Double Mutualism Between the Black-crowned Palm-Tanager (Passeriformes, Pheanicophilidae, Phaenicophilus palmarum) and the Beach Creeper (Rubiaceae, Ernodea littoralis) on Hispaniola, Greater Antilles, Caribbean

Authors: Møller-Stranges, Fredrik, Hedegaard, Line Maj, and Dalsgaard, Bo

Source: Caribbean Journal of Science, 51(1) : 86-91

Published By: University of Puerto Rico at Mayagüez

URL: https://doi.org/10.18475/cjos.v51i1.a10

Caribbean Journal of Science (2021), 51: pp. 86–91.

Double Mutualism Between the Black-crowned Palm-Tanager (Passeriformes, Pheanicophilidae, *Phaenicophilus palmarum*) and the Beach Creeper (Rubiaceae, *Ernodea littoralis*) on Hispaniola, Greater Antilles, Caribbean

Fredrik Møller-Stranges[1,*], Line Maj Hedegaard[2], and Bo Dalsgaard[1]

[1]*Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Denmark*
[2]*Department of Plant and Environmental Sciences, Section for Plant and Soil Sciences, University of Copenhagen, Denmark*

**Corresponding author: fredrikstranges@gmail.com*

Abstract—**Double mutualism describes the situation where two species interact for the benefit of both in more than one type of interaction. For instance, if a given plant species is both pollinated and has its seeds dispersed by the same animal species. Double mutualism is thought to be more present in ecosystems where organisms are generalized, such as on oceanic islands. In the Caribbean islands, double mutualism has only been reported four times, of which only one involves a bird, between the widespread Bananaquit (*Coereba flaveola*) and the plant *Cordia bicolor* (Boraginaceae) on the continental island of Tobago. Here, for the first time, we report an observation of double mutualistic behaviour of a bird on Caribbean oceanic islands: The Black-crowned Tanager (*Phaenicophilus palmarum*), a bird endemic to Hispaniola, and the widespread plant Beach Creeper (*Ernodea littoralis*, Rubiaceae). Whereas hummingbirds and insects were more frequent visitors to the flowers of *E. littoralis* compared to *P. palmarum*, only *P. palmarum* was observed as a seed-disperser of *E. littoralis*. Based on our observations, we conclude that *P. palmarum* and *E. littoralis* show double mutualistic behaviour, though more detailed studies are needed to quantify the importance of this mutualistic behaviour, both from the bird's point of view and from the plant's point of view regarding the effectiveness of *P. palmarum* as pollinator and seed-disperser, respectively. We believe that double mutualism has been overlooked in the Caribbean, and, thus, we hope our observations will stimulate research into the importance of double mutualism across the Caribbean.**

In order for plant populations to regenerate, most plant species depend on their flowers being animal-pollinated and their fruits being dispersed by animals (Jordano 2009; Rech et al. 2016). These two distinct mutualistic processes are often served by different animal species, but for some plant species, the same animal is both a pollinator and a seed-disperser. Such cases where the same animal first pollinate the flowers and later disperse the resulting seeds is coined 'double mutualism' (Hansen and Müller 2009; Olesen et al. 2018; Fuster et al. 2019).

Double mutualism is thought to be more common in the tropics than in other climatic zones, mainly because there is a higher number of mutualistic relationships (Fuster et al. 2019). Double mutualism is also thought to be more common in ecosystems where organisms tend to be more generalized, as normally the most generalized species function as double mutualists (Fuster et al. 2019). For instance, it is known that oceanic islands far from the mainland have fewer but more generalized species (MacArthur and Wilson 1967; Dalsgaard et al. 2021) and, therefore, double mutualism is more common on islands (Olesen et al. 2018; Fuster et al. 2019). According to Fuster et al. (2019), who made a review of all known double mutualistic interactions, the number of double mutualistic relationships between birds and plants were four times higher on islands compared to the mainland. This may be because birds on oceanic islands are forced to explore other food sources beyond just insects, as insects are in scarcity on oceanic islands (Olesen et al. 2002; Olesen and Jordano 2002; Olesen and Valido 2003; Traveset et al. 2015). However, double mutualistic interactions between birds and plants may often be overlooked, as most research has focused on either pollination or seed-dispersal, but rarely examining both mutualistic processes.

In the Caribbean, the review by Fuster et al. (2019) only reported four animal species interacting in double mutualistic relationships and only one was a bird, the widespread Bananaquit (*Coereba flaveola* (Linnaeus, 1758)) both pollinating the flowers and dispersing the seeds of the plant *Cordia bicolor* A.DC. (Boraginaceae) on the continental island of Tobago. Biogeographically, however, the flora and fauna on Tobago is more related to mainland South America than the oceanic islands of the Caribbean north of Bond's line (Carstensen et al. 2012). Therefore, contrary to the general pattern of birds on tropical oceanic islands showing double mutualistic behavior, to our knowledge there is no observation of a bird-plant double mutualistic relationship on oceanic Caribbean islands.

Study Subjects and Methods

On the Caribbean island of Hispaniola, we observed the Black-crowned Tanager (*Phaenicophilus palmarum* (Linnaeus, 1766)) both pollinating and acting as a seed-disperser of the Beach Creeper (*Ernodea littoralis* Sw.) plant in the Rubiaceae family. *Phaenicophilus palmarum* is endemic to the island of Hispaniola, where it is widespread throughout the main island of Hispaniola as well as its satellite islands. It is only absent from Gonâve Island and the southern peninsula of Haiti, where the closely related Grey-crowned Tanager (*Phaenicophilus poliocephalus* (Bonaparte, 1851)) occurs instead (McDonald and Smith 1994). Despite the common name, the Black-crowned Tanager, *P. palmarum*, is no longer placed in the Thraupidae family (tanager family), but has been moved to the Phaenicophilidae family together with three other birds endemic to Hispaniola (Barker et al. 2013). Although *P. palmarum* is often characterized as an insectivore (Latta and Wunderle 1996; Wunderle and Latta 1998), it has also been reported to forage on fruits, seeds, and occasionally drink nectar (Johnson 2011; Birds Caribbean 2020).

The plant *Ernodea littoralis* is a woody shrub in the Rubiaceae family. It grows primarily on sandy, sun-exposed sites, often close to the coast. It is widespread and native in all of the Caribbean and in Florida (Negron-Ortiz and Hickey 1996b). The white flowers are frequently visited by both hummingbirds and insects (Negron-Ortiz and Hickey 1996a; Dalsgaard et al. 2021; Fig. 1A). Although it flowers year around, the flowering peaks in December to February (Negron-Ortiz and Hickey 1996b), resulting in an extended fruit bearing period (Fig. 1B). The flowers of *E. littoralis* are actinomorphic (i.e. has radial symmetry), a trait often seen among plants involved in double mutualism (Fenster et al. 2004; Fuster et al. 2019).

Our observations were conducted in Cotubanamá National Park, Dominican Republic (GPS: 18°19'19.3"N; 68°48'22.2"W), as part of a community study focusing on hummingbird-pollinated flowers. The duration of the study was approximately three months, from the 7th of March to the 5th of June 2020. The study area was a 200 m long, and 5 m wide transect within which the flowering of all plants was quantified and observed for animal visitation. The flowers of *E. littoralis* were popular among hummingbirds, and less so among various species of insects. Additionally, we occasionally observed *P. palmarum* visiting the flowers to drink nectar. The first certain observation of *P. palmarum* visiting *E. littoralis* flowers was made on the 28th of March, where *P. palmarum* was observed to both visit the flowers for nectar and eat the fruits (Fig. 1C–D). Even though *E. littoralis* was abundant inside the transect, *P. palmarum* was primarily observed interacting with *E. littoralis* outside the study area for our abovementioned community study, perhaps because the density of *E. littoralis* was higher outside our study area.

After the first opportunistic observations, we decided to conduct more focused observations on pollination and seed-dispersal of *E. littoralis*, to examine whether it was an isolated instance of double mutualistic behaviour of *P. palmarum*. Because *P. palmarum* preferred bushes adjacent to the transect, we decided to conduct the observations for this study outside the transect, focusing on the areas we knew *P. palmarum* preferred. During these observations, we focused only on *P. palmarum* rather than recording if hummingbirds or insects were pollinating the flowers (as these were recorded during our community study, see above). In total, we made 16 hours of observations, simultaneously recording both pollination and seed dispersal of *P. palmarum* of *E. littoralis*.

Results

During these 16 hours of observations, we estimated that *Phaenicophilus palmarum* visited 21 flowers and ate 78 berries of *Ernodea littoralis*. When drinking nectar, *P. palmarum* chose the flowers that it could reach without too much hazard and often it visited two to five flowers within one feeding bout. As mentioned above, *E. littoralis* flowering peaks in the period December to February. As we began our fieldwork on the 7th of March, flowering and, thus nectar-feeding, may have been more intense earlier in the flowering season. A few times we checked the flowers after a visit from *P. palmarum* and noted that some of these flow-

FIG. 1. Interactions between the bird *Phaenicophilus palmarum* and the plant *Ernodea littoralis* in Cotubanamá National Park, Dominican Republic. A. Flower from *E. littoralis* after a visit from *P. palmarum*. Note that the floral tube is torn, probably because the bill of *P. palmarum* is thicker than the floral tube; B. Fruits of *E. littoralis*; C. *P. palmarum* drinking nectar from the flowers of *E. littoralis*; D. *P. palmarum* eating fruits of *E. littoralis*. Photos by F. Møller-Stranges.

ers were damaged (Fig. 1A), maybe as a result of the bill of *P. palmarum* being too wide for the flower. We have no data on how this damage is affecting the pollination of the flower, but as not all flowers were damaged, we judge that *P. palmarum* may still act as an effective pollinator. Besides the hummingbirds and *P. palmarum* we also observed other passerine birds, the bananaquit (*Coereba flaveola*), and various species of warblers feeding on the nectar of *E. littoralis*. To compare the flower visitation rate of *P. palmarum* with the other pollinators, we calculated the visitation frequency of each pollinator group by dividing the number of feeding bouts of a given pollinator group (ignoring how many flowers it visited during each visit) by the number of flowers observed within a given time period (see Bárrios et al. in press). By calculating visitation rate as number of feeding bouts per floral unit, we are able to compare the insects against the birds, even though the observations were conducted in two different ways: insects were caught as soon as they had been scored as pollinators, whereas birds were allowed to continue feeding. We found that the most frequent pollinator group was the hummingbirds (Kruskal-Wallis test with a Dunn-Bonferroni post hoc test; $P < 0.001$; Fig. 2), whereas there was no difference between the insect group, *P. palmarum*, and other passerine birds (Kruskal-Wallis test with a Dunn-Bonferroni post hoc test; $P > 0.05$; Fig. 2). Thus, we judge hummingbirds to be

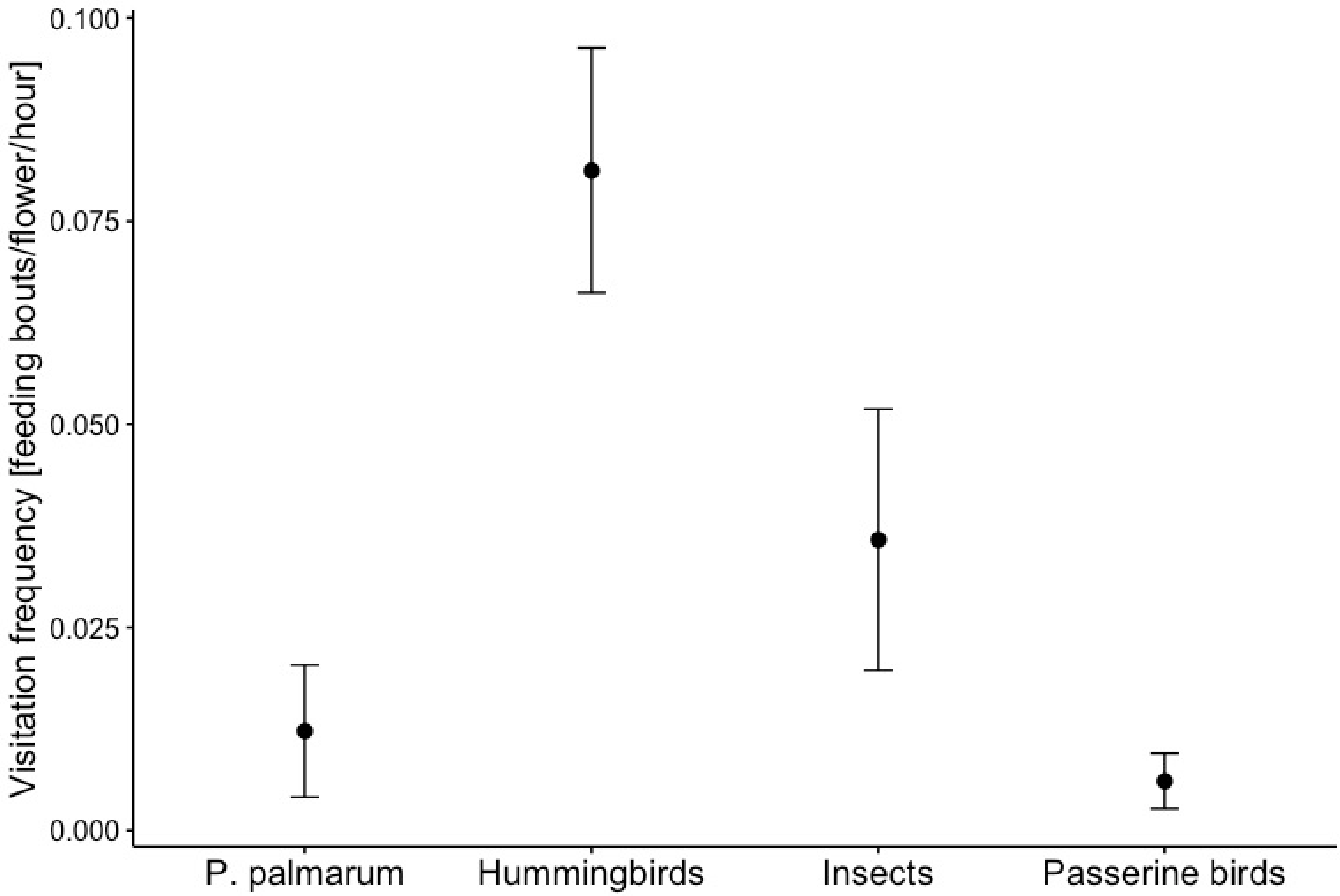

FIG. 2. Mean (± SE) visitation rate of different pollinator groups, i.e. hummingbirds, insects, *Phaenicophilus palmarum*, and other passerine birds. The visitation frequency index is calculated by dividing the number of nectar-feeding bouts with the number of flowers observed, ignoring the number of probes during each visit (see text for details). Comparing the visitation frequencies by a Dunn-Bonferroni post hoc after a Kruskal-Wallis test, we show that hummingbirds are the most important pollinator group ($P < 0.001$), whereas there is no difference between the other pollinator groups ($P > 0.05$).

the most important pollinators of *E. littoralis*, with *P. palmarum*, insects, and other passerine birds playing a lesser role as pollinators of *E. littoralis*.

It was clear that the fruits of *Ernodea littoralis* were the main interest for *Phaenicophilus palmarum*. When *P. palmarum* was feeding in bushes of *E. littoralis*, it was slowly jumping around searching for the ripest fruits, which it either ate whole or sometimes ate only the fleshy part of the fruit. During three months of fieldwork, although the visitation rate for fruits was low (0.006 visits/fruit/hour, SE ± 0.003) due to the high number of observed fruit-set, we did not observe *P. palmarum* feeding on other food sources than the fruits and nectar of *E. littoralis*, indicating that the fruits were a major part of its diet during March to the beginning of June.

DISCUSSION

Taken together, the observations reported here indicate a double mutualistic relationship between *Phaenicophilus palmarum* and *Ernodea littoralis*, with *P. palmarum* both pollinating and dispersing the seeds of *E. littoralis*. Although its role as a pollinator may be minor, the mutualistic benefits are much clearer with regards to seed dispersal, where *P. palmarum* appears to be the most important species as we observed no other seed-dispersers. This dependence seems to go both ways, as the fruits appear to be an important part of the diet of *P. palmarum*, at least during March to the beginning of June when we conducted our fieldwork. In the literature, *P. palmarum* is often described as an insectivore, but with our observations, combined with casual observations by various ornithologists (Johnson

2011; Birds Caribbean 2020), it would be more precise to categorize it as an omnivore or a highly adaptive opportunist that is capable of using numerous types of available food resources. As such, it may not differ from many other Caribbean birds, which are often thought to be generalists to cope with the frequent natural disturbances happening in the Caribbean (Caviedes 1991; Wiley and Wunderle 1993; Rathcke 2000; Dalsgaard et al. 2007). Therefore, as observed in other archipelagos in the tropics (Fuster et al. 2019), we hypothesize that numerous other species in the Caribbean may engage in double mutualistic associations and, thus, we hope our findings stimulate research into the importance of double mutualism across the Caribbean.

Acknowledgements—We would like to thank Jose Delio Guzman for help with obtaining a research permit. We would also like to thank our contact in the *Ministerio de Medio Ambiente y Recursos Naturales de República Dominicana*, Luis Reynoso, for his work and sincere help in understanding the local rules. None of the fieldwork would have been possible without the grants from the "Ingeniør Svend G. Fiedler & Hustrus" Foundation and from "Herboms Bog-legat for botanikstuderende." Bo Dalsgaard thanks Independent Research Fund Denmark (grant no. 0135-00333B). Finally, we thank 'Kati,' a friend in The Dominican Republic, who gave accommodation under the difficult time caused by the coronavirus.

Literature Cited

Barker, F. K., K. J. Burns, J. Klicka, S. M. Lanyon, and I. J. Lovette. 2013. Going to Extremes: Contrasting Rates of Diversification in a Recent Radiation of New World Passerine Birds. *Systematic Biology* 62: 298–320.

Bárrios, S., M. Dufke, M. Hamilton, R. Cowan, N. Woodfield-Pascoe, B. Dalsgaard, J. Hawkins, and C. Cubbe. In press. The conservation status and ecology of the British Virgin Islands endemic tree, *Vachellia anegadensis*. *Oryx*.

Birds Caribbean. 2020. From the Nest–Day 16. https://www.birdscaribbean.org/2020/05/from-the-nest-day-16/

Carstensen, D. W, B. Dalsgaard, J.-C. Svenning, C. Rahbek, J. Fjeldså, W. J. Sutherland, and J. M. Olesen. 2012. Biogeographical modules and island roles: A comparison of Wallacea and the West Indies. *Journal of Biogeography* 39: 739–749.

Caviedes, C. N. 1991. Five hundred years of hurricanes in the Caribbean: Their relationship with global climatic variabilities. *GeoJournal* 23: 301–310.

Dalsgaard, B., G. M. Hilton, G. A. L. Gray, L. Aymer, J. Boatswain, J. Daley, C. Fenton, J. Martin, L. Martin, P. Murrain, W. J. Arendt, D. W. Gibbons, and J. M. Olesen. 2007. Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. *Ibis* 149: 298–312.

Dalsgaard, B., A. C. Baquero, C. Rahbek, J. M. Olesen, and J. W. Wiley. 2016. Speciose opportunistic nectar-feeding avifauna in Cuba and its association to hummingbird island biogeography. *Journal of Ornithology* 157: 627–634.

Dalsgaard, B., P. Kiyoshi Maruyama, J. Sonne, K. Hansen, T. B. Zanata, S. Abrahamczyk, R. Alarcón, A. C. Araujo, F. P. Araújo, S. Buzato, E. Chávez-González, A. G. Coelho, P. A. Cotton, R. Díaz-Valenzuela, M. F. Dufke, P. L. Enríquez, M. Martins Dias Filho, E. Fischer, G. Kohler, C. Lara, F. M. G. Las-Casas, L. Rosero Lasprilla, A. O. Machado, C. G. Machado, M. A. Maglianesi, T. S. Malucelli, O. H. Marín-Gómez, V. Martínez-García, S. Mendes de Azevedo-Júnior, E. Nunes da Silva Neto, P. E. Oliveira, J. Francisco Ornelas, R. Ortiz-Pulido, R. Partida-Lara, B. Itzel Patiño-González, S. Najara de Pinho Queiroz, M. B. Ramírez-Burbano, A. Rodrigo Rech, M. A. Rocca, L. C. Rodrigues, A. M. Rui, I. Sazima, M. Sazima, B. I. Simmons, B. A. Tinoco, I. G. Varassin, M. F. Vasconcelos, J. Vizentin-Bugoni, S. Watts, J. D. Kennedy, C. Rahbek, M. Schleuning, and A. M. Martín González. 2021. The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird-plant networks. *Functional Ecology*: https://doi.org/10.1111/1365-2435.13784

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* 35: 375–403.

Fuster, F., C. Kaiser-Bunbury, J. M. Olesen, and A. Traveset. 2019. Global patterns of the double mutualism phenomenon. *Ecography* 42: 826–835.

Hansen, D. M. and C. B. Müller. 2009. Reproductive ecology of the endangered enigmatic mauritian endemic *Roussea simplex* (Rousseaceae).

International Journal of Plant Sciences 170: 42–52.

Johnson, S. 2011. *Black-crowned Palm Tanagers*. https://www.beautyofbirds.com/blackcrowned-palmtanagers.html

Jordano, P. 2009. *Fruits and frugivory: Seeds: the ecology of regeneration in plant communities*. Cabi Publishing.

Latta, S. C. and J. M. Wunderle. 1996. The Composition and Foraging Ecology of Mixed-Species Flocks in Pine Forests of Hispaniola. *The Condor* 98: 595–607.

MacArthur, R. H. and E. O. Wilson. 1967. *Area and Number of Species Theories: The Theory of Island biogeography*. Princeton University Press.

McDonald, M. A. and M. H. Smith. 1994. Behavioral and Morphological Correlates of Heterochrony in Hispaniolan Palm-Tanagers. *The Condor* 96: 433–446.

Negron-Ortiz, V. and R. J. Hickey. 1996a. The Genus *Ernodea* (Rubiaceae) in the Caribbean Basin. I. Allozyme Variation and Mating Systems. *Systematic Botany* 21: 433–443.

Negron-Ortiz V. and R. J. Hickey. 1996b. The Genus *Ernodea* (Rubiaceae) in the Caribbean Basin. II. *Systematic Botany* 21: 445–458.

Olesen, J. M., C. F. Damgaard, F. Fuster, R. H. Heleno, M. Nogales, B. Rumeu, K. Trøjelsgaard, P. Vargas, and A. Traveset. 2018. Disclosing the double mutualist role of birds on Galápagos. *Scientific Reports* 8: 1–11.

Olesen, J. M., L. I. Eskildsen, and S. Venkatasamy. 2002. Invasion of pollination networks on oceanic islands : importance of invader complexes and endemic super generalists. *Diversity and Distributions* 8: 181–192.

Olesen, J. M. and P. Jordano. 2002. Geographic Patterns in Plant-Pollinator Mutualistic Networks. *Ecology* 83: 2416–2424.

Olesen, J. M. and A. Valido. 2003. Lizards as pollinators and seed dispersers: An island phenomenon. *Trends in Ecology and Evolution* 18: 177–181.

Rathcke, B. J. 2000. Hurricane causes resource and pollination limitation of fruit set in a bird-pollinated shrub. *Ecology* 81: 1951–1958.

Rech, A. R., B. Dalsgaard, B. Sandel, J. Sonne, J.-C. Svenning, N. Holmes, and J. Ollerton. 2016. The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. *Plant Ecology and Diversity* 9: 253–262.

Traveset, A., J. M. Olesen, M. Nogales, P. Vargas, P. Jaramillo, E. Antolín, M. Mar Trigo, and R. Heleno. 2015. Bird-flower visitation networks in the Galápagos unveil a widespread interaction release. *Nature Communications* 6: 2–7.

Wiley, J. W. and J. M. and Wunderle. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conservation International* 3: 319–349.

Wunderle, J. M. and S. C. Latta. 1998. Avian resource use in Dominican shade coffee plantations. *Wilson Bulletin* 110: 271–281.