

USE OF MAINLAND HABITATS BY SUPPOSED RIVER-ISLAND OBLIGATE BIRDS ALONG THE AMAZON RIVER IN PERU

J. W. ARMACOST JR.¹ AND ANGELO P. CAPPARELLA

School of Biological Sciences, Illinois State University, Normal, IL 61790

Abstract. Eighteen species of Amazonian birds have been considered river-island obligates in northeastern Peru, but some of these species have been detected recently at mainland sites along the Amazon River. We document the presence of supposed river-island obligate birds at riparian sites on the mainland and characterize these birds' habitat use on the islands and the mainland on the basis of point counts at five island sites, five riparian mainland sites, and five upland mainland sites. We regularly encountered seven species of supposed river-island obligates on the islands and four of them, including the Ash-breasted Antbird (*Myrmoborus lugubris*), Black-and-white Antbird (*Myrmochanes hemileucus*), Castelnau's Antshrike (*Thamnophilus cryptoleucus*), and Fuscous Flycatcher (*Cnemotriccus fuscatus*), also occurred regularly at the riparian mainland sites, but none occurred at the upland mainland sites. These four species are primarily birds of early-successional scrub or forest, but they also used agricultural habitats on both the islands and the mainland. The presence of these species on the mainland may have been overlooked by previous researchers, who may neglect human-dominated habitats during avifaunal surveys, or these species may have only recently colonized the mainland in response to an increase in the amount of small-scale agricultural plots in the region. Supposed river-island obligate birds are, in fact, habitat specialists, and can occur on the mainland if appropriate natural or anthropogenic habitat exists there. Human-dominated tropical landscapes may provide habitat suitable for disturbance-adapted bird species and should not be overlooked during avifaunal surveys.

Key words: *habitat specialization, habitat colonization, agricultural disturbance, river islands, river-island obligates, Amazonia, Peru.*

Uso de Hábitats de Tierra Firme por parte de Aves Supuestamente Específicas de Islas Ribereñas a lo largo del Río Amazonas en Perú

Resumen. Dieciocho especies de aves amazónicas han sido consideradas como habitantes obligados de las islas ribereñas en el noreste de Perú, pero algunas de estas especies han sido detectadas recientemente en sitios de tierra firme a lo largo del Río Amazonas. Documentamos la presencia de aves supuestamente específicas de islas de ríos en sitios ribereños de tierra firme y caracterizamos el uso de hábitat de estas aves en las islas y en tierra firme basándonos en puntos de conteo en cinco sitios en las islas, cinco sitios ribereños en tierra firme y cinco sitios altos en tierra firme. En las islas encontramos siete especies de aves supuestamente exclusivas de las islas ribereñas, y cuatro de ellas, incluyendo a *Myrmoborus lugubris*, *Myrmochanes hemileucus*, *Thamnophilus cryptoleucus* y *Cnemotriccus fuscatus*, también de modo regular en los sitios ribereños de tierra firme, pero ninguna en los sitios altos de tierra firme. Estas cuatro especies son principalmente aves de arbustal o bosque en estadios sucesionales tempranos, pero también usaron ambientes agrícolas tanto en la isla como en tierra firme. La presencia de estas especies en tierra firme puede haber pasado desapercibida por previos investigadores, que pueden haber desatendido los hábitats antropizados durante los muestreos de aves, o estas especies pueden haber colonizado recientemente la tierra firme en respuesta a un incremento en la cantidad de parcelas de agricultura de pequeña escala en la región. Las aves supuestamente específicas de las islas ribereñas son, de hecho, especialistas de hábitat, y pueden presentarse en la tierra firme si existen allí los hábitats naturales o antrópicos apropiados. Los paisajes tropicales dominados por el hombre pueden brindar hábitat adecuado para las especies de aves adaptadas a los disturbios y no deben ser pasados por alto en los muestreos de aves.

INTRODUCTION

There is a strong latitudinal gradient in avian diversity, with higher species richness at lower latitudes, and the avifauna of the Neotropical Region is particularly diverse (Stotz et al. 1996,

Stutchbury and Morton 2001). One hypothesis to explain this pattern suggests that it results from increased habitat specialization by tropical species (Klopper and MacArthur 1960, Remsen and Parker 1983, Marra and Remsen 1997). For example, there are about 170 species of birds restricted to

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¹Current address: Biology Department, Lamar University, P. O. Box 10037, Beaumont, TX 77710.

E-mail: jim.armacost@lamar.edu

river-created habitats in Amazonia (Remsen and Parker 1983) and 18 species of birds further restricted to river islands in northwestern Amazonia (Rosenberg 1990). Although in general tropical species are expected to be more specialized than temperate-zone species (Klopfer and MacArthur 1960, Marra and Remsen 1997), those of disturbance-prone habitats (e.g., birds of ephemeral islands in Amazonian rivers) are predicted to retain high ability for dispersal and plasticity in habitat use (Rosenberg 1990, Hilty and Ascanio 2009), traits that might make them particularly suited to exploiting small-scale anthropogenic disturbances.

In northwestern Amazonia, 18 species of landbirds have been described as river-island obligates, even though islands of the Amazon and its tributaries may be separated from the mainland by only hundreds of meters (Rosenberg 1990). Extensive field work along the Amazon and Napo rivers in northeastern Peru in the 1980s by researchers from the Louisiana State Museum of Natural Science (LSUMNS) and Academy of Natural Sciences of Philadelphia (ANSP) did not detect these river-island obligate species at mainland riparian sites (Cardiff 1983, Rosenberg 1990, Robbins et al. 1991); however, it is thought that these species, rather than being island specialists per se, are specialists of early-successional vegetation types that just happen to be most common on sandbar islands of the Amazon and its tributaries.

More recently, JA encountered birds supposedly restricted to river islands at mainland riparian sites along the Amazon in northeastern Peru: the Ash-breasted Antbird (*Myrmoborus lugubris*), Black-and-white Antbird (*Myrmochanes hemileucus*), Castelnau's Antshrike (*Thamnophilus cryptoleucus*), and Fuscous Flycatcher (*Cnemotriccus fuscatus*). The river-island birds were present in both natural and agricultural habitats within a landscape that is moderately disturbed by humans, creating a mosaic of natural habitats interspersed by clearings for small-scale, traditional agriculture on both the islands and the mainland. JA studied river-island birds at multiple field sites from June to August of 2003 and 2004 with the objectives of documenting the occurrence of supposed river-island obligates on the mainland, characterizing these species' use of habitat on the islands and the mainland, and determining if river-island birds occurred at mainland sites away from the river.

METHODS

The riparian ecosystem of western Amazonia is strongly affected by the annual flood pulse. At Iquitos, Peru, the water level of the Amazon fluctuates an average of 8 m through the year, and may fluctuate as much as 16 m (Goulding et al. 2003). Field work for this study extended from June to August, when the water level of the Amazon is dropping following the annual peak, which usually occurs in May. Sedimentation creates sandbar islands, which become vegetated if they do not erode. In western Amazonia,

succession follows a predictable pathway, proceeding from grass (mainly *Paspalum* sp.) to cane (*Gynerium* sp.) or shrubs (*Tesaria* sp.), then to *Cecropia* forest, and finally to riparian forest (*varzea*) of mixed tree species (Terborgh 1985, Salo et al. 1986, Rosenberg 1990, Kalliola et al. 1991, Robinson and Terborgh 1997). *Varzea* forests, which are seasonally flooded, occur along rivers in Amazonia, while *terra firme* forests occur on unflooded uplands farther from the rivers.

Along the Amazon and other rivers near Iquitos, the natural riparian vegetation is fragmented by small clearings made by subsistence farmers for homes, garden plots, and small (mostly 0.5–2 ha) farm fields (*chacras*). The local farmers practice small-scale, shifting cultivation, creating a mosaic of natural, cleared, and regenerating habitats (Hiraoka 1985). Farm fields are often polycultures, in which crops ranging from *yuca* (*Manihot esculenta*) to papaya (*Carica papaya*) are grown together, creating structurally diverse agricultural habitats. Groves of bananas and plantains (*Musa* spp.) are also common and retain some of the structure of natural forest.

JA studied 15 sites in the Amazon Basin downstream from the city of Iquitos (Fig. 1). Five study sites (island sites) were on islands in the Amazon River. Another five study sites (riparian sites) were mainland sites paired with the island sites, such that each riparian site was on the mainland riverbank immediately across from an island site. The mean width of the river channel between an island site and its paired riparian site was 840 m (Table 1). Each island/riparian pair of sites was separated from other pairs of sites by at least 5 km (Fig. 1). A final five study sites (upland sites) were mainland sites well away from the Amazon River. Two of the upland sites were located along Quebrada Yanayacu, one along Quebrada Maniti, and two along the

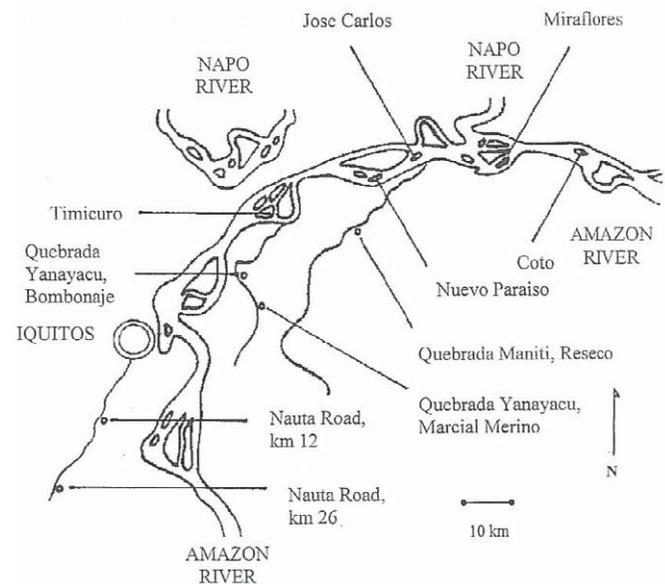


FIGURE 1. Locations of the fifteen study sites near Iquitos, Peru. The city of Iquitos is represented by the double ring at the left.

TABLE 1. Description of study sites along the Amazon near Iquitos, Peru.

Site	Distance to Iquitos (km)	Number of count points	Degree of disturbance	Island size (ha)	Island age (years)	Distance from island to mainland (m)
Island						
Timicuro	30	10	moderate	420	25	300
Coto	85	5	moderate	150	25	1600
Jose Carlos	60	5	low	320	10	1000
Nuevo Paraiso	50	5	low	660	5	900
Miraflores	65	5	low	430	5	400
Riparian						
Timicuro	30	10	moderate			
Coto	85	5	low			
Jose Carlos	60	5	high			
Nuevo Paraiso	50	5	low			
Miraflores	65	5	moderate			
Upland						
Quebrada Yanayacu, Bombonaje	30	5	moderate			
Quebrada Yanayacu, Marcial Merino	25	5	moderate			
Quebrada Maniti, Reseco	50	5	moderate			
Iquitos–Nauta Road, km 12	10	5	high			
Iquitos–Nauta Road, km 26	25	5	high			

road between Iquitos and the city of Nauta. Each upland site was separated from other upland sites by at least 5 km (Fig. 1). Some of the sites included in this study had been visited by researchers from the LSUMNS and ANSP in the 1980s (Cardiff 1983, Rosenberg 1990, Robbins et al. 1991).

At each of the 15 study sites, JA established a transect consisting of 5–10 count points, each separated by 200 m. At the island and riparian sites, the transects were parallel to the Amazon River. There were a total of 85 count points (Table 1). JA conducted one count at each point each year (2003 and 2004), except at the Timicuro island and riparian sites, where he made three point counts per field season at roughly 2-week intervals, and at the upland sites, where he made one point count in 2004 only. Counts took place during the first 4 hr after dawn, lasted 10 min, encompassed a radius of 100 m, and all birds detected were recorded (Ralph et al. 1993). Point counts were not conducted during heavy rain or high winds.

We estimated population densities of supposed river-island obligates for island, riparian, and upland sites. For a given species, we calculated the mean number of birds recorded per point for each of the three types of sites, averaging over repeated visits. To obtain an estimate of population density, we then divided the mean number of individuals per point by the area of the circle (3.14 ha). We used nonparametric Mann–Whitney tests in SigmaPlot 11 to compare the mean densities of a given species at island sites with those at riparian or upland sites.

Each of the 15 study sites encompassed a mosaic of natural and agricultural habitats, but we assigned each point within

a site to a particular habitat type on the basis of the dominant vegetation. Natural habitat types encountered at the island and riparian sites included grass, cane, and forest (including both *Cecropia*-dominated and mixed-species *varzea* forest). At upland sites, *terra firme* forest was the only natural habitat encountered. Agricultural habitats at the island and riparian sites included *chacras* and banana groves, and agricultural habitats at the upland sites included *chacras*, banana groves, and pastures.

We characterized habitat use of those species of supposed river-island obligates that were encountered commonly on the mainland by comparing habitat use (observed frequency) to availability (expected frequency) at island sites and at riparian mainland sites. For a given species, observed frequencies were the sum of the average number of birds detected per point in a given habitat (to correct for the unequal number of counts at different sites). Expected frequencies were calculated by multiplying the frequency of a given habitat (the percent of points assigned to that habitat) by the sum of the average number of birds detected at all points. We used chi-squared tests to determine if there were statistically significant differences between habitat use (observed frequency) and availability (expected frequency).

RESULTS

Seven species of supposed river-island obligate birds were detected at island sites during the point counts. Of those seven

species, six were also detected at riparian sites on the mainland during the point counts. None of the seven species was detected at any of the upland sites on the mainland (Table 2).

Three species were absent from or uncommon at riparian mainland sites. The Lesser Hornero (*Furnarius minor*) was never detected during point counts and should still be considered a river-island obligate. On the mainland, the Parker’s Spinetail (*Cranioleuca vulpecula*) was detected at only two points at two different riparian sites, and its density was significantly lower on the mainland than on the islands (Table 2). Similarly, the White-bellied Spinetail (*Synallaxis propinqua*) was detected only on the mainland at two points at the same riparian site, and its density was also significantly lower on the mainland than on the islands (Table 2).

Four species were commonly encountered at riparian mainland sites. The Ash-breasted Antbird was detected on the mainland only at five points at the same riparian mainland site, but its density on the islands and on the mainland was statistically similar (Table 2). The density of the Black-and-white Antbird was significantly higher on the islands than on the mainland, but it was detected on the mainland at 11 points (37% of all riparian points) at three riparian sites (Table 2). The Castelnau’s Antshrike was also detected at 11 points at four riparian mainland sites, and its density on the islands and on the mainland was statistically similar (Table 2). Finally, the Fuscous Flycatcher was detected on the mainland at seven points (23% of all riparian points) at four riparian sites, and its density on the islands and on the mainland was statistically similar (Table 2).

On the islands, the Ash-breasted Antbird used habitats in proportion to availability, but on the mainland, its use differed significantly from availability (Table 3). On the mainland, the Ash-breasted Antbird avoided forest and preferred banana groves and, unexpectedly, grassy areas (Fig. 2). Habitat use of the Black-and-white Antbird differed significantly from availability on the islands (Table 3), where it avoided natural habitats and preferred agricultural habitats (Fig. 2). On the mainland, it used habitats in proportion to availability (Table 3). Habitat use by the Castelnau’s Antshrike differed

significantly from availability on the islands (Table 3), where it preferred forest and *chacras* (Fig. 2), but on the mainland it used habitats in proportion to availability (Table 3). Finally, the Fuscous Flycatcher used habitats in proportion to availability on both the islands and the mainland (Table 3, Fig. 2).

DISCUSSION

This study suggests that three species of supposed river-island obligate birds should still be considered river-island obligates. The Lesser Hornero was not encountered at mainland sites, so it may still be considered a river-island obligate. Parker’s Spinetail and the White-bellied Spinetail were each detected at only 7% of the count points at the riparian mainland sites, and population densities of both species were significantly lower on the mainland than on the islands, so these two species may also remain classified as essentially river-island obligates. Four other species, the Ash-breasted Antbird, Black-and-white Antbird, Castelnau’s Antshrike, and Fuscous Flycatcher, should no longer be considered river-island obligates. These species occurred at similar population densities on the islands and at riparian mainland sites, except for the Black-and-white Antbird, whose population density was significantly higher on the islands than on the mainland, but it was detected at 37% of the points at the riparian mainland sites. The Castelnau’s Antshrike has been reported nesting on the mainland (Armacost 2004), and the Fuscous Flycatcher is known to occur in mainland habitats in other parts of its range (Rosenberg 1990).

It is unlikely that the supposed river-island obligates were detected on the mainland because individual birds were regularly crossing between the islands and the mainland. At the paired Timicuro study sites, birds were captured and color-banded. During three field seasons (2002–2004), 55 individuals of five species of supposed river-island obligates were banded, but no individual banded on the island was subsequently recaptured on the mainland or vice versa, despite a recapture rate of 38%. In contrast, riparian birds of the temperate zone may more readily move between mainland and river-island sites

TABLE 2. Densities (mean ± SE birds ha⁻¹) of supposed river-island obligate birds at island and riparian mainland sites. None of the species was detected at upland mainland sites. Results of comparison by a Mann–Whitney test.

Species	Island	Mainland	<i>U</i>	<i>P</i> ^a
Lesser Hornero	5.43 ± 0.75	0.00 ± 0.00	75.0	<0.001**
White-bellied Spinetail	5.34 ± 1.10	0.94 ± 0.69	191.5	<0.001**
Parker’s Spinetail	4.30 ± 0.77	0.41 ± 0.29	162.5	<0.001**
Ash-breasted Antbird	1.16 ± 0.44	0.94 ± 0.43	417.5	0.50
Black-and-white Antbird	6.37 ± 0.97	1.57 ± 0.45	173.5	<0.001**
Castelnau’s Antshrike	1.57 ± 0.47	1.79 ± 0.49	414.0	0.55
Fuscous Flycatcher	0.85 ± 0.33	0.94 ± 0.34	430.0	0.69

^aLevel of significance: **<0.001.

TABLE 3. Results of chi-squared tests comparing habitat use versus availability for four species of river-island birds at island and riparian mainland sites.

Species	Island		Mainland	
	χ^2_5	<i>P</i> ^a	χ^2_4	<i>P</i> ^a
Ash-breasted Antbird	7.15	0.25	20.87	0.01**
Black-and-white Antbird	11.85	0.10	6.35	0.25
Castelnau’s Antshrike	12.31	0.05*	0.60	0.98
Fuscous Flycatcher	4.63	0.75	2.12	0.50

^aLevels of significance: *0.05, **0.01.

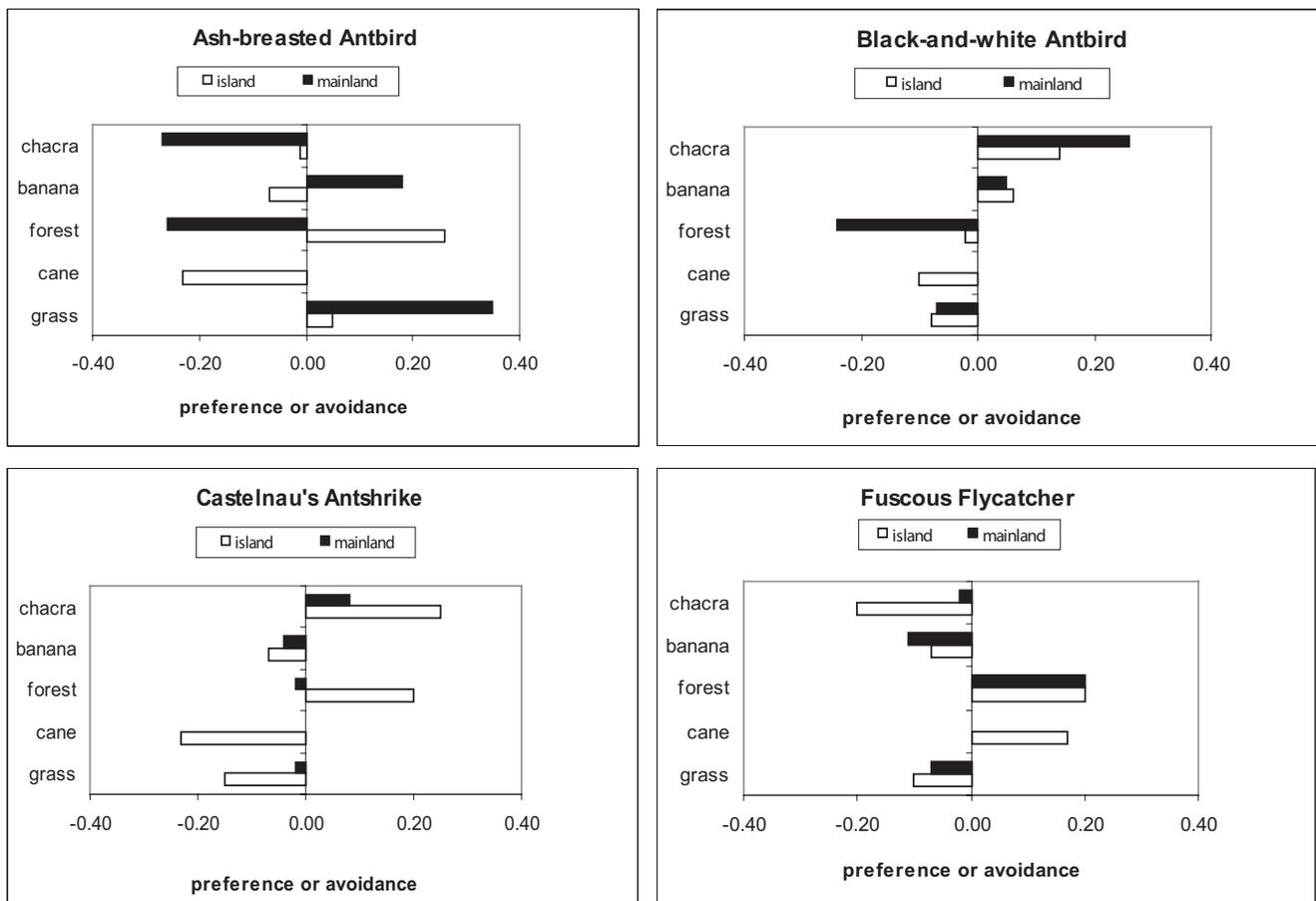


FIGURE 2. Habitat use by four species of river-island specialist birds at island and riparian mainland sites. Positive values represent preference; negative values represent avoidance.

(Scharf 2007), although even temperate-zone riparian birds may be somewhat reluctant to cross rivers (Shirley 2006).

The four species of supposed river-island obligates that we found to be common on both the islands and at riparian mainland sites are generally considered birds of early-successional scrub or forest (Ridgely and Tudor 1994, Stotz et al. 1996). Interestingly, even on the islands they either used agricultural habitats in proportion to availability or preferred one or more types of agricultural habitats. On the islands, the Ash-breasted Antbird used all habitats (including agricultural ones) in proportion to availability, though it was most common in forest. Rosenberg (1990) considered it to be an understory specialist of *Cecropia* forest on river islands. The Black-and-white Antbird preferred agricultural habitats on the islands. It was especially common along edges between forests and *chacras*. Rosenberg (1990) considered it to be a habitat generalist but with a preference for understory vine tangles in all habitats. The Castelnau's Antshrike preferred both forest and *chacras* on the islands. Rosenberg (1990) considered it to be a habitat generalist. Finally, the Fuscous Flycatcher used all

habitats in proportion to availability on the islands. Rosenberg (1990) considered it to be a habitat generalist.

At the riparian mainland sites we studied, the Black-and-white Antbird, Castelnau's Antshrike, and Fuscous Flycatcher used all habitats in proportion to availability, while the Ash-breasted Antbird preferred banana groves, and, unexpectedly, grassy areas. Thus these four species colonize appropriate natural habitats if they occur on the mainland, and they exploit agricultural habitats on the islands and the mainland. These species may adapt well to small-scale, shifting agriculture because such anthropogenic disturbance mimics the natural disturbance regime of the region and creates appropriate substitutes for the early-successional natural habitats that these birds prefer (Andrade and Rubio-Torgler 1994, Vereá and Solorzano 2005).

It is uncertain why previous researchers failed to detect these supposed river-island obligates on the mainland. It is possible that the birds were present on the mainland but were overlooked by ornithologists. Researchers from the LSUMNS and ANSP did extensive avifaunal surveys along the Amazon and Napo rivers in northeastern Peru in the 1980s (Cardiff 1983, Rosenberg 1990,

Robbins et al. 1991), but they did not specifically target *chacras* and other human-disturbed habitats, so they may have missed river-island birds on the mainland. Alternatively, it is possible that the river-island birds have only recently (since the 1980s) colonized the mainland, perhaps in response to an increase in the amount of small-scale agricultural plots. Although the dispersal abilities of river-island birds have not been well studied (Agreda et al. 2006), the river-island specialists do inhabit ephemeral habitat patches that vary from season to season as well as from year to year, so they are probably pre-adapted for finding and exploiting habitat patches created by small-scale agricultural disturbances (Remsen and Parker 1983, Rosenberg 1990, Hilty and Ascanio 2009), but they are not expected to disperse overland to upland habitats away from rivers, and upland sites may be unsuitable because of differences in hydrology between *varzea* and *terra firme* forests.

Amazonian river islands are notable for their high productivity and high densities of birds. Rosenberg (1990) estimated that a community of 16 bird species on an island in the Napo River in northeastern Peru had a combined density of 160 birds ha⁻¹. The seven species of supposed river-island obligate birds we detected at the island sites had a combined density of 25 birds ha⁻¹, and this estimate does not include any of the non-obligate species that were also present.

In conclusion, at least four species of birds (the Ash-breasted Antbird, Black-and-white Antbird, Castelnau's Antshrike, and Fuscous Flycatcher) previously considered river-island obligates, at least in northeastern Peru, also occur at riparian mainland sites. They are habitat specialists but can no longer be considered river-island obligates, as they colonize appropriate habitat where it occurs on the mainland. Interestingly, these four species all exploit agricultural habitats, and this ability may contribute to their colonization of riparian mainland sites. Anthropogenic habitats may provide suitable habitat for these species if it consists of small-scale plots of traditional agriculture near the river bank. Finally, this study emphasizes the need for ornithological surveys to include anthropogenic habitats, especially as such habitats come to dominate many landscapes, even in the neotropics.

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