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SITE-FIDELITY OF THE NORTHERN WATERTHRUSH (*PARKESIA NOVEBORACENSIS)* AND THE YELLOW WARBLER (*SETOPHAGA PETECHIA*) IN JAMAICAN MANGROVES: COMPARING BANDING DATA FROM A MIGRANT AND A RESIDENT SPECIES

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Abstract · Between September 1999 and January 2002, a banding study was conducted at standardized mist net locations in coastal mangroves in south-central Jamaica (Two Sisters, in the Portland Bight Protected Area). Captures included 427 birds of 31 species, resulting in 183 local recaptures of banded birds and no foreign recaptures. Two Parulidae species dominated the captures, including the winter resident Nearctic migrant Northern Waterthrush (*Parkesia noveboracensis*), with 183 individuals banded, and the resident Yellow Warbler (*Setophaga petechia*), with 45 individuals banded. The data on phenology and philopatry within and between years were compared for the two species. A quarter (25%, N = 45) of all banded Northern Waterthrushes was recaptured on average 1.6 times, and almost half (47%, N = 21) of all banded Yellow Warblers were recaptured on average 3 times during this study. Captures of Northern Waterthrushes peaked during migration season (i.e., in September, October, and March) and were absent from mid-May to mid-August. Altogether, almost 18% of Yellow warblers were recaptured again during the following winter, in contrast to only 3–4% of the marked Northern Waterthrushes.

Resumen · Filopatría de la reinita charquera norteña (*Parkesia noveboracensis*) y la reinita de manglar (*Setophaga petechia*) en manglares de Jamaica: comparación de datos de anillado para una especie migratoria y una residente.
Entre septiembre de 1999 y enero de 2002 se condujo un estudio de anillado, usando redes de niebla, en sitios de captura estandarizados de manglares costeros del centro-sur de Jamaica (Two Sisters, en el área protegida Portland Bight). Se capturaron 427 individuos de 31 especies, que resultaron en 183 recapturas de aves anilladas localmente, mientras que no hubo recapturas de individuos anillados en otros sitios. Dos especies de la familia Parulidae dominaron las capturas: el migrante neártico *Parkesia noveboracensis*, con 183 individuos anillados, y la residente *Setophaga petechia,* con 45 individuos anillados. Con base en esto, comparamos la fenología y filopatría de ambas especies dentro y entre años. Una cuarta parte (25%, N = 45) de todos los individuos anillados de *Parkesia noveboracensis* fueron recapturados en promedio 1,6 veces, mientras que casi la mitad (47%, N = 21) de los individuos anillados de *Setophaga petechia* fueron recapturados en promedio 3 veces durante este estudio. Las capturas de *Parkesia noveboracensis* tuvieron su pico durante la temporada de migración (en Septiembre–octubre y marzo) y no hubo capturas entre la última mitad de mayo y la primera mitad de agosto. En total, casi el 18% de todos los *Setophaga petechia* anillados fueron recapturados el invierno siguiente, comparado con el 3–4% de los individuos de *Parkesia noveboracensis*.

Key words: Caribbean · Coastal wetland · Mist-netting · Phenology

INTRODUCTION

Mangrove ecosystems are found globally along tropical and subtropical coastlines, covering approximately 151,000 km^2 worldwide (Luther & Greenberg 2009). Most mangroves are home to two sets of avian inhabitants: resident species living there year-round and migratory species spending part or most of their non-breeding season in them. The species composition of the avian fauna has been studied in various mangrove habitats, e.g., in Guinea-Bissau (Altenburg & Van Spanje 1989, Zwarts et al. 2014), Singapore (Sodhi et al. 1997), Venezuela (Lefebvre et al. 1992, 1994), Costa Rica (Warkentin & Hernandez 1996, Woodcock & Woodcock 2007), Cuba (Wallace et al. 1996, Parada Isada et al. 2015), St. Croix, US Virgin Islands (McNair 2008), and Puerto Rico (Acevedo & Aide 2008, Gemmill 2015).

The family of New World Warblers (Parulidae) contains 122 species living exclusively in the Americas (del Hoyo & Collar 2016). Out of these, only two species breed in Jamaica: the resident subspecies of the Yellow Warbler (*Setophaga petechia eoa*) and the endemic Arrowhead Warbler (*Setophaga pharetra*). Among the Parulidae, two species have been identified as either being restricted to mangroves (i.e., the Yellow 'Mangrove' Warbler), or being dependent on mangrove habitats (i.e., the

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Northern Waterthrush (*Parkesia noveboracensis)* (Luther & Greenberg 2009). In Jamaica, the Yellow Warbler is a common resident in mangroves, as well as other wooded wetlands and cays, and nests close to the ground or in low canopy in mangroves and scrub forests (Haynes-Sutton et al. 2009). Some 23 other species of Parulidae frequently visit from their North American breeding grounds to winter in Jamaica. North American migrant warblers have been studied extensively in Jamaica using mist-netting and banding for several decades (e.g., by Diamond & Smith 1973, Diamond et al. 1977, Holmes & Sherry 1989, Holmes et al. 1989, Wunderle & Waide 1993; see also Latta et al. 2003 for a history of research). The overwintering habits of Northern Waterthrushes were studied in detail in other tropical mangrove localities, such as Trinidad, by Snow & Snow (1960) and especially Puerto Rico by Reitsma et al. (2002), Burson et al. (2005) and Smith et al. (2008, 2010, 2011). However, as for most tropical warbler species, baseline ecological data is lacking (Salgado-Ortiz et al. 2008).

The Northern Waterthrush is known to defend territories on its wintering grounds (Schwartz 1964, Greenberg 1988), which can lead to density-dependence in population regulation if habitat availability is limited (Rappole & Warner 1976, DeSante et al. 2015). Therefore, DeSante et al. (2015) recommend that the efforts to preserve diminishing mangrove habitats on its winter range should also be considered a high priority conservation strategy for this species. Besides numerous anthropogenic impacts on mangroves in the Caribbean, two natural factors can influence Waterthrush habitat quality on different temporal scales. A lack of precipitation can influence the water level, especially in brackish mangrove stands, over periods of weeks or months, whereas hurricanes may severely impact mangroves once every decade (or even less frequently, but the damage may endure for even longer periods). Mangroves increasingly suffer from various effects of a changing climate, including sea level rise, increased occurrence of severe weather events, and increased frequency of the most powerful hurricanes (Emanuel 2005, Neelin et al. 2006). A recent review emphasized the impacts of new drivers, in particular those resulting from global climate change and the expansion in aquaculture, on mangroves in the Caribbean and Latin America (Lacerda et al. 2019). Furthermore, detrimental effects limiting migrant populations on the wintering grounds can be exacerbated by factors limiting populations during migration and on the breeding grounds (e.g., Warkentin et al. 2003, Frantz et al. 2018).

During our 16-month study, we investigated the presence of the two warbler species common in mangrove habitats: a Nearctic-Neotropical migrant, the Northern Waterthrush, and the resident Yellow Warbler, as well as their differences in site-fidelity, in a Jamaican mangrove forest during the non-breeding season by documenting capture phenology and recaptures of these two warblers. In addition, we described the species composition of captures in the mangrove habitat. Our mark-recapture study allows inferences about the use of mangroves by the two species and hence, about its conservational value for these species.

METHODS

Study area The Portland Bight Protected Area (in Clarendon Parish) lies on the south coast of Jamaica, west of Kingston and south of Spanish Town and May Pen. Its total area is 1,896.2 km^2, of which 72.2% is sea and 27.8% land area, and it includes the longest contiguous mangrove coastline in Jamaica.

Four species of mangrove live in Jamaica and predominate the vegetation in the siltation zone: the Red Mangrove (*Rhizophora mangle*), the Black Mangrove (*Avicennia germinans*), the White Mangrove (*Laguncularia racemosa*), and the Button Mangrove (*Conocarpus erectus*), in order of their tolerance of salt water to frequent drying. The maximum tidal range in Old Harbour Bay (at the northern end of Portland Bight) measures ~30 cm. Seasonal changes in water levels are mostly due to precipitation.

The climate in the wetlands of Portland Bight is warm and humid. It is characterized by relatively low rainfall, a high but seasonal tropical temperature regime (20–31°C), high relative humidity (67-88%), and moderate winds. During the day, there is a sea breeze, mainly from the SE, with velocities up to 12 m/s. In the late afternoon, this tends to be replaced by a land breeze from the NW (Hendry 1983). The thirty-year average annual rainfall for West Portland Bight, in the center of the study area, varies between 886 mm and 1052 mm per year, with a bimodal seasonal pattern that is typical of Jamaica. The wettest months are from May to June and August to November, when rainfall exceeds evaporation (Chow 1989). The rainfall during the study period was atypical, however, with more rain than average in November 1999 and September 2000, and less from December 1999 to August 2000, including the absence of the May-June rains.

Mist-netting Our banding operation occurred in a large stand of fringe and basin mangroves at a site in West Harbour, known as Two Sisters (17° 46.987’ N/ 77° 12.771’ N), where 10 mist nets were operated. The position of pre-existing dyke roads at the study site facilitated the placement of nets in a standard pattern, with five nets in an unbroken line on an east-west dyke road, and other five on the adjacent north-south dyke. The nets included up to five 12 meter nets, three 20 meter nets and three 9 meter nets with a mesh size of 30 or 35 mm. The nets were operated for a minimum of six hours per day, between dawn and 13.00 h, except when they were closed early in response to rain or high winds. Netting sessions occurred approximately for 16 months, once every 14 days. Migratory birds were banded using United States Geological Survey bird bands, whereas year-round resident species were banded using private bands. The number of net hours was calculated as net-meter-hours to correct capture rates (per 100 net-meter*hours) for any variation in effort. Between September 1999 and November 2000, usually 130 m of nets were operated on 23 banding days, with 781.1 ± 111.41 ($\bar{X}$ ± SD) net-meter*hours per day. The total netting effort for these 23 days was 17,965 net-meter*hours.

When considering the three wintering seasons involved (i.e., 1999/2000, 2000/2001, and 2001/2002), it becomes apparent that the banding effort was spread unevenly, with 14, 4, and 1 banding day each winter respectively. Both warbler species were subjected to this uneven netting effort among winters so that comparisons between the recapture rates for the two species within this study were possible. However, direct comparisons of our recapture results with other published recapture rates for these two species, based on different

Table 2. Interseasonal recapture rates of Northern Waterthrushes (*Parkesia noveboracensis*) in Jamaican mangroves (number of banded individuals per banding day as catch per unit effort measured for each season).

	Banded in first winter season (Sep 1999 - May 2000) = 14 banding days	Banded in second winter season (Aug 2000 - Nov 2000) = 4 banding days	Banded in third winter season (Jan 2002) = 1 banding day
Total banded	138 (9.9 per banding day)	36 (9.0 per banding day)	9 (9.0 per banding day)
Recaptured in same season	38 (27.5%)	2 (5.6%)	n/a
Recaptured in following season	6 (4.3%)	1 (2.8%)	n/a
Recaptured in subsequent season	1 (0.7%)	n/a	n/a

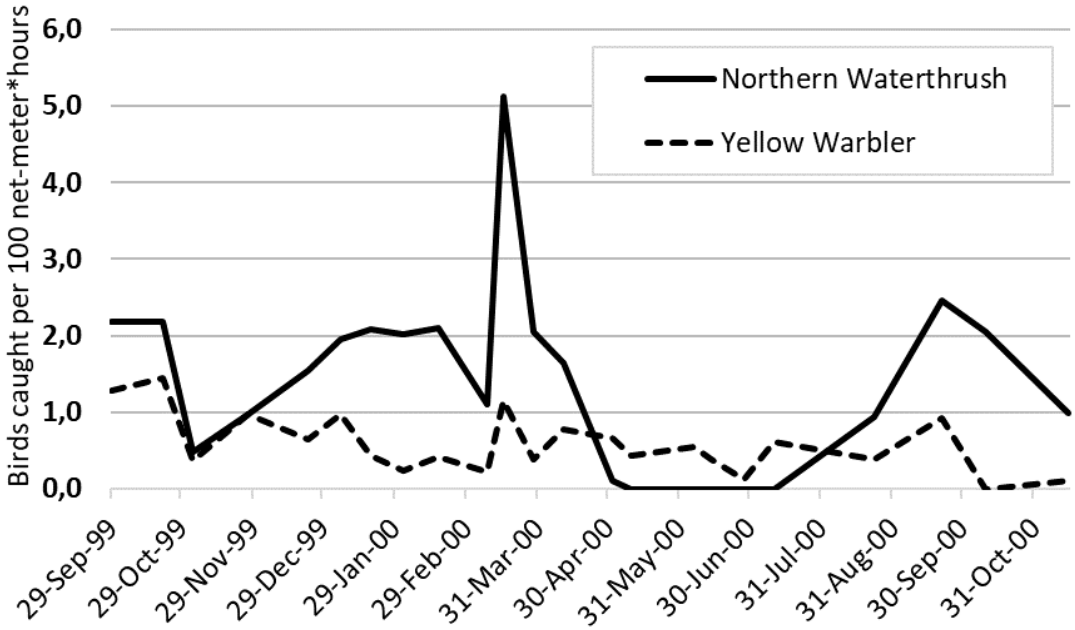

Figure 1. Effort-corrected capture rates of Northern Waterthrushes (*Parkesia noveboracensis*) and Yellow Warblers (*Setophaga petechia*) in Jamaican mangroves between September 1999 and November 2000.

netting efforts, may yield different results.

RESULTS

Species captured. During the 25 banding days over three winters between September 1999 and January 2002, a total of 427 individuals of 31 species were captured and banded (Supplementary Table 1). Of these species, the following Parulidae were most numerous: Northern Waterthrush (N = 183), American Redstart (*Setophaga ruticilla*; N = 48), and Yellow Warbler (N = 45). Other seven warbler species were captured less frequently, and together constituted the bulk of the migratory species. Because of their abundance, we concentrated our following analyses on the migrant Northern Waterthrush and the resident Yellow Warbler, which together accounted for 37% of all birds banded during this study.

Phenology. Overall, the two warbler species provided the most recaptures of any species, with 71 recaptures of 45 individual Northern Waterthrushes and 64 recaptures of 21 individual Yellow Warblers. This means that a quarter (25%) of all banded waterthrushes was recaptured on average 1.6 times, and almost half (47%) of all banded Yellow Warblers were recaptured on average 3 times during this study. Captures of Northern Waterthrushes peaked during migration (i.e., in September, October, and March) and were absent from mid-May to mid-August; overall, $\bar{X}$ = 1.34 captures per 100 net-meter*hours, from Sep 1999 until Nov 2000, or $\bar{X}$ = 1.62 captures per 100 net-meter*hours, excluding June and July, when waterthrushes were absent. Yellow Warblers were captured at a lower rate of $\bar{X}$ = 0.57 captures per 100 net-meter*hours (Figure 1).

Out of the 46 Northern Waterthrushes banded in 1999, 26 individuals (57%) were recaptured on average 1.8 times, whereas among the 127 Northern Waterthrushes banded in 2000, only 19 individuals (15%) were recaptured on average 1.2 times. Out of the 22 Yellow Warblers banded in 1999, 16 individuals (73%) were recaptured on average 3.4 times, whereas out of the 19 Yellow Warblers banded in 2000, only five individuals (26%) were recaptured on average 1.8 times.

Site fidelity. The 45 waterthrushes were recaptured up to five additional times, and the 21 Yellow Warbler up to seven additional times. Final recaptures of 21 Yellow Warblers took place 1–23 months after the initial banding ($\bar{X}$ ± SD = 8.7 ± 4.55 months). Most recaptured birds were retrieved over a maximum period of 5–12 months, possibly reflecting survival and/or simply the duration of the study (Figure 2). Although distribution of banding days (i.e., the netting effort) over the

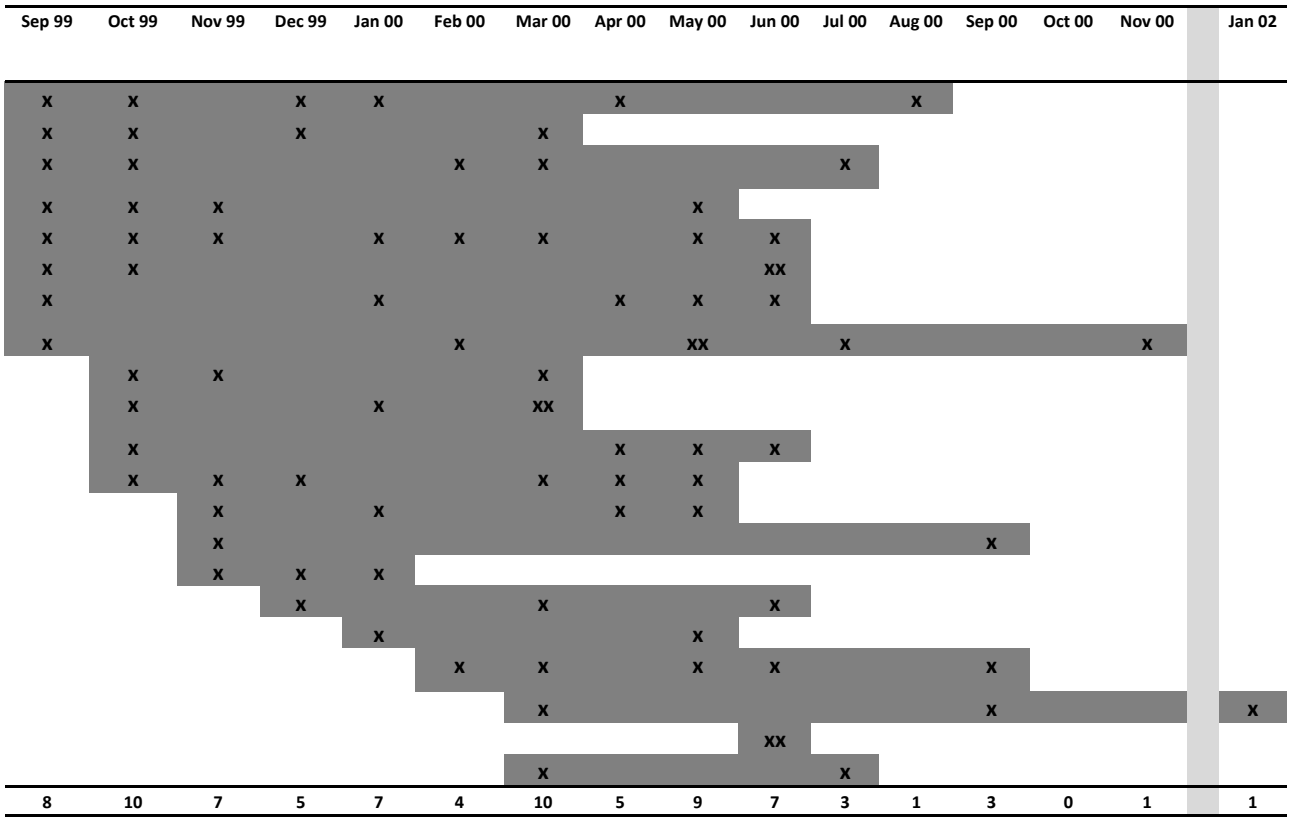

Figure 2. Capture histories of 21 Yellow Warblers (*Setophaga petechia*) recaptured in Jamaican mangroves (out of 45 banded in total) between September 1999 and January 2002.

three wintering periods was skewed (Table 2), the banding rate of Northern Waterthrushes remained constant, with 9.0 to 9.9 birds per banding day. Among the 138 Northern Waterthrushes banded between September 1999 and May 2000 (14 study days), 38 individuals (27.5%) were recaptured during the same period (winter 1999/2000), six individuals (4.3%) during the second season (winter 2000/2001), and only one individual (0.7%) during the third season (winter 2001/2002; Figure 3). Out of the 36 individuals banded between August and November 2000 (four study days), two (5.6%) were recaptured in the same season and one individual (2.8%) the following season (with only one study day). Altogether, only 3–4% of the marked individuals were recaptured again during the following winter season (Table 2).

DISCUSSION

Of the 31 species mist-netted in Jamaican mangroves during this study, 58% were permanent resident species, whereas the remaining 42% were Nearctic-Neotropical migrant winter resident species. Although numerous bird species occupy the mangrove forest, few appear to depend on this habitat as much as the two Parulidae species studied here, one for year-round territories and reproduction and the other for overwintering. According to our own observations in Jamaica and numerous published studies (e.g., Lack 1976, Wunderle & Waide 1993, Reitsma et al. 2002, Burson et al. 2005, Acevedo & Aide 2008, Smith et al. 2008, 2010, 2011, Howard & Brown 2013, Gemmill 2015), the mangrove forest appears to be the primary wintering habitat for Northern Waterthrushes in the Caribbean region. Only one study describes the occurrence of a more terrestrial wintering habitat in Venezuela (Schwartz 1964). This habitat, however, is threatened by direct human activities such as mangrove destruction and overexploitation, as well as by more indirect anthropogenic effects like climate change (Luther & Greenberg 2009, Lacerda et al. 2019).

The Yellow Warbler was the most common and widespread resident species. During concurrent point counts (results not presented here), Yellow Warblers were even more frequently recorded than Northern Waterthrushes, but both were consistently, by far, the most common species. The fact that Northern Waterthrushes were caught four times more often than Yellow Warblers probably reflects their lifestyle, with Yellow Warblers usually foraging higher in the canopy and Northern Waterthrushes close to the ground, where they are more likely to be captured (cf. McNair 2008). In his study of habitat use by Jamaican warblers, Lack (1976) characterized the two species: the Northern Waterthrush is abundant in mangroves and regular but scarce in lowland woods on muddy ground, usually near standing water or a muddy stream. The resident Yellow Warbler is easily separated, as it is the only common leaf-gleaning warbler in mangroves, where it takes nearly all its food off the leaves. His observations of the two different feeding niches may also explain the discrepancy between our banding results and our point counts. Other warbler species, such as the American Redstart, are not specialized on mangrove habitats and thus were not included in this analysis.

Based on their external appearance, all Yellow Warblers captured belonged to the resident subspecies–unlike in Central America, where approximately one fifth of the Yellow Warblers studied were migrants (Weidenfeld 1992). This can be explained by Witynski & Bonter (2018), who state

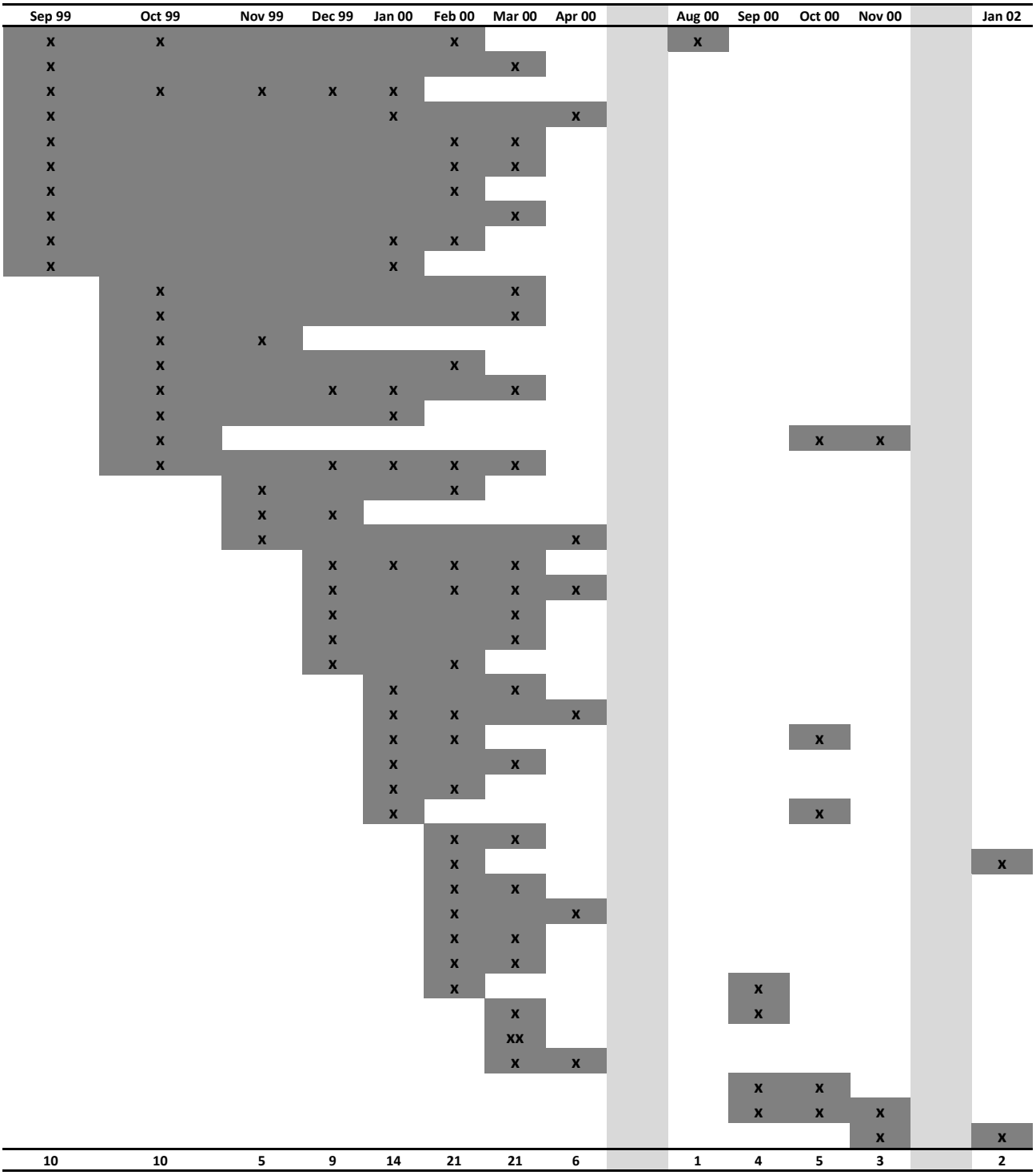

Figure 3. Capture histories of 45 Northern Waterthrushes (*Parkesia noveboracensis*) recaptured in Jamaican mangroves (out of 183 banded in total) between September 1999 and January 2002.

that migratory Yellow Warblers may bypass Jamaica on their migration from North America to either Central or South America.

The Northern Waterthrush was most abundant among White, mixed and Red Mangrove vegetation. We were unable to determine whether the birds left that habitat at times to forage in other places (Smith et al. 2008, Smith et al. 2011) or if they move during the day between mangrove species (Reitsma et al. 2002, Burson et al. 2005). The lower waterthrush recapture rate within a given winter season (25% of individuals, compared to 46% for Yellow Warblers) is consistent with the possibility that waterthrushes were more likely to leave the mangrove netting site than Yellow Warblers. These recapture rates occurred despite expectations of higher recaptures for the Northern Waterthrush, given its tendency to forage at mist net level, in contrast to Yellow Warblers, which forage above the nets (Lack 1976). Additionally, wintering Northern Waterthrushes may use various individual strategies, such as seasonal transients or floaters, in the study area (cf. Lefebvre et al. 1992, Smith et al. 2011). However, we did not collect any evidence for these behaviors.

Northern Waterthrushes and Yellow Warblers are common in many mangrove forests throughout the Caribbean and display similar occurrence patterns. In Puerto Rico, for example, Northern Waterthrushes are particularly abundant

Table 3. Caribbean-wide comparison of inter-annual recapture rates in Northern Waterthrushes (*Parkesia noveboracensis*) and Yellow Warblers (*Setophaga petechia*). Number of returning individuals in parentheses.

Species	Proportion of birds recaptured	Location	Source
Northern Waterthrush	1.4% (1 ind.)	Jamaica	Smith (1971), Diamond & Smith (1973)
Northern Waterthrush	4.3% (6) and 2.8% (1)	Jamaica	This study (Table 2)
Northern Waterthrush	9.1% (22)	St. Martin	Howard & Brown (2013)
Northern Waterthrush	21.4% (30)	Costa Rica	Warkentin & Hernandez (1996)
Northern Waterthrush	21.5% (81)	Costa Rica	Woodcock & Woodcock (2007)
Northern Waterthrush	27.5% (40)	Puerto Rico	Schaffner et al. (2017)
Northern Waterthrush	52% (12) and 31% (8)	Puerto Rico	Reitsma et al. (2002)
Yellow Warbler	5.9% (1)	Costa Rica	Warkentin & Hernandez (1996)
Yellow Warbler	12.5% (39)	Costa Rica	Woodcock & Woodcock (2007)
Yellow Warbler	17.8% (8)	Jamaica	This study
Yellow Warbler	21.4% (24)	Cuba	Parada Isada et al. (2015)

during a brief migration period from late February to early March (Gemmill 2015), i.e., shortly before capture rates peaked in our study area. Although this peak could also be a product of a seasonal habitat shift or birds being captured while moving to or from roost sites, we believe it is related to migrants starting to move around because the net sites and the operating times of the nets were standardized.

Ever since Snow & Snow (1960) found a Northern Waterthrush returning to the same winter quarters in Trinidad in successive winters (i.e., in December 1958 and December 1959), there have been many studies showing some winter site-fidelity in this species (see Table 3 for examples). The inter-seasonal recovery rates of Northern Waterthrushes in our study (3–4% of individuals recaptured during next winter season) were low compared to those of other studies in the region (Table 3). The recapture rate of Yellow Warblers in our study over 10 months (8 of 45 individuals) fits into the pattern of other studies, although it was not possible to distinguish seasons clearly.

Occasional hurricanes can destroy large swaths of mangrove habitat, impacting songbirds directly and in the long-term (Reitsma et al. 2002). On the other hand, water level changes can impact habitat quality far more frequently through a reduction of arthropod biomass (Lefebvre et al. 1994). In Puerto Rico, flooding conditions reduced the number of returning Northern Waterthrushes (Reitsma et al. 2002), but wetter territories had higher food availability and facilitated faster fat deposition and body mass gain (Smith et al. 2010, 2011).

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