

SPATIAL AND TEMPORAL ABUNDANCE PATTERNS OF RUDDY QUAIL-DOVES (*GEOTRYGON MONTANA*) NEAR MANAUS, BRAZIL¹

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Abstract. We analyzed patterns of abundance of Ruddy Quail-Doves (*Geotrygon montana*) based on 12 years of mist-net data (457 captures) from *terra firme* forest near Manaus in central Amazonian Brazil. Unlike most understory birds at the study site, *G. montana* varied greatly in abundance. Quail-doves disappeared for months and then reappeared, usually during the wet season. In some months they became one of the most frequently netted birds. Quail-doves avoided isolated forest fragments of one ha, although abundance did not differ among fragments of 10 ha, 100 ha, and continuous forest. Peak abundance varied among years, as did the timing of peak abundance. In general, the annual pattern of quail-dove abundance was correlated with the annual rainfall pattern. Considering all 12 years of data, however, quail-dove abundance during a given three-month period was not correlated with rainfall during that period, but with rainfall in the same period in the previous year. No quail-doves were recaptured more than a few weeks apart; thus individual birds did not return to the same site from year to year. Since quail-doves feed mainly on fallen fruit, these results suggest that they may range over wide areas to exploit regional differences in fruit production.

Key words: Amazonian Brazil; *Geotrygon montana*; migration; rainfall; Ruddy Quail-Dove; seasonal movements.

INTRODUCTION

The understory bird community of *terra firme* forest in central Amazonian Brazil is characterized by permanently resident species that show little seasonal variation in abundance as measured by mist net captures (Bierregaard 1990a). This area is south of the wintering range for most neotropical migrants (e.g., Blake et al. 1990, Stotz et al. 1992). Austral migrants that winter in equatorial Brazil include few forest birds (Bierregaard 1990a). In other tropical regions, forest birds commonly make relatively small scale migrations to take advantage of seasonal variation in resources, especially differences in flower and fruit production as a function of habitat or altitude (Morton 1977, Blake and Loiselle 1991, Date et al. 1991, Levey and Stiles 1992). Such movements appear to be much less common in the Amazon Basin than in Central America (Terborgh and Weske 1969, Lovejoy 1975, Terborgh et al. 1990).

One reason such migrations are less common in Amazonia may relate to the geography of the region. By virtue of its vast expanse with little altitudinal variation, Amazonia offers little op-

portunity for relatively short distance altitudinal migration such as is common in Central America (Levey 1988a, Stiles 1988, Loiselle and Blake 1991) and southeastern Brazil (Sick 1983). A second reason for the lack of migration may relate to the difference in structure of understory communities between well-studied sites in Central America and Amazonia. Among species sampled by mist-netting, frugivores and nectarivores are more common in Central America (Karr et al. 1990), and are more prone to large- and small-scale movements than are insectivores (Terborgh and Weske 1969, Levey and Stiles 1992).

The Ruddy Quail-Dove (*Geotrygon montana*) is one of the few species that exhibit pronounced variation in abundance in the forests near Manaus, Brazil, presumably as a result of large-scale population movements (Bierregaard 1990a). Based on over seven years of mist net data, Bierregaard (1990a) found it to be more abundant in the wet season, although there was strong variation among years. Of the 37 common species examined, *G. montana* was the most variable in abundance, disappearing for months at a time. In Panama and at La Selva, Costa Rica, abundance of *G. montana* is also highly variable (Stiles and Levey, in press; Karr, pers. observ. cited in Karr et al. 1990).

G. montana is distributed from southern Mexico to northern Argentina, including Caribbean

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islands (AOU 1983). It is generally found in the interior of moist to wet forests, where it feeds on fallen fruits, digesting both pulp and seeds (Skutch 1949; Schubart et al. 1965; Cruz 1974; Davis et al. 1985; Hilty and Brown 1986; pers. observ.). It nests in low vegetation or on decaying stumps (Skutch 1949). Active nests were found on the study site in 1983, 1987, and 1992, and we suspect the bird nested on the site in other years of high abundance (D. F. Stotz and A. Whittaker, pers. comm., pers. observ.). This quail-dove is especially well suited to a study based on mist net captures (see below) as it rarely perches off the ground and typically flies only one to two m above the ground.

As for many understory birds, preliminary analysis suggested that *G. montana* shows spatial variation in abundance associated with fragment size. Data presented in Bierregaard and Lovejoy (1989; Appendix) suggest that *G. montana* decreased in abundance in one ha forest fragments in comparison to larger fragments and continuous forest.

Here we examine the patterns of spatial and temporal abundance of *G. montana* based on 12 years of mist net capture data. We asked the following questions. How does abundance vary within and among years? Are quail-doves equally abundant in continuous forest and in patches of one, 10 and 100 ha? How is temporal variation related to seasonal variation in rainfall? Does temporal variation represent a consistent migration pattern? How can this pattern be explained based on the ecological characteristics of the bird?

METHODS

This study was conducted in *terra firme* forest 80 km north of Manaus, Brazil (2°30'S, 60°W) in the study area of the Biological Dynamics of Forest Fragments Project. Although some parts of the area have been cleared for cattle ranching, providing the opportunity to study the effects of fragmentation (e.g., Bierregaard 1990b, Lovejoy and Bierregaard 1990), these local disturbances are within an area of unbroken forest that extends for hundreds of km. Here we include data from five fragments of one ha, four fragments of 10 ha, two fragments of 100 ha, and continuous forest. Continuous forest data include the fragments before they were isolated by cutting the surrounding forest, and five sites that have not been isolated. The greatest distance between sites is about 60 km.

The forest is characterized by an average canopy height of 30–35 m with occasional emergents that reach up to 55 m. The understory is relatively open and dominated by palms. Density of fertile understory plants is low compared to other neotropical sites, probably because of poor soils (Gentry and Emmons 1987; see a more complete description of the study area in Lovejoy and Bierregaard 1990). Rainfall at Reserva Ducke, 50 km south of the study site, averaged about 2.5 m/year from 1966 to 1990, with annual peaks from January to April (see also RESULTS; rainfall data courtesy of the Departamento de Climatologia of INPA).

Results presented here are based on a netting and banding program that began in 1979. All nets were NEBBA-type ATX (36 mm mesh, 12 × 2 m). A larger mesh would be more efficient for quail-doves, but since we used the same net size at all times, this does not bias our results. A total of over 55 transects of 100 m (8 nets), 200 m (16 nets), or 400 m (30 nets) were netted for one day at a time (06:00 to 14:00) at various intervals (see Bierregaard 1990a for more details). Although interspecific differences in abundance based on mist net capture data must be viewed cautiously (see discussion in Karr 1981, Remsen and Parker 1983), we consider the technique effective for determining abundance of *Geotrygon montana* based on our knowledge of the bird's behavior (see also INTRODUCTION).

For most analyses we lumped captures and net-hours for three month periods ("quarters" hereafter) that correspond to rainfall seasonality. Capture rate was distributed bimodally across fragment sizes because of the low number of captures in one ha fragments and frequent absences from larger reserves, so we analyzed fragment size effects using a non-parametric test for randomized blocks (Sokal and Rohlf 1981:446). We counted each quarter with samples from the three fragment sizes and continuous forest as a block, thus controlling for variation among quarters and years. We analyzed relationships among rainfall, mass, and abundance using Spearman rank correlation. Mass data did not violate assumptions of parametric analyses, allowing us to estimate the variance in mass due to variation among years using a model II ANOVA (Sokal and Rohlf 1981:205). We provide details on other tests as they are used.

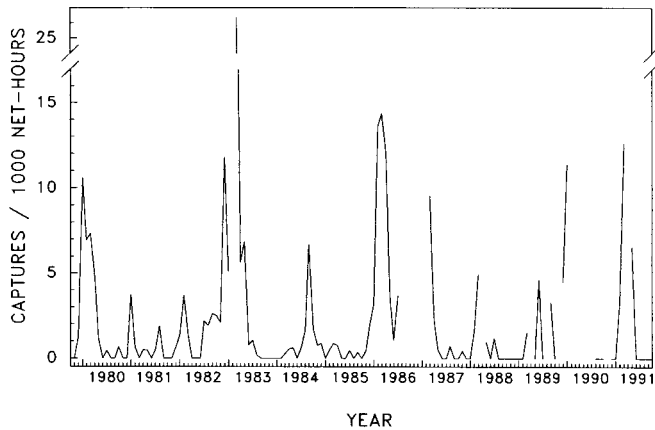


FIGURE 1. Monthly capture rate of *Geotrygon montana* from October 1979 to October 1991, excluding same-day recaptures. This figure only includes months with >200 net-hours, so gaps in the line represent periods with reduced sampling (e.g., late 1986 and early 1990).

RESULTS

CAPTURE RATE

A total of 457 captures of quail-doves (excluding same day recaptures) were recorded in 239,000 net-hr between October 1979 and October 1991 (Fig. 1). Runs tests for the two longest periods of uninterrupted data, November 1979 through January 1983 and March 1983 to July 1986 showed significant variation in capture rates (both $P < 0.005$). In general, the times of highest quail-dove abundance were January through April, although peak capture rate varied from <4 to >19 captures/1,000 net-hr (Figs. 1, 2). During capture

peaks the abundance of quail-doves relative to other understory birds became quite high; quail-doves were the most frequently netted bird in March 1983 (10.6% of captures) and in March 1986 (8.3% of captures), and they were the second most commonly netted species in several other months. In most years no or very few quail-doves were captured between June and November. There were some irregularities in this pattern, however. Quail-doves were present from June 1982 through July 1983, after which there were almost no captures until August 1984. A striking feature of quail-dove captures was an absolute lack of recaptures across years—only

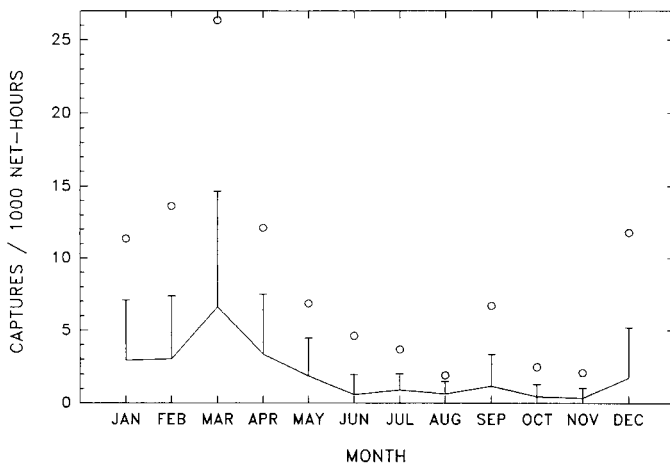


FIGURE 2. Monthly mean capture rate +SD. Also shown is the maximum for each month. All months had a minimum capture rate of zero.

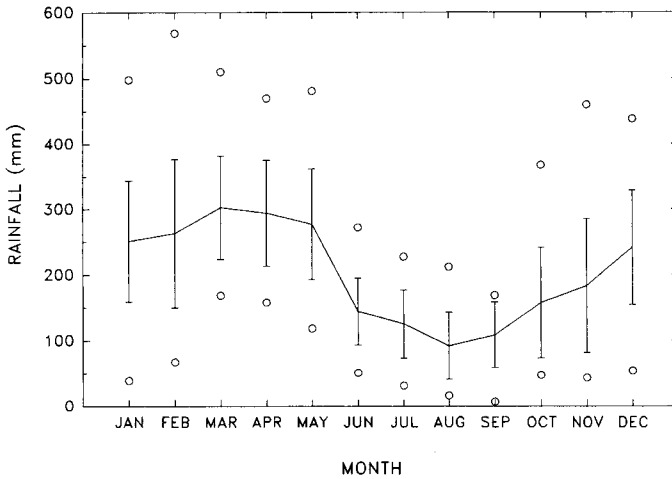


FIGURE 3. Monthly rainfall \pm SD at Reserva Ducke from 1965–1991. Also shown is the minimum and maximum for each month.

nine quail-doves were recaptured, none more than five weeks after it was first banded.

CAPTURE RATE AND FRAGMENT SIZE

To analyze fragment size effects we lumped captures by quarters based on rainfall (Fig. 3: early wet season, Dec–Feb; late wet season, Mar–May; early dry season, June–Aug; and late dry season, Sept–Nov). For 26 quarters with data from all size classes, one ha fragments had lower capture rates than larger fragments and continuous forest (Table 1, $\chi^2 = 13.035$, $df = 3$, $P < 0.005$), but there was no difference among fragments of 10 ha, 100 ha, and continuous forest ($\chi^2 = 0.122$, $df = 2$, $P > 0.9$). Hereafter in analyses based on capture rate, we exclude captures and net-hours from one ha reserves.

RAINFALL AND CAPTURE RATE

Rainfall data from Reserva Ducke show the wettest months to be December through May (Fig. 3). March through May were the most consistently wet months; in some years almost no rain fell earlier in the wet season, from December through February. June through September were the driest months, with the lowest among-year variation. Among-year variation was pronounced in October and November, as the rains came in some years but the dry season continued in others. In general, capture rate and rainfall were positively correlated (Spearman rank correlation of monthly means: $r = 0.755$, $P = 0.0045$).

Despite the clear relationship between mean

capture rate and mean rainfall for all years combined (Figs. 2, 3), rainfall and capture rate were not correlated when the data were examined quarter by quarter for the entire period (Fig. 4a, $r = 0.160$, $P = 0.283$). Rainfall in the same quarter one year previous was significantly correlated with capture rate, however (Fig. 4b, $r = 0.369$, $P = 0.011$). This relationship was especially close from 1979 to 1983. Capture rate was not related to capture rate one year before ($r = 0.274$, $P = 0.124$), which suggests that abundance cycles were not due to population cycles.

CONDITION AND CAPTURE RATE

Male and female quail-doves differed in mass (ANOVA $P = 0.0014$), and both sexes showed substantial variation (adult males: $\bar{x} = 115.6$ g, $SD = 15.7$, range = 70–165 g, $n = 169$; adult females: $\bar{x} = 111.4$ g, $SD = 16.5$, range = 74–170 g, $n = 154$). We used quarterly mean mass to examine the relationships between quail-dove abundance and mass and between rainfall and

TABLE 1. Quail-dove captures in forest fragments and in continuous forest. Capture rates followed by the same letter do not differ.

Reserve size (ha)	Number of captures	Number of net-hours	Capture rate/1,000 net-hr
1	6	13,400	0.448 A
10	41	27,940	1.467 B
100	39	21,970	1.775 B
≥ 100	330	201,800	1.635 B

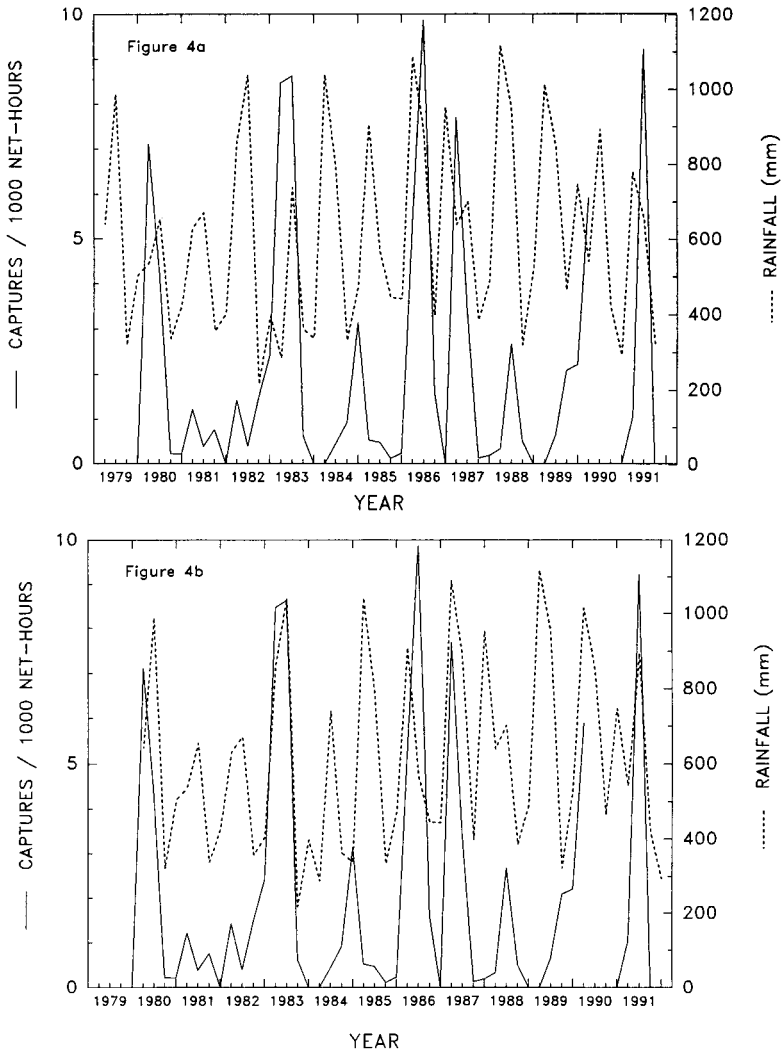


FIGURE 4. Quarterly capture rate and quarterly rainfall (a). Quarterly capture rate and rainfall in the same quarter in the previous year (b).

mass. After adjusting for sexual dimorphism, quarterly mean mass was not significantly correlated with abundance or rainfall, although the positive relationship between capture rate and mass approached significance (capture rate: $r = 0.320, P = 0.053$; rainfall: $r = -0.115, P = 0.498$; rainfall in the same quarter one year before: $r = -0.107, P = 0.530$). Mass varied significantly among years ($F = 2.13, P = 0.0408$), but inter-annual variation accounted for only 3.4% of mass variation.

DISCUSSION
ABUNDANCE PATTERNS

Analysis of abundance data clearly indicated that quail-doves avoided one hectare fragments but did not discriminate among larger fragments and continuous forest (Table 1). This result was also suggested by the capture data presented in Bierregaard and Lovejoy (1989). Canopy fruit production is probably lowest per unit area in one hectare reserves because many large trees die or

blow over. Also, most accounts of *Geotrygon montana* suggest that it prefers areas of closed forest to edges and treefall gaps (e.g., Skutch 1949), as was quantitatively shown for *G. veraguensis* in Costa Rica (Levey 1988b). One hectare fragments are hotter and drier than larger fragments (Kapos 1989) and thus may be microclimatically unsuitable for *G. montana*, which has been shown to prefer wetter sites in a heterogeneous forest in Panama (Karr and Freemark 1983).

Since quail-doves recolonized larger fragments, their absence from one hectare fragments was due to active avoidance of these habitat patches, a different process than that which leads to long-term absence of other understory birds from fragments. Obligate ant-followers and some species that typically forage in mixed-species flocks are also especially vulnerable to fragmentation (Bierregaard and Lovejoy 1989). These species quickly leave fragments after isolation (Bierregaard and Lovejoy 1989), and do not recolonize fragments that remain isolated. Absence from isolated fragments appears to be due to the unwillingness of these species to cross open areas. Most of these species become more likely to reappear in fragments (although they do not necessarily persist) as the secondary growth that connects fragments to continuous forest becomes taller (P. C. Stouffer and R. O. Bierregaard, unpubl. data). Other forest species that use edges and secondary growth persist even in one ha fragments (Bierregaard and Lovejoy 1989). Canopy species that readily cross open areas, such as pigeons, parrots, oropendolas, and some toucans and tanagers, also use fragments (pers. observ.).

Capture data also clearly showed a relationship between quail-dove abundance and rainfall. As was previously noted by Bierregaard (1989a) and by Tostain (1989) in French Guiana, quail-doves were most abundant during the wet season. Quail-doves responded not to rain directly, but with a time lag of one year (Fig. 4). Since quail-dove abundance is not linked directly to rainfall, quail-dove appearances and disappearances were not a response to physiological stress (*sensu* Karr and Freemark 1983). Data from other neotropical forests show that canopy fruits are most abundant in the late dry season or wet season (e.g., Frankie et al. 1974; Terborgh 1983, Ch. 2; see summary of data from Barro Colorado Island, Panama and La Selva, Costa Rica in Levey et al., in press). At Reserva Ducke a sample of 81

individuals of 27 species of canopy tree showed highest fruit production between September and May, after a flowering peak from July to September (Alencar et al. 1979). Presumably fruit production is determined by rainfall before the period of flowering and fruit maturation, accounting for the time lag between rainfall and quail-dove appearances.

Studies of tropical birds have not addressed multi-year patterns in fruit and fruit-eating bird abundance, but the relationship between bird density and food availability across years has been examined for sparrows in arid areas of the western US, where overwintering birds eat seeds produced the summer before. Summer rainfall influences seed production (Pulliam and Brand 1975), and correlates with sparrow abundance in southeastern Arizona (Dunning and Brown 1982). An alternative explanation for the time lag in quail-dove response to rainfall is that abundance in Manaus correlates with reproductive success of the population the year before, which in turn relates to rainfall during the period of reproduction. Unfortunately, this hypothesis is difficult to consider because of the lack of recapture data.

Patterns of quail-dove abundance were not related to regular movements by individual birds or to population cycles. No birds were captured in two different years; even though quail-doves bred successfully on the site, we know of no adults or juveniles that returned to the area. Thus individual quail-doves were not making predictable movements, such as returning to a breeding site. This low recapture rate contrasts markedly with most understory species at the site. On regularly netted lines in continuous forest the overall recapture rate for all species was about 40% (Bierregaard 1990a).

Finally, capture rate and rainfall did not significantly affect mass. If anything, there may be a positive relationship between capture rate and mass. Variation in mass was mostly due to intra-quarterly differences rather than variation among quarters or years.

POSSIBLE MOVEMENT PATTERNS

Although it is clear that quail-doves disappear from the Manaus area, the extent and direction of their movements are unknown. We doubt that quail-doves simply move from *terra firme* forest into *várzea* or *igapó* forest along watercourses, since they have not been recorded from those

habitats around Manaus. Regional variation in phenology has not been studied, but rainfall data suggest that latitudinal movements from Manaus to the north would allow quail-doves to most easily track changes in fruit resources. Rainfall patterns shift most dramatically to the north of Manaus. In Roraima, about 800 km to the north, rainfall seasonality is the reverse of that in Manaus (SUDAM 1984). D. Stotz (pers. comm.) has observed quail-doves there in September, during Roraima's wet season, but not in March, during Roraima's dry season. Rainfall patterns differ little to the east and west of Manaus, and seasonality changes much more gradually to the south (SUDAM 1984).

Because it has a large range without subspecific variation, *G. montana* appears to be predisposed to making movements without regard for geographical barriers (see discussion in Bierregaard 1990a). Indeed, quail-doves move between Caribbean islands (Robertson and Given 1980). This contrasts markedly with many Amazonian understory birds, which differ at the species or subspecies level across most major rivers (see discussion in Haffer 1985).

An exception to the typical pattern of quail-dove abundance occurred in 1984 and, to a lesser extent, 1985 (Fig. 1). This may have been related to an *El Niño* event in 1983, which dramatically altered rainfall patterns in parts of the neotropics. The 1983 *El Niño* strongly affected rainfall around Manaus, but only for three months. It may have also altered phenology and fruit production elsewhere in the range of the Manaus quail-dove population. Thus quail-dove abundance may reflect not only local availability of food, but also the availability in other parts of the population's range. A similar relationship was proposed by Pulliam and Parker (1979) to account for variation in winter sparrow abundance in the deserts of the southwestern US.

Other birds that feed on canopy fruits have been suspected of making seasonal movements near Manaus, but abundance of these birds is difficult to quantify. Willis (1977) reported seasonal variation of *Amazona autumnalis* at Reserva Ducke, which we also suspect for *A. fari-nosa* at our site (pers. observ.). *Ramphastos* toucans, including many individuals in very poor condition, invaded Manaus from the south in great numbers in 1990 (T. M. Sanaiotti and R. Frola, pers. comm.). Presumably this invasion was the result of failure of some key food plant.

We suspect that *G. montana* is rarely forced to make such desperate movements, since we found little variation in condition among years. The relatively high variation in quail-dove mass may reflect an ability to store fat during times of food abundance or before moving to another area.

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