

is consistent with Kontogiannis' (1967) finding that captive birds of this species showed maximum rate of increase in mass during the first 2.5 hours of the day.

Black-capped Chickadee-RWR, the dominant female, gained, on average, nearly twice as much mass over the course of the day in comparison to the dominant male RBR (1.08g vs 0.62 g, representing an average daily change of 9.6% vs 5.6%). RBR exhibited the smallest daily amplitude of mass variation, suggesting that being the dominant male may facilitate energy conservation in roosting.

Acknowledgments.—We are indebted to Mary Doscher for instruction in banding technique, John Fennimore for apparatus modification, and Douglas White, Charles Leck, Richard Kane, Paul Kerlinger, Bertram Murray, Thomas Graedel and three anonymous reviewers for valuable technical and editorial advice.

LITERATURE CITED

- CASTRO, G., B. A. WUNDER, AND F. L. KNOFF. 1991. Temperature-dependent loss of mass by shorebirds following capture. *J. Field Ornith.* 62:314–318.
- HAFTORN, S. 1989. Seasonal and diurnal body weight variation in Titmice, based on analyses of individual birds. *Wilson Bull.* 101:217–235.
- HOWITZ, J. L. 1981. A population study of the Black-capped Chickadee. Ph.D. diss., Univ. of Minnesota, Minneapolis, Minnesota.
- KING, J. R. AND S. FARNER. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. *Am. Nat.* 100:403–418.
- KONTOGIANNIS, J. E. 1967. Day and night changes in body weight of the White-throated Sparrow, *Zonotrichia albicollis*. *Auk* 84:390–395.
- LAWRENCE, L. DEK. 1958. On regional movements and body weight of Black-capped Chickadees in winter. *Auk* 75:415–443.
- NATIONAL CLIMATIC DATA CENTER. 1989–91. Climatological Data New Jersey Vols. 94–96, passim. NOAA, Asheville, North Carolina.
- REFSNIDER, J. M. 1993. Weight loss by birds when held for banding. *N. Am. Bird Bander* 18:90–97.
- ROGERS, C. M. AND J. N. M. SMITH. 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves? *Ecology* 74:419–426.
- SAS. 1985. SAS Institute Inc., Box 8000, Cary North Carolina.
- STEEL, R. G. D. AND J. H. TORRIE. 1960. Pp. 338f in *Principles and procedures of statistics, with special reference to the biological sciences*. McGraw-Hill, New York, New York.

SUSANNAH K. GRAEDEL, *New Jersey Audubon Society, P.O. Box 693, Bernardsville, New Jersey 07924 (Present address: 3 Talmage Road, Mendham, NJ 07945); AND ROBERT E. LOVELAND, Dept. of Biological Sciences, FAS, and Bureau of Biological Research, Rutgers Univ., New Brunswick, New Jersey 08903. Received 8 March 1995, accepted 22 May 1995.*

Wilson Bull., 107(4), 1995, pp. 727–733

Detectability and population density of Scaly-naped Pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island.—Detectability and density of Scaly-naped Pigeons before and after Hurricane Hugo hit northeastern Puerto Rico with sustained winds of 30–40 m/s (gusting from 50–60 m/s) on 18 September 1989 (see Boose et al.

1994). With the exception of some protected vegetation pockets, forest habitats along the coastline and in the mountains were devastated. Unprotected forests were completely stripped of leaves and fruits. As a result, some canopy and ground-dwelling frugivore/seed-eater bird populations were severely impacted both directly and indirectly by the hurricane (Waide 1991; but also see Askins and Ewert 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993). This large-scale perturbation provided the opportunity of studying the resiliency of columbid populations under prolonged environmental stress (e.g., cover and food limitations).

Elsewhere I reported that Puerto Rican columbid populations sampled in September and October 1989 did not differ significantly from those sampled during the same time in 1986–87, and that increased detectability following the hurricane may have biased the counts since individuals and flocks were more visible when searching for food and cover in less affected areas (Rivera-Milán 1990a).

Here I provide data on the status of Scalynaped Pigeon (*Columba squamosa*) nesting populations, and examine changes in the detectability and density of the species before and after Hurricane Hugo hit Puerto Rico and Vieques Island (1986–92). Roadside counts should be adjusted for detectability in different habitats, especially when vegetation cover conditions change drastically as a result of defoliation (Rotella and Ratti 1986, Raphael 1987). Moreover, roadside counts are not necessarily reliable indicators of short-term changes in the size and success of nesting populations at local scales (Baskett 1993, and references therein). Therefore, I combined fixed- and unfixed-radius point counts along secondary and tertiary roads and strip-transect nest-counts to assess the effect of Hurricane Hugo on Scalynaped Pigeon nesting populations in Puerto Rico and on Vieques Island.

The Scalynaped Pigeon is an arboreal frugivore with a diverse diet (Pérez-Rivera 1978). The species is common in mesic habitats on the Puerto Rican mainland, and in xeric habitats on Vieques and Culebra islands (Rivera-Milán 1990b, 1992, 1993). It is the second most important game species of Puerto Rico (Rivera-Milán et al. 1990), hence accurate abundance estimates are needed to monitor population changes and guide management actions to maintain sustainable populations.

Study sites and methods.—Pre- and post-hurricane roadside counts were conducted in nine 8 km routes in the wet and moist zones of the Puerto Rican mainland (September–October 1986–89, and May 1987–92; Fig. 1 and Table 1). In May 1991–92, three routes with variable lengths were sampled in the dry zone of Vieques Island (Fig. 1 and Table 1). Vieques Island is the largest offshore territory (167 km²) and lies 9.7 km from the Puerto Rican mainland (8903 km²).

Six permanent stations at 1.6-km intervals were sampled/route on the Puerto Rican mainland. Because of the length of available secondary and tertiary roads, stations were at 0.8 km intervals on Vieques Island (four stations along road 995, six stations in Camp García and along Road 997, and ten stations inside the Naval Base Storage Facility). Call- and sight-counts were conducted for three minutes at each station in Puerto Rico and on Vieques Island from 06:00–10:30 AST (see Rivera-Milán 1993).

Detectability ($\hat{C}$) and density ($\hat{D}$) estimates were obtained from the combination of unfixed- and fixed-radius point counts (radius [r] = 60 m) at each station. Aural and visual detections outside the fixed area of the stations (πr^2) were used as supplementary data to estimate a species-specific constant to approximate the distance at which detectability dropped to zero. Detectability was estimated as $\hat{C} = 1 - (1 - P)^{0.5}/r$, where P equaled the number of detections inside 60 m (i.e., fixed count) divided by the number of detections inside and outside 60 m (i.e., unfixed count). Density was estimated as $\hat{D} = 3(10^6)N\hat{C}^2/\pi$, where N equaled the number of detections inside 60 m. The constant 10^6 was used to express $\hat{D}$ in km² (see Järvinen and Väisänen 1975, Järvinen 1978).

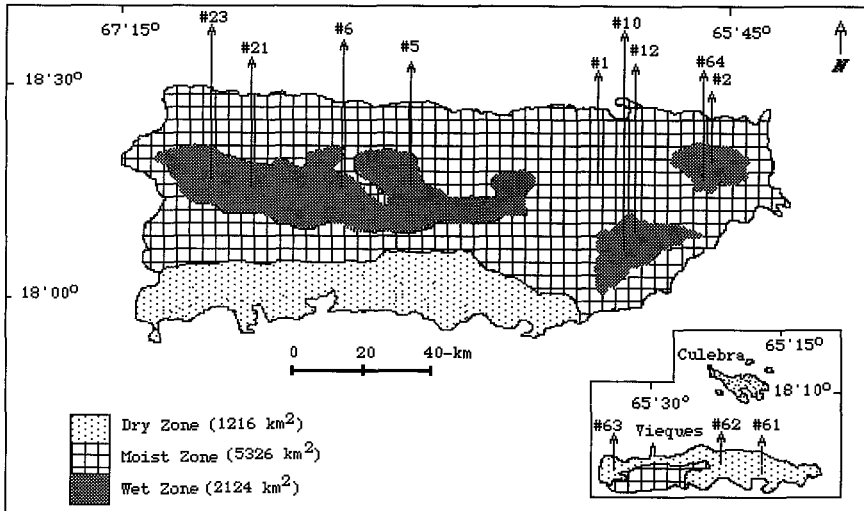


FIG. 1. Study sites and the three major life zones on Puerto Rico and its two major offshore territories, Vieques and Culebra islands.

TABLE 1
ROUTES USED TO EVALUATE THE EFFECT OF HURRICANE HUGO ON SCALY-NAPED PIGEON POPULATIONS

Location ^a	Habitat type
Puerto Rico	
Cidra	Moist montane forest
Luquillo	Rain forest
Barranquitas	Wet montane forest
Ciales	Wet montane forest
Cayey	Wet montane forest
Cayey	Wet montane forest
Adjuntas	Wet montane forest
Maricao	Wet montane forest
Naguabo	Rain forest and wet montane forest
Vieques Island	
Camp García and Road 997	Dry coastal forest
Road 995	Dry interior forest
Naval Base Storage Facility	Dry coastal forest

^a See Fig. 1.

TABLE 2

DETECTABILITY ($\hat{C}$) AND DENSITY ($\hat{D}$) ESTIMATES OF SCALY-NAPE PIGEONS BEFORE AND AFTER HURRICANE HUGO IN PUERTO RICO AND ON VIEQUES ISLAND^a

Date	Unfixed counts	Fixed counts	$\hat{C}$	$\hat{D}$
Puerto Rico				
Sept–Oct, 1986	22	7	0.00295	58.2
Sept–Oct, 1987	16	4	0.00223	19.0
Sept–Oct, 1989	18	8	0.00424	137.3
May, 1987	44	6	0.00118	8.0
May, 1988	60	13	0.00192	45.6
May, 1989	74	13	0.00154	29.2
May, 1990	101	27	0.00240	148.6
May, 1991	55	11	0.00176	32.5
May, 1992	60	12	0.00176	35.4
Vieques Island				
May, 1991	21	7	0.00306	62.5
May, 1992	16	6	0.00349	69.8

^a $\hat{C}$ and $\hat{D}$ estimates were obtained from 72 km sampled in Puerto Rico and 15.2 km sampled on Vieques Island (see Methods).

Nest counts were conducted in 32 0.1-ha (10 × 100 m) strip-transects in Cidra and Cayey (Fig. 1: #1 and #12) from May–June 1987–92. A total of 314 transects were sampled on Vieques Island in May–June 1989; 344 were sampled in May–June 1990; and 52 in May–June 1991–92 (Fig. 1: #61–63). The habitat types sampled in Cidra and Cayey were second-growth montane forests characteristic of the moist and wet zones of Puerto Rico; whereas the habitat types sampled on Vieques Island were characteristic of coastal and interior dry forests (see Ewel and Whitmore 1973). Forests of Cidra and Cayey were little impacted by Hurricane Hugo unlike those of Vieques Island, which were damaged severely.

Wilcoxon's signed-rank test, which is the nonparametric equivalent of a two group paired *t*-test, was used to compare pre- and post-hurricane changes in detectability (significance $P \leq 0.05$).

Results.—Detectability ($\hat{C}$) of Scaly-naped Pigeons was higher immediately after (Sept.–Oct., 1989) than before (Sept.–Oct., 1986–87) Hurricane Hugo (z corrected for ties = -2.383 , $P = 0.017$; z corrected for ties = -2.585 , $P = 0.009$; Table 2). As a result, density ($\hat{D}$) estimates obtained from the combination of fixed- and unfixed-radius point counts along roads were higher immediately after than before the hurricane (Table 2). The detectability of Scaly-naped Pigeons in May 1990 did not differ significantly from that of May 1987–89 and 1991–92 on the Puerto Rican mainland (Wilcoxon's signed-rank tests, $P > 0.05$; Table 2). Detectability approached average levels in May 1990 (wet zone [1986–88]: mean $\hat{C} = 0.00132$, SE = 0.00041, $N = 24$; 95% CI = 0.0005–0.00214; Rivera-Milán 1990b); and it returned to pre-hurricane levels in May 1991–92 (Table 2).

Detectability of Scaly-naped Pigeons in May 1991–92 (combined) on Vieques Island was significantly higher than that in May 1987 and 1989 on the Puerto Rican mainland (z corrected for ties = -1.997 , $P = 0.046$; z corrected for ties = -2.201 , $P = 0.028$); whereas

the other years (May 1988, 1990–92) did not differ significantly (Wilcoxon's signed-rank tests, $P > 0.05$; Table 2).

Scaly-naped Pigeons were not detected nesting on Vieques Island in May–June, 1990. But nesting populations rebounded to pre-hurricane levels after one year in Cidra and Cayey (low effect areas), and after two years on Vieques Island (high effect areas; Fig. 2A–C).

Discussion.—Detectability ($\hat{C}$) and density ($\hat{D}$) estimates increased as a result of Scaly-naped Pigeons being more visible when dispersing from high to low effect areas in search of cover and food. In Sept.–Oct. 1989, I observed 50–75 Scaly-naped Pigeons feeding at ground-level on fallen seagrapes (*Coccoloba uvifera*) on Culebra Island. Similarly, I observed flocks of 10–25 pigeons feeding on fallen fruits of yellow prickly-ash (*Zanthoxylum monophyllum*) and shortleaf fig (*Ficus laevigata*) on Vieques Island. I did not observe Scaly-naped Pigeons feeding on the ground on the Puerto Rican mainland; but flocks of 10–20 pigeons were seen feeding at canopy-level on fruits of Puerto Rican royal palm (*Roystonea borinquena*), trumpet tree (*Cecropia schreberiana*), and matchwood (*Didymopanax morototoni*).

In Sept.–Oct. 1989, I also saw flocks of 3–15 Scaly-naped Pigeons flying from Culebra and Vieques islands to the northeastern corner of the Puerto Rican mainland. From 1986–92, I did not observe Scaly-naped Pigeons moving from Puerto Rico to Culebra or Vieques islands. They were seen moving from Vieques Island to Puerto Rico before Hurricane Hugo, but mostly as singles or flying couples; their flocking behavior appeared to be more conspicuous immediately after the hurricane. The increase in density in Sept.–Oct. 1989 and May 1990 reflected in part an increase in the detectability of Scaly-naped Pigeons moving from high to low effect areas in Puerto Rico and on Vieques Island. That pigeons from Culebra and Vieques islands dispersed to Puerto Rico after the hurricane mainly in search of food and cover is supported by the lack of nesting activity found in May–June 1990 (the peak of the nesting season; Rivera-Milán 1990b) on Vieques Island. Nesting populations rebounded to pre-hurricane levels after one year in low effect areas on the Puerto Rican mainland, and after two years in high effect areas on Vieques Island. Scaly-naped Pigeon populations in the moist and wet zones of the Puerto Rican mainland increased slightly from May–June 1987–92. The density increase detected in May 1990 was followed by an increase in the number of active nests of Scaly-naped Pigeons in May 1991–92 (Table 2 and Fig. 2A–C). This appeared to be a response of the populations to a year of below normal reproduction (1990) in Puerto Rico and on Vieques Island.

The combination of unfixed- and fixed-radius point counts (“simple” vs “adjusted”; Raphael 1987) helped to account for changes in the detectability of Scaly-naped Pigeons before and after Hurricane Hugo. The unfixed and fixed roadside counts of Scaly-naped Pigeons were probably biased high on the Puerto Rican mainland in Sept.–Oct. 1989 and in May 1990, and on Vieques Island in May 1991–92. Detectability was higher immediately after (1989–90) than before (1987–88) the hurricane, because of the drastic loss of vegetation cover at canopy-level and the increased visibility of dispersing and foraging Scaly-naped Pigeons (Wiley and Wunderle 1993; J. M. Wunderle, unpubl. data).

Management decisions about the sustainability of nesting populations (e.g., reopening of the hunting season [September–November] on Vieques Island; Rivera-Milán et al. 1990) should be guided by standardized monitoring efforts. The combination of fixed- and unfixed-radius point counts along secondary and tertiary roads and strip-transect nest-counts facilitated the examination of changes in the size of Scaly-naped Pigeon nesting populations at local scales before and after Hurricane Hugo.

Acknowledgments.—I thank A. Ortiz, D. Ramos, E. Ramos, and A. Matos for spending many hours afield. F. Schaffner, J. Wiley, J. Wunderle, and two anonymous reviewers helped me to improve a previous version of the manuscript. This study was supported by Pittman-

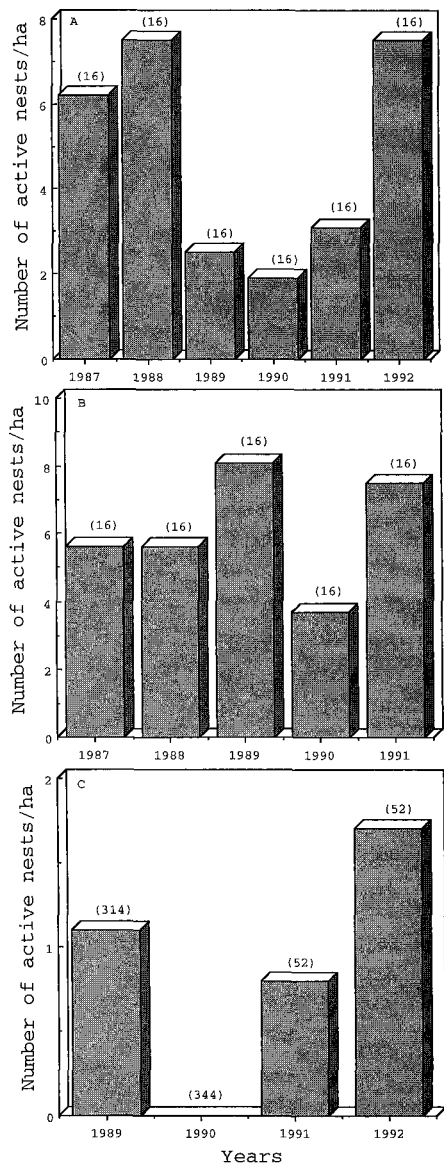


FIG. 2. Nesting density of Scały-naped Pigeons before and after Hurricane Hugo in Cidra (A), Cayey (B), and on Vieques Island (C). Numbers in parentheses correspond to the number of 0.1-ha strip-transects sampled before and after the hurricane.

Robertson Funds grant-in-aid to the Terrestrial Ecology Section, Scientific Research Area, Puerto Rico Dept. of Natural Resources.

LITERATURE CITED

- ASKINS, R. A. AND D. N. EWERT. 1991. Impact of Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. *Biotropica* 23:481–487.
- BASKETT, T. S. 1993. Biological evaluation of the call-count survey. Pp. 253–268 in *Ecology and management of the mourning dove* (T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, eds.). Sateckpole Books, Harrisburg, Pennsylvania.
- BOOSE, E. R., D. R. FOSTER, AND M. FLUET. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64:369–400.
- JÄRNIVEN, O. 1978. Estimating relative densities of land birds by point counts. *Ann. Zool. Fenn.* 15:290–293.
- AND R. A. VÄISÄNEN. 1975. Estimating relative densities of breeding birds by the line transect method *Oikos* 26:316–322.
- PÉREZ-RIVERA, R. A. 1978. Preliminary work on the feeding habits, nesting habitat and reproductive activities of the Plain Pigeon (*Columba inornata wetmorei*) and the Red-necked Pigeon (*Columba squamosa*), sympatric species: an analysis of their interaction. *Science-Ciencia* 5:89–98.
- RAPHAEL, M. G. 1987. Estimating relative abundance of forest birds: simple versus adjusted counts. *Wilson Bull.* 99:125–131.
- RIVERA-MILÁN, F. F. 1990a. Preliminary assessment of the impact of Hurricane Hugo to columbid populations in Puerto Rico and offshore satellite islands. *El Pitorre* 2:2.
- . 1990b. Distribution and abundance of columbids in Puerto Rico. Ph.D. diss. Univ. of Maryland, College Park.
- . 1992. Distribution and abundance patterns of columbids in Puerto Rico. *Condor* 94:224–238.
- . 1993. Standardization of roadside counts of columbids in Puerto Rico and on Vieques Island. U.S. Department of the Interior, Fish and Wildl. Serv. Res. Publ. 197.
- RIVERA-MILÁN, F. F., G. BONILLA, A. ORTIZ, D. RAMOS, AND E. RAMOS. 1990. Final Report. Project W-11. Puerto Rico Dept. Nat. Res.
- ROTELLA, J. J. AND J. T. RATTI. 1986. Test of a critical density index assumption: a case study with gray partridge. *J. Wildl. Manage.* 50:532–539.
- WAIDE, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:475–480.
- WAUER, R. H. AND J. M. WUNDERLE, JR. 1992. The effect of Hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. *Wilson Bull.* 104:656–673.
- WILEY, J. W. AND J. M. WUNDERLE, JR. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Cons. Intl.* 3:319–349.

FRANK F. RIVERA-MILÁN, *Dept. of Natural Resources, Scientific Research Area, Terrestrial Ecology Section, Stop 3 Pta. de Tierra, San Juan, Puerto Rico 00906. Current address: U.S. Fish and Wildlife Service, Office of International Affairs, 4401 North Fairfax Drive, Suite 860-ARLSO, Arlington, Virginia. Received 9 Nov. 1994, accepted 1 May 1995.*