ECOLOGICAL CORRELATES OF RARITY IN A TROPICAL FOREST BIRD COMMUNITY

JAMES R. KARR

ABSTRACT.—Many species were rare and a few species and individuals seasonal at a lowland seasonally wet forest site in central Panama. Rare species decreased in April–June, either because of nesting peaks or because food supplies are better (hence wandering less necessary) in these months. Of the rare species, many are large species with large home ranges and others wander from nearby second-growth or forest-edge habitats. Some are associated with a small stream adjacent to the study plot. Some follow army ants or have other specialized hunting techniques that may be correlated with their rarity. For a number of species rarity may also be correlated with limits to physiological capabilities and exclusion by local congeneric competitors, but definitive evidence for these patterns is hard to muster. Some species wander seasonally from wetter or dryer habitats in central Panama, suggesting some seasonal flux that keeps birds within forests of correct moisture (or other) characteristics at all times. The magnitude of these seasonal movements varies among wet and dry years. When the ecological correlates of rarity are compared for two Middle American forests, a number of similarities are found. Differences in the two areas are attributed to differences in sampling or to characteristics of the climate and/or nearby habitats.—*Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907. Present address: Department of Ecology, Ethology and Evolution, Vivarium Building, University of Illinois, Champaign, Illinois 61820.* Accepted 1 October 1975.

Low densities of many tropical forest organisms have long been recognized by tropical biologists (Richards 1966). For birds, the abundance per species is lower in tropical forest habitats than in similar temperate habitats (Orians 1969, Karr 1971a, MacArthur 1972).

I conducted an intensive study of the birds of a forest plot along the Pipeline Road in the Panama Canal Zone. Earlier papers discuss the avifauna of the area from a variety of viewpoints (Karr 1971a, 1971b, 1975, 1976a, 1976b; Karr and Roth 1971; Karr and James 1975). This paper asks: For what ecological reasons might a species occur irregularly at a tropical forest locality?

STUDY AREA AND METHODS

The study area is in a region of humid forest that is seasonally dry. Annual precipitation averages about 260 cm and falls primarily in a rainy season lasting from late April to mid-December. The forest canopy often exceeds 40 m and stays predominantly green throughout the year. The 2-ha study plot is contiguous with a much larger expanse of relatively undisturbed forest. Further details of the habitat are provided in Karr (1971a).

Data for this analysis derive from 1 year of intensive fieldwork on the study area in 1968–69 and brief return visits in 1971, 1973, and 1975. Following the convention established earlier (Karr 1971a), each species observed on the study plot was categorized according to its status there: *resident,* a species that could be seen or netted almost daily on the study area; *regular,* species seen during many months, but generally on less than 50% of the surveys in any particular month; *irregular,* species that were seen only once, or at most, a few times during the study; and *migrant,* nonbreeding transients involved in long-distance migration, or winter visitors. Most of the migrants breed in North America (Karr 1976a).

Any attempt to assign species from a continuum to discrete classes, as this system does, is open to criticism. This system is developed to facilitate comparison of the status of species on any study plot. It should, at best, be considered an artificial system. It has heuristic value in that it does provide insights into the structure of avian communities.

More than 300 hours of field observations and 2400 mist-net hours were accumulated on the study plot in the 1968–69 period. Surveys of the area were done throughout the year during most weeks and one 3-to-6-day period was spent mist-netting each month (Karr 1971a).

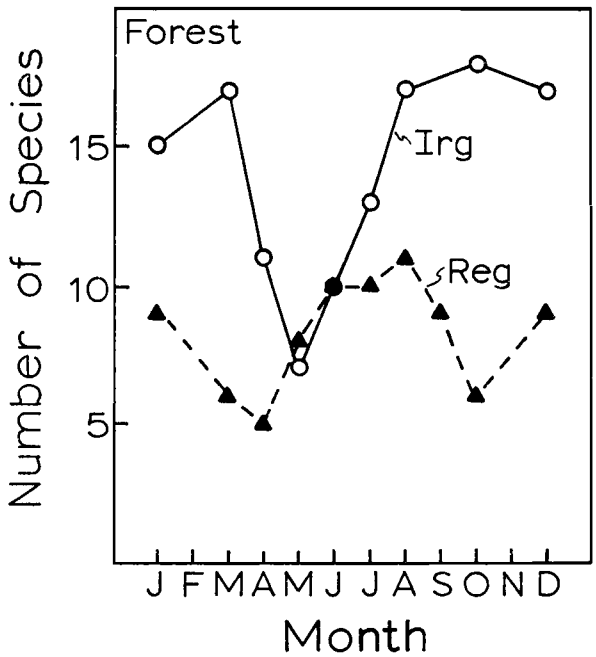

Fig. 1. Seasonal variation in the number of regular and irregular species in a tropical forest bird community.

Results

Of the 165 species seen in the forest study area in 1968–69, 15 were classed as regular and 70 as irregular. In addition, 7 other species observed on recent trips were classed as irregular, yielding a total of 77 irregular species. An additional 56 species are considered resident (Karr 1971a) and 22 are migrants from North America (Karr 1976a). Not including migrants, 62% of the species seen on the 2-ha forest study plot are relatively rare, or occur sporadically on the area.

Regular species were commonly large species that traveled over large home ranges relative to the size of the study area, and were consequently difficult to census accurately. As pointed out earlier, their inclusion in the resident list could lengthen it but have little impact on counts of biomass or number of individuals per unit area (Karr 1971a). These include such species as two vultures, a quail, a large canopy-feeding pigeon, two parrots, a cuckoo, and about a half dozen small-to-medium-sized insectivores of several passerine families. Most are found on the study plot sporadically throughout the year; 5 to 11 of these species are seen on the forest plot each month (Fig. 1).

Of the 77 irregular species noted in the forest study plot 24 species were seen only once and 22 were seen only twice. The remainder were seen more frequently, but still either sporadically or in only a single portion of the year. Notice that the number of irregular species seen per month varies seasonally (Fig. 1). In the last half of the wet season and most of the dry season the number of irregular species is high, averaging slightly above 15. At the end of the dry season (April), the number declines with a low in May of 7 and climbs to above 15 by August. This low in the late dry season may be due to decreased wandering during periods of high food abundance or to movements being restricted during a period of intense nesting activities. The peak in

TABLE 1

ECOLOGICAL CORRELATES OF RARITY IN A TROPICAL FOREST AVIFAUNA ON THE PIPELINE ROAD STUDY PLOT.[1]

I. Species associated with other habitats
  A. Aquatic forms—5 species
  Butorides virescens (2); *Agamia agami* (1); *Eurypyga helias* (1); *Chloroceryle inda* (1); *C. aenea* (3).
  B. Wander from nearby habitats (second-growth and forest-edge)—16 species
  Heliothrix barroti (2); *Jacamerops aurea* (3); *Xiphorhynchus guttatus* (2); *Myrmotherula brachyura* (1); *Myrmeciza exsul* (6); *Manacus vitellinus* (2); *Tityra semifasciata* (1); *Tyranniscus vilissimus* (4); *Neochelidon tibialis* (2); *Zarhynchus wagleri* (3); *Thraupis episcopus* (2); *T. palmarum* (1); *Habia fuscicauda* (4); *Tachyphonus luctuosus* (1); *Mitrospingus cassinii* (1); *Arremon aurantiirostris* (2).
  C. Foothill forms—6 species
  Geotrygon veraguensis (4); *Klais guimeti* (1); *Selenidera spectabilis* (1); *Thamnistes anabatinus* (5); *Mionectes olivaceus* (10); *Euphonia minuta* (1).
  D. Species that tend to be more abundant in dry forest—4 species
  Trogon violaceus (9); *Dendrocincla homochroa* (1); *Sclerurus mexicanus* (1); *Hylophilus ochraceiceps* (1).

II. Species for which sampling problems may account for rarity
  A. Large species that tend to have large home ranges—15 species
  Sarcoramphus papa (2); *Harpagus bidentatus* (2); *Leucopternis albicollis* (3); *L. semiplumbea* (1); *Spizaetus ornatus* (2); *S. tyrannus* (4); *Micrastur semitorquatus* (3); *Odontophorus gujanensis* (3); *Pionus menstruus* (6); *Amazona autumnalis* (7); *A. farinosa* (5); *Pteroglossus torquatus* (6); *Dryocopus lineatus* (2); *Phloeceastes melanoleucos* (2); *P. haematogaster* (3).
  B. Difficult to observe (mostly canopy) species—4 species
  Leptotila cassinii (4); *Laniocera rufescens* (3); *Rhytipterna holerythra* (4); *Myiopagis caniceps* (2).
  C. Nocturnal species easily overlooked—4 species
  Otus guatemalae (2); *Ciccaba nigrolineata* (1); *Lurocalis semitorquatus* (1); *Nyctibius grandis* (2).

III. Species exhibiting seasonal movements
  A. Move out in late wet and much of dry season—6 species
  Cotinga nattererii (2); *Cyanerpes cyaneus* (2); *C. lucidus* (2); *Dacnis cayana* (3); *Tangara inornata* (2); *T. gyrola* (4).
  B. Move into forest from Pacific slope areas during dry season—7 species
  Claravis pretiosa (3); *Florisuga mellivora* (2); *Thalurania colombica* (2); *Damophila julie* (2); *Amazilia amabilis* (1); *Legatus leucophaius* (4); *Ramphocaenus rufiventer* (1).

IV. Rare in area due to food or feeding behavior
  A. Food resource rare (follow army ants)—4 species
  Dendrocolaptes certhia (1); *Phaenostictus mcleannani* (10); *Pittasoma michleri* (3); *Eucometis penicillata* (3).
  B. Specialized hunting technique—3 species
  Accipiter superciliosus (1); *Micrastur mirandollei* (1); *M. ruficollis* (1).

V. Reason unknown—3 species
  Threnetes ruckeri (5); *Sirystes sibilator* (3); *Conopias parva* (1).

[1] Number of observations of each species in parentheses.

availability of animal-dispersed fruits (Foster 1973), and in biomass of insects (Smythe 1974) in the forests of nearby Barro Colorado Island coincides with the low in numbers of irregular species (Fig. 1). In addition, this is the peak of the breeding season for many species (Skutch 1950) so corresponds to the season when movements are restricted by domestic responsibilities. The August increase occurs after the completion of the breeding season, thereby corresponding to the period of wandering by immature birds.

The seasonal patterns of these irregular species are considerably more complex than indicated in Fig. 1. Species might be classed as irregular on my study plot for any of several reasons. For example, a competitor species that is successful in the Canal Zone may prevent them from increasing their populations. Alternatively, they may be rare because they are at the edge of their physiological tolerance limits for some physical (environmental) factor. A third possibility is that they are rare because

the resource that they depend on is rare in the region. A specialized frugivore or species requiring a specialized nest site might be rare if its food or habitat requirements are not plentiful. In addition to rarity within its habitat, a species might be irregular in my study plot if it were only an accidental wanderer from other nearby habitats. A species may also be nomadic with patterns of movement correlated with a seasonal climatic pattern and/or associated changes in resource abundance.

In addition, rarity in my samples may be due to artifacts of sampling. For example, birds active at a time of day that is inadequately sampled might actually be abundant (e.g. owls), or secretive forest species might be overlooked. When these factors seem to be responsible for a species' rarity in my data, they are noted. Each of the irregular species seen on the forest study tract was classed according to the probable reason for its sporadic or irregular appearance on the study plot (Table 1).

Species associated with other habitats.—Of the 77 species observed irregularly, 31 could reasonably be associated with other habitats (Table 1). Five species were recorded because a small stream bordered the study plot on the south boundary. A much larger number of species (16) occurred within the study plot because of its close proximity to a large road cut 200 m from the study plot. These include undergrowth species (*Manacus vitellinus* and *Myrmeciza exsul*), canopy species (*Tityra semifasciata* and *Zarhynchus wagleri*), aerial feeders (*Neochelidon tibialis*), and species of midlevel vine tangles (*Myrmotherula brachyura*). Six other species seem to reach their highest densities in the nearby foothills that tend to be less seasonal. Because of its relative isolation from contiguous foothill forest, the Pipeline receives fewer species than Caribbean coastal lowlands east of the Canal Zone (pers. obs.) or similar forest at La Selva in Costa Rica (see below). Apparently a number of foothill and Caribbean lowland species have been moving into the Canal Zone in recent years (Karr 1971b). It could be very interesting to study their effect on congeneric species already present there. Some of these species seem to move into the Pipeline Road region during the wet season and they might be included in the next section dealing with species exhibiting seasonal movements. Four other species tend to reach higher abundances in forest that is somewhat drier than that along the Pipeline Road.

Species exhibiting seasonal movements.—Seasonal movements to and from temperate forest habitats are well documented. Unfortunately, few workers recognize the magnitude of seasonal movements in lowland tropical forest habitats, although the phenomenon has been mentioned by many researchers (Slud 1960, 1964; Wetmore 1968; Willis 1974; Karr 1976b). Two distinct patterns of seasonal movement can be detected in the rare species seen on the Pipeline Road study plot. A group of six fruit-and-flower-associated species move out of the vicinity of the forest study area during the late wet and much of the dry season. Presumably this is a response to the decreased food avilability during this time of the year as Leck (1972) and Willis (pers. comm.) have suggested. Another 10 species move into the forest study area vicinity during the dry season from their major habitat of drier forest and second growth in the Pacific coastal part of Panama. Two species, *Claravis pretiosa* and *Ramphocaenus rufiventris*, even vocalize as if on territory in the Pipeline Forest region.

The magnitude of this dry season movement varies from year to year. During the dry season of 1975, one of the driest on record in the Canal Zone, I found an unusual number of individuals of birds more typical of dry forest. These included species seen in 1968–69 and a number of species not seen there in that wetter year. Many were not seen on the study plot but were recorded in the immediate vicinity. These included *Notharchus macrorhynchus, Turdus grayi,* and *Oryzoborus funereus* among others.

Species with specialized feeding ecology.—Seven species seem to be rare either because they are associated with a rare food resource, following army ants, or have a specialized hunting technique that depends on rarity for success. Three of the four ant-followers are the largest of the ant-following species. Three small-to-medium-sized raptors are rare. *Accipiter superciliosus* is rare throughout its range and the two *Micrastur* species have specialized hunting techniques (Smith 1969) that may depend on the relative rarity of the hawk for their success. In addition *Micrastur roficollis* is commonly found in association with army ants (pers. obs.; Willis, pers. comm.). *Dendrocincla homochroa,* listed with species generally found in drier forest, also seems to be an ant-following species.

Species for which sampling problems might result in rarity.—The 23 species in this group are in three distinct subgroups; 15 are large species with large territories or home ranges, 7 are large raptors or carrion feeders, and 3 are woodpeckers that have large territories (Schoener 1968) and traverse portions of their territories only irregularly. The remaining 5 species are primarily fruit and/or seed feeders, 4 in the forest canopy and 1 on the ground. These 5 species include 3 parrots, 1 araçari, and a wood quail. All seem to wander over large areas in flocks in search of local spots of fruit abundance.

A second group includes three species that are difficult to observe as they forage in forest canopy thickets for insects, and one species, a dove, that is hard to see and rarely caught in mist nets.

Four nocturnal species are known from the study plot but are seen or heard only on the less regular nocturnal surveys.

Rare for unknown reasons.—The factor associated with the rarity of these species is not clear. The hummingbird *Threnetes ruckeri* was captured in mist nets regularly in August, September, and October 1968, but none were seen or captured on the study plot in the following nine months of the study. Two other species, both medium-to-large forest-canopy flycatchers, are difficult to evaluate. *Conopias* is abundant to the north and the south of the Canal Zone. Slud (1964) found it associated with habitats at the edge of tall forest and often found it wandering. I suspect it is a bird of the canopy of mature forest that is more easily seen at the edge of the forest. *Sirystes* is a forest canopy species with similar irregular distribution patterns in Panama.

DISCUSSION

The general rarity of many tropical forest birds is well known. This analysis focuses on the 77 rarest species known from a forest plot in the Panama Canal Zone. Although I have tried to correlate each species' rarity with some ecological or sampling problem, it is clear that many of the species are rare from a complex of factors. The forest-falcon *Micrastur ruficollis,* for example, might be classed as a large species, as a species commonly associated with army ants, or as a species with a specialized foraging technique. In fact it is probably the combination of these factors that makes it rarer than might be predicted from any one factor.

Similarly there is a clear interaction between rarity in a marginal habitat and some complex of physiological and competitive limits. *Trogon violaceus* tends to be more abundant in "the trees along streams, at the forest edge, the borders of clearings, and similar more open cover" (Wetmore 1968) while *T. rufus* is found in denser forest. Some *T. violaceus* do occur in dense forest, but are they limited in that habitat by

behavioral habitat selection mechanisms, or are they restricted to moister (?) denser forest by their physiological capabilities? Another possibility is that they are competitively inferior to *T. rufus* in dense forest. As it is not possible to distinguish among those alternatives, I have categorized species according to habitat factors; the other alternatives should be kept in mind.

When the avifauna of the Perlas Archipelago (MacArthur et al. 1972) is considered, the known patterns of niche shifts strongly suggest that competition may be a primary factor in restricting species' distributions and abundances. But it is also true that physiological capabilities limit the competitive ability of inferior species. Examples of species pairs in which one species may be excluded by a superior competitor (in this habitat) include *Dendrocincla*, *Geotrygon* and *Sclerurus*. A possible intergeneric example of competition involves the antwrens (*Myrmotherula* and *Microrhopias*) and the greenlet (*Hylophilus ochraceiceps*). At Finca La Selva in Costa Rica the greenlet is abundant, while the antwrens are quite rare. The reverse is true in the Panama Canal Zone region.

The importance of physiology is implicated in the seasonal movements of a number of species. Various species wander seasonally (or in dry vs. wet years) from wetter or dryer habitats in central Panama, suggesting some seasonal flux that keeps birds within forests of correct rainfall characteristics and/or humidity conditions at all times. This may be a reason for extinction on Barro Colorado Island; in their relative isolation on the island, birds cannot shift about in dry (wet) weather or in exceptional years (Willis 1974). As Willis pointed out, this would argue for the inclusion of corridor zones between forest reserves to allow recolonization following unusually stressful periods.

Rare species at La Selva, Costa Rica.—In an effort to determine the generality of these patterns, I analyzed species considered rare, uncommon, or seasonal at the La Selva forest in Costa Rica (Slud 1960). While my Pipeline Road data derive from studies on a 2-ha study plot, Slud's intensive study tract included an area of 1 sq km. I counted 82 rare, uncommon, or seasonal species for La Selva using data from Slud and my own experience at La Selva in July of 1973 and 1974. This involves some subjectivity, as I had to depend on Slud's excellent but sometimes brief discussions. In addition I excluded from consideration a number of thicket species associated with small clearings in Slud's study tract, but not found in mature forest.

Several ecological differences between the study plots in Panama and Costa Rica should be noted. The La Selva area is wetter; according to the Holdridge system La Selva is a Tropical Wet Forest with about 380 cm of rain per year, while the Pipeline area receives only about 260 cm. Furthermore the Pipeline Road region has a longer and more severe dry season. The Holdridge system classes it as a Tropical Moist Forest. In addition the La Selva site is more broadly connected with subtropical habitat. The study plot is bordered by a large river, Rio Puerto Viejo, and includes several small streams. Finally, in addition to some small clearings, plantations of several trees such as cacao and palm occur within the La Selva site.

The total number of species Slud observed on his study tract was 331, compared to 170 on my Pipeline Road plot. The difference is due to two factors: Slud's tract was larger and it included a greater variety of habitats. Still, the number of rare or uncommon species on the two plots was similar with 77 in Panama and 82 in Costa Rica. The number for La Selva is artificially low because I no doubt excluded some species which rarely occurred in forest because Slud associated them with the cleared or otherwise disturbed areas. Furthermore many rare large species should be re-

TABLE 2

ECOLOGICAL CORRELATES OF RARITY IN PIPELINE ROAD, PANAMA CANAL ZONE (2 HA) AND LA SELVA, COSTA RICA (100 HA) STUDY PLOTS.[1]

	Panama	Costa Rica
I. Species associated with other habitats		
A. Aquatic	5	12
B. Second growth, forest edge	16	13
C. Foothill species	6	20
D. Dry forest	4	6
II. Sampling problems		
A. Large species with large home range	.15	6
B. Difficult to observe species	4	4
C. Nocturnal species	4	2
III. Seasonal movements		
A. Out in dry season	6	4
B. In during dry season	7	3
IV. Specialized species		
A. Ant-following species	4	2
B. Specialized hunting technique	3	4
V. Unknown	3	6
Total number of "rare" species	77	82

[1] La Selva data modified from Slud 1960 and pers. obs.

corded more regularly on a large tract, where the sampling problems of a small study plot would be eased. This is clear in that the number of large species with large home ranges is smaller in Costa Rica (6) than in Panama (15). Numbers of difficult-to-observe and nocturnal species are similar in the two areas (Table 2).

The increased availability of aquatic and foothill habitats at La Selva is reflected in the higher number of species associated with these habitats in Costa Rica than in Panama. The numbers of dry-forest-associated rare species in the two areas are similar, but some species in this category in Costa Rica (e.g. *Onychorhynchus mexicanus, Centurus pucherani*) are residents in the seasonally dry forest in Panama.

Numbers of species exhibiting seasonal movements in Costa Rica are somewhat below those in Panama. Although it is not reflected in the Table, about half of the species in the foothill group also exhibit some seasonality in their occurrence at La Selva.

The number of ant-following species is lower at La Selva, reflecting the trend in reduced numbers of ant-followers to the north in Middle America. Several other groups contain similar numbers of species in the two places.

In general the patterns discussed in the Panama study plot are similar to those in Costa Rica except when sampling problems differ (small vs. large study tract), where climate varies (La Selva wetter and less seasonal), and when habitat varies (presence of second growth, nearness of foothills).

ACKNOWLEDGMENTS

The Smithsonian Tropical Research Institute supported most of the fieldwork for this project. Fieldwork for the 1975 dry season was supported by a grant from the National Geographic Society. Special thanks to go these organizations and their staff. E. O. Willis, C. Leck, and R. S. Ridgely made helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

FOSTER, R. B. 1973. Seasonality of fruit production and seed fall in a tropical forest ecosystem in Panama. Unpublished Ph.D. dissertation, Durham, North Carolina, Duke Univ.

KARR, J. R. 1971a. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41: 207–233.

———. 1971b. Ecological, behavioral, and distributional notes on some central Panama birds. Condor 73: 107–111.

———. 1975. Production, energy pathways, and community diversity in forest birds. Pp. 161–176 *in* Tropical ecological systems: Trends in terrestrial and aquatic research (F. B. Golley and E. Medina, Eds.). New York, Springer-Verlag.

———. 1976a. On the relative abundances of north temperate migrants in tropical habitats. Wilson Bull. 88: 433–458.

———. 1976b. Seasonality, resource availability, and community diversity in tropical bird communities. Amer. Naturalist. 110: 973–994.

———, AND F. C. JAMES. 1975. Eco-morphological configurations and convergent evolution in species and communities. Pp. 258–291 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, Eds.). Cambridge, Massachusetts, Harvard Univ. Press.

———, AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several new world areas. Amer. Naturalist 105: 423–435.

LECK, C. F. 1972. Seasonal changes in feeding pressures of fruit and nectar eating birds in the neotropics. Condor 74: 54–60.

MACARTHUR, R. H. 1972. Geographical ecology. New York, Harper & Row.

———, J. M. DIAMOND, AND J. R. KARR. 1972. Density compensation in island faunas. Ecology 53: 330–342.

ORIANS, G. H. 1969. The number of bird species in some tropical forests. Ecology 50: 783–801.

RICHARDS, P. W. 1966. The tropical rain forest. Cambridge, England, Cambridge Univ. Press.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123–141.

SKUTCH, A. F. 1950. The nesting seasons of Central American birds in relation to climate and food supply. Ibis 92: 185–222.

SLUD, P. 1960. The birds of Finca "La Selva," Costa Rica: A tropical wet forest locality. Bull. Amer. Mus. Nat. Hist. 121: 53–148.

———. 1964. The birds of Costa Rica: distribution and ecology. Bull. Amer. Mus. Nat. Hist. 128: 1–430.

SMITH, N. G. 1969. Provoked release of mobbing—a hunting technique of *Micrastur* falcons. Ibis 111: 241–243.

SMYTHE, N. 1974. Pp. 70–115 *in* Environmental monitoring and baseline data (R. W. Rubinoff, Ed.). Smithsonian Inst. Environ. Sci. Program.

WETMORE, A. 1968. The birds of Panama, part 2, Columbidae (pigeons) to Picidae (woodpeckers). Smithsonian Misc. Coll. No. 150.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Monogr. 44: 153–169.