecked Crow specimens measured by Johnston (1961) is 7.80 ± 2.37 for four measurements (Wing = 7.19, Tail = 4.72, Tarsus = 9.89, Culmen = 9.41). Males are significantly larger than females in each of these measurements (Wing: P = 0.001, df = 20; Tail: P = 0.01, df = 17; Tarsus: P << 0.001, df = 11; Culmen: P < 0.001, df = 24; Fisher-Behrens t-test). Cuban Crows (mean_{D.I.} = 2.47 \pm 0.78), Palm Crows (mean_{D1} = 2.45 \pm 2.19), and Jamaican Crows (mean_{D.I.} = 2.41 ± 1.51) show less sexual size dimorphism than the White-necked Crow

There has been substantial debate over the relationship and taxonomy of the Whitenecked Crow. Johnston (1961) placed *leucognaphalus* in a group that included the American Crow (*Corvus brachyrhynchos*) and Cuban Crow, and apart from a second group that included the other West Indian crows. In contrast, Goodwin (1976) and Jollie (1978) placed *leucognaphalus* with *jamaicensis* and *nasicus*, separate from *brachyrhynchos* and *palmarum*. Based on results using DNA hybridization to determine relationships among taxa, Monroe & Sibley (1993) similarly arranged *leucognaphalus* next to nasicus, jamaicensis, and palmarum. Indeed, much earlier, leucognaphalus, jamaicensis, and nasicus were placed together in a separate genus, Microcorax (Sharpe 1877). Dorst (1947) and Brodkorb (1959) considered C. nasicus to be a subspecies of C. leucognaphalus. Based on vocalizations, Bond (1977) suggested a relationship among C. nasicus, C. leucognaphalus, and C. jamaicensis, all of which he believed to be most closely related to C. cryptoleucus of the mainland. Bond (1977) further suggested that C. palmarum was derived from C. ossifragus (Fish Crow) and represents a later invasion of the Greater Antilles.

RANGE AND STATUS

The White-necked Crow formerly occurred in Hispaniola, Puerto Rico, and St. Croix. In St. Croix, the crow is known solely from aboriginal kitchen middens (Wetmore 1918, 1925). The crow's decline and disappearance from Puerto Rico is well documented. It was common during the earliest years of exploration of the island (Abbad & Lasierra 1788). In the last quarter of the nineteenth century, Gundlach (1874, 1878) reported the Whitenecked Crow could still be found in good numbers in interior and eastern Puerto Rico (i.e., Lares, Pajita, Utuado, Caguana), and was told that the crow was still common in the eastern region of the island where he did not visit. When Wetmore (1916, 1927) visited Puerto Rico in 1911-1912, however, the crow was almost extirpated. Wetmore encountered the crow in the Sierra de Luquillo, where it was still fairly common, and learned of other individuals below San Sebastian, northwestern Puerto Rico. Wetmore (1916) observed that the White-necked Crow could not adapt to changed conditions and he expected it would only survive in the government forest reserve (now the Caribbean National Forest) in the Sierra de Luquillo. The last Puerto Rican population of the crow did persist in

WHITE-NECKED CROW ECOLOGY AND CONSERVATION

the Sierra de Luquillo but, unfortunately, Wetmore's prediction for its survival there did not come true.

My interviews with older woodsmen who had a long familiarity with the Sierra de Luquillo area yielded a unanimous opinion that the crow became quite rare or disappeared from the Sierra in the 1930s or 1940s. Manolo Vázquez (age 65 years in 1976) saw about 40 crows at Icacos Valley in 1950. By the late 1950s, few crows remained there (Mason 1960). Moises Parilla recalled the crow occurred near his home in Sonadora in the 1940s, but reported it as gone by the late 1950s. The crow was last sighted in the Sierra de Luquillo in 1963 by H. A. Raffaele (Bond 1973, Raffaele 1983) and Cayo Burgos (pers. com.), an area resident and former woodsman. Despite numerous, spurious reports of White-necked Crows in Puerto Rico, all proved to be escaped American Crows, imported as pets (Raffaele 1983, pers. com.; pers. observ.).

The White-necked Crow formerly occurred in large numbers throughout much of Hispaniola (see Wetmore & Swales 1931 for review). Württemberg (1835) described flocks of hundreds of whitenecks in the early 19th century. Beck (1916) observed several hundred crows in the swamp near the mouth of río Bararrote on 23 November 1916. By 1927, the White-necked Crow was still considered common in some areas, but was becoming rare in many regions (Wetmore & Swales 1931). Dod (1978, 1992) described it as declining and extirpated from the larger part of its former range in the Dominican Republic. She described the crow as very common in many localities as late as 1950, but since that time it numbers were reduced because of hunting. Most recently, Keith et al. (2003) described the White-necked Crow as a locally common to uncommon resident island-wide, but by 1982 it had become rare in pine forest habitat and at high elevations, so that now it is

only locally distributed in lowlands.

Little has been reported of the crow's present status and distribution in Haiti. Although Wetmore & Swales (1931) encountered it to 2650 m in Massif de la Selle in April 1927, it has more recently been reported as uncommon above 1500 m (A. O. U. 1998). Bond (1928) found it "very common in the northern pine belt" of Haiti. Woods & Ottenwalder (1983, 1992) recorded it from the Citadelle region, but absent from the Morne la Viste and Pic Formon-Pic Macaya regions in the high mountains. Golding (1983) recently reported the White-necked Crow in northwestern Haiti. Dod (1992) reported that in Haiti it "is very common around Port-au-Prince, where there are trees, and at an agricultural station at Damian...since the Haitians are not allowed to have guns." The crow was reported as "casual" on Île de la Gonäve (A. O. U. 1998).

In the Dominican Republic, I found the White-necked Crow restricted mainly to large tracts of habitat, and there it was local in distribution. Dod's (1978) distribution map is deceptive in showing the crow occurring throughout the Dominican Republic, whereas its distribution is actually quite uneven. Areas where I observed substantial crow populations included Los Haitises, Miches, the Samaná Peninsula, and the Sierra de Bahoruco. Also, it was seasonally abundant on Isla Saona during the aggregated breeding of White-crowned Pigeons (*Patagioenas leucocephala*). Nowhere did crow numbers approach those described by early visitors.

HABITAT

Sallé (1857) and Wetmore (1916) suggested that the White-necked Crow requires large expanses of natural forest and soon disappears where its habitat is degraded. When Wetmore visited Puerto Rico in 1911–1912, he found the White-necked Crow primarily in

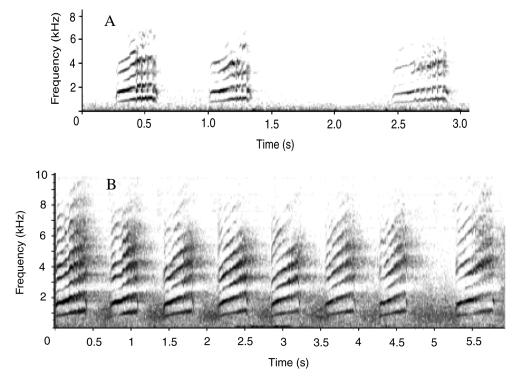


FIG. 5. A: *Caw* vocalization of White-necked Crow, Los Haitises, Dominican Republic, 1976. B: *High can*, Los Haitises, Dominican Republic, 2001.

rugged forested terrain of the inland mountains. This may indicate a preference for this habitat, but may also reflect the near-complete destruction of the island's lowland habitat by the time of Wetmore's visit.

In Hispaniola, records exist for the crow's occurrence in several habitat types, including pine forests (Danforth 1929, Bond 1947, Dod 1978), broadleaf forests, cactus forests (Peters 1917), mangrove swamps (Beck 1916, Peters 1917, Abbott *in* Wetmore & Swales 1931, Wetmore & Swales 1931), and palm savannas (Dod 1978). I found it most often in wet forests, particularly the extensive tracts in Los Haitises, but also the remnant coastal rain forest (Sabana de la Mar, Peninsula de Samaná) and degraded rain forests in the mountains above Miches. A small breeding population

has persisted in the dry coastal woodland in southwestern Dominican Republic (Pedernales). Whitenecks were also regular visitors to the dry woodlands and agricultural areas surrounding Lago Enriquillo (particularly the western and northwestern shores), moving between the lowlands and nearby foothills and mountains to the north. The crow was seasonally abundant (during pigeon breeding season) in the dry coastal forest of southeastern Dominican Republic and Isla Saona, but otherwise was not common there. I did not find it to be common in the dry foothill and scrub habitats, nor in the pine forests. There, the Palm Crow was locally common, as reported by Danforth (1929), Wetmore & Swales (1931), Bond (1947), and Dod (1992). The two species are sympatric in some areas,

114

WILEY

WHITE-NECKED CROW ECOLOGY AND CONSERVATION

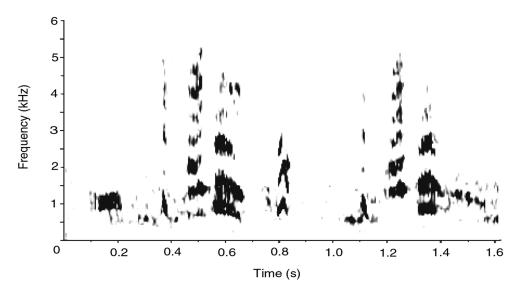


FIG. 6. Bubbling call of White-necked Crow, Los Haitises, Dominican Republic, 1976.

but the Palm Crow is the more abundant in drier sites. The White-necked Crow is apparently less tolerant of human activity than the Palm Crow, as I saw few White-necked Crows around human habitations. The exception to that pattern was the breeding population at Pedernales, where pairs nested in palms close to houses and active agricultural fields. The Palm Crow often nested, roosted, and fed in palm groves about small towns (e.g., Duvergé).

VOCAL BEHAVIOR

Corvids are typically highly vocal, with a complex repertoire of calls; e.g., Chamberlain & Cornwell (1971) catalogued 23 distinct vocalizations of the American Crow, each with a unique environmental and behavioral context, whereas Connor (1985) noted 18 call types in the Common Raven (*C. corax*). The complex and diverse vocal behavior of the Whitenecked Crow is more like that of ravens than of crows (Cherrie 1897, Danforth 1929, Wetmore & Swales 1931, Bond 1947). Madge & Burn (1994) described its vocalizations as "An extraordinary mixed babbling, bubbling and squawking, very varied in content, some notes rich and sweet, others raucous and squawked." Gundlach (1874) noted that the voice of the White-necked Crow was like that of C. nasicus. Württemberg (1835) and Cherrie (1897) reported the whiteneck forming noisy flocks. Cherrie (1897) remarked that "Their noise can be heard a long way off when a number are collected together. The note in itself is very peculiar, and appears to be compounded of a half musical cackle and a whistling kind of laugh, but sometimes it is harsh and discordant. It is one of the most strange noises I have ever heard from any bird." Here I describe some of the more common vocalizations and their contexts. Chick vocal behavior is described in the Nestlings section.

Cam. This was the most common Whitenecked Crow vocalization I heard (Fig. 5a). The *cam* was typically used in advertisement on the territory, including when the adult crows entered or left the nest site. It was also

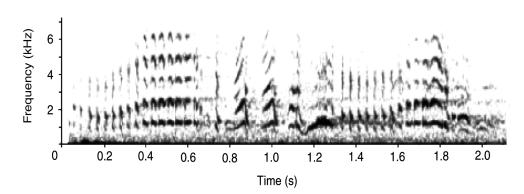


FIG. 7. Week-woo call of White-necked Crow, Los Haitises, Dominican Republic, 1976.

used when residents chased territorial invaders (especially Red-tailed Hawks *Buteo jamaicensis*, Ridgway's Hawks *Buteo ridgmayi*, Turkey Vultures *Cathartes aura*) or when a human approached the nest. On occasion I heard a retreating crow (territorial invader) give *can*'s as it was pursued by territory holders. When an adult called with *can*'s after discovering me at its nest, or in response to a territorial invader entering the nest territory, its mate quickly approached to join in the defense.

Meinertzhagen (1926) noted that Corvus brachyrhynchos minutus "...and C. b. palmarum [= C. palmarum] are the only West Indian crows which 'caw'; all others, 'leucognaphalus, nasicus, and jamaicensis,' babbling and chattering."

High-can: This vocalization was similar to the advertisement *can*, but was higher in tone, more intense, and was used in contexts of greater excited than more guttural *canv* (Fig. 5b).

Bubbling call. This is a complex call with several variations, but having a general phonetic pattern of "Gollygop" (Fig. 6). It was used in several contexts, including duets by mated pairs in flight, in greetings by pair members, intraspecific supplantations (by aggressors and chased birds), and when other species (e.g., Cattle Egret Bubulcus ibis) were chased. *Bubbling* calls were occasionally given by the chased crow in interspecific interactions. When a foraging pair of adult crows discovered me in a treetop lookout, they flew over my head giving *bubbling* vocalizations, then landed in a nerby tree, where they continued to direct these calls at me as they displayed the white base of their neck feathers.

Week-woo call. A complex "week-woo-oo" or "week-wick-woo-oo" (Fig. 7) was given by the territory holder as it returned from evicting a territory invader Rowley (1974) described a "Victory" call given in similar context for the Australian Raven (*Corvus coronoides*).

Guk calls. These are a complex series of calls with several variations, but with the general form of "guk - guk - gu-woo" (Fig. 8), and sometimes with the bubbling "gollygop" as the final element. The gollygop element was sometimes used alone by the chased crow in interspecific interactions. *Guk* calls were used in high intensity intra- and inter-specific interactions, usually by the chaser, but occasionally by the chased birds, too.

Weeak call. A loud, gutteral "*weeak-weeak-weeah*" was intermittently given by birds as they gathered twigs for nest building.

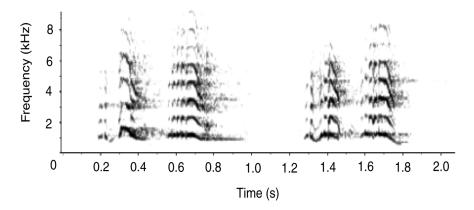


FIG. 8. "Guk" vocalization of White-necked Crow, Los Haitises, Dominican Republic, 1976.

Wag call. A gargling "*wag*" was given by birds flying to their nests with building materials.

Gauch call. Adult White-necked Crows occasionally gave a loud, rauchous "gauch-gauchgauch" as they left the nest after delivering materials.

Hic-gu-gik-gu call. A high-intensity *bic-gu-gik-gu* call was given during intraspecific interactions, typically by members of territorial pairs directed toward territory invaders, but also by supplanted invaders.

High-low gargles. Gargles are complex vocalizations consisting of alternating high-pitched calls and low guttural sounds, typically given by several birds during apparent high-anxiety situations, particularly in congregations of many birds.

"Nah" Older chicks gave begging calls, sounding like a soft version of the *caw*: "nah."

VISUAL DISPLAYS

Assertion. Low- and moderate-intensity assertion consisted of the crow orienting toward another bird and calling, usually with can's. In more intense assertion bouts, the crow's body was held horizontal, with its neck outstretched and neck feathers splayed. At these times the white bases of the neck feathers were clearly visible.

Anxiety and excitement. In some territorial defense bouts, one or both resident pair members landed next to an intruding crow. Usually the residents, but sometimes also the intruder, lowered their heads and forcefully hammered on their perches with their bills. Leaves and vines were also plucked and shredded with the bill. Such displays of possible tension were common among crows that gathered in groups. Displays involving lowering the head, or "Herabstarren," have been reported as displacement behavior for other species of *Corrus*, as has hammering (Poncy 1938, Skead 1952, Coombs 1960, Gwinner 1964, Wittenberg 1968).

Tail flipping is apparently associated with anxiety and was the most consistent display during assertion bouts. The tail flips were of low amplitude and were rapidly executed. The crow held its head down at the plane of the back or slightly below it when the angle of the back was about 10° below horizontal. Crows displaying high anxiety lowered their head farther and the tail was held more upright

(Fig. 4). White-necked Crows tail flipped (5-6 flips) when they landed after a flight, when they arrived at the nest with twigs or food, when one crow "greeted" another (usually its mate), and when a bird perched after an aerial attack during intra- and interspecific chases (including mobbing humans at the nest). Tail flips were sometimes given during vocal bouts. In high-intensity territorial interactions, crows called with high-can's, oriented toward the intruder with heads down, then quickly moved to an upright position and gave a quick tail flip. Tail flips were a downward movement with retrices quickly splayed so the tail was 1/4-opened. During the display, the crow's throat feathers are somewhat erect and the bird's wings are held slightly out from the body and above the head. Palm Crows also tail flip when aggitated but, although they hold their body horizontal as do Whitenecked Crows, the tail is flipped down, rather than up as in the White-necked Crow. Palm Crows give individual tail flips after each caw call element. Holvoak (1983) suggested these tail movements in Palm Crows function as flight intentions or self-assertive movements. Tail flipping has been reported for several other corvid species (e.g., Eurasian Rook Corvus frugilegus and Carrion Crow; Coombs 1960). Madge & Burn (1994) reported that the White-necked Crow lacked the tail flicking movement, but that the behavior is characteristic of the Palm Crow.

Alarm. When potential predators (including humans) approached a crow's nest, the residents exhibited a more intense version of the Assertion Display. The body and tail were held horizontal, with the neck outstretched and the bird's head held slightly below the plane of the back. The bird partially extended and raised its wings and splayed its neck feathers, showing the white bases. The bird gave vigorous tail flips and called with *caw*'s. Wetmore (1916) reported that White-necked

Crows responded to his presence by landing high in a tree, where they "crouched" and called, lifting their wings nervously.

Antagonistic display. In this display, the territory holder leaned forward, lowered its head below the plane of its back, held its body horizontal, fanned its tail, hung its wings somewhat, and called with bubbling calls and hic-gu-gik-gu vocalizations, while directing these activities at an intruding White-necked Crow. Sometimes, however, the displaying birds were more upright with the tail down and neck curved down somewhat. The feathers of the bird's head, throat, and back were elevated, and the white feather bases were clearly exposed on the neck. Supplanted invaders, if not expelled from the area, sometimes responded with similar visual and vocal displays, directed at the resident birds. Johnston (1958) reported the Chihuahuan Raven assuming a similar posture and exposing hidden white on the neck during aggressive and defensive behavior. Although Blake (1957) had suggested an epigamic function of the concealed white neck feathers in the Chihuahuan Raven, Johnston (1958) was unable to find support for this explanation in captive and wild birds. Bowing and tail flaring have been reported for the Eurasian Rook during territorial conflicts (Coombs 1960).

Supplantation display. White-necked Crows performed a ritualized display after being supplanted by another crow or other species. The supplanted crow moved away from the chasing bird and, perching, held its head below its feet, hung its wings down, fanned its tail, and called (*bubbling* calls). The neck was curved downward with splayed neck feathers, showing their white bases. This position was sometimes associated with a re-directed behavior in which the crow hammered its perch with its bill or broke off a twig and carried it away. During more intense supplantation bouts (e.g., multiple, intraspecific), the harassed crow broke off nearby twigs for up to 1.5 min. Thereafter, the alien flew with a twig in its bill and when it was 40–90 m from the aggressor, transferred the twig to its feet, dropped it in mid-flight, and flew into dense forest.

Aerial displays. White-necked Crows occasionally interrupted nest building to circle over the nest area while calling with *can*'s. Birds soared to heights of 50–200 m before dropping back to the forest.

Attacks on some large birds (crows, vultures, hawks) involved complex aerial displays. Crows chased the intruders in strong flapping, spiraling flights, sometimes to altitudes where the birds were barely visible to the human eye. During these ascending chases, crows called vigorously with high-can's. If these chases failed in expelling the intruder, the crows flew above and dove on the intruder, sometimes striking the invader with their feet. After a successful eviction of an intruder from its territory, the resident flew to its nest area, frequently giving an aerial display, wherein it half raised its wings above its back in a "V," momentarily held them stationary in that position, dropped through the air for several meters, then gave a few strong flaps and repeated the display, dropping closer to the forest canopy with each display. When the crow was over its nest area, it lowered its legs, elevated its wings and tail, and dropped to the nest in a series of parachuting glides. Week-woo calls were given during the display. Sometimes crows descended rapidly with wings 1/2 to 2/3 closed, varying the wing position to control their descent, directly into the forest. The aerial display was typically followed by perched crows calling with high-can's. Coombs (1960) described dihedral flights and glides by Eurasian Rooks and Carrion Crows, with some elements similar to the aerial display of the White-necked Crow.

Greeting display. An incoming crow often gave a *bubbling* call as it approached its mate or nest site. After landing, the pair performed a mutual bowing display, with tail flips, and tail and wings partially spread. The birds then touched bills and allopreened.

Allopreening. White-necked Crows displayed mutual allopreening between pair members and, rarely, among other crows. This behavior usually followed a greeting display. The preened individual loosened its feathers, bowed its head, and held its wings loose at its sides. The white of the neck feather bases was visible during allopreening. The preened bird frequently reciprocated and preened its mate's neck. This may be what Dod (1978, 1992) reported as courtship behavior. Kilham (1989), however, noted that other species of Corvus clearly allopreen with neck feathers raised outside of the breeding season and outside of a courtship context. Blake (1957) reported Chihuahuan Ravens also show the otherwise hidden white bases of the neck feathers during courtship displays. Allopreening has been reported for several species of Corvus (e.g., Lorenz 1931, Skead 1952, Lamm 1958, Coombs 1960, Gwinner 1964, Wittenberg 1968).

Twig gathering. After gathering a twig for its nest, a White-necked Crow occasionally bowed its head down below its feet, then held that position for 5–15 s before flying to its nest.

Food exchange. I observed food exchanges between adult crows from courtship through the post-fledging period. A crow (individual "A") silently delivered the prey in its bill to its perched mate ("B"). B sometimes performed low intensity wing-fluttering, then quietly received the prey in its bill, moved 1–10 m away after 5–20 s, and ate the prey, fed it to nestlings, or cached it nearby.

Items observed	Number of observations	Percent of observations
Plant material		
Hispaniolan royal palm (R <i>oystonea hispaniolana</i>)	13	7.5
Cupey (Clusia rosea)	24	13.8
Masa (Tetragastris balsamifera)	6	3.4
Fourleaf buchenavia (Buchenavia capitata)	2	1.1
Bullytree (Pouteria multiflora)	28	16.1
Palo de Hierro (Ixora ferrea)	4	2.3
Bastard redwood (Chrysophyllum argenteum)	5	2.9
Urban's holly (<i>Ilex riedlaei</i>)	1	0.6
Bulletwood (Manilkara bidentata)	7	4.0
Rough strongwood (Bourreria succulenta)	2	1.1
Tietongue (Coccoloba diversifolia)	6	3.4
White pricklyash (Zanthoxylum martinicense)	1	0.6
Unidentified plants	34	19.5
Total plants	133	76.4
Animal material		
Common green treesnake (Uromacer oxyrhynchus)	1	0.6
Unidentified snakes	5	2.9
Haitian giant anole (Anolis ricordii)	2	1.1
Dominican giant anole (Anolis baleatus)	2	1.1
Unidentified Anolis	13	7.5
Unidentified frogs	5	2.9
Nestling Bananaquit (Coereba flaveola)	1	0.6
Nestling Plain Pigeon (Patagioenas inornata)	2	1.1
Nestling Scaly-naped Pigeon (Patagioenas squamosa)	3	1.7
Crustacean	1	0.6
Snails	6	3.4
Total animals	41	23.6
Total items	174	

TABLE 1. Food items observed taken by adult White-necked Crows foraging at Los Haitises and Pedernales, Dominican Republic, 1976, 2000, 2001, and 2002.

FOOD, FORAGING, AND DRINKING

Depending upon season and locality, even individual species of crows may occupy various feeding niches; e.g., Common Raven has been described as primarily a scavenger in southwestern Virginia (Harlow *et al.* 1975), omnivorous in the Canary Islands (Nogales & Hernandez 1994), nest and chick predators in Norway (Byrkjedal 1987, Jacobsen & Ugelvik 1992), Oregon (Littlefield 1995), and Manitoba (Evans 1970), feeding on cereal grains in southwestern Idaho (Engel & Young 1989), small vertebrates in Oregon (Stiehl & Trautwein 1991), and invertebrates (summer) and plant materials (autumn and winter) in the Canary Islands (Nogales & Hernandez 1997). Some species or populations have been considered specialists (e.g., Hooded Crow, Gotmark *et al.* 1990), whereas others are considered generalists (Common Raven, Nogales & Hernandez 1994, 1997). West Indian crows occupy broad feeding niches (Gosse 1847, Cruz 1972, Goodwin 1976, Lack 1976, Garrido & Kirkconnell 2000). White-necked Crows are omnivorous and

WILEY

TABLE 2. Food items brought to nests	by adult	White-necked	Crows,	Los	Haitises	and	Pedernales,
Dominican Republic, 1976, 2001, and 2002.							

Items	Number of item	s delivered (%)
	Observed delivered	Remains found
Plant material		
Hispaniolan royal palm (Roystonea hispaniolana)	10 (3.5)	12 (18.2)
Cupey (Clusia rosea)	53 (18.5)	7 (10.6)
Bullytree (Pouteria multiflora)	19 (6.7)	7 (10.6)
Bastard redwood (Chrysophyllum argenteum)	4 (1.4)	2 (3.0)
Urban's holly (<i>Ilex riedlaei</i>)	—	3 (4.5)
Coccoloba sp.	2 (0.7)	_
Tietongue (Coccoloba diversifolia)	_	2 (3.0)
Bulletwood (Manilkara bidentata)	5 (1.8)	1 (1.5)
Smooth manjack (Cordia nitida)	—	1 (1.5)
Camasey (Miconia sp.)	_	1 (1.5)
Sweet acacia (Acacia farnesiana)	4 (1.4)	
Unidentified plants	41 (14.4)	9 (13.6)
Total plants	138 (48.4)	45 (68.2)
Animal material		
Common green treesnake (Uromacer oxyrhynchus)	14 (4.9)	1 (1.5)
W-headed racer (Ialtris dorsalis)	2 (1.7)	_
Unidentified snakes	3 (1.1)	3 (4.5)
Haitian giant anole (Anolis ricordii)	7 (2.5)	2 (3.0)
Dominican giant anole (Anolis baleatus)	12 (4.2)	3 (4.5)
Unidentified Anolis	27 (9.5)	2 (3.0)
Unidentified Ameiva	1 (0.4)	—
Hispaniolan giant eleuth (Eleutherodactylus inoptalus)	5 (1.8)	1 (1.5)
Unidentified frogs	22 (7.7)	4 (6.1)
Nestling Bananaquit (Coereba flaveola)	5 (1.8)	—
Nestling Patagioenas spp.	5 (1.8)	_
Nestling passerines	12 (4.2)	_
Columbid eggs	5 (1.8)	—
Walking sticks (Orthoptera)	7 (2.5)	1 (1.5)
Beetles	12 (4.4)	4 (6.1)
Beetle larvae	8 (2.8)	—
Total animals	147 (51.6)	21 (31.8)
Total items	285	66

have been reported feeding on a variety of food types, including fruits (Beck 1916, Wetmore 1916, Wetmore & Swales 1931, Dod 1978, Biaggi 1983), seeds (Wetmore 1916), grains (Dod 1978, Biaggi 1983), bird's eggs and nestlings (Wetmore 1916; Dod 1978, 1992), insects (Dod 1978, Biaggi 1983), small reptiles (Biaggi 1983), and *Eleutherodactylus* frogs (Wetmore 1916). Esquemeling (1684– 1685) noted that "Their ordinary food is the flesh of wild-dogs, or the carcases of those beasts the buccaneers kill and throw away."

I observed White-necked Crows feeding on all reported food categories (Tables 1 and 2). Small items (e.g., invertebrates, small amphibians) were probably more common

than I report, because they were difficult to identify from a distance and were usually passed quickly to chicks before I could determine identity. Like Wetmore (1916), I found that adult crows consumed mostly plant materials (76.4% of my observations of foraging crows; Table 1). Nevertheless, animals were more prevalent (51.6%) among items delivered to nestlings, compared with my observations of items taken by foraging crows ($\chi^2 = 35.07$, df = 1, P < 0.0001; Table 2). Although I observed carcasses (dogs, livestock) within some of the rural areas where crows occurred in the Dominican Republic, no White-necked Crows were observed feeding on carrion. Palm Crows, however, were observed feeding at carcasses (contra Madge & Burn 1994) along with Turkey Vultures.

Interviews of older woodsmen provided information on native plant species eaten by White-necked Crows in Puerto Rico. Several people reported crows fed on the fruit of the Puerto Rican royal palm (*Roystonea borinquena*); other species included sierra palm (*Prestoea montana*; fruit), candletree (*Dacryodes excelsa*, fruit), mucilage manjack (*Cordia sulcata*; fruit), and doncella (*Byrsonima coriacea*; fruit). Some woodsmen reported finding seeds of several plant species in and under nests, as did I. White-necked Crows, similar to some other corvids (e.g., Common Raven; Nogales & Hernández 1994), are undoubtedly important seed dispersal agents.

Although White-necked Crows descended to the ground to forage on crops, in forests they were strictly arboreal. Non-breeding crows formed small foraging flocks that ranged widely in search of food. Breeding pairs spent most of the day within their territories and foraged primarily within those areas, although individuals (especially males) were unaccounted for during long periods when they could have been foraging elsewhere. Foraging crows often worked in pairs as they systematically moved through the upper- and mid-sections of trees, where they searched up and down the trunk and branches investigating hiding places for prey. They were particularly active among vines, bromeliads, and orchid masses, where they probed for invertebrates, reptiles, and amphibians. Crows were observed to hang on the vertical cliff faces of karst areas and probe in the pock-marked face for prey while maintaining balance by flapping their wings. Crows flew to fruit masses on Hispaniolan royal palms, hanging on the side of the cluster, with body horizontal or vertical (head up), and plucked fruits. Crows held hard objects (e.g., snails, large seeds and fruits) in their feet and hammered them open with their bills. I occasionally saw crows hammering on dead branches and trunks, as well as chipping away at bark on live trees, apparently to extract insects. On Isla Saona, I watched several White-necked Crows moving systematically, but as individuals, from nest to nest in a White-crowned Pigeon colony, where they preyed on the pigeon eggs and squabs. The crows were so thorough in this nest depredation that in some years local residents believed crows had caused the failure of the pigeon colony. Vargas & Arendt (1978) noted White-necked Crows were common on Isla Saona, where the pigeons were breeding in large aggregations, but were not found there when the pigeons were not breeding. Similarly, Cherrie (in Wetmore & Swales 1931) reported crows opportunistically banding together in immense flocks to exploit the regional availability of fruits. Other corvids are known to exploit concentrations of prey (eggs, nestlings) in nesting colonies of birds (e.g., Common Ravens; Parmelee & Parmelee 1988, Gaston & Elliot 1996).

I observed crows caching food (plant and animal) in tree cavities and crotches, and in bromeliads. The birds sometimes returned to their caches, but often the food was not

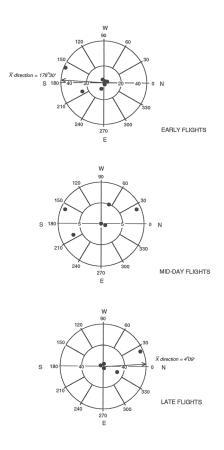


FIG. 9. Flight patterns of White-necked Crows during three time periods, Los Haitises, Dominican Republic, 1976: A. 05:00–09:59 h (N = 97), B. 10:00–13:59 h (N = 33), C. 14:00–18:59 h (N = 121). Scale on horizontal axis is frequency of flights toward compass bearings on perimeter of outer circle.

retrieved. Such food hiding behavior is common among corvids (reviewed by Turcek & Kelso 1968; see also James & Verbeek 1985, Verbeek 1997, Heinrich 1999).

I saw an adult White-necked Crow capture a small (15 cm) snake (*Uromacer oxyrhynchus*) on a tree branch 5 m from the crow's nest. The adult crow had been perched an additional 5 m from the nest. It flew 10 m, grabbed the WHITE-NECKED CROW ECOLOGY AND CONSERVATION

snake in its bill, pinned it between the branch and its foot, then tore pieces of flesh from the snake. After it had eaten about half of the prey, it took the remainder to its nest, where it fed it to one chick. The other adult crow flew to the site where the snake had been captured and thoroughly searched the area. Larger lizards (e.g., *Anolis ricordii*) were handled and eaten in a fashion similar to that described for the snake.

Standing water was generally not available in Los Haitises, but temporary pools did form after rains. Nevertheless, I did not observe crows coming to the ground to drink. Rather, they took water from cups in leaves, from the axils of bromeliad bracts, and from bowls formed in tree crotches.

MOVEMENTS AND FLOCKING

White-necked Crows made regular flights during the day (Fig. 9). Whereas directions of midday (10:00-14:00 h EST) flights at Los Haitises were random (R = 7.11, N = 33, P >0.05; Rayleigh test), morning (> 10:00 h; R =69.11, N = 97, P < 0.001) and late afternoonevening (14:00 h to dusk; R = 97.87, N = 121, P < 0.001) flights were not uniformly distributed. The mean compass direction of flights before 10:00 h was 178°30', whereas flights after 14:00 h had a mean direction of 04°09'; i.e., crows flew south in the morning and back north in the late day. Midday flights represented local movements within the study area. Breeding crows infrequently made long flights, although some (non-breeding?) individuals continued to do so through the nesting period. I believe these movements were to foraging sites, probably crops about 3 km south of my study area, where I observed gatherings of crows.

Verrill & Verrill (1909) and Verrill (1926) reported that White-necked Crows in the Dominican Republic formed immense feeding flocks in lowland swamps, which the WILEY

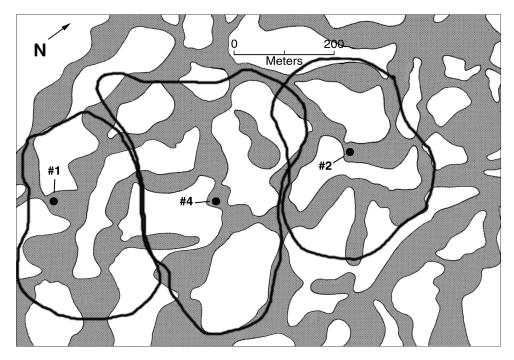


FIG. 10. Activity areas of three White-necked Crow pairs, Los Haitises, Dominican Republic, 1976. Dots represent nest sites: # 1 = H1976 # 1, # 2 = H1976 # 2, # 4 = H1976 # 4. Shaded areas represent ridges and uplands.

crows visited daily from their roosts in the mountains. In eastern Dominican Republic, Beck (1916) observed hundreds of crows descending from mountains to forage in lowland swamps by 10:30 h, then returning to those mountains from 14:00 to 16:00 h. As recently as 21 March 1997, a flock of at least 300 White-necked Crows was observed in Los Haitises (Keith et al. 2003). Wetmore & Swales (1931) noted nightly roosting congregations of White-necked Crows in Haiti, where the birds moved from roosts in early morning and returned at night. Dod (1978) also reported distant movements wherein the crows foraged in lower sites in the mornings, then flew to regular roost sites in trees in the high mountains. Wetmore (1916) noted long distance flights by White-necked Crows in eastern Puerto Rico that were related to

weather. On days when it was cold and rainy on the summit of El Yunque, crows descended into the warmer valleys. When the weather cleared, they moved back to the higher peaks. Along the northern shore of Lago Enriquillo, Dominican Republic, I watched crows form pre-roost flocks in June through September. Flights from the staging sites were made en mass, with as many as c. 60 crows flying into high mountain valleys to the north. Communal roosting and pre-roosting are common among corvids (e.g., Engel & Young 1992). American Crows have been reported forming pre-roosting aggregations before flying into a night roost, with the aggregation sites perhaps serving as information centers for location of either daytime foraging areas or nighttime roosts, as well as lowering predation risk (Moore & Switzer 1998). Common Ravens formed large communal roosts, which varied in number of individuals seasonally (Engel *et al.* 1992), although Heinrich *et al.* (1994) found individuals in a raven population showed considerable independence of one another with no indication of flock cohesiveness. Hooded Crows gathering in pre-roosts perched in a highly aggregated and exposed group that did not forage (Hansen *et al.* 2000). Hansen *el al.* (2000) suggested the pre-roost gathering had a function of maximizing the probability of finding rewarding food sites the next day.

During the breeding season, Whitenecked Crows usually associated as pairs. Non-breeding, yet paired, birds formed small groups that occupied areas peripheral to nesting areas. Breeding crows occasionally congregated with other breeding and nonbreeding crows in moderate-sized groups (up to 20 birds). A flock of 18 crows formed at 08:00 h on 10 April 1976. The birds arrived on a hilltop as singles (N = 4) or pairs (7), and perched within 30 m of one another in trees. There were continual supplantations and calling with complex high-low gargles. All of the crows slowly dispersed in their respective pairs or as singles in various directions after about 5 min. Two birds made midair attacks on a third crow as the group disbanded. Groups of crows were commonly seen after the breeding season, when groups contained adult pairs, as well as some fledglings. The paired adults frequently allopreened. Chasing within the groups was common.

I observed sentinel behavior among White-necked Crows, particularly when flocks fed on crops on or near the ground. Foraging under those circumstances probably placed birds at greater risk to predation, especially from humans. As in other corvids, the increased risk probably favored the presence of sentinels (e.g., Maccarone 1987).

ACTIVITY AREA AND TERRITORY

Core activity areas of members of three breeding pairs averaged 9.8 ± 3.7 (range = 7.6–11.9) ha (Fig. 10). One or both members, however, occasionally made long forays, where I was unable to determine distances.

Several species of corvids have been reported as defending territories (reviewed by Kilham 1985a). Although they are somewhat gregarious in feeding and roosting, Whitenecked Crows maintain strict breeding territories (Dod 1978). Territories were defended year-round, but less vigorously in the nonbreeding season than during the nesting period. The mean distance among the three nests I measured in Los Haities was 392 + 98.3 (range = 282-620) m. White-necked Crows were highly defensive of nesting areas and chased intruders with direct supplantation flights and vocalizations. Crows noisily chased other birds, and dove at them, occasionally striking even large aggressive raptors (Red-tailed Hawk, Ridgway's Hawk). I observed cooperative attacks by several crows on other species more often in the non-breeding season than when pairs were nesting ($\chi^2 =$ 4.71, df = 1, P = 0.03). Typically, pairs of crows attacked an intruder in series as it flew through each of the residents crows' territories. But if the alien landed, or began soaring, members of two or more pairs (mean = $5.0 \pm$ 0.93 individuals; N = 140 bouts) mobbed the intruder. When perched, the crows oriented toward the intruder, tail flipped, and called with loud can's. Mobbing of perched Redtailed Hawks that remained in the crows' activity area continued for up to 1 hour. Neighbors (up to 4 pairs) were involved in cooperative attacks on other species (Redtailed and Ridgway's hawks, Turkey Vultures) in 61% (N = 179) of interspecific conflicts.

Intruding White-necked Crows were vigorously chased from territories by residents. Both resident sexes defended territories

Statistics	Distance (m)/species								
	Ridgway's Hawk	White-necked Crow	Red-tailed Hawk	Sharp-shinned Hawk	Turkey Vulture	Hispaniolan Parrot	Pigeons ^a		
Mean	47	102	90	111	31	20	8		
SD	11.5	36.9	16.5	41.8	4.9	6.8	3.2		
Ν	30	309	84	15	66	38	16		
Range	20-70	40-225	45-120	60-225	20-40	5-30	5–15		

TABLE 3. Distance of initial response by adult nesting White-necked Crow to territorial intruders at three crow nests, Los Haitises, Dominican Republic, 1976.

^aPigeons = Scaly-naped Pigeon (*Patagioenas squamosa*), Plain Pigeon (*P. inornata*), and White-crowned Pigeon (*P. leucocephala*).

against intruding conspecifics and nests were left unguarded during the chases. At the approach of the defending residents, aliens usually left the area. Residents pursued the fleeing crow with a close tail chase. When the intruding crow did not leave with the residents' approach, the territory holders landed next to the alien and performed an antagonistic display directed at the intruder. The intruder, when supplanted, sometimes moved only a short distance, then perform a headdown, tail-fanned display, while giving a hic-gugik-gu call. The intruder either flew from the area or the resident(s) made additional short supplantation flights before the intruder left. Less intense threat displays consisted of caw and *bubbling* calls, and tail flipping.

Most chases and supplantations did not involve physical contact. Occasionally, however, pursuing crows struck fleeing birds on the back with their feet. Fleeing crows fended off the aggressors by turning upside down and presenting their outstretched talons toward the incoming bird. After turning back from the chase, the territorial birds performed an aerial display and gave *week-woo* vocalizations. At the nest area, both resident birds gave *bubbling* calls.

Different species evoked initial responses by White-necked Crows at distinct distances from the crow nest |P < 0.05 for all compari-

sons, except White-necked Crow vs Sharpshinned Hawk (Accipiter striatus), P = 0.35; unpaired t-test; sample sizes as in Table 3]. Sharp-shinned Hawks (N = 15 defenses) elicited territorial defense by nesting Whitenecked Crow pairs from the farthest distances (mean = 111 ± 41.8 m), followed by alien White-necked Crows (mean = 102 ± 36.9 m; Table 3). Other raptors (Red-tailed Hawk: mean = 90 ± 16.5 m; Ridgway's Hawk: 47 \pm 11.5 m; Turkey Vulture: 31 ± 4.9 m) apparently caused greater concern by the nesting crows than did intruding Hispaniolan Parrots (Amazona ventralis; mean = 20 ± 6.8 m) or pigeons [primarily Plain Pigeon (Patagioenas inornata) and Scaly-naped Pigeon (P. squamosa); collectively mean = 8 ± 3.2 m]. Sharpshinned and Ridgway's hawks were usually chased from the crow nesting area. Neither of these hawks was mobbed by several crow families to the same extent as were Red-tailed Hawks. One White-necked Crow pair built its nest within 30 m of an active Ridgway's Hawk nest. At that territory, I observed several supplantations and chases of hawks pursuing crows and crows chasing hawks during early nest-building. Later in the breeding season, however, few encounters were observed. Nevertheless, when an alien immature Ridgway's Hawk entered that crow pair's nesting territory, it was immediately and vigorously

WILEY

chased from the vicinity by the crows. Although the resident female Ridgway's Hawk perched as close to the crow's nest as the alien juvenile hawk, she was not attacked by the resident crows.

Resident crows aggressively chased Turkey Vultures whenever the vultures passed through the crows' territory. In the air, the crows struck the vultures with their feet. When the vultures landed within the crows' territory, they were driven off with a supplantation flight after the crow had first landed near the vulture, tail-flipped, and sometimes called with caw and bubbling calls.

Crows and Hispaniolan Parrots nested close to one another in Los Haitises and I observed frequent interactions between these species. Each species showed dominance over the other near their respective nests. Parrots were chased by crows, which gave caw or bubbling calls during pursuits. A pair of parrots that landed in a White-necked Crow nest tree was supplanted by a direct flight by an adult crow, which had been perched 10 m away. The parrots immediately left the area. The crow soared low over the nest tree, returning to the tree with its legs dangling, and wings elevated in a glide. As it glided to its nest, the crow called with a *week-woo* call, then gave a raspy, guttural gurr. Parrots supplanted crows with a direct (usually silent) flight; rarely a parrot struck a crow with its feet during aggressive encounters. Parrots sometime gave take-off calls and flight bugles as they flew toward intruding crows (Snyder et al. 1987).

Immediately around their nests, Whitenecked Crows were aggressive toward columbids. Pigeons were chased from the crow nest area in silent supplantations or the crow(s) gave raspy, short, *bubbling* calls. Pigeons flying through the nest area were occasionally pursued by crows.

Based on these observations of crow defenses against conspecifics and other species, I estimated the average territory size of three nesting pairs was 5.5 ± 5.2 (range = 1.1– 11.3) ha. That estimated territory size is moderate compared with those reported for other corvid species; e.g., 0.5 ha – Northwestern Crow (*Corvus caurinus*) (Butler *et al.* 1984), 4 ha – Little Raven (*C. mellori*) (Rowley 1967), 27 ha – Carrion Crow (Wittenberg 1968), 60 ha – Black Crow (*C. capensis*) (Skead 1952).

Both sexes of the White-necked Crow attacked intruders equally ($\chi^2 = 0.443$, P = 0.513, N = 207; Fisher exact test). In contrast, male Northwestern Crows performed 81% of territorial defense (Butler *et al.* 1984).

NEST BUILDING

In Los Haitises, I first observed crows nest building on 24 January 1976, although sustained building did not begin until 24 February. Nest building at Miches also began in February, although there a pair was observed nest building as late as 28 April. Nest building activities of White-necked Crows varied through the day ($F_{0.05(1),3,16} = 19.42$, P < 0.001; one-factor ANOVA) and were greatest at mid- to late morning (09:00-11:59 h) and late afternoon to evening (15:00-18:59 h; Fig. 11). Nest materials were gathered 3-80 m (mean = 33.2 ± 21.6 m; N = 34 trips) from the nest. All nest material was gathered from trees; although twigs were abundant on the forest floor, I saw no birds descend to gather materials there. While gathering twigs, adults (both sexes) occasionally called with loud guttural weeak-weeak-weeah vocalizations. White-necked Crows called (can, wag) in 32% of my observations (N = 81) as material was delivered to nests, but otherwise entered the area silently. During early nest building (week one: 24-25 January, Los Haitises), crows occasionally performed a bowing display after plucking a stick from a tree. With the twig in its bill, the crow bowed its head below its feet, held it there up to 15 s, then stood upright for about 50 s before flying to its nest. The bird usually did

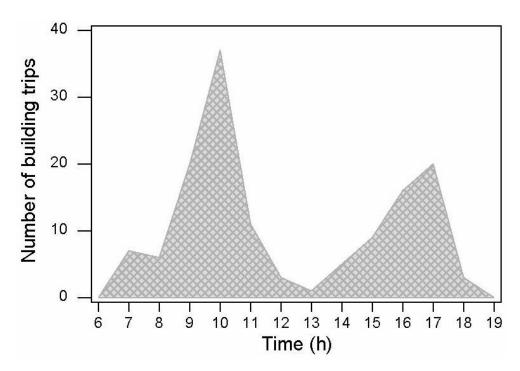


FIG. 11. Time of nest building by three pairs of White-necked Crow, Los Haitises, Dominican Republic, 1976.

not fly directly to it, but landed 9–18 m from the nest where it walked among the branches, flipping its tail, for a few seconds, apparently surveying the area for predators, then flew directly to the nest. Both adults collected materials and built the nest; at one nest (H1976 # 1), individual "A" (sex undetermined) made 64% (N = 28) of the nest-building trips; at the H1976 # 2 nest, individual "A" made 71% (N = 7) of the deliveries. Coombs (1960) reported male Eurasian Rooks gathered most materials and constructed nests.

At the height of nest-building activity, the collecting adult was at the nest for an average of 36 s (range = 10-120 s; N = 34). The material brought to the nest was either worked into the structure by the member who had been laboring at this task while its mate collected material or, if both birds were gath-

ering, by the member making the delivery. Fresh nest materials were delivered to the nest through the mid-nestling stage, possibly functioning to renew the parasite repellency of the nest as in some species (e.g., Wimberger 1984, Clark et al. 1990, Petit et al. 2002).

After placing materials, crows left to gather more material, giving loud calls (*can*, gauch) in 80% of my observations (N = 75). On occasion, an adult would perform a post-delivery flight over the nest after depositing the nest material. The adult circled low over the nest tree, calling with *caw*'s, then flew to the twig-collecting site.

Construction at nests was slow and intermittent for up to four weeks before intensive building began. Then, two crow nests I closely watched took four and five days, respectively, to complete. These periods were comparable to nest-building times

128

WILEY

Nest	Tree species	Tree height (m)	Nest height (m)	Tree diameter at nest (cm)	DBH (m)	Distance nest from center (m)	Location	Support for nest
H1976 # 1	Clusia rosea ^a	30.3	28.8	25.4	?°	0.9	SE slope	<i>Clusia</i> branches
H1976 # 2	Clusia rosed ^a	21	20	19.3	۶ ^с	1.7	SE slope	Clusia branches
H1976 # 3	Buchenavia capitata ^b	26	23	18.5	1.3	0.7	NW slope	Clusia branches & vines
H1976 # 4	Buchenavia capitata	9.0	8.5	19.8	0.9	0.2	E slope	Upper branches
H1996 # 1	Clusia rosed ^a	18	15	14.5	? ^c	0.6	NW slope	Clusia rosed ^a
H1996 # 2	Buchenavia capitata ^b	25	18	18.4	1.9	0.8	SE slope	Clusia rosed ^a
H2002 # 1	Guarea guidonia	18	13	21.6	0.8	0.8	SE slope	Clusia rosed ^a
H2002 # 2	Buchenavia capitata ^b	13	8.9	20.3	1.5	1.0	N slope	Clusia rosed ^a
P2000 # 1	Roystonea hispaniolana	9.2	8.3	29.5	0.6	0.1	Woodlot in urban area	Upper frond axils
P2001 # 1	Roystonea hispaniolana	10.2	9.2	30.2	0.6	0.1	Woodlot in urban area	Upper frond axils
B2002 # 1	Roystonea hispaniolana	15.4	12.3	24.4	0.5	0.2	Forest edge	Upper frond axils
B2002 # 2	Roystonea hispaniolana	18.6	15.4	23.8	0.7	0.1	Forest edge	Upper frond axils

TABLE 4. Characteristics of 12 White-necked Crow nests, Los Haitises (H), Barahona (B), and Pedernales (P), Dominican Republic, 1976, 1996, 2000, 2001, and 2002.

^aHost tree completely gone, with only formerly dependent *Clusia* remaining. ^bNest built in *Clusia*, which dominated upper portion of host tree. ^{cue}Trunk" consisted of multiple stems of the dependant *Clusia*.

reported for American Crows by Kilham (1984; 5–9 days), but were shorter than the average of 13 days reported by Emlen (1942).

Although cliffs with pot holes and ledges were available in Los Haitises, all crow nests were placed high in tall trees or, in Pederales and Barahona, in palms (mean tree and palm height = 17.8 ± 6.9 m, range = 9.0-30.3m; mean nest height = 15.0 ± 6.5 m, range = 8.3-28.8 m; N = 12), with nest placement averaging 84.4 + 9.5% (range 68.5-95.2%) of the tree or palm's height. Sites selected did not differ in height of tree versus palms (mean tree height = 20.0 ± 7.0 m, range = 9.0-30.3 m, N = 8; mean palm height $= 13.4 \pm 4.4$ m, range = 9.2-18.6 m, N = 4; t = 2.01, df = 9, P > 0.05). Nest sites were typically in emergent trees or palms. Nests in trees (mean nest height = 16.9 ± 7.0 , range = 8.5-28.8 m; N = 8; Table 4) averaged slightly higher than those in palms (mean nest height = 11.3 ± 3.2 m, range = 8.3-15.4 m, N = 4; t = 1.90, df = 9, P > 0.05), likely related to greater average tree height compared to palm heights. Nest placement in palms and trees averaged 84.3 \pm 9.5% of tree height, with no difference between heights at which nests were built in trees (mean = 83.6 + 11.3%, range = 68.5-95.2%, N = 8) and palms (mean = $85.8 \pm 5.3\%$, range = 79.9-90.3%, N = 4; t = -0.45, df = 9, P > 0.05). Others also reported White-necked Crow nests placed high in trees (Wetmore 1916, Wetmore & Swales 1931, Dod 1978, Biaggi 1983).

Nests were bulky platforms in crotches or supported by limbs of dense *Clusia* or vines. They were constructed of branches (3–13 mm diameter), with a lining of orchid and other leaves, fine twigs, bromeliad bracts, and moss. Nests in palms included considerable dried palm frond material among the twig and stick structure. Four nests averaged 56.6 ± 2.4 (range = 53.3–61.1) cm in diameter and 55.1 \pm 3.8 (range = 47.4–59.3) cm in depth. The shallow cup averaged 10.1 \pm 1.3 (range = 7.9–12.3) cm deep.

Two closely watched nests were built in palms within 2 m of active Palmchat (*Dulus dominicensis*) nest colonies. Palmchats consistently gave alarm calls, scattered from the nest en masse, and displayed excited behavior with the arrival and departure of nesting crows. Crows occasionally took nest twigs from the Palmchat colony, either dropping the material or carrying it to their nest. Crows also appeared to be probing the Palmchat nest entrances, although I observed no depredations of contents. Nevertheless, Palmchats became increasingly excited as crows probed among their nest colony.

Although "helpers" have been reported for other corvids (e.g., American Crow: Forbush 1927, Good 1952, Kilham 1984, 1985b, Caffrey 2000; Carrion Crow: Charles 1972; Northwestern Crow: Verbeek & Butler 1981), I found no evidence of this behavior at nests of White-necked Crows. Similarly, I detected no extra-pair birds (other than neighboring breeding pairs) assisting in territorial defense.

NESTING CHRONOLOGY

Egglaying at four nests (H1976 # 1, H1976 # 2, H1976 # 3, H1976 # 4) at Los Haitises occurred from 27 February to 10 March. At the nest (H1976 # 1) I watched most intensively, egglaying began on 6 March 1976, 8 days after the nest was completed (27 February). The nest held four eggs on 9 March. Egglaying at daily intervals appears to be a general trait for the genus *Corrus* (Holyoak 1967, Wittenberg 1968, Butler *et al.* 1984). A pair (H1976 # 3) whose nest fell in a wind storm, built a new nest 15 m from the first site and began laying eggs about 4 April, 25 days after its first clutch was lost. The incubation period lasted about 18–22 days and the

Nests		Number						
	Eggs	Chicks hatch	Older chicks	Chicks fledge				
H1976 # 1	4	3	3	3				
H1976 # 2	4	3	3	3				
H1976 # 3	3 ^a	0	0	0				
H1976 # 4	4	4	3	3				
P2000 # 1	4	4	4	4				
P2001 # 1	4	4	4	4				
H2002 # 1	4	4	3	3				
H2002 # 2	3	3	2	2				
Mean + SD	3.8 ± 0.5	$3.6 \pm 0.5^{\mathrm{b}}$	$3.1 \pm 0.7^{\mathrm{b}}$	$3.1 \pm 0.7^{\mathrm{b}}$				
Ν	8	7	7	7				

TABLE 5. Outcome of eight White-necked Crow nesting attempts, Los Haitises (H) and Pedernales (P), Dominican Republic, 1976, 2000, and 2001.

^aNest falls in wind-storm during egglaying/incubation. ^bNests with competed clutches.

nestling period was approximately 35-44 days. Common Ravens have a similar incubation period of about 21 days (Stiehl 1985). American Crows fledge at 30-34 days of age (Ignatiuk & Clark 1991). Although I had few opportunities to observe fledglings, I believe adults continued to attend them for at least two weeks after young birds fledged. I observed adults carrying food to fledglings near the nest tree (radius of about 30 m from nest) for 14 days after chicks had fledged. Adults were characteristically silent during food transfers, but nestlings gave soft naw calls. The breeding season (excluding replacement nests) lasted about 94 days; i.e., 24 February to 28 May. I did not find evidence of second clutches. In Haiti, nests were reported on 24 April and 2 May (Wetmore & Swales 1931, Bond 1947). Biaggi (1983) reported the White-necked Crow nested from March to May in Puerto Rico. Wetmore (1916) found nests containing eggs and others with well-grown chicks in March in lowland Puerto Rico, suggesting that the crow may begin breeding earlier at lower elevations.

EGGS

Clutch size averaged 3.9 ± 0.4 (range = 3–4) eggs at the seven nests I inspected at clutch completion. Another nest contained three eggs when it fell in a storm during the egglaying period (Table 5). Dod (1978) reported clutch size in the Dominican Republic as three to four eggs.

Twelve eggs (from 3 nests) I measured averaged 42.3 ± 0.42 (range = 40.3-44.6) mm in length and 29.1 ± 0.41 (27.5–31.6) mm in breadth. Gundlach (1874) reported the size of a White-necked Crow egg from Puerto Rico as $44 \ge 29$ mm. The 12 eggs I weighed averaged 30.3 ± 0.34 (range = 28-32) g at about mid-incubation.

The egg is hazel (varying from pale greenish-blue to greenish-brown) in ground color, and is speckled with maroon to brown throughout, but more heavily on the rounded end. Dod (1978) described the egg as pale green, marked with maroon. Gundlach (1874) noted that the coloration of the Whitenecked Crow's egg resembled that of the Cuban Crow, which is greenish with spots of

WILEY

brownish violaceous (Garrido & Kirkconnell 2000).

NESTLINGS

Of the eight nests I watched closely, one fell in a windstorm during the incubation stage and the other seven hatched 25 chicks from 27 eggs (0.93 hatching rate; Table 5). All chicks at four nests fledged, whereas three nests lost one chick each between hatching and fledging, for an overall fledging success of 81.5% (N = 22/27) of eggs laid at the seven successful nests; productivity was 2.8 ± 1.3 young per nest and 3.1 ± 1.3 0.7 young per successful nest (Table 5). At the four nests where four chicks hatched, the first two hatched on the same day, but chick # 3 hatched on the second day and the fourth chick hatched two days later. Asynchronous hatching has been reported for several corvids, including Chihuahuan Raven (Haydock & Ligon 1986), Northwestern Crows (Butler et al. 1984), Eurasian Jackdaws (Corvus monedula, Lockie 1955), and Carrion Crows (Wittenberg 1968).

Hatchlings were naked with charcoal-colored skin. The rictus was bright fuscia, whereas the gape was bright red. Their eyes remained closed at least through the sixth day after hatching. Primary sheaths began to emerge on day six. The six-day-old chicks were quite helpless and gave soft creaking calls when I visited the nest. Average weights of chicks were: Day 1: 43 g (N = 1), Day 3: 60.3 ± 3.9 g (N = 3, range = 55–66 g), Day 5: 103 ± 4.0 g (N = 2, range = 99–107 g), Day 6: 112 ± 3.0 g (N = 2, range = 109–115 g). The chicks acquired a coat of charcoal down by days 6-9. At the mid-nestling stage the flanges were cream colored, from the gape to near the upper and lower mandible tips. By age 17-22 days, the nestlings gave several calls. As the adult landed at the nest, the

chicks gave a low gargling call. They outstretched their necks, lifted their heads, and opened their bills to the sky. While being fed by the adults, the chicks sometimes gave creaking calls, which sounded like a rusty door hinge (but rapidly repeated). When adults were absent from the nest vicinity, chicks at the mid-nestling stage remained crouched low in the nest bowl, with only the tops of their heads and part of the backs visible above the rim. Chicks were occasionally active, autopreening and exploring nest material with their bills. When an adult was present in the nest vicinity, mid-stage nestlings often exercised their wings and autopreened. Adults allopreened nestlings at this stage. Older chicks, when alone at the nest, alternated their activities among dozing, preening, and calling with soft cawing calls while scanning the surroundings for the adults. At that age, chicks actively moved out on branches supporting and adjacent to the nest, flapping vigorously, to meet incoming adults; sometimes all chicks were vigorously begging from adults on the outskirts of the nest. After receiving food, the chicks returned to the nest bowl, where they occasionally flapped their wings vigorously in exercise. As the birds matured, they moved farther from the nest during exercise bouts, often when an adult was out of sight, flapping wings and hopping, but returned to the nest thereafter. By day 20, chicks were mostly feathered, although some charcoal-colored down remained on the head and body. At fledging, the chicks' eyes were a milky blue color (appearing dark gray from a distance) and their plumage was a dull black, lacking the glossy sheen of adults. The bases of neck feathers were light gray rather than white as in adults. The large, white "lips" appearance of the rictal flanges had been lost, and the bright fuchsia color of the gape had dulled to a pinkish-red. Fledglings, like adults, used an over-the-wing movement to scratch their head.

Stages ^a	No. observation periods	Time (h)							
		Observations	One or both adults on nest (%)	No. adult on or near (within 15 m) nest (%)	Adult within 15 m of nest (%)				
Incubation	2	21.0	20.2 (96.2)	0.8 (3.6)	0.1 (0.5)				
Early-nestling	2	19.0	16.0 (84.2)	2.1 (11.1)	0.9 (4.7)				
Mid-nestling	5	43.8	21.1 (48.2)	19.3 (44.1)	3.4 (7.8)				
Late-nestling	5	34.5	10.4 (30.1)	21.1 (61.2)	3.0 (8.7)				
Total		118.3							

TABLE 6. Adult White-necked Crow attendance behavior at two nests, Los Haitises and Pedernales, Dominican Republic, 1976 and 2000.

^aEarly nestling stage = days 0–13, mid-nestling stage = days 14–28, late nestling stage = days 29–44.

ADULT ATTENDANCE AND BEHAVIOR AT NEST

I watched two crow nests from incubation through fledging for a total of 118.3 h (Table 6). Adult attendance declined significantly from the incubation through the late nestling periods ($F_{0.05(1),3,10} = 38.09, P < 0.0001$; oneway ANOVA). Although normally only female corvids incubate (Goodwin 1976, Butler et al. 1984, Verbeek 1995), and Dod (1978) reported the female White-necked Crow performed all the incubation, I observed both sexes sitting on eggs at the one nest (H1976 # 1) I watched from a blind placed close enough to note individual differences in adults. One of the pair members ("A," sex not determined), however, was on the nest more (89%) than the other (11%) in those incubation bouts when I was able to distinguish individuals (N = 17.8 hours; Z = 1.83, P = 0.06, Wilcoxon paired-sample test). One adult (consistently "A") remained on the nest overnight through late brooding. The other adult normally roosted within 10-20 m of the nest.

During incubation and early nestling (days 0–13) stages, "A" only left the nest for short (5–15 min) periods, usually when its mate relieved it. During the incubation and early

nestling stages, at least one adult was on the nest 96.2% and 84.2% of observation time, respectively (t = 3.3, df = 1, P > 0.05; Table 6). Adults normally left the nest during food transfers (within 3 m), although on 12 occasions (N = 229) at the H1976 # 1 nest, one bird ("B") delivered food items to its mate at the nest. When food was brought to the nest area, the incubating bird flew to the incoming bird and, with mutual soft gik calls and tail flipping, quickly took the item. The attending bird then flew a short distance and consumed the food while the incoming bird flew to the nest and covered the eggs. After finishing the food item, the bird returned to the nest and the other adult flew off silently. At other times, "B" flew directly to the nest and assumed incubation duty, while "A" flew off, probably to forage and preen.

Although adult attendance remained high during the early nestling period, the amount of time the nest was left unguarded (11.1% during early nestling stage vs. 3.6% during incubation) or when one or both adults were in the vicinity of the nest (within 15 m; "guarding") when not covering eggs or chicks (4.7% vs. 0.5%) increased above that during incubation (Table 6).

By the mid-nestling stage (days 14-28),

Observation periods (No. observation periods: total hours)			Whitney est		
	Feeding trips	Hours	Feedings/h	U	P
Early (06:00-09:59 h; N = 8, Σ = 26.9 h)	160	26.9	5.6 ± 1.3		
Early vs Mid-day deliveries				96.5	0.0031
Mid-day (10:00-14:59 h; N = 8, Σ = 37.7 h)	107	37.7	3.4 ± 0.8		
Mid-day vs Late deliveries				36.0	0.0040
Late (15:00-18:59 h; N = 5, Σ = 15.6 h)	120	15.6	7.7 ± 1.11		
Early vs Late deliveries				41.5	0.0396

TABLE 7. Time of food deliveries to nestlings at five White-necked Crow nests at Los Haitises and Pedernales, Dominican Republic, 1976, 2000, and 2001.

adult nest attendance had declined to 48.2% (early vs. mid-nestling: t = 6.7, df = 1, P >0.05; incubation vs. mid-nestling: t = 15.9, df = 4, P < 0.0001), whereas the amount of time adults remained in the vicinity of the nest increased (Table 6). Attendance reached a low point during the late nestling stage (days 29-44; adults on nest 30.1% of observed time; incubation vs. late nestling: t = 11.9, df = 4, P < 0.0001; early vs. late: t = 8.0, df = 4, P = 0.001; mid vs. late: t = 3.99, df = 5, P = 0.01), with a slight increase (8.7%) in presence near the nest when not brooding. During mid and late nestling periods, adult crows did not brood the chicks, but cleaned the nest and preened young when at the nest. Verbeek (1995) reported female Northwestern Crows essentially ceased brooding chicks by day 15, when they participated fully in food gathering. The cessation of daytime brooding coincided approximately with the eruption of feathers from their sheaths, attainment of effective endothermy, start of maximum daily growth rate of the feathers, and point of inflection of the chicks' growth curve.

Adult White-necked Crows fed nestlings throughout the day but feedings were more frequent during the early morning and late afternoon than at midday ($U_{0.05(2),8,8} = 96.5, P = 0.003, U_{0.05(2),8,5} = 36.0, P = 0.004$, respectively; Table 7). Both adults fed the young,

although occasionally one adult would pass food to its mate, who then carried it to the nest and fed the chicks. On several occasions, I observed both adults at the nest simultaneously feeding the nestlings.

Larger food items were carried to the nest in the adult's bill, whereas smaller items and much of the plant materials were delivered in the adult's sublingual pouch and regurgitated into the chicks' mouths. Whole food was carried to the nest or nearby limb in the bill, then broken apart with heavy blows of the bill while the item was held in the bird's feet.

Although mean food deliveries to nestlings per hour were consistently higher at four-chick nests compared with three-chick nests, feeding rates at the latter did not differ from those at four-chick nests (early nestling period, t = -1.22, df = 2; mid-nestling, t =-2.042, df = 2; late nestling = 0.81, df = 1; all P > 0.05; Table 8); i.e., adults did not adjust for the greater food demands of four chicks, or were unable to do so. Nevertheless, both of the closely watched nests with four chicks fledged all young. Three nests, including two with four nestlings, lost one chick during the nestling period, perhaps related to food stress (Table 5). Thus, mean feedings per chick at four-chick nests was somewhat lower (P >0.05) than at three-chick nests. Because the feeding rates showed no significant difference

WILEY

TABLE 8. Feeding rates at White-necked Crow nest with three and four chicks during three periods of observation, Los Haitises (N = 3 chicks each) and Pedernales (N = 4 chicks each), Dominican Republic, 1976, 2000, and 2001.

Stages ^a			Number of		
	Hours of observation	Food deliveries	Mean deliveries per h	Mean feedings per chicks	Mean feedings per chick per h
Three-chick nests $(N = 3)$					
Early nestling	19.0	111	5.8	37.0	1.9
Mid-nestling	26.0	97	3.7	32.2	1.2
Late-nestling	17.5	80	4.6	26.7	1.5
Totals	62.5	288			
Four-chick nests $(N = 2)$					
Early nestling	12.9	89	6.9	22.3	1.7
Mid-nestling	17.0	94	5.5	23.5	1.4
Late-nestling	13.3	64	4.8	16.0	1.2
Totals	43.2	247			
All nests $(N = 5)$					
Early nestling	31.9	200	6.3	58.8	1.9
Mid-nestling	43.0	191	4.4	56.2	1.3
Late-nestling	30.8	144	4.6	42.4	1.4
Totals	105.7	535			

^aEarly nestling stage = days 0-13, mid-nestling stage = days 14-28, late nestling stage = days 29-44.

in three- and four-chick nests, I combined all nests to compare feeding rates among nestling periods (Table 8). Feeding rates at nests with early nestlings (mean = 6.3 deliveries per h) were significantly higher than those at midnestling (4.4 per h; t = 2.62, df = 7, P = 0.035) and late nestling (4.6 per h; t = -3.27, df = 7, P = 0.014) stages. Feeding rates at mid and late nestling periods showed no difference (t = -0.09, df = 6, P = 0.928). Butler *et al.* (1984) noted that the feeding rates of nestling Northwestern Crows peaked in the second week, then declined to a low in the last week of nestling life.

Estimated sizes (animal matter) and quantities (plant) of items delivered by Whitenecked Crows were smaller during the midnestling period (mean = 27.5 ± 0.61 g/h) than during the early nesting period (mean = 33.1 ± 1.02 g/h; $F_{0.05(1),1.4}$ = 14.81, P = 0.018). Biomass delivered to nests increased in the late nestling period (mean = 35.3 ± 0.28 g/h; midvs late-nestling periods: $F_{0.05(1),1,4}$ = 104.0, P = 0.0005; early- vs late-nestling periods: $F_{0.05(1),1,4}$ = 5.04, P = 0.088). Both adults fed chicks nearly equally, with one individual delivering slightly more food than the other parent; individual "A": mean = 1.5 deliveries/ h, individual "B": 2.2/h (Z = 1.60, P = 0.105, N = 102; Wilcoxon paired-sample test). Butler *et al.* (1984) reported male Northwestern Crows fed chicks more during the first week (when the adult female was most attentive at the nest), but that females did most feeding thereafter.

When an attending crow detected me in its nest area, it called loudly with *can's*, oriented toward me, and performed an Alarm Display. The calling attracted the other adult, which joined in the calling. WILEY

nests.

When I was able to sneak into the nest area NATURAL PREDATION so that I was quite close to the nest before the adult detected me, the attending adult In Los Haitises, adult White-necked Crows assumed a low-profile "hiding" posture on

the nest until I was not looking in that direction or had passed the nest tree. Then the adult silently left the nest, circled around and returned to the area, loudly calling with can's. Frequently, both adults would return from the circling flight, then mob me. The crows displayed the same "hiding" and sneaking off behavior when Turkey Vultures and Red-tailed Hawks passed over their Adult crows frequently cleaned the nests.

Adults ate or carried off small food scraps and excreta of the chicks. They excavated in the nest bowl; i.e., grabbed bowl twigs in their bills and vigorously shook the material in a rapid back and forth movement, presumably to "sift" food, feces, and other debris out of the chicks' bowl (Kilham 1984). Adults carried off large uneaten pieces of food, sometimes to cache them nearby, but usually more than 15 m and out of my sight. Nest sanitation activity by adults continued until the last chick fledged.

ECTOPARASITES

Warble flies [Philornis (Neomusca) pici] are common ectoparasites of birds at Los Haitises (Wiley & Wiley 1981, Snyder et al. 1987). I inspected six White-necked Crow chicks (2 nests) closely for ectoparasites. Three of these (from one nest) had minor infestations of warble fly larvae, distributed as follows: Chick # 1: three larvae on head, one on right thigh; Chick # 2: one larva on head; Chick # 3: two larvae on breast, one on abdomen. All chicks survived to fledging. One woodsman in Puerto Rico, Garciano Torres (age 83 years when interviewed in 1976), remembered seeing warble fly larvae on White-necked Crow nestlings.

apparently have few natural enemies other than man, and I observed few attempts at predation of adult crows. Red-tailed Hawks made what I considered the only "serious" attempts to take crows, although I observed no captures. Ridgway's Hawks sometimes chased crows, apparently to supplant them from their nest area. I found no Whitenecked Crow remains at 18 Red-tailed Hawk and 14 Ridgway's Hawk nests in my study areas. Other potential nest predators include black rats (Rattus rattus), boas (Epicrates spp.), and arboreal lizards (especially Anolis ricordii). I did not find evidence of depredation at crow nests, and observed a low incidence of predation on nests of other large bird species in the areas (Wiley & Wiley 1981, Snyder et al. 1987).

CAUSES OF DECLINE OF WHITE-NECKED CROW POPULATIONS

As with most recent declines or extirpations of avian populations in the West Indies, the decline of White-necked Crow populations has been the result of many factors, most of which are related to man's activities.

The most important of these factors has been habitat destruction. The history of the crow's decline and extinction in Puerto Rico is particularly instructive in demonstrating the importance of habitat change. In Puerto Rico, the crow's decline in numbers and range is closely related to the history of that island's loss of old age forests (see Wadsworth 1949 and Snyder et al. 1987 for history). The crow's last refuge in Puerto Rico was apparently in the mostly uncut forest in the Sierra de Luquillo, which was also the last sanctuary of the Puerto Rican Parrot (Amazona vittata) (Snyder et al. 1987). But, even though the Sierra de Luquillo forest and its wildlife were

given legal protection, the forest was degraded through several activities, including timber stand improvement and charcoal harvesting (Snyder *et al.* 1987), and the Whitenecked Crow continued to decline and eventually disappeared.

Degradation and loss of habitat were not the only factors involved in the crow's extirpation from Puerto Rico. Although Sallé (1857) and Wetmore (1916) believed the Whitenecked Crow required extensive tracts of natural forest, my observations of sizable populations of crows surviving in quite degraded habitat in the Dominican Republic suggest that pristine tracts of forest are not essential for the species' survival (see below).

Hurricanes may have been direct and secondary factors in the disappearance of the White-necked Crow from Puerto Rico, as the crow became rarer there after Hurricane San Felipe (1928; Danforth 1936, Rolle 1961). As the once extensive old-growth forest habitat was fragmented for agriculture, crows were not only exposed to greater "edge," with the temptation of crop depredation and increased susceptibility to shooting, but the crow's large contiguous populations were segregated into smaller units separated from one another by unsuitable habitat. These fragmented populations were more vulnerable to the random tropical storms that savage the Caribbean region. When habitat was widespread and crow populations were extensive in number and distribution, hurricanes had only local effects. Populations affected by the storms were quickly replaced by surrounding reservoirs of birds. Birds in storm-ravaged areas could easily move into nearby, less affected areas for food and shelter (Wiley & Wunderle 1993). But, when wildlife populations are small and habitat is reduced to small "islands," surrounded by agriculture, a direct hit by a hurricane (such as occurred in 1928, when Hurricane San Felipe hit the limestone karst area of western Puerto Rico) has a severe negative effect on bird populations. Leonardo Bonnano Marques (90 years old in 1976) noted that crows became scarce in the Sierra de Luquillo after Hurricane San Ciprian (1932), whereas Gilberto Torres (83 years old in 1976) recalled that crows disappeared from areas after Hurricane San Ciriaco (1899).

Shooting has undoubtedly contributed to the crow's decline. Most of the older woodsmen interviewed in the Sierra de Luquillo and Río Abajo areas of Puerto Rico reported that crows were shot in the past. One such person, Bernardo Vaquier (58 years old when interviewed in 1976), believed the crow disappeared from around his home in Carite because of excessive shooting. Because they are noisy and aggressive around the nest and in feeding flocks, White-necked Crows are easy to find and shoot. Esquemeling (1684-1685) wrote, "These clamorous birds do no sooner hear the report of a fowling piece or musket but they gather from all sides into whole flocks, and fill the air and woods with their unpleasant notes." Such noisy congregations must have made the crow easy prey for a man with a gun.

The White-necked Crow has been considered a game species whose flesh was valued (Abbad y Lasierra 1788, Wetmore 1916, Verrill 1926, Wetmore & Swales 1931, Raffaele 1983). Verrill (1926) reported that during the periods when they congregated for feeding, thousands of crows were shot and sold in markets. The appeal of the species as food varies locally. I found hunters in some areas of the Dominican Republic who considered crows undesirable as a game bird. Conversely, most of the interviewed older woodsmen who were familiar with the crow in Puerto Rico reported that it was a favorite local food. Garciano Juarbez Torrez (96 years old when interviewed in 1976) remembered that crows were taken as nestlings for food. Despite laws to prevent it, illegal hunting continued in the Sierra de Luquillo through the mid-1970s, when stepped-up enforcement substantially reduced the activity. That enforcement was, regrettably, too late for the White-necked Crow.

White-necked Crows eat corn, beans, and other crops (Gundlach 1874, Dod 1978; pers. observ.), and many are shot to protect crops (interviews of older residents of Puerto Rico and the Dominican Republic). Württemberg (1835) noted that White-necked Crows formerly came fearlessly about houses in flocks of hundreds of birds, perhaps to feed on crops.

Disease is a possible factor in the extirpation of the White-necked Crow in Puerto Rico and has been suggested as a potential reason for the decline of the Puerto Rican Parrot (Snyder *et al.* 1987). Disease has proven to be an important factor in the decline of the Hawaiian Crow (*Corvus hawaiiensis*) and is now perhaps the most critical problem in preventing that species' recovery (Giffin *et al.* 1987, Jenkins *et al.* 1989).

Predation by Pearly-eyed Thrashers (Margarops fuscatus) and introduced rats (Rattus norvegicus and R. rattus) likely contributed to the crow's decline in Puerto Rico. Rats are common throughout habitats used by crows. They are known to eat bird eggs and chicks, but normally will not enter a large bird's nest when an adult is present (Snyder et al. 1987). Also, they are normally active only during the night, when adult White-necked Crows are consistently at the nest. Nevertheless, rats may have occasional opportunities to invade a crow nest when the adult has been scared off for the night or a marauding rat may take an egg or chick during the day.

The Pearly-eyed Thrasher is a recent invader of Puerto Rican forests (Snyder *et al.* 1987) and, apparently, is only beginning to colonize mainland Hispaniola (Wiley & Ottenwalder 1990, Keith *et al.* 2003). Thrashers are aggressive predators of birds' eggs and chicks but, like rats, will not normally attack an attended nest. The recent arrival of the thrasher into an environment with no such nest predator perhaps exposed the naïve crow, which likely had no effective defense to counter the threat. Indeed, I observed White-necked Crows leaving eggs and young chicks unguarded (3.6% and 11.1%, respectively, of daytime observation periods) for sufficient time to allow a thrasher to destroy a nest unchallenged by an adult crow. Predation by thrashers may have been the "coup-de-grâce" for the crow in the Sierra de Luquillo.

The hypothesis that thrashers played a critical role in the extirpation of the Whitenecked Crow from Puerto Rico is supported by events in my Los Haitises study area over the period 1974-1996. When I began fieldwork in Los Haitises in 1974, the area was largely continuous forest, with small inroads of local cultivation. White-necked Crows were in good numbers and evenly distributed through the forest. By 1996, the forest had been largely cleared, with only small (0.05 ha) fragments remaining, separated by large areas of active and abandoned cultivation. Nevertheless, crow populations remained unchanged in numbers and general distribution. Using the same methods as in 1976 surveys, I found an average of 0.020 crows detected per minute in 1996 (total = 1600 min of surveys), whereas I encountered 0.029 crows per minute in 1976 (total = 5940 min). Crows were breeding (incubating) in March-April 1996 and were well distributed in the degraded habitat. All other pressures apparently remained the same: shooting was, as in the 1970s, at a low level. If anything, I would expect persecution from humans protecting their crops to have increased with the more active agriculture in the area in the 1990s. Rat populations were still quite high, as they were in the 1970s. The only major element that differed between Puerto Rico and Los Haitises was the absence of the Pearly-eyed Thrasher in the latter site. Crow egg and chick depredation by the thrasher, combined with nearcomplete habitat destruction and shooting, seem to be the most likely causes of the White-necked Crow's disappearance from Puerto Rico.

REINTRODUCTION TO PUERTO RICO

Little has been done (of an effective nature) toward conservation of the White-necked Crow. A petition for listing the crow as a species of special concern was reviewed by the U. S. government in 1986–1987 (Federal Register 1987). The review concluded that more information was needed to determine the status of the crow in Hispaniola. Furthermore, as a foreign species the priority for seeking the necessary data was deemed somewhat lower than that accorded domestic species, while costs to obtain the data were expected to be higher. The conclusion was that "... the best scientific and commercial information available support a finding that the action (listing as endangered) requested is warranted, but precluded by work on other species judged to be in greater need of protection."

I suggest that a program to re-establish the crow should be undertaken in Puerto Rico. I feel it would be prudent to harvest White-necked Crows from Hispaniola and attempt releases in Puerto Rico for several reasons. First, the crow is declining in numbers and range with the accelerating habitat destruction in Hispaniola, and may become extinct there, too, without additional conservation measures. With the current desperate state of the country's economy and limited habitat for crows, there is little reason for optimism for the crow in Haiti. The Dominican Republic is also experiencing a severely poor economic period, wherein concern for the country's natural resources has become secondary to the primary needs of humans. Nevertheless, the Dominican Republic is perhaps 100 years "behind" Puerto Rico, where the cutting of forests peaked in the first quarter of the 20th century (Wadsworth 1949, Snyder et al. 1987). Although considerable area has been set aside in natural reserves, and several of these have been quite effective in conserving natural resources, human exploitation has continued unchecked at others, including Parque Nacional Los Haitises. Although the Dominican government initially took a strong position within the Park, relocating people out of Los Haitises, providing food subsidies to people to dissuade further cutting of vegetation, and levying fines and jail penalties for persons convicted of farming or cutting within the Park, forest clearing has continued within the protected area. Continued exploitation of important crow habitat, along with other negative factors (e.g., spread of the Pearly-eyed Thrasher), could result in the loss of the White-necked Crow in the Dominican Republic.

A second reason for re-introducing crows in Puerto Rico is that an opportunity still exists to obtain crows from Hispaniolan populations that would not be affected by such a harvest. A suitable source of White-necked Crows still exists in parts of the Dominican Republic. Although Cory (1886) suggested Puerto Rican specimens differed somewhat from Hispaniolan birds, and Ridgway (1904:279) recognized racial differences between the "Haitian" [= Hispaniola] crow (C. l. erythrophthalmus) and Puerto Rican populations (C. l. leucognaphalus) of the Whitenecked Crow, other workers concluded that the Puerto Rican and Hispaniolan populations do not differ enough to warrant treatment as subspecies (Meinertzhagen 1926, Wetmore 1927, Wetmore & Swales 1931, Johnston 1961). Thus, at least morphologically, crows introduced from Hispaniola would be similar to those formerly inhabiting Puerto Rico.

Third, many of the problems responsible for the crow's loss from Puerto Rico are now

controllable: (1) habitat destruction has ebbed. More forest and woodland habitat exists now (40% of the island in forests, albeit second-growth; Schmidt 1982) than in 1912 (< 2%). (2) The large area of second-growth forest in Puerto Rico would now serve to absorb effects of a severe storm. A direct hit by a storm would only be serious during the initial stages of reintroduction, when numbers are low and the populations are concentrated about the release areas. When each of several introduced populations grows in number and range, storms would become what they once were - threats to only local communities and not to the species. (3) Agriculture is not as important now as formerly; fewer farms are active and there would be fewer conflicts over crop depredation. (4) Hunting is much better controlled.

Pearly-eyed Thrashers (and rats to a lesser degree) would still be a threat to crows reintroduced to Puerto Rico. Areas with relatively low densities of thrashers exist (e.g., Río Abajo; Snyder et al. 1987), however, and reintroductions could be first attempted there. Río Abajo is a wet limestone area, similar to the Haitises area used by White-necked Crows in Hispaniola, and was formerly inhabited by the crow. Reintroduced crows could share resources of conservation projects already planned for the Commonwealth of Puerto Rico Río Abajo Forest; i.e., releases of the Puerto Rican Plain Pigeon (Patagioenas inornata wetmorei) and Puerto Rican Parrot (Wadsworth et al. 1982, Wiley et al. 1982). The crow reintroduction could be part of a conservation effort to "reconstruct" a part of Puerto Rico's recent ecosystems (Wiley 1985). Eventually, other extirpated species, such as the Limpkin (Aramus guarauna) and perhaps the ground iguana [Cyclura pinguis (= C. portoricensis)], still extant in other countries, could be re-established in Puerto Rico. Such a refuge would establish additional disjunct populations of animals whose populations may be declining toward extinction, or as supplementary populations to help secure species now confined to small areas (e.g., *C. pinguis* on Anegada). Certainly, under current conditions and prognoses, the White-necked Crow can be expected to decline further in Hispaniola. Another population established in Puerto Rico could serve as insurance against the species' extinction if the Hispaniolan population disappears.

Being as adaptable as apparently the crow has been during changing environments in the Dominican Republic, and with its generalistic food habits, I suspect that reintroduction problems would be few. One concern, however, might be for other endangered bird species planned for introduced into the Río Abajo Forest, if that site is chosen for crow releases. I suspect the most serious problem among these birds would come from nest depredations, although all forms once coexisted in the karst zone obviously with some kind of natural balance. Crows are known to be predators of pigeon eggs and squabs and may thereby pose a threat to the recovery efforts for the Plain Pigeon. Similarly, parrot nests are often depredated by Cuban Crows (pers. observ.), and reintroduced populations of the Whitenecked Crow to the karst zone of Puerto Rico may thereby have negative effects the re-establishment of Puerto Rican on Parrots there. Competition for food and habitat should be a minor issue in a sympatric release.

Although other species of endangered crows (e.g., Hawaiian Crow) have been successfully managed in captive breeding programs (Giffin 1989, Whitmore & Marzluff 1998), it would seem more prudent for the release in Puerto Rico to consist of birds caught wild from Hispaniola as free-flying birds. Juvenile White-necked Crows associate for considerable time with their parents and large flocks of crows, likely gaining substantial survival skills. Further, they may be similar to many other crow species in not breeding until after their second year. Thus, if young birds are used in translocations, it would be advisable to release groups of birds containing older as well as recently fledged individuals to improve the chance of success of introduction efforts. If naïve young crows are used, prerelease aversion training would be advisable to enhance their predator recognition and avoidance skills (Wiley *et al.* 1992).

A potentially serious threat to efforts to re-establish White-necked Crow populations in Puerto Rico and, indeed, to the conservation of the species range-wide, is disease. West Nile virus has been reported from all of the Greater Antilles (Komar et al. 2003b, Dupuis et al. 2005), and virus-neutralizing antibodies have been found in resident birds in Cuba, Jamaica, Dominican Republic, and Puerto Rico (Dupuis et al. 2003, Komar et al. 2003b, Dupuis et al. 2005). The virus is likely transmitted by infected migratory birds from North America (Dupuis et al. 2005). American Crows are highly susceptible to the West Nile virus (Caffrey et al. 2003, Komar et al. 2003a), and some crow populations have undergone an unprecedented and sustained decline since the virus arrived (Caffrey & Peterson 2003, Caffrey et al. 2005). It is likely that West Indian crows will show similar susceptibility to the arbovirus, and may also decline as a result of the disease. In 2002, Komar et al. (2003b) tested resident and migratory birds for flavivirus-neutralizing antibodies at Los Haitises and Sierra de Bahoruco, two strongholds of the White-necked Crow in the Dominican Repulic. Their results suggested that transmission of West Nile virus among bird populations at Los Haitises was widespread. The presence of the virus in Hispaniola poses a grave threat to the crow, particularly in combination with colonization of the island by the Pearly-eved Thrasher (Keith et al. 2003).

ACKNOWLEDGMENTS

I was ably assisted in the field by Julio Cardona, Joan Duffield, Elizabeth Litovich, John Taapken, and Beth Wiley. Tudy and Don Dod, José A. Ottenwalder, and Sixto Inchaustugui generously provided logistical and technical support for the study. I thank the administration and staff of the Museo Nacional de Historia Natural (Santo Domingo) for logistical support. The research was funded by the Commonwealth of Puerto Rico Departamento de Recursos Naturales (1974), U. S. Department of Agriculture - Forest Service (1975-1977), and U.S. Department of the Interior - Fish and Wildlife Service (1978–1989), National Biological Survey (1996), and U. S. Geological Survey (2000-2004).Additional support came from National Science Foundation, Wildlife Preservation Trust International, World Parrot Fund, and the International Crane Foundation. I thank my supervisors for their support during the fieldwork: Drs. Eduardo Cardona and Eduardo Angel, Puerto Rico Departmento de Recursos Naturales, Dr. Frank H. Wadsworth, Institute of Tropical Forestry, Drs. Ray C. Erickson and H. Randolph Perry, Patuxent Wildlife Research Center, and Drs. Reed Goforth, Michael Tome, and James Fleming, Cooperative Research Units. Carlos A. Delannoy, Dwight Smith, and Julio Cardona facilitated interviews in Puerto Rico, for which I thank them. Matilda Mota G. (Parques Nacionales, República Dominicana) provided permits to work in the national parks of the Dominican Republic. Dr. Mary LeCroy provided access to the field notes of Rollo Beck at the American Museum of Natural History. I thank Gina Mori and Alma Ramírez for their help with the resumen. The manuscript was improved through the suggestions of A. B. Clark and two anonymous reviewers.

REFERENCES

- Abbad y Lasierra, I. 1788. Historia geográfica, civil y politica de la isla de San Juan Bautista de Puerto Rico. Madrid. (1979 edition, Editorial Universitaria, Río Piedras, Puerto Rico).
- A. O. U. 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, DC.
- Barbour, T. 1943. Cuban ornithology. Nuttall Ornithological Club, Cambridge, Massachussetts.
- Baumel, J. J. 1953. Wing claws in the White-necked Crow (*Corvus leucognaphalus*). Auk 70: 373.
- Beck, R. H. 1916. Dominican Republic. Unpublished field notes deposited at the American Museum of Natural History, New York, New York.
- Biaggi, V. 1983. Las aves de Puerto Rico. 3rd ed. Editorial Universitaria, Univ. de Puerto Rico, San Juan, Puerto Rico.
- Blake, S. F. 1957. The function of the concealed throat-patch in the White-necked Raven. Auk 74: 95–96.
- Bond, J. 1928. The distribution and habits of the birds of the Republic of Haiti. Proc. Acad. Nat. Sci. Phila. 80: 483–521.
- Bond, J. 1947. Field guide to birds of the West Indies. Macmillan Co., New York, New York.
- Bond, J. 1973. Eighteenth supplement to the check-list of birds of the West Indies (1956). Academy of Natural Sciences, Philadelphia, Pennsylvania.
- Bond, J. 1977. Twenty-first supplement to the check-list of birds of the West Indies (1956). Academy of Natural Sciences, Philadelphia, Pennsylvania.
- Brodkorb, P. 1959. Pleistocene birds from New Providence Island, Bahamas. Bull. Fla. State Mus. Biol. Sci. Ser. 4: 349–371.
- Butler, R. W., N. A. M. Verbeek, & H. Richardson. 1984. The breeding biology of the Northwestern Crow. Wilson Bull. 96: 408–418.
- Byrkjedal, I. 1987. Antipredator behavior and breeding success in Greater Golden-Plover and Eurasian Dotterel. Condor 89: 40–47.
- Caffrey, C. 2000. Correlates of reproductive success in cooperatively breeding western American Crows: if helpers help, it's not by much.

Condor 102: 333–341.

- Caffrey, C., & C. C. Peterson. 2003. West Nile virus may not be a conservation issue in northeastern United States. Am. Birds 103rd Christmas Bird Count: 14–21.
- Caffrey, C., S. C. R. Smith, & T. J. Weston. 2005. West Nile virus devastates an American Crow population. Condor 107: 128–132.
- Caffrey, C., T. J. Weston, & S. C. R. Smith. 2003. High mortality among marked crows subsequent to the arrival of West Nile virus. Wildl. Soc. Bull. 31: 870–872.
- Chamberlain, D. R., & G. W. Cornwell. 1971. Selected vocalizations of the Common Crow. Auk 88: 613–634.
- Charles, J. K. 1972. Territorial behavior and the limitation of population in the crow, *Corvus cor*one and *Corvus cornix*. Ph.D. thesis, Aberdeen Univ., Aberdeen, Scotland.
- Cherrie, G. K. 1897. Contributions to the ornithology of San Domingo. Field Columbian Museum, Publication 10, Ornithological Series, Volume 1, No. 1, Chicago, Illinois.
- Clark, C. C., L. Clark, & L. Clark. 1990. Anting behavior by Common Grackles and European Starlings. Wilson Bull. 102: 167–169.
- Connor. R. N. 1985. Vocalizations of Common Ravens in Virginia. Condor 87: 379–388.
- Coombs, C. J. F. 1960. Observations on the Rook *Corvus frugilegus* in southwest Cornwall. Ibis 102: 394–419.
- Cory, C. B. 1886. The birds of the West Indies, including the Bahama Islands, the Greater and Lesser Antilles, excepting the islands of Tobago and Trinidad. Auk 3: 187–245.
- Cruz, A. 1972. Food and feeding behavior of the Jamaican Crow, *Corvus jamaicensis*. Auk 89: 445– 446.
- Danforth, S. T. 1929. Notes on the birds of Hispaniola. Auk 46: 358–375.
- Danforth, S. T. 1936. Pájaros de Puerto Rico. Rand McNally & Co., New York, New York.
- Dod, A. S. 1978. Las aves de la República Dominicana. Museo Nacional Historia Natural, Santo Domingo, República Dominicana.
- Dod, A. S. 1992. Endangered & endemic birds of the Dominican Republic. Cypress House Press, Fort Bragg, California.
- Dorst, J. 1947. Révision systématique du genre Cor-

WILEY

vus. Oiseau 17: 44-87.

- Dupuis, A. P., II, P. P. Marra, & L. D. Kramer. 2003. Serological evidence of West Nile virus transmission, Jamaica, West Indies. Emerging Infectious Diseases 9: 860–863.
- Dupuis, A. P., II, P. P. Mara, R. Teitsma, M. J. Jones, K. Louie, & L. D. Kramer. 2005. Serologic evidence for West Nile virus transmission in Puerto Rico and Cuba. Am. J. Trop. Med. Hyg. 73: 474–476.
- Emlen, J. T., Jr. 1942. Notes on a nesting colony of western crows. Bird-Banding 13: 143–154.
- Engel, K. A., & L. S. Young. 1989. Spatial and temporal patterns in the diet of Common Ravens in southwestern Idaho. Condor 91: 372–378.
- Engel, K. A., & L. S. Young. 1992. Movements and habitat use by Common Ravens from roost sites in southwestern Idaho. J. Wildl. Manage. 56: 596–602.
- Engel, K. A., L. S. Young, K. Steenhof, J. A. Roppe, & M. N. Kochert. 1992. Communal roosting of Common Ravens in southwestern Idaho. Wilson Bull. 104: 105–121.
- Esquemeling, J. 1684–1685. The buccaneers of America. George Routlege & Sons, Ltd., London, UK.
- Evans, R. M. 1970. Oldsquaws nesting in association with Arctic Terns at Churchill, Manitoba. Wilson Bull. 82: 383–390.
- Federal Register. 1987. [White-necked Crow petition.] Federal Register 52 FR 24485, July 1, 1987. Washington, DC.
- Fisher-Meerow, L. L. 1983. Floristics, ecology, phytogeography, and history of botanical exploration of the Sierra de Bahoruco, Dominican Republic. M. Sc. thesis, Univ. Florida, Gainesville, Florida.
- Fisher-Meerow, L. L., & W. S. Judd. 1989. A floristic study of five sites along an elevational transect in the Sierra de Baoruco, Prov. Pedernales, Dominican Republic. Moscosoa 5: 159– 185.
- Forbush, E. H. 1927. Birds of Massachusetts and other New England states. Vol. 2. Massachusetts Dept. Agric., Boston, Massachusetts.
- Garrido, O. H., & A. Kirkconnell. 2000. Field guide to the birds of Cuba. Cornell Univ. Press, Ithaca, New York.
- Garrido. O. H., G. B. Reynard, & A. Kirkconnell.

1997. Is the Palm Crow, *Corvus palmarum* (Aves: Corvidae), a monotypic species? Ornitol. Neotrop. 8: 15–21.

- Gaston, A. J., & R. D. Elliot. 1996. Predation by ravens *Corvus corax* on Brunnich's Guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. Ibis 138: 742–748.
- Giffin, J. G. 1989. Captive propagation of birds. Pp. 103–106 in Stone, C. P., & D. B. Stone (eds.). Conservation biology in Hawaii. Univiversity of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, Hawaii.
- Giffin, J. G., J. M. Scott, & S. Mountainspring. 1987. Habitat selection and management of the Hawaiian Crow. J. Wildl. Manage. 51: 485–494.
- Golding, P. 1983. Haitian birds. Gosse Bird Club Broadsh. 40: 15.
- Good, E. E. 1952. The life history of the American Crow – Corvus brachyrhynchos Brehm. Ph.D. diss., Ohio St. Univ., Columbus, Ohio.
- Goodwin, D. 1976 Crows of the world. Cornell Univ. Press, Ithaca, New York.
- Gosse, P. H. 1847. The birds of Jamaica. John van Voorst, London, UK.
- Gotmark, F., R. Neergaard, & M. Ahlund. 1990. Predation of artificial and real Arctic Loon nests in Sweden. J. Wildl. Manage. 54: 429–432.
- Greenway, J. C., Jr. 1958. Extinct and vanishing birds of the world. American Committee for International Wild Life Protection, Spec. Publ. 13, New York, New York.
- Gundlach, J. 1874. Beiträge zur Ornithologie del Insel Portorico. J. Ornithol. 22: 304–315.
- Gundlach, J. 1878. Neue Beiträge zur Ornithologie der Insel Porto Rico. J. Ornithol. 26: 157–194.
- Gwinner, E. 1964. Untersuchungen über das Ausdrucks– und Sozialverhalten des Kolkraben (*Corvus corax corax* L.). Z. Tierpsychol. 21: 657– 748.
- Hansen, H., C. A. Smedshaug, & G. A. Sonerud. 2000. Preroosting behaviour of Hooded Crows (*Corvus corone cornix*). Can. J. Zool. 78: 1813– 1821.
- Harlow, R. F., R. G. Hooper, D. R. Chamberlain, & H. S. Crawford. 1975. Some winter and nesting season foods of the Common Raven in Virginia. Auk 92: 298–306.
- Haydock, J., & J. D. Ligon. 1986. Brood reduction

in the Chihuahuan Raven: an experimental study. Ecology 67: 1194–1205.

- Heinrich, B. 1999. Planning to facilitate caching: possible suet cutting by a Common Raven. Wilson Bull. 111: 276–278.
- Heinrich, B., D. Kaye, T. Knight, & K. Schaumburg. 1994. Dispersal and association among Common Ravens. Condor 96: 545–551.
- Holyoak, D. T. 1967. Breeding biology of the Corvidae. Bird Study 14: 153–168.
- Holyoak, D. T. 1983. Notes on the Palm Crow Corvus palmarum in Haiti. Bull. Br. Ornithol. Club 103: 81–82.
- Ignatiuk, J. B., & R. G. Clark. 1991. Breeding biology of American Crows in Saskatchewan parkland habitat. Can. J. Zool. 69: 168–175.
- Jacobsen, O. W., & M. Ugelvik. 1992. Anti-predator behavior of breeding Eurasian Wigeon. J. Field Ornithol. 63: 324–330.
- James, P. C., & N. A. M. Verbeek. 1985. Clam storage in a Northwestern Crow (*Corvus caurinus*): dispersion and sequencing. Can. J. Zool. 63: 857–860.
- Jenkins, D. C., S. A. Temple, C. van Riper, & W. R. Hansen. 1989. Disease-related aspects of conserving the endangered Hawaiian Crow. Pp. 77–87 *in* Cooper, J. E. (ed.). Disease and threatened birds. ICBP Tech. Publ. No. 10, International Council for Bird Preservation, Cambridge, UK.
- Johnston, D. W. 1961. The biosystematics of American crows. Univ. Washington Press, Seattle, Washington.
- Johnston, R. F. 1958. Function of cryptic white in the White-necked Raven. Auk 75: 350–351.
- Jollie, M. 1978. Phylogeny of the species of *Corrus*. Biologist 60: 73–108.
- Keith, A. R., J. W. Wiley, S. C. Latta, & J. A. Ottenwalder. 2003. The birds of Hispaniola. Haiti and the Dominican Republic. BOU Checklist No. 21, British Ornithologists' Union, Tring, UK.
- Kilham, L. 1984. Cooperative breeding of American Crows. J. Field Ornithol. 55: 349–356.
- Kilham, L. 1985a. Territorial behavior of American Crows. Wilson Bull. 97: 389–390.
- Kilham, L. 1985b. Behavior of American Crows in the early part of the breeding cycle. Fla. Field Nat. 13: 25–31.

- Kilham, L. 1989. The American Crow and the Common Raven. W. L. Moody, Jr. Natural History Series, No. 10. Texas A&M Univ. Press, College Station, Texas.
- Komar, N., S. Langevin, S. Hinten, N. Nemeth, E. Edwards, D. Hettler, B. Davis, R. Bowen, & M. Bunning. 2003a. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. Emerg. Infect. Dis. 9: 311–323.
- Komar, O., M. B. Robbins, K. Klenk, B. J. Blitvich, N. L. Marlenee, K. L. Burkhalter, D. J. Gubler, G. Gonzálvez, C. J. Peña, A. T. Peterson, & N. Komar. 2003b. West Nile virus transmission in resident birds, Dominican Republic. Emerg. Infect. Dis. 9: 1299–1302.
- Lack, D. 1976. Island biology. Illustrated by the land birds of Jamaica. Univ. California Press, Berkeley, California.
- Lamm, D. W. 1958. A nesting study of the Pied Crow at Accra, Ghana. Ostrich 29: 59–70.
- Little, E. L., Jr., & F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. Agriculture Handbook No. 249, United States Department of Agriculture – Forest Service, Washington, DC.
- Little, E. L., Jr., R. O. Woodbury, & F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands, second volume. Agriculture Handbook No. 449, United States Department of Agriculture – Forest Service, Washington, DC.
- Littlefield, C. D. 1995. Demographics of a declining flock of Greater Sandhill Cranes in Oregon. Wilson Bull. 107: 667–674.
- Lockie, J. D. 1955. The breeding and feeding of Jackdaws and Rooks with notes on Carrion Crows and other Corvidae. Ibis 97: 341–369.
- Lorenz, K. 1931. Beiträge zur Ethologie sozialer Corviden. J. Ornithol. 79: 511–519.
- Maccarone, A. D. 1987. Sentinel behavior in American Crows. Bird Behav. 7: 93–95.
- Madge, S., & H. Burn. 1994. Crows and jays. A guide to the crows, jays and magpies of the world. Houghton Mifflin Co., New York, New York.
- Mason, C. R. 1960. Log of the Caribbean....April 1–12, 1958. Florida Nat. 33: 30–37.
- Meinertzagen, R. 1926. Introduction to a review of

the genus Corvus. Nov. Zool. 33: 57-119.

- Monroe, B. L., Jr., & C. S. Sibley. 1993. A world checklist of birds. Yale University Press, New Haven, Connecticut.
- Moore, J. E., & P. V. Switzer. 1998. Preroosting aggregations in the American Crow, *Corvus* brachyrhynchos. Can. J. Zool. 76: 508–512.
- Nogales, M., & E. C. Hernández. 1994. Interinsular variations in the spring and summer diet of the Raven *Corvus corax* in the Canary Islands. Ibis 136: 441–447.
- Nogales, M., & E. C. Hernández. 1997. Diet of Common Ravens on El Hierro, Canary Islands. J. Field Ornithol. 68: 382–391.
- Olson, S. L., & W. B. Hilgartner. 1982. Fossil and subfossil birds from the Bahamas. Pp. 22–56 in Olson, S. L. (ed.). Fossil vertebrates from the Bahamas. Smithsonian Institution Contributions Paleobiology No. 48, Washington, DC.
- Parmelee, D. F., & J. M. Parmelee. 1988. Ravens observed killing roosting Kittiwakes. Condor 90: 952.
- Peters, J. 1917. Birds of the northern coast of the Dominican Republic. Bull. Mus. Comp. Zool. 61: 391–426.
- Petit, C., M. Hossaert-McKey, P. Perret, J. Blondel, & M. M. Lambrechts. 2002. Blue Tits use selected plants and olfaction to maintain an aromatic environment for nestlings. Ecology Letters 5: 585–589.
- Poncy, R. 1938. Observations concernant le Corbeau Corneille. Ornithol. Beob. 35: 138–139.
- Raffaele, H. A. 1983. A guide to the birds of Puerto Rico and the Virgin Islands. Fondo Educativo Interamericano, San Juan, Puerto Rico.
- Ridgway, R. 1904. The birds of North and Middle America. United States National Museum Bulletin 50, part III. Washington, DC.
- Rolle, F. J. 1961. Notes and records of little-known species of birds from Puerto Rico. J. Agric. Univ. P. R. 45: 333–341.
- Rowley, I. 1967. Sympatry in Australia ravens. Proc. Ecol. Soc. Aust. 2: 107–115.
- Rowley, I. 1974. Display situations in two Australian ravens. Emu 74: 47–52.
- Saino, N., & F. De Bernardi. 1994. Geographic variation in size and sexual dimorphism across a hybrid zone between Carrion Crows (*Corrus* corone corone) and Hooded Crows (*C. c. cornix*).

Can. J. Zool. 72: 1543–1550.

- Sallé, M. A. 1857. Liste des oiseaux rapportés, et observés dans la Republique Dominicaine (Ancienne partie espagnole de l'Ile St. Domingue ou d'Haiti) par M. C. Sallé, pendant son voyage de 1849 à 1851. Proc. Zool. Soc. London 1857: 230–237.
- Schmidt, R. 1982. Forestry in Puerto Rico. Pp. 69– 71 in Lugo, A. E., & S. Brown (eds.). Forestry in the Caribbean. U. S. Man & Biosphere Report No. 7, Washington, DC.
- Sharpe, R. B. 1877. Catalogue of the birds in the British Museum. Volume 3 (Cat. of the Passeriformes or perching birds, in the Brit. Museum: Coliomorphae, containing the families Corvidae, Paradiseidae, Oriolidae, Dicruridae, and Prionopidae). Taylor & Francis, London, UK.
- Skead, C. J. 1952. A study of the Black Crow Corvus capensis. Ibis 94: 434–451.
- Snyder, N. F. R., J. W. Wiley, & C. B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California.
- Stiehl, R. B. 1985. Brood chronology of the Common Raven. Wilson Bull. 97: 78–87.
- Stiehl, R. B., & S. N. Trautwein. 1991. Variations in diets of nesting Common Ravens. Wilson Bull. 103: 83–92.
- Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83: 423–436.
- Turcek, F. J., & L. Kelso. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communs. Behav. Biol. 2: 127–297.
- USDA, NRCS. 2004. The PLANTS Database, version 3.5 (http://plants.usda.gov). National Plants Data Center, Baton Rouge, Louisiana.
- Vargas Mora, T. A., & W. J. Arendt. 1978. Estudio sobre la Paloma Coronita (*Columba leucocephala*) (Febrero–Septiembre, 1978). Unpubl. report dated 15 September 1978, Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic.
- Verbeek, N. A. M. 1995. Body temperature and growth of nestling Northwestern Crows, *Corvus caurinus*. Can. J. Zool. 73: 1019–1023.
- Verbeek, N. A. M. 1997. Food cache recovery by Northwestern Crows (Corrus caurinus). Can. J.

WILEY

Zool. 75: 1351–1356.

- Verbeek, N. A. M., & R. W. Butler. 1981. Co-operative breeding of the Northwestern Crow Corvus caurinus in British Columbia. Ibis 123: 183–189.
- Verrill, A. E., & A. H. Verrill. 1909. Notes on the birds of San Domingo, with a list of the species, including a new hawk. Proc. Acad. Nat. Sci. Phila. 61: 352–366.
- Verrill, A. H. 1926. Porto Rico, past and present, and San Domingo of to-day. Dodd, Mead & Co., New York, New York.
- Wadsworth, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. Ph.D. diss., Univ. Michigan, Ann Arbor, Michigan.
- Wadsworth, F. H., N. F. R. Snyder, H. A. Raffaele, J. W. Wiley, & A. Rodriguez. 1982. Puerto Rican Parrot recovery plan. U. S. Fish & Wildlife Service, Atlanta, Georgia.
- Wetmore, A. 1916. Birds of Porto Rico. U. S. Dep. Agric. Bull. 326: 1–140.
- Wetmore, A. 1918. Bones of birds collected by Theodoor de Booy from kitchen midden deposits in the islands of St. Thomas and St. Croix. Proc. U. S. Natl. Mus. 54: 513–522.
- Wetmore, A. 1920. Five new species of birds from cave deposits in Puerto Rico. Proc. Biol. Soc. Wash. 33: 77–78.
- Wetmore, A. 1925. Another record for the genus *Corrus* in St. Croix. Auk 42: 446.
- Wetmore, A. 1927. The birds of Porto Rico and the Virgin Islands. Pp. 409–598 in Scientific Survey of Porto Rico and the Virgin Islands. Volume 9, Parts 3 & 4. New York Academy of Science, New York, New York.
- Wetmore, A. 1937. Ancient records of birds from the island of St. Croix with observations on extinct and living birds of Puerto Rico. J. Agric. Univ. P. R. 21: 5–16.
- Wetmore, A., & B. H. Swales. 1931. The birds of Haiti and the Dominican Republic. U. S. Natl. Mus. Bull. 155: 1–483.
- Whitmore, K. D., & J. M. Marzluff. 1998. Handrearing corvids for reintroduction: importance of feeding regime, nestling growth, and dominance. J. Wildl. Manage. 62: 1460–1479.
- Wiley, J. W. 1985. Bird conservation in the United

States Caribbean. Bird Conserv. 2: 107-159.

- Wiley, J. W., & J. A. Ottenwalder. 1990. Birds of Islas Beata and Alto Velo, Dominican Republic. Stud. Neotrop. Fauna Environ. 25: 65–88.
- Wiley, J. W., N. F. R. Snyder, R. Cotte, W. Parker, & A. Rodríguez. 1982. Puerto Rican Plain Pigeon recovery plan. U. S. Fish & Wildlife Service, Atlanta, Georgia.
- Wiley, J. W., N. F. R. Snyder, & R. S. Gnam. 1992. Reintroduction as a conservation strategy for parrots. Pp. 165–200 *in* Beissinger, S. R., & N. F. R. Snyder (eds.). New World parrots in crisis. Solutions from conservation biology. Smithsonian Institution Press, Washington, DC.
- Wiley, J. W., & B. N. Wiley. 1981. Breeding season ecology and behavior of Ridgway's Hawk (*Buteo* ridgwayi). Condor 83: 132–151.
- Wiley, J. W., & J. M. Wunderle, Jr. 1993. The effects of hurricanes on island birds, with emphasis on the Caribbean. Bird Conserv. Int. 3: 319–349.
- Wimberger, P. H. 1984. The use of green plant material in bird nests to avoid ectoparasites. Auk 101: 615–618.
- Wittenberg, J. 1968. Freilanduntersuchungen zu Brutbiologie und Verhalten der Rabenkrähe (*Corvus c. corone*). Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere 95: 16–146.
- Woods, C. A., & J. A. Ottenwalder. 1983. The montane avifauna of Haiti. Pp. 607–622 in Risser, A. C., Jr., & F. S. Todd (eds.). Proceedings of the Jean Delacour/IFCB Symposium on breeding birds in captivity. International Foundation for the Conservation of Birds, Los Angeles, California.
- Woods, C. A., & J. A. Ottenwalder. 1992. The natural history of southern Haiti. Florida Museum of Natural History, Gainseville, Florida.
- Württemberg, P. W. H. von. 1835. Erste Reise nach dem nordlichen America in den Jahren 1822 bis 1824. J. G. Cotta, Stuttgart and Tübingen, Germany.
- Zanoni, T. A., M. M. Mejía P., J. D. Pimentel B., & R. G. García G. 1990. La flora y la vegetación de Los Haitises, República Dominicana. Moscosoa 6: 46–98.
- Zar, J. H. 1975. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.