SIBLEY, C. G. AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven, Connecticut.

SKUTCH, A. F. 1976. Parent birds and their young. Univ. of Texas Press, Austin.

STEPHENS, M. 1984a. Interspecific aggresive behavior of the polyandrous Northern Jacana (*Jacana spinosa*). Auk 101:508–518.

STEPHENS, M. 1984b. Intraspecific distraction displays of the polyandrous Northern Jacana, *Jacana spinosa*. Ibis 126:70–72.

STRAHL, S. D. 1987. The social organization and behaviour of the Hoatzin *Opisthocomus hoazin* in central Venezuela. Ibis 130:483–502.

WILKINSON, L. 1997. SYSTAT 7.0: the system for statistics. SYSTAT Inc., Evanston, Illinois.

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# Rapid Long-distance Colonization of Lake Gatun, Panama, by Snail Kites

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ABSTRACT.—The distribution of the Snail Kite (Rostrhamus sociabilis) is closely tied to that of apple snails (Pomacea spp.), its nearly exclusive food. Before the early 1990s, the species occurred in Panama primarily as a vagrant. Apple snails were introduced to Lake Gatun in central Panama in the late 1980s, and by 1994 Snail Kites had colonized the lake from population sources at least 350 km away and initiated breeding. Since 1994 the population has increased rapidly and the species can now be found throughout the lake. Received 7 Oct. 1998, accepted 6 Jan. 1999.

The Snail Kite (Rostrhamus sociabilis) is a highly specialized raptor that ranges from southern Florida and Mexico, through Central America, to Bolivia, northern Argentina and Uruguay (Beissinger 1988). Its distribution is closely tied to that of apple snails (Pomacea spp.), which form its diet almost exclusively (Beissinger 1988). The kite uses its exceptionally thin upper mandible to extract snails from their shells (Snyder and Snyder 1969). Other species of snails, turtles, crabs and other items are taken on occasion (Beissinger 1990a, Snyder and Kale 1983, Sykes and Kale 1974). The species is nomadic, moving in response to changes in the availability of its favored prey because of fluctuating water levels (Sykes 1979, 1983; Beissinger and Takekawa 1983, Takekawa and Beissinger 1989).

Snail Kites are rare in southern Central

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America, and there have been only seven previous reports from Panama (Ridgely and Gwynne 1989). The sole Panama specimen, an immature female, was collected near the Colombian border at Permé, near Puerto Obaldía, San Blas Province, in 1929 (Wetmore 1965). There were four reports of single birds, all either females or immatures, at marshes near Panama City, in 1971, 1973, 1977, and 1979. There were two reports from Chiriquí province in western Panama; an adult male and a female or immature near Gualaca in 1965, and several pairs and a nest in a marsh near Remedios in 1973, the latter being the only previous report of breeding activity in Panama (Ridgely and Gwynne 1989). The closest significant populations of Snail Kites to Panama are in western Colombia, on the west side of the Gulf of Urabá (Hilty and Brown 1986), about 350 km from the Panama Canal area, and the Tempisque Basin in northern Costa Rica (Stiles and Skutch 1989), approximately 650 km away.

## STUDY AREA

Lake Gatun (420 km²) is an artificial lake created by the damming of the Chagres River to form the central part of the Panama Canal in 1914. The lake level is controlled by the Panama Canal Commission, and may vary several meters between wet and dry seasons as water is released when ships pass through the locks. The Canal area experiences a strong four-month long dry season from mid-December to mid-April.

The introduced aquatic plant *Hydrilla verticillata* is a major problem in the lake. It apparently first became established in the late 1920s or early 1930s, and had

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become a significant problem by the 1960s (Maturell and Salazar 1994). Rooting in shallow water, it now occurs in huge beds in many parts of the lake.

The apple snail Pomacea lattrei was introduced to Panama from Guatemala in the early 1980s by Panama's National Directorate of Aquaculture. Snails were established at a research station at Divisa, Herrera Province, approximately 130 km west of Lake Gatun. for use in rural aquaculture programs. Between 1986 and 1988, the owner of a sportfishing business in the town of La Arenosa on the southwestern arm of Lake Gatun obtained 15 snails from the Divisa station and introduced them to a small artificial pond next to Lake Gatun. After they had reproduced, she distributed some to neighbors and introduced others into the lake. A few months later it was noticed that the snails were feeding on and reducing the abundant Hydrilla around the community's public dock and in surrounding areas. Residents of other lakeside communities began deliberately introducing snails to their areas in an effort to control Hydrilla (Maturell and Salazar 1994), a major impediment to small boat travel. The snails are also used for food by some local people.

Surveys by the Panama Canal Commission found that the snails were distributed throughout the southeastern arm of the lake by 1991, were in the northwestern part by 1992, and had reached the town of Gamboa at the east end of the lake by 1993. In some areas *Hydrilla* cover was reduced by as much as 94% in three years. Deliberate introduction by humans evidently allowed the snail to disperse quickly around the lake. The snails also spread by floating in currents and by egg masses fixed to floating vegetation, logs, and boats (Maturell and Salazar 1994).

A native species of apple snail, *Pomacea cumingi*, occurs in the Canal area. It is a bottom-dwelling species that typically occurs in low densities. It mostly inhabits small streams, but is sometimes found in larger rivers. The combination of habitat, bottom dwelling habit, and low density evidently makes this species unsuitable as prey for Snail Kites (F. G. Thompson, pers. comm.).

### **RESULTS**

M. Santamaría (pers. comm.), a game warden at the Barro Colorado Nature Monument, a reserve managed by the Smithsonian Tropical Research Institute, first observed unusual hawklike birds eating snails in Gigante Bay, south of Barro Colorado Island, in May or June 1994. On 3 February 1995 Santamaría and I visited an area where he had recently seen birds building nests in Guindilla Cove, a narrow inlet about 1500 m long on the south shore of Gigante Bay. We saw at least 14 Snail Kites in the cove at that time, including at least two adult males in black plumage. The remaining birds were in brown plumage. Im-

matures and adult females have brown plumage and cannot reliably be distinguished in the field (S. Beissinger, pers. comm.).

At four locations we observed nests consisting of loose platforms of twigs at various stages of construction. One small vine-covered tree standing in water (Site 1) had seven nests while the other sites had one nest each. No eggs or chicks were evident at that time, although we could not see the contents of high nests. Santamaría recently had seen birds bringing twigs to add to the nests.

The area was visited again on 20 May 1994 by D. and L. Engleman. They did not see any active nests at Site 1, but at least 17 kites were soaring or perched in the area. They observed five nests at another site (Site 2) about 300 m north of Site 1. These were located on a small island composed of Annona glabra shrubs overgrown with vines. Three nests were complete, one with two eggs and another with at least one egg and perhaps more. A third nest appeared to have eggs but they could not be counted. The remaining two nests were under construction and were visited by birds in brown plumage carrying twigs. At least 20 kites were present at this site, yielding a total of at least 37 in the cove (D. and L. Engleman, pers. comm.).

I visited Guindilla Cove again on 15 July 1994. At that time seven nests were present at Site 2. Two nests had three well-feathered nestlings, while two more fledglings were perched together on a branch near a third nest. Three other birds which took flight from the island had very short tails and appeared to have recently fledged. On 27 August 1994 two nests at Site 1 each had a single large downy young. No active nests were present at Site 2, but I saw two birds that apparently had recently fledged. On 14 October no activity was seen at Site 1, but three apparently recently fledged birds were present at Site 2. On this date I also surveyed several other areas in Gigante Bay that I had not previously investigated. One nest with two small nestlings was found near an island at the mouth of Guindilla Cove, and a second nest with two fledglings on the verge of flying was found on a large Annona glabra island about 3 km west of Guindilla. Approximately 15 adults and three apparently recently fledged young were also seen at this site.

#### DISCUSSION

Apple snails probably reached the area of Gigante Bay in 1991 (Maturell and Salazar 1994). I am certain no kites were present in the area before 1992, because I made three surveys of the shoreline of parts of the bay by canoe in 1991 and 1992, and surveyed Guindilla Cove itself on 23 August 1992. Guindilla Cove probably was colonized by kites in either 1993 or 1994.

In 1995, in the central part of the lake near the Panama Canal channel, Snail Kites were restricted to Gigante Bay, based on information from Smithsonian game wardens and researchers who worked on the lake. Kites were rarely if ever seen at the Smithsonian research station on the north side of Barro Colorado Island 4 km away.

Since 1995, kites have been seen more often in other parts of Lake Gatun and the Canal area in general, ranging from the northern end of the lake near the Gatun Locks to Miraflores Locks near the Pacific entrance to the Panama Canal. Although no comprehensive surveys of kite distribution and numbers have been made, Snail Kites appear to have spread throughout the lake and occur wherever suitable habitat is present.

In 1995 nest construction evidently began in January, during the early dry season. A few small nestlings were still present in mid-October, during the late rainy season. These latter birds would probably have fledged in November, so that in 1995 the breeding season was at least 10 months long. In Florida, the main nesting season is January-August, peaking in February-June, although in years of high water breeding may begin in December and extend to September (Beissinger 1986, 1988; Snyder et al. 1989). Nesting seasonality is poorly known elsewhere in the tropics, but may be tied to the rainy season. Nesting takes place during the wettest period in Surinam, Argentina and Venezuela (Beissinger 1988).

At Gigante, clutch or brood size ranged from one to three. In Florida, clutch size presently ranges from one to three with the latter much more frequent. However, clutch size appears to have declined historically in Florida, with four-egg clutches previously having been common (Beissinger 1986). The decline may be attributable to habitat deterioration. Al-

though there are few data, clutch size elsewhere in the kite's range seems typically to be two to three, although four-egg clutches often occur in Argentina (Beissinger 1990b) and clutch size may range up to six (Beissinger 1988). Despite a presumably superabundant food supply at Gigante in 1995, there was no evidence that kites increased their clutch size in response.

The Snail Kite colony in Guindilla cove increased from no birds in 1992 to at least 37 in 1995, an extraordinarily high rate of increase if only a single founding pair had been involved. Because Kites are highly sociable, initial colonization could have been by a small flock of birds rather than a single pair. It is possible that Guindilla Cove was not the initial site of colonization of Lake Gatun. Snails were present in the southwestern arm of the lake by the late 1980s. Kites could have colonized that area first, and then spread to Guindilla. The southwestern arm of the lake is large and remote from population centers, so a colony there could easily have gone undetected.

Nevertheless, Snail Kite populations increase rapidly under favorable conditions (Snyder et al. 1989, Beissinger 1995), such as the essentially unlimited food supply Lake Gatun would have offered the first colonists. The age at first reproduction in Snail Kites is very low, with some females nesting at 10 months. In favorable years in Florida, the breeding season may last up to 10 months, and some kites may re-nest and raise second broods (Beissinger 1986, Snyder et al. 1989). Parents of either sex may desert a nest leaving the other member of the pair to continue to raise the young alone (Beissinger and Snyder 1987). The remaining parent almost always is able to rear the young to independence by itself, while the deserting parent has the opportunity to re-nest with another partner.

The rapid colonization by Snail Kites of Lake Gatun and subsequent population expansion provides an interesting example of the dispersal capabilities of this highly opportunistic species. The most likely source of colonizing birds would have been the Colombian population, approximately 350 km from Lake Gatun. This population is much closer than the one in Costa Rica, and there are several large areas of freshwater habitat, including

Lake Bayano and several large rivers, in the intervening area. Dispersers discovered the newly suitable habitat of Lake Gatun within only a few years after the introduction of their preferred food, and rapidly spread throughout the available area.

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## LITERATURE CITED

- Beissinger, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the Snail Kite. Ecology 67:1445–1459.
- BEISSINGER, S. R. 1988. Snail Kite. Pp. 148–165 in Handbook of North American birds. Vol. 4 (R. S. Palmer, Ed.). Yale Univ. Press, New Haven, Connecticut.
- Beissinger, S. R. 1990a. Alternative foods of a diet specialist, the Snail Kite. Auk 107:327–333.
- Beissinger, S. R. 1990b. Experimental brood manipulations and the monoparental threshold in Snail Kites. Am. Nat. 136:20–38.
- BEISSINGER, S. R. 1995. Modeling extinction in periodic environments: everglades water levels and Snail Kite population viability. Ecol. Applications 5:618–631.
- Beissinger, S. R. and N. F. R. Snyder. 1987. Mate desertion in the Snail Kite. Anim. Behav. 35:477–487.

- BEISSINGER, S. R. AND J. E. TAKEKAWA. 1983. Habitat use and dispersal by Snail Kites in Florida during drought conditions. Fla. Field Nat. 11:89–106.
- HAVERSCHMIDT, F. 1970. Notes on the Snail Kite in Surinam. Auk 87:580-584.
- HILTY, S. L. AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.
- MATURELL, J. C. AND A. J. SALAZAR. 1994. Aspectos de la introducción y diseminación del caracol gigante *Pomacea* sp. en el Lago Gatún y sus efectos sobre la abundáncia de *Hydrilla verticillata*. Panama Canal Commission, Bureau of Engineering and Construction, Balboa, Panama.
- RIDGELY, R. AND J. GWYNNE. 1989. A guide to the birds of Panama. Princeton Univ. Press, Princeton, New Jersey.
- SNYDER, N. F. AND H. A. SNYDER. 1969. A comparative study of mollusc predation by Limpkins, Everglade Kites, and Boat-tailed Grackles. Living Bird 8:177-233.
- SNYDER, N. F. AND H. W. KALE, II. 1983. Mollusk predation by Snail Kites in Colombia. Auk 100: 93-97.
- SNYDER, N. F., S. R. BEISSINGER, AND R. F. CHANDLER. 1989. Reproduction and demography of the Florida Everglade (Snail) Kite. Condor 91:300–316.
- STILES, F. G. AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.
- SYKES, P. W., Jr. 1979. Status of the Everglade Kite in Florida 1968–1978. Wilson Bull. 91:495–511.
- SYKES, P. W., JR. 1983. Recent population trends of the Everglade Kite in Florida and its relationship to water levels. J. Field Ornithol. 54:237–246.
- SYKES, P. W., JR. AND H. W. KALE, II. 1974. Everglades Kites feed on non-snail prey. Auk 91:818– 820.
- Takekawa, J. E. and S. R. Beissinger. 1989. Cyclic drought, dispersal, and the conservation of the Snail Kite in Florida: lessons in critical habitat. Conserv. Biol. 3:302–311.
- WETMORE, A. 1965. The birds of the Republic of Panama. Vol. I. Tinamidae to Rynchopidae. Smithsonian Institution Press, Washington, D.C.