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### Intra-annual variations in abundance of Collared Plover *Charadrius collaris* in coastal French Guiana: the potential influence of rainfall, interspecific competition and breeding activities

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The Collared Plover Charadrius collaris is a year-round resident in the Neotropics, mainly associated with inland habitats but regularly inhabiting seashores. Abundance patterns of some coastal populations in Brazil vary throughout the year indicating seasonal movements. Variability of food resources, seasonal competition with Nearctic migrants, and breeding activity are suspected reasons for these movements. Along the coast of French Guiana, the species is regularly observed on sandy beaches, but no monitoring had ever been conducted on these populations. We investigated intra-annual variations in abundance of Collared Plovers in the Kourou River estuary, French Guiana during 2004–2008. Along three sandy beaches near the city of Kourou, we counted Collared Plovers and the two most abundant Nearctic migrants, Sanderlings Calidris alba and Red Knots Calidris canutus. While conducting censuses we looked for evidence of breeding activity and extracted all local data available from the French Guiana wildlife database. Collared Plovers were found on sandy beaches from December to August, with a peak during the short dry season (mid-Feb-mid-Apr) that coincided with low abundances of Nearctic migrants. During the long dry season (Aug-Nov), plovers almost disappeared from sandy beaches, coinciding with the period of greatest abundance of Nearctic migrants, but also with the period of increased availability of suitable inland habitat. Periods of moderate abundance of both plovers and Nearctic migrants occurred during the two rainy seasons, which coincided with breeding activity of Collared Plovers being reported at inland habitats. Our data indicate that intra-annual abundance of Collared Plovers on the coast of French Guiana varies with rainfall patterns. Breeding activity in inland habitats and competition with Nearctic migrants may influence the observed abundance patterns in coastal areas, meriting further investigation.

#### Keywords

short-distance movements distribution change sandy beach Nearctic shorebird migration Neotropics

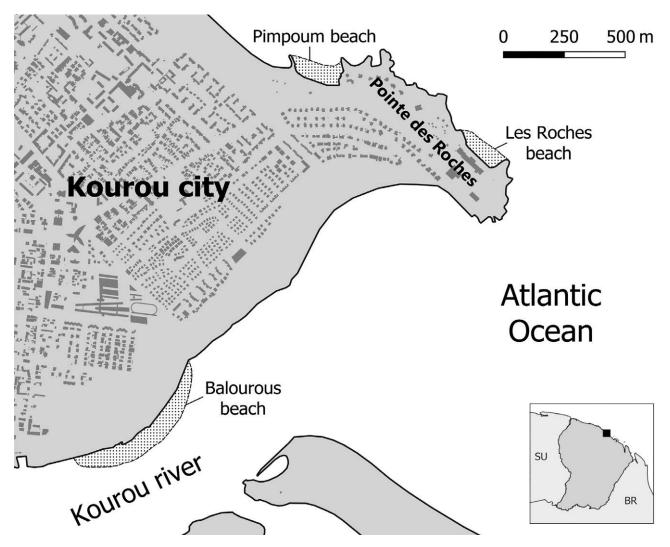
#### INTRODUCTION

In the Neotropics, some resident bird species perform periodic short-distance movements between habitats, resulting in local intra-annual variations in abundance. Such movements may be related to seasonal changes in the environment (Martin & Karr 1986, Poulin *et al.* 1993). For example, rainfall patterns can drive habitat use by influencing food and habitat availability (Hayes & Fox 1991, Canepuccia *et al.* 2007, Macías-Duarte *et al.* 2009, Boyle 2011). Birds may also move to and from suitable breeding habitats (Poulin *et al.* 1993). Moreover, an influx of migrants may generate interspecific competition for critical resources (Greenberg *et al.* 1994, Powell *et al.* 2021). Therefore, behavioral segregation such as shifts in territorial behavior and habitat use could be important to minimize interspecific competition (Recher 1966, Waide 1981, Jedlicka *et al.* 2006, Bensusan *et al.* 2011).

The Collared Plover *Charadrius collaris* is a widespread resident shorebird in the Neotropics, distributed from Mexico to central Argentina and Chile, and in the southern Lesser Antilles. The species uses a wide range of wetland habitats, including beaches, sand spits, estuary mudflats, riverbanks, inland marshes, and open sandy savannas (Hayman *et al.* 1986) and is mainly found inland, although some populations are coastal (Hilty 2003, Restall 2007). On the Atlantic coast of South America, the species is known to use open sandy beaches, sand dunes, and muddy lagoons (Spaans 2003, Alfaro *et al.* 2008, Almeida & Rodrigues 2015). Coastal populations feed on polychaetes, bivalves, and crustaceans in the inter-tidal zone (Kober & Bairlein 2006).

Although generally considered to be a sedentary species (Hayman *et al.* 1986), there have been indications of seasonal movements (Canevari *et al.* 2001). On the shores of Brazil, Collared Plovers showed seasonal variations in abundance, with different patterns depending on latitude and habitat type (Vooren & Chiaradia 1990, Barbieri & Mendonça 2005, Cabral *et al.* 2006, Almeida & Rodrigues 2015). It has been hypothesized that such variations may be linked to competition for space and food with migrating Nearctic shorebirds (Sick 1997) or to seasonal variations in the availability of some inland habitats for breeding and foraging (Resende & Leeuwenberg 1987, Rodrigues & Lopes 1997).

Along the French Guiana coast, Collared Plovers are regularly observed on beaches, backshore open areas, and estuaries (Groupe d'Etude et de Protection des Oiseaux en Guyane [GEPOG] unpubl. data), but they have not been monitored. Patterns of occupancy and use of coastal habitats, as well as breeding activity, along the Guiana coast are poorly documented. Only Renssen (1974) and



**Fig. 1**. Map of the study area in the Kourou River estuary, French Guiana. Stippled areas indicate the sandy beaches where birds were counted. The inset shows the location of the study area within French Guiana (dark grey) and the bordering countries Suriname (SU) and Brazil (BR).

Spaans (2003) observed nests during the long rainy season (Apr–Aug) on the coast of neighboring Suriname. Therefore, we assessed the seasonal changes in the abundance of Collared Plover coastal populations of French Guiana and determined the possible causes of the observed variations by focusing on fluctuations in environmental conditions and breeding behavior.

#### **METHODS**

The study area was located on the estuary of the Kourou River (5°10'N, 52°40'W), near Kourou city, French Guiana (Fig. 1). It comprised different shoreline types that provide resting and feeding areas for many shorebird species: rocky shores, sandy beaches, and mudflats. Because of its accessibility and diversity of habitats, the site represents one of the best areas to monitor shorebirds in French Guiana, and Collared Plovers are commonly observed there. We focused on three sandy beaches (Fig. 1). Balourous beach is located along the mouth of the Kourou River and is 700 m long and 30 m wide on average. This beach is backed by White Mangroves Laguncularia racemosa and has a soft mudflat along the river. The limited upper part of the beach is colonized by rare psammophilous creepers such as Bayhops Ipomea pes-caprae. It has a slight slope, is partially covered with organic debris up to the high tide line, and is almost totally submerged at high tide. Les Roches beach and Pimpoum beach are on the north side of Pointe des Roches, an urbanized peninsula. These beaches extend over 160 m and 320 m respectively, with an average width of 30 m. They are edged by rocky outcrops and mudflats. Except for some psammophilous creepers and palm tree plantations on their higher reaches, there is no vegetation covering them and they are only partially submerged at high tide.

Collared Plovers were counted at low tide with a telescope  $(20-60 \times 85 \text{ mm})$  approximately once every 10 days during three periods: February–September 2004, October 2005–October 2006, and July 2007–July 2008. As Sanderling *Calidris alba* and Red Knot *C. canutus* are the main migrating Nearctic shorebirds using sandy beaches in French Guiana (unpubl. data), they were counted at the same time. On Balourous beach, censuses were conducted from two points 350 m apart. As we walked between the two points along the inland edge of the beach, we noted any movement of birds from the first to the second part of the

beach to avoid double-counting. Les Roches and Pimpoum beaches were each counted from a single central point located on the inland edge. Any breeding behaviour was also recorded. In addition, all data available on nests or any other indications of breeding activities of Collared Plover in and around Kourou city to the end of 2022 were extracted from the 'Faune Guyane' database (GEPOG unpubl. data).

An analysis of intra-annual variations in abundance was performed using the monthly means of all counts. Mean abundance was calculated for each month given that this minimizes variance problems associated with repeated measures within a month (Hurlbert 1984). We also compared abundance between dry and rainy seasons: short rainy season (Dec-mid-Feb), short dry season (mid-Feb-mid-Apr), long rainy season (mid-Apr-July) and long dry season (Aug-Nov). Kruskal-Wallis tests were used to test for significant differences ( $\alpha = 0.05$ ) in median abundances among seasons. Post-hoc comparisons were conducted using the Mann-Whitney *U*-test.

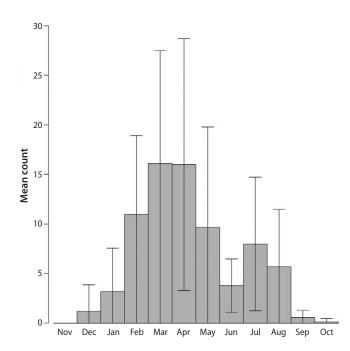
To test the relationship between Collared Plover and Nearctic shorebird abundances, we performed a regression analysis. As preliminary examination of plots suggested that abundances did not follow linear trajectories, they were analyzed by fitting a polynomial regression. A best-fitting polynomial model was identified using five degrees (h = 1-5) of polynomials to fit and *K*fold cross validation with k = 10 folds to calculate the mean squared errors for each model (Ostertagová 2012, Chatterjee & Simonoff 2020). Both variables were log(1+x) transformed to achieve normality and homoscedasticity of residuals. All statistical tests and figures were performed using R v.4.2 (R Development Core Team 2022).

#### RESULTS

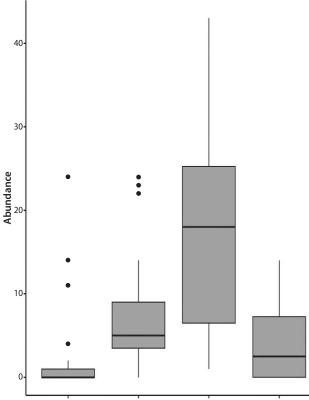
Collared Plovers were present in the Kourou River estuary from December to August, but were virtually absent from September to November (Fig. 2). From December and January, abundance gradually increased to a peak in March and April (mean = 16, SD = 14 individuals in both months) with a maximum count in April 2004 of 43 individuals. The population then declined rapidly until June (mean = 4, SD = 2 individuals), increased in July and August, but did not reach the numbers seen in March and April (Fig. 2).

**Table 1.** Observations of breeding evidence for Collared Plovers in the Kourou region between 1980 and 2022. Data extracted from Faune Guyane database.

Date	Place	Habitat	Latitude	Longitude	Observations
7 Mar 2007	Savane Guatemala	Savannah/grassland	05°07′31.28″N	52°36′44.51″W	Juvenile
12 May 2012	Pointe des Roches	Sandy beach	05°09′36.45″N	52°37′33.65″W	Adults with immatures
5 May 2014	Guiana Space Center	Artifical open sandy area	05°09′59.90″N	52°41′2.56″W	Adults with chicks
7 Jul 2021	Guiana Space Center	Artifical open sandy area	05°15′48.29″N	52°47′29.45″W	Adult with chick-rearing behavior

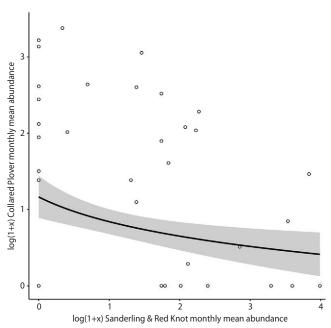


**Fig. 2**. Mean monthly counts (±SD) of Collared Plovers *Charadrius collaris* at the Kourou River estuary, French Guiana, during February–September 2004, October 2005– October 2006, and July 2007–July 2008 (data for month is of all years combined).



Long dry season Long rainy season Short dry season Short rainy season

**Fig. 3**. Abundance of Collared Plovers *Charadrius collaris* in the Kourou River estuary, French Guiana, according to season. The box plots show the medians (thick horizontal line), interquartile ranges (box), ranges (whiskers), and outliers (dots) of abundances per count for each season during February–September 2004, October 2005–October 2006, and July 2007–July 2008.



**Fig. 4**. Predicted monthly mean abundance (heavy line) and 95% CI (shaded area) of Collared Plover *Charadrius collaris* in relation to Sanderling *Calidris alba* and Red Knot *C. canutus* combined monthly mean abundance (open circles) at the Kourou River estuary, French Guiana.

Abundance differed among seasons (Kruskal-Wallis test,  $\chi^2 = 33.7$ , df = 3, P < 0.001). It was highest during the short dry season (median = 18; 95% Confidence Interval [CI] = 9–26 individuals) and lowest during the long dry season (median = 0, 95% CI = 0–12 individuals). Both were significantly different from the two rainy seasons (Fig. 3). The short rainy season and the long rainy season had intermediate abundances and did not differ from each other (Mann-Whitney *U*-test, z = -1.85, P = 0.064).

Sanderlings and Red Knots arrived in late August and reached their maximum abundance between September and November, with peak dates varying among years (peaks ranged between 39 and 56 individuals for both species combined). Their abundance then generally decreased, but we noted groups of birds in January (up to 34 individuals) and May (up to 79 individuals) 2006. Similar peaks were also observed in 2008, although to a much lesser extent. The comparison of monthly mean abundances between Collared Plover and the two Nearctic shorebirds indicated a moderate negative relationship ( $R^2 = 0.3$ , P < 0.001). Collared Plovers were most numerous when Sanderlings and Red Knots were absent or very few, but their numbers decreased when the abundance of Sanderlings and Red Knots increased (Fig. 4).

We found no evidence of breeding during our surveys and there are only four instances of breeding evidence reported in and around Kourou city in the 'Faune Guyane' database. No nests were reported, but chicks and adults with chick-rearing behavior ('broken wing' display) were observed in May 2014 and July 2021 on sandy open areas of the Guiana Space Center (~3 km from the coast). Additionally, a juvenile was reported in a backshore grassland in early March 2007, and a group of immatures was noted in May 2012 on a sandy beach (Table 1).

#### DISCUSSION

Our study provides new knowledge on the ecology of a poorly known Neotropical shorebird species. Previously, abundance data for Collared Plover on the coast have only been published for some sites in Brazil (e.g., Barbieri & Voietta Pinna 2005, Cabral et al. 2006, Almeida & Rodrigues 2015). On the coast of French Guiana, we observed wide fluctuations in the numbers of Collared Plovers throughout the year, with peaks in March and April, an absence from September to November and few birds outside of these two periods. The lowest abundance occurred during the long dry season, whereas high abundance largely corresponded to the short dry season. In northern Brazil, where there is no short dry season, Collared Plovers also tended to be absent from the beaches during the dry season (Rodrigues & Lopes 1997, Almeida & Rodrigues 2015). Further south, where the climate is not equatorial, they reach maximum abundances during the drier seasons (Barbieri & Mendonça 2005, Barbieri & Hvenegaard 2008, Scherer & Petry 2012).

Patterns of occurrence seem to be related to local rainfall and preferential conditions appear to change with latitude and climate. In South America, rainfall increases wetland water surface and reduces riparian habitat and habitat diversity, thus reducing habitat availability for shorebirds (Hayes & Fox 1991, Canepuccia et al. 2007), whereas food resources, such as meiofauna, may increase in estuarine beaches such as our study site (Baia et al. 2021, Checon et al. 2023). By contrast, low water in rivers and inland wetlands during the dry season, provide suitable habitats and food resources for shorebirds (Rodrigues & Lopes 1997, Almeida & Rodrigues 2015). In French Guiana, the short dry season is characterized by variable repetitions of dry periods lasting a few days interspersed by rainier periods, unlike the long dry season which is more continuous and drier (see *https://meteofrance.gf/fr/climat*). During the short dry season, food resources on the beaches may be sufficient to support shorebirds when most inland habitats are still flooded or difficult to access. However, to date no information is available to confirm this.

Sick (1997) assumed that Collared Plovers stop feeding on beaches when large numbers of Nearctic shorebirds arrive and compete for food resources. As migrants may have less opportunity to shift their behavior and habitat use to avoid overlap with residents (Bensusan *et al.* 2011), residents would need to alter their ecology to reduce interspecific competition (Keast & Morten 1980, Jedlicka *et al.* 2006). In French Guiana, Sanderlings and Red Knots mainly use sandy beaches to forage during migration (unpubl. data). In northern Brazil, Red Knots mainly feed on large bivalves and snails whilst Sanderlings and

Collared Plovers are more specialized on bivalves and polychaetes (Kober & Bairlein 2006). As the diet of Collared Plovers seems to overlap to some extent with that of Sanderlings, they may compete for food. We noted that Collared Plover abundance is moderately and negatively correlated with the Sanderlings and Knots. Collared Plovers reach their lowest abundance when Nearctic shorebirds arrive in large numbers during southward migration in the long dry season, and few are present when moderate numbers of Nearctic shorebirds use the area during the non-breeding season and northward migration. However, the low abundance between June and August cannot be explained by interspecific competition with Nearctic shorebirds. All along the Atlantic coast of South America, maximum Sanderling and Red Knot abundance seems to match with the periods of absence or low abundance of Collared Plovers (Rodrigues 2000, Scherer & Petry 2012, Roselli & Barbieri 2022) but also with their breeding season (Resende & Leeuwenberg 1987, Barbieri 2007). So, this observed correlation is probably not the result of food competition.

The inconspicuous behavior of this species makes courtship and nesting behavior difficult to observe. Inland populations are known to nest on exposed sandbanks in rivers during the dry season, from January to April in Venezuela (Navarro et al. 2011) and in January in Argentina (Maugueri 2005). In French Guiana, nesting habitat and season for inland populations are unknown. Coastal populations were found breeding in backshore wetlands, grasslands, dunes, and lagoons, from January to June in Colombia (Ruiz-Guerra & Cifuentes-Sarmiento 2013), from June to July in Suriname (Renssen 1974, Spaans 2003), from May to June in northern Brazil (Rodrigues & Lopes 1997), from November to January in southern Brazil (Resende & Leeuwenberg 1987, Vooren & Chiaradia 1990, Barbieri 2007), and from November to February in Uruguay (Alfaro et al. 2008). At our study site, no nesting birds or chicks were found. Nesting apparently takes place inland, during the period of absence or low abundance on the beaches. The few observations collected in Kourou indicated that the breeding period on the coastal strip could extend at least during the two rainy seasons. This is consistent with the observations for Suriname and northern Brazil. Adjustment of reproduction with the rainy seasons is a common pattern in tropical birds (Marchant 1960, Stutchbury & Morton 2001), and this adjustment may lead to biannual breeding activities where there are two rainy seasons (Miller 1962, Wilkinson 1983). Thus, the few plovers observed feeding on the beach throughout the rainy seasons would likely be non-breeders or off-duty breeders, as breeding pairs share incubation duties (Ruiz-Guerra & Cifuentes-Sarmiento 2013). Chicks and suspected broods were found in welldrained open areas and juveniles in grasslands. In precocial bird species, like shorebirds, the parent(s) may lead their downy chicks away from the nest to broodrearing habitats where they can obtain more food and/or better protection from predators until they attain full independence (Loegering & Fraser 1995, Kosztolányi et

*al.* 2007). We assume that Collared Plovers in coastal French Guiana prefer to nest in open uplands and rear their broods in more vegetated habitats, where they probably find more food and protection than on beaches.

In summary, Collared Plovers use sandy beaches to forage when suitable habitats and food availability would be higher than inland due to rainfall and possibly when competition for food with Nearctic shorebirds is reduced. They likely move to inland habitats during the rainy seasons to breed. Nevertheless, Collared Plovers observed on the beaches may also be birds from more inland populations moving from flooded habitats to the coast during rainy seasons and returning inland at the beginning of the long dry season to breed. Deployment of GPS devices on some individuals, coupled with a diet survey and assessment of beach food availabilities throughout the year, would be needed to confirm our statements and gain a better understanding of the ecology of Collared Plovers in French Guiana.

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