



RESEARCH ARTICLE

Tropical montane birds have increased nesting success on small river islands

David Ocampo^{1,2*} and Gustavo A. Londoño^{3,4}

¹ Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia

² Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

³ Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA

⁴ Departamento de Ciencias Biológicas, Universidad ICESI, Cali, Colombia

* Corresponding author: d.ocampo10@uniandes.edu.co

Submitted March 30, 2014; Accepted July 20, 2014; Published October 1, 2014

ABSTRACT

Predation is the most important cause of nest failure in birds, and variation in predation risk has been associated with changes in nesting behaviors such as nest-site selection. Some birds choose favorable breeding sites on oceanic or large lake islands to increase their nesting success, but we do not know whether river islands with smaller water barriers provide similar “safe” conditions that decrease predation risk. We tested this in tropical birds by comparing daily survival rates (DSR; i.e. the probability that a nest will survive a single day) and predators identified at nests among bird species that nest on river edges and islands in the Andes. We monitored natural nests of 9 species and placed 70 artificial nests of different shapes (dome, cup, and ground nests) on islands and along river edges. We found that nest survival rates were greater on islands than on river edges for both natural nests (0.989 ± 0.004 vs. 0.0975 ± 0.004) and artificial nests (0.977 ± 0.007 vs. 0.944 ± 0.012). Isolation and nest height significantly explained ($w_i = 0.65$) differences in DSR among islands and river edge. Among nest types, ground nests had higher DSR on islands and river edges than cup and dome nests. Birds were the principal predators in both areas, whereas small mammals, marsupials, and reptiles (i.e. snakes) preyed on nests exclusively on the river edges. Andean river islands—despite their small size and small distances from river edges—provided a refuge for nesting birds by isolating important nest predators such as mammals and snakes. Because birds that nest on islands have higher fitness, natural selection should favor individuals that select Andean river islands as nesting sites.

Keywords: Andes, artificial nests, nest predation rates, nest predator identity, river islands

Las aves montanas neotropicales aumentan su éxito de nidificación en pequeñas islas de río

RESUMEN

La depredación es la causa más importante de fracaso de los nidos de aves, y se ha asociado a la variación en el riesgo de depredación con los cambios en el comportamiento de nidificación, como la selección del sitio de ubicación del nido. Algunas aves eligen sitios de nidificación favorables en islas oceánicas y en grandes lagos para aumentar su éxito de nidificación, pero no sabemos si las islas de río, con pequeñas barreras de agua, brindan condiciones de “seguridad” similares que disminuyan el riesgo de depredación. Evaluamos si las islas de río pueden servir como refugio de la depredación del nido para las aves tropicales comparando las tasas de supervivencia diaria (TSD; probabilidad de supervivencia diaria del nido) y los depredadores identificados en nidos de especies de aves que anidan en los bordes y en islas de río en los Andes. Observamos nidos naturales de 9 especies y colocamos 70 nidos artificiales de diferentes formas (domo, taza y sobre el suelo) en islas y a lo largo de los bordes de río. Encontramos que las tasas de supervivencia de los nidos fueron mayores en las islas que en los bordes de río, tanto para los nidos naturales (0.989 ± 0.004 vs. 0.0975 ± 0.004) como para los artificiales (0.977 ± 0.007 vs. 0.944 ± 0.012). El aislamiento y la altura del nido explicaron diferencias significativas ($w_i = 0.65$) en la TSD entre las islas y los bordes de río. Entre los tipos de nido, los terrestres presentaron mayor TSD en las islas y en los bordes de río, comparados con los nidos con forma de taza y cúpula. Las aves fueron los principales depredadores en ambas áreas, mientras que los pequeños mamíferos, marsupiales y reptiles (i.e. víboras) depredaron nidos exclusivamente en los bordes de río. Las islas de río de los Andes—a pesar de su tamaño pequeño y las pequeñas distancias a los bordes del río—brindaron refugio para las aves nidificantes, aislando de importantes depredadores de nidos como mamíferos y reptiles. Debido a que las aves que anidan en las islas tienen una mayor adecuación biológica, la selección natural debería favorecer a los individuos que seleccionan a las islas de río de los Andes como sitios de nidificación.

Palabras clave: Andes, identidad de depredadores de nido, islas de río, nidos artificiales, tasas de depredación de nidos



FIGURE 1. The Ladder-tailed Nightjar (*Hydropsalis climacocerca*) is a ground-nesting bird, and nests are found on islands and river edges. (A) Female incubating eggs and (B) 3-day-old nestling. Photo credit: David Ocampo

INTRODUCTION

Avian nesting success is principally affected by nest predation (Ricklefs 1969, Skutch 1985, Brawn et al. 2011). Behavior before birds start nesting, during incubation, or during the nestling period can decrease nest predation risk (Ricklefs 1969, Skutch 1985, Fontaine et al. 2007, Brawn et al. 2011). For example, selecting sites inaccessible to nest predators (e.g., islands) is an important nesting strategy to reduce nest predation risk (Robinson 1985, Boag 1987, Martin 1987, 2001, Lloyd 2004, Fontaine and Martin 2006). The absence of avian nest predators (i.e. snakes and mammals) from many oceanic islands is likely a major advantage of nesting on islands for species with long nesting periods, such as marine birds (Wright et al. 2013). Many colonial icterids, such as oropendolas and caciques, also show strong preferences for nesting on islands in large tropical rivers,

because of the protection they afford against mammals and snakes (Robinson 1985). However, we do not know whether much smaller and less isolated islands, such as those occurring along tropical montane rivers and streams, may also provide protection against nest predators.

We hypothesized that the isolation created by small montane rivers might reduce the overall nest predation rates on islands by excluding terrestrial animals (Robinson 1985, Weatherhead and Blouin Demers 2004, Zoellick et al. 2004), but not flying predators such as birds. To test this, we monitored natural nests of 9 species nesting on islands and river edges and conducted an experiment using artificial nests of different shapes (i.e. dome, cup, and ground) located on different islands and river edges. We restricted our “mainland” species to those nesting along river edges because they nest in essentially the same microhabitats, have similar risks of flooding, and therefore should be facing otherwise similar selective pressures, except for possible differences in predator assemblages. Figure 1 depicts the one ground-nester in our study, the Ladder-tailed Nightjar (*Hydropsalis climacocerca*).

METHODS

Study Area

We worked in the Kcosñipata Valley at the Cock-of-the-Rock Field Station ($13^{\circ}0.4'19.4''S$, $71^{\circ}3.3'48.5''W$), located in the buffer area of Manu National Park, Cusco, Peru. The study area is located at 1,450 m elevation in an Andean cloud forest with a canopy height of ~ 25 m, a mean temperature of $18.3^{\circ}C$ (range: 12.1 – $26.6^{\circ}C$), and mean annual precipitation of 1,521 mm, with a rainy season from November through April and a dry season from May through August (Ocampo and Londoño 2011). We studied 5 islands with an average area ($\pm SD$) of 986 ± 595 m 2 along 3 km of the Kcosñipata River (Figure 2A); 4 of those islands were considered small (< 891 m 2), and 1 was considered large (2,034 m 2). During the study season (September–November), the river's flow rate was 11.3 ± 1.5 m 3 s $^{-1}$ (Clark et al. 2014). The islands were isolated from the edge of the river by 7.25 ± 4.40 m (range: 13.0–2.5 m), with a water depth of 76 ± 31 cm ($n = 10$). Island and river edges had similar vegetation, dominated by cane (Poaceae: *Gynerium sagittatum*), several shrub species, and some small trees (<5 m height; Figure 2B).

Natural Nests

Following the protocol of Martin and Geupel (1993), we searched for nests on islands and river edges from August through December in 2008 and 2009. We detected 36 bird species (see Table 4 in the Appendix) that were using

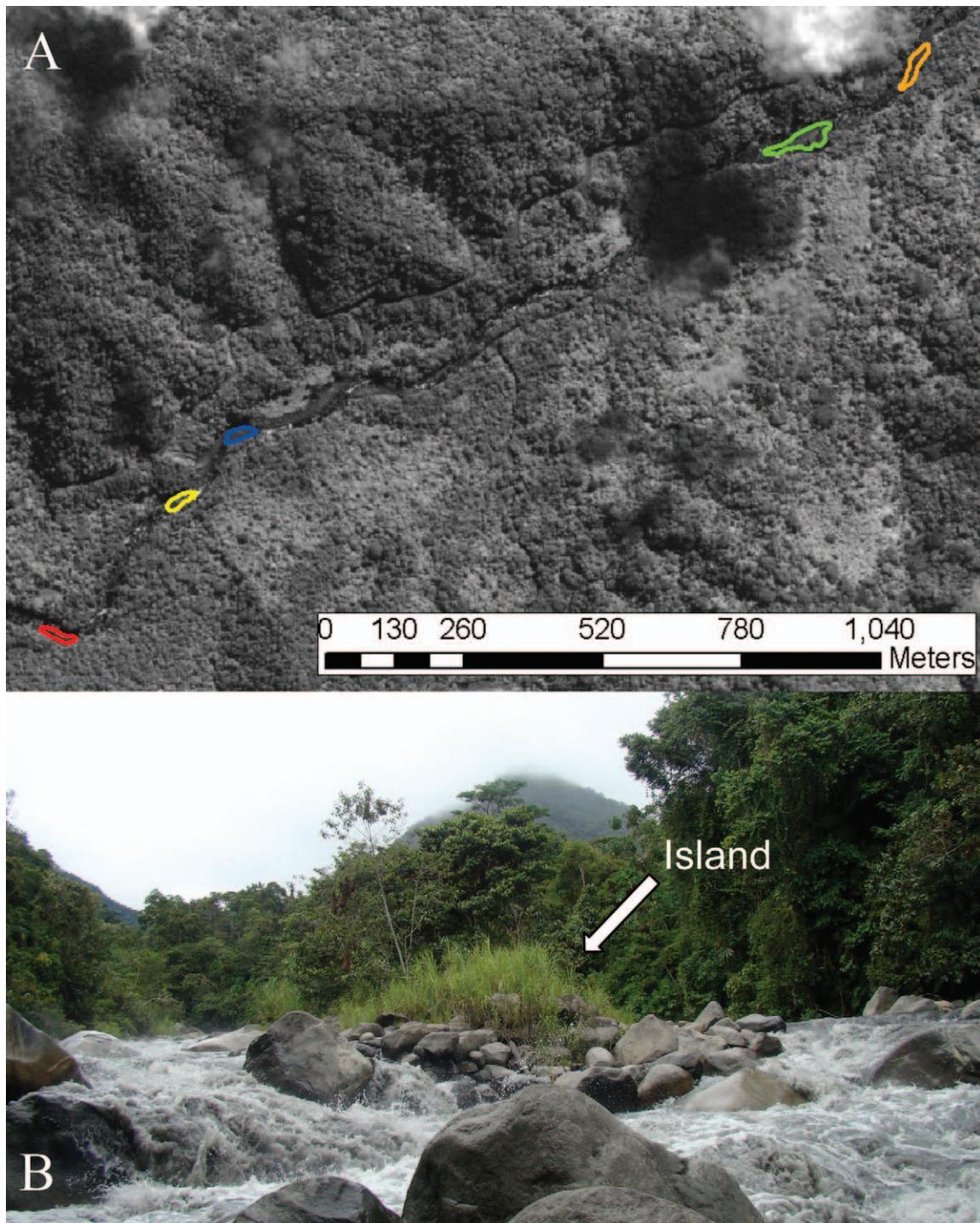


FIGURE 2. Views of the Kcosñipata Valley. (A) Five islands along 2 km of the river (satellite photo, Quickbird 2009, pan-sharpened in ArcMap 9.3.1). (B) Vegetation present in edges and islands of the Kcosñipata river.

habitats created by rivers. Most nests were found during the dry season, when flooding was at a minimum. We observed reproductive activity in 29 of these species (80%); some species bred in vegetation along creeks and banks, and 16 bred exclusively on islands and river edges. We

found a total of 137 nests of 12 species, but we analyzed data for only 65 nests of 9 species for which we had data on nesting success (successful–failed) and on the number of days that the nest was exposed during the incubation and nestling periods.

TABLE 1. Total numbers of natural and artificial nests used in the analysis, numbers of nests depredated (Pred.; with percentage of nests failed in parentheses), and daily survival rates of nests (DSR \pm SE) among islands and river edges and within different nest types in an Andean river habitat in southeastern Peru.

Nest type	Islands			River edges			Total		
	n	Pred.	DSR	n	Pred.	DSR	n	Pred.	DSR
Natural nests: incubation period only									
Dome	2	0 (00)	1.000 \pm 0.000	8	3 (38)	0.977 \pm 0.014	10	3 (30)	0.977 \pm 0.013
Cup	13	3 (23)	0.994 \pm 0.007	33	6 (18)	0.987 \pm 0.005	46	9 (20)	0.987 \pm 0.013
Ground	5	0 (00)	1.000 \pm 0.000	4	0 (00)	1.000 \pm 0.000	9	0 (00)	1.000 \pm 0.000
Total	20	3 (15)	0.990 \pm 0.005	45	9 (20)	0.987 \pm 0.004	65	12 (18)	0.988 \pm 0.003
Natural nests: nesting period (incubation + nestling)									
Dome	2	1 (50)	0.993 \pm 0.004	8	7 (88)	0.957 \pm 0.015	10	8 (80)	0.963 \pm 0.012
Cup	13	5 (38)	0.988 \pm 0.007	33	22 (67)	0.976 \pm 0.005	46	27 (59)	0.980 \pm 0.004
Ground	5	1 (20)	0.996 \pm 0.005	4	1 (25)	0.991 \pm 0.015	9	2 (22)	0.993 \pm 0.012
Total	20	7 (35)	0.989 \pm 0.004	45	30 (67)	0.975 \pm 0.004	65	37 (57)	0.980 \pm 0.003
Artificial nests									
Dome	9	4 (44)	0.969 \pm 0.012	9	5 (56)	0.924 \pm 0.026	18	9 (50)	0.953 \pm 0.015
Cup	16	7 (44)	0.971 \pm 0.009	16	13 (81)	0.928 \pm 0.018	32	20 (63)	0.952 \pm 0.011
Ground	10	1 (10)	0.990 \pm 0.005	10	4 (40)	0.976 \pm 0.011	20	5 (25)	0.984 \pm 0.007
Total	35	12 (34)	0.977 \pm 0.007	35	22 (63)	0.944 \pm 0.012	70	34 (49)	0.963 \pm 0.006

Artificial Nest Experiments

We placed 35 artificial nests on islands and an equal number along river edges. We divided the islands and river edges into small plots with both vegetation and open sandy areas, with the aim that the nests were uniformly distributed along the areas; nests were placed randomly near sites where nesting birds had been observed previously. Artificial nests had different shapes (18 were domes, 32 were cups, and 20 were ground nests) and sizes to resemble the nest architecture and materials of the species nesting in the area (Figure 3). The external average (\pm SD) measurements of the dome nests were 97.41 \pm 24.86 mm \times 118.76 \pm 134.22 mm \times 127.90 \pm 51.41 mm (length, width, and height, respectively; $n = 140$). The nest

entrance was 44.13 \pm 6.55 mm \times 41.01 \pm 6.30 mm (length and width, respectively), average nest thickness was 21.66 \pm 9.56 mm, and distance from the entrance of the vertical tunnel to the roof was 70.23 \pm 13.34 mm ($n = 137$). The inside depth was 41.05 \pm 9.92 mm ($n = 135$). For the artificial cup nests, the inner diameters were 58.80 \pm 18.14 mm \times 54.87 \pm 13.85 mm ($n = 36$). The wall thickness and cup depth were 21.77 \pm 5.21 mm and 41.06 \pm 9.91 mm ($n = 35$), respectively, and the outer dimensions of the nests were 95.57 \pm 21.16 mm \times 89.51 \pm 17.18 mm and 66.63 \pm 14.50 mm ($n = 36$) high. To build these nests, we used materials from old nests of bird species that nested on the islands or from nests of other species of similar size. The only ground-nester on the islands, the Ladder-tailed Nightjar (Figure 1), does not build a nest; thus, for this nest category, we simply placed the eggs on the ground. To control for possible density effects, the number of artificial nests placed on each island was based on the maximum number of active nests recorded simultaneously on a given island in 2008, and we placed the same number of nests on the river edge to match each island (Figure 2A: red, $n = 5$; yellow, $n = 6$; blue, $n = 8$; green, $n = 12$; orange, $n = 4$). We placed artificial nests at similar locations and heights as natural nests: Ground nests were placed in open sandy areas, whereas cup and dome nests were placed \sim 1.5 m above the ground on similar vegetation. In each artificial nest, we placed 2 plasticine eggs (Figure 3A), matching the most common clutch size of nesting birds on the study area. Because egg coloration and size varied among nest types, we placed handmade, light-brown plasticine eggs with reddish brown spots in cup and ground nests and white eggs in dome nests. Because egg sizes vary among nest

TABLE 2. Summary of model selection results for nest survival in an artificial nest experiment in an Andean river habitat in southeastern Peru. Models are ranked by ascending value of Akaike's Information Criterion corrected for small sample sizes (AIC_c); w_i is the model weight, and K is the number of parameters. Factors in models included location of nests on islands and river edges (A), nest height (H), and nest type (NT), and a model with constant daily nest survival (BO). Deviance is computed as $-2[\log(L(\theta)) - 2\log(L_s(\theta))]$, where θ represents a maximum-likelihood estimate whose log likelihood is evaluated for the model in question [$L(\theta)$] and for the saturated model [$L_s(\theta)$].

Model	Deviance	K	AIC _c	Δ AIC _c	w_i
{BO + A + H}	200.90	3	206.92	0.00	0.65
{BO + A + NT}	200.79	4	208.83	1.91	0.25
{BO + A}	207.59	2	211.60	4.68	0.06
{BO + NT}	207.47	3	213.49	6.57	0.02
{BO}	214.10	1	216.10	9.18	0.01
{BO + H}	214.10	1	216.10	9.18	0.01

TABLE 3. Summary of bill marks, tooth (or claw) marks, and marks by unknown predators on plasticine eggs in artificial nests on islands and river edges in an Andean river habitat in southeastern Peru (n = total number of nests depredated; number of each type of mark is shown, with percentage of total depredated in parentheses).

Nest type	Islands				River Edges				Total			
	<i>n</i>	Bill	Tooth	Unknown	<i>n</i>	Bill	Tooth	Unknown	<i>n</i>	Bill	Tooth	Unknown
Dome	4	3 (75)	0 (0)	1 (25)	5	1 (20)	2 (40)	2 (40)	9	4 (45)	2 (22)	3 (33)
Cup	7	5 (71)	0 (0)	2 (29)	13	7 (54)	3 (23)	3 (23)	20	12 (60)	3 (15)	5 (25)
Ground	1	0 (0)	0 (0)	1 (100)	4	1 (25)	0 (0)	3 (75)	5	1 (20)	0 (0)	4 (80)
Total	12	8 (67)	0 (0)	4 (33)	22	9 (41)	5 (23)	8 (36)	34	17 (53)	5 (22)	12 (35)

type, we made the eggs 20×15 mm, 17×13 mm, and 27×21 mm for cup, dome, and ground nests, respectively.

The artificial nest experiment was conducted during October 3–22, 2009. Nests were checked every third day (days 4, 6, 9, 12, 15, and 18) for a total of 19 days. We ran the experiment for 19 days because this is the average incubation period documented for birds that nest in this island habitat (19 ± 4 days; $n = 8$ species). Nests in which either one or both eggs were missing or damaged were considered to have been depredated. We inspected plasticine eggs for signs of bill, tooth, or claw marks to determine the type of predator responsible for attacking the nest; 12 nests (35%) had marks that we could not identify, so we placed them in the “unknown predator” category; 58% of these nests had eggs missing or eggs with rhomboid marks, and in 1 nest, the marks seemed to have been made by ants. In an additional analysis, we compared nests depredated between small islands ($n = 4$) and the 1 large island, to explore a possible size effect in the predation rates on the islands.

Statistical Analyses

To compare predation rates between natural and artificial nests, we used a Wilcoxon signed-rank test for paired samples. We used contingency-table analyses to test our response variable (successful–failed nest) against our possible predictor variables: location of nest (island–river edge), type of nest (dome–cup–ground), and height of nest (ground–vegetation). Additionally, we calculated daily survival rates (DSR; i.e. the probability that a nest will survive a single day) using Program Mark (White and Burnham 1999) with a generalization of the estimator of maximum-likelihood analysis (Bart and Robson 1982). For each nest, the model required (1) the day it was found; (2) the last day it was checked when alive; (3) the last day it was checked; and (4) its fate (0 = successful, 1 = depredated). We incorporated nest location, type of nest, and height as covariates. Model support was evaluated using Akaike's Information Criterion (AIC; Dinsmore et al. 2002). To calculate the probability of nesting success, we used species with known nesting periods (duration of incubation and

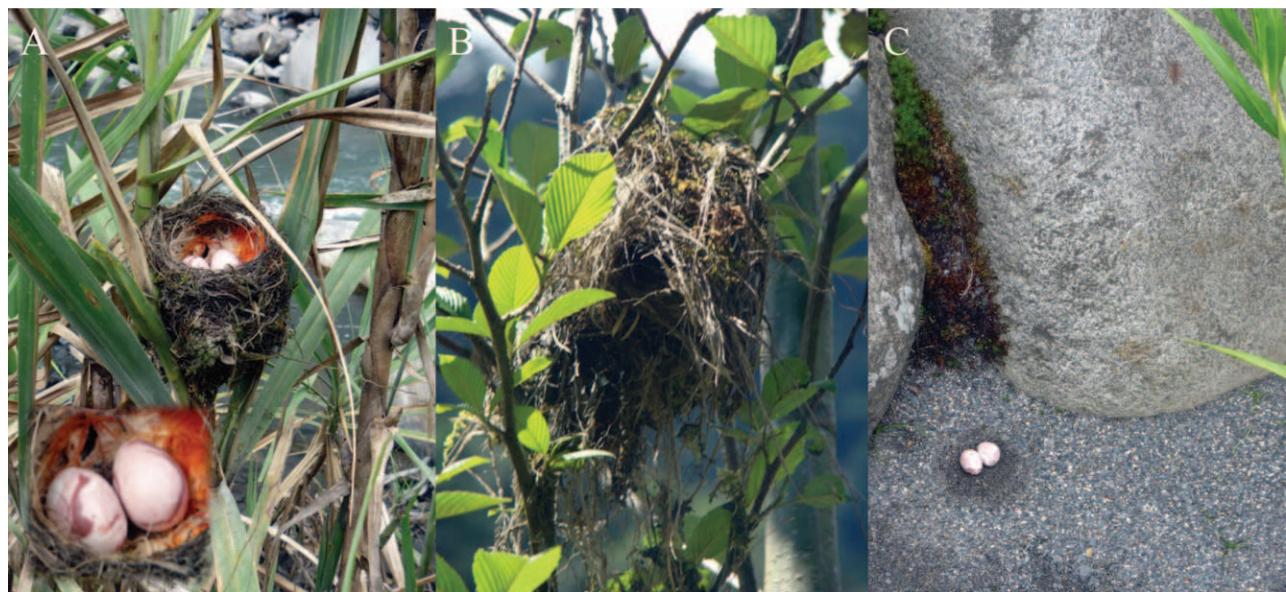


FIGURE 3. Nest types used during the artificial nest experiment. (A) Cup nest, and a close-up of the 2 plasticine eggs. (B) Dome nest. (C) Ground nest.

nesting period), in which the DSR values for each species were raised to the power of the length of the nesting period (e.g., *Ramphocelus carbo*: 0.952²³; Mayfield 1975).

RESULTS

Overall, there were no differences in the nest predation rate between natural and artificial nests ($P = 0.625$). Although 57% of the natural nests were depredated, compared with 49% of the artificial nests, daily survival rate (DSR \pm SE) was higher in natural nests (0.980 ± 0.003) than in artificial nests (0.963 ± 0.006). However, in agreement with our first hypothesis, both natural and artificial nests had higher DSR on islands than on river edge ($\chi^2 = 5.719$, df = 1, $P = 0.017$; Table 1).

Among natural nests on the river edges, 67% were depredated (DSR = 0.975 ± 0.004), whereas only 35% of the nests on the islands were depredated (DSR = 0.989 ± 0.004). When only the incubation period is taken into account, patterns of DSR in natural nests were similar (i.e. higher nest predation at the river edge), though the magnitude of the differences decreased to 20% (DSR = 0.987 ± 0.004) on river edges and 15% (DSR = 0.990 ± 0.005) on islands, compared with the entire nesting period (incubation + nesting period). Data from artificial nests also supported our hypothesis. Along river edges, 63% of artificial nests were depredated (DSR = 0.944 ± 0.012), whereas on islands only 34% of artificial nests were depredated (0.977 ± 0.007 ; Table 1). DSR also varied among nest types ($\chi^2 = 6.337$, df = 2, $P = 0.042$). On both islands (0.990 ± 0.005) and river edges (0.976 ± 0.011), ground nests had higher DSR than domes and cups, which presented similar DSR (<0.971; Figure 3). The model that included nest height and location (island or river edge) explained most of the variation in DSR ($w_i = 0.65$; Table 2). Based on the probability of survival, correcting for the length of the nesting period in each species, overall nesting success was higher on islands than on river edge for all species and nest types (Figure 4). Also, we found higher rates of success on the small islands (83%; DSR = 0.990 ± 0.007) than on the large island (30%; DSR = 0.936 ± 0.015).

We observed differences in nest predators between islands and river edge ($\chi^2 = 9.290$, df = 3, $P = 0.026$). Although birds were the most common nest predators (53%), and unknown predators the least frequent, on both islands and river edges (35%; Table 3), we often recorded small mammals preying on nests along river edges (22%)—but never on islands, consistent with our hypothesis. Nest predators did not attack different nest types equally ($\chi^2 = 14.411$, df = 6, $P = 0.025$). Birds preyed on cup (12/20) and dome (4/9) nests more frequently than ground nests (1/5). Similarly, small mammals frequently preyed on cup (3/20) and dome (2/9) nests located above ground (Table 3).

Unfortunately, we could not assign most of the ground-nest predation to a particular predator (4/5; Table 3), although for 3 of these nests, marks suggested predation by snakes (Marini and Melo 1998).

DISCUSSION

As we predicted, avian nesting success was higher on islands than on mainland river edges. Furthermore, data from artificial nests provided evidence that increased nesting success may result from some kinds of predators (e.g., mammals or snakes) being absent or scarce on islands, or at least on small islands. Therefore, even small patches of open, running water provide barriers to certain kinds of nest predators. Our results suggest that even in areas where nest predation is high, such as the tropics (Ricklefs 1969, Skutch 1985, Martin et al. 2006), nest predation risk can vary among habitats (Chalfoun and Martin 2009), which implies that there are potential refugia where species might be able to produce enough young to sustain local populations. Alternatively, the advantages of nesting on islands may be offset by the costs of flooding during the rainy season.

In temperate regions, studies that evaluated avian breeding success in lakes (Willms and Crawford 1989, Lokemoen and Woodward 1992) and river islands (Zoellick et al. 2004) found that visits of terrestrial predators to islands, and variance in predation rates, decreased as island isolation increased, similar to what is observed in oceanic islands (Losos and Ricklefs 2010). However, the increase in nesting success observed in temperate bird species nesting on islands may not be an important advantage, because nest predation risk is already lower in this region than in the tropics (Skutch 1985, Martin et al. 2006). Similar studies with artificial nests in the Neotropics (Loiselle and Hoppes 1983, Sieving 1992) found that birds on Barro Colorado Island had lower nest success than birds on the mainland, which the researchers associated with differences in predator assemblages. However, Roldán-Clarà et al. (2013) documented higher nest loss for Black Catbirds (*Melanoptila glabrirostris*) on mainland sites (74% failed) than on island sites (21% failed) that were ~30 km from the continent. Thus, it is not clear whether tropical birds that nest on continental islands consistently increase their nesting success. Furthermore, islands in those studies were separated by >1 km, so it is not surprising that large bodies of water are important barriers for tropical nest predators (e.g., *Cebus capucinus*, *Eira barbara*, *Nasua narica*, *Pseustes poecilonotus*, and *Spilotes pullatus*; Sieving 1992).

Given strong differences in nesting success between islands and river edges, it is possible that there is competition among and within species for nesting on

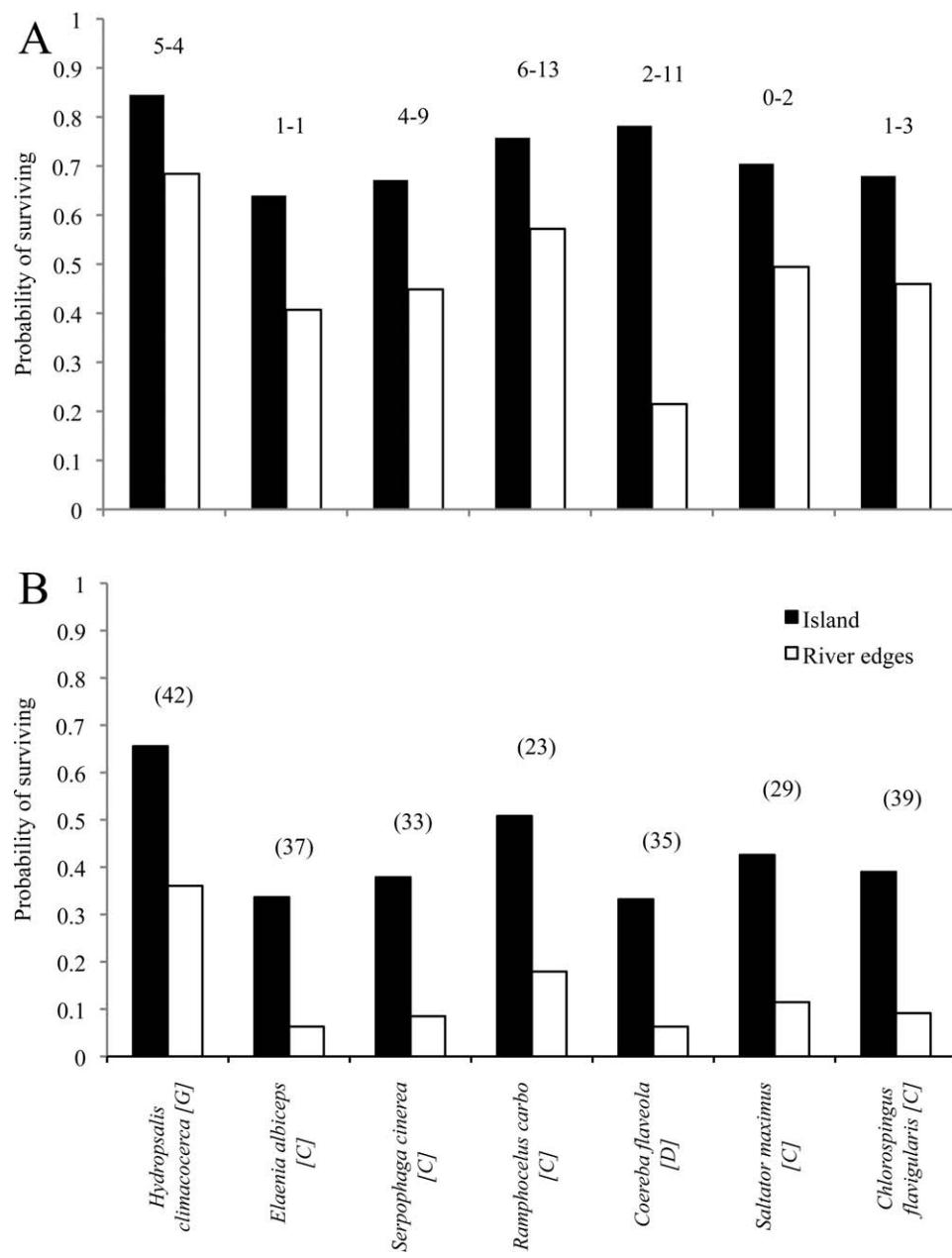


FIGURE 4. Probability of survival for 7 species nesting on islands (black bars) and on river edges (white bars) in southeastern Peru. (A) Natural nests; above bars are the numbers of nests found on islands or river edges (island-river edge; calculation was made with the daily survival rate for natural nests of each nest type). (B) Artificial nests; the length of the nesting period of each species is in parentheses above the bars. Nest types: G = ground, C = cup, D = dome.

these islands. Caciques, for example, compete intensely for access to nest sites on islands, where nesting success can be several times greater than on the mainland (Robinson 1985). Older and larger females dominate these habitats and are able to exclude many newcomers from nesting in these populations (S. Robinson personal communication). It would be interesting to determine whether similar competitive interactions occur in the more territorial species that we studied.

The difference in predation rates among the 3 types of nests means that the height of the nest could influence a predator's ability to detect it (Colombelli-Négrel and Kleindorfer 2008). In general, the nests we placed above ground in vegetation (domes and cups) suffered more predation than ground nests, which is consistent with results from previous studies (Loiselle and Hoppes 1983, Auer et al. 2007, Brawn et al. 2011, Roldán-Clarà et al. 2013). These differences may result from differences in

predator searching strategy: Nests located in vegetation above the ground, such as cup and dome nests, were located more reliably than ground nests.

We found that birds were the main predators on both islands and river edges and that they mostly preyed on cup and dome nests. Nests above ground can be more readily encountered by visual predators such as birds (Howlett and Stutchbury 1996). Additionally, the islands provided isolation from small mammal predators, which can be important predators in some habitats (Schmidt et al. 2001, Hausmann et al. 2005). Predation by unknown predators, some of which may have been snakes (Marini and Melo 1998), was mainly confined to river edges, but we found 3 events on the large island (twice the size of the others; green island in Figure 2A), which had higher predation rates than the small islands. This suggests that island size can influence the faunal assemblage (possible nest predators), which has been widely documented on a large scale in island systems (MacArthur and Wilson 1967, Jørgensen et al. 2007, Losos and Ricklefs 2010, Covas 2012).

We tested the assumption of similar predation rates on artificial and natural nests (Moore and Robinson 2004) by comparing our experimental results with results from natural nests. We found comparable predation rates, which supports the use of artificial nests to help elucidate factors that influence the success of natural nests (Berry and Lill 2003, Boyle 2008, Major and Kendal 2008). We found that artificial nests provide useful additional data, including sufficient numbers of nests for comparative analyses and information about predators in the area. However, it must be noted that artificial nests assess predation only during the incubation period; thus, we may have underestimated the DSR in artificial nests, because they were exposed for fewer days than the nesting period of natural nests. But considering just the incubation period, nest predation was still higher on the river edge than on the island, though the magnitude of these differences was smaller. Another consideration when using artificial nests is that parental activities, which could serve as an important cue for predators in finding bird nests (Martin et al. 2000), are not taken into account. However, the high rate of predation on artificial nests in our study suggests that the predators were as successful in finding artificial nests as in finding natural ones, so bird activity may not have been an important cue. Finally, we were unable to identify the predators of natural nests, so we cannot compare specific types of predators. However, data from nests away from the river in this area (G. Londoño personal observation) show that artificial nests may be undersampling snakes (Marini and Melo 1998).

In summary, we found that despite the small expanse of water between the river edge and the islands, the river was a strong barrier to predators. Thus, islands can serve as

nest-predation refugia for tropical birds. The extent to which these islands can act as a population source (*sensu* Pulliam 1988) that can sustain populations in tropical landscapes where nest predation rates tend to be high (Stutchbury and Morton 2001) depends on many other variables, including the size of the island, which determines how many individuals of a population can breed there, and the additional costs of nest flooding during rain events.

ACKNOWLEDGMENTS

We thank E. Tenorio, C. Flórez, A. Carter, R. Hannauer, M. Sánchez, and J. C. Bermudéz for help in the field. D. Blanco allowed us to work at Cock-of-the-Rock Field Station. K. Clark from the Environmental Change Institute, School of Geography and the Environment, Oxford, helped us with satellite photo and GIS analysis of the study area. J. Bailey, M. C. Estrada F., and C. Ramirez provided valuable comments and corrections on an early draft of the manuscript. This paper was written as part of a graduate course directed by F. Brown, E. Lasso, and A. Crawford. D. Cadena, S. Robinson, and D. Steadman provided insightful comments that improved the manuscript. Our research on animals was approved by the University of Florida's Institutional Animal Care and Use Committee. Financial support was provided by the Katherine Ordway Foundation, the Dexter Fellowships in Tropical Conservation, and the undergraduate thesis project fund from the Universidad de Antioquia (CODI).

LITERATURE CITED

- Auer, S. K., R. D. Bassar, J. J. Fontaine, and T. E. Martin (2007). Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *The Condor* 109:321–333.
- Bart, J., and D. S. Robson (1982). Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078–1090.
- Berry, L., and A. Lill (2003). Do predation rates on artificial nests accurately predict predation rates on natural nests? The effects of nest type, egg type and nest-site characteristics. *Emu* 103:207–214.
- Boag, P. T. (1987). Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). *The Auk* 104:155–166.
- Boyle, W. A. (2008). Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia* 155:397–403.
- Brown, J. D., G. Angehr, N. Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater (2011). Sources of variation in the nesting success of understory tropical birds. *Journal of Avian Biology* 42:61–68.
- Chalfoun, A., and T. E. Martin (2009). Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. *Journal of Animal Ecology* 78:497–503.
- Clark, K. E., M. A. Torres, A. J. West, R. G. Hilton, M. New, A. B. Horwath, J. B. Fisher, J. M. Rapp, A. Robles Caceres, and Y. Malhi (2014). The hydrological regime of a forested tropical

- Andean valley. *Hydrology and Earth System Sciences Discussions* 18:1–46.
- Colombelli-Négrel, D., and S. Kleindorfer (2008). Nest height, nest concealment, and predator type predict nest predation in Superb Fairy-wrens (*Malurus cyaneus*). *Ecological Research* 24:921–928.
- Covas, R. (2012). Evolution of reproductive life histories in island birds worldwide. *Proceedings of the Royal Society of London, Series B* 279:1531–1537.
- Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin (2007). Testing ecological and behavioral correlates of nest predation. *Oikos* 116:1887–1894.
- Fontaine, J. J., and T. E. Martin (2006). Habitat selection responses of parents to offspring predation risk: An experimental test. *American Naturalist* 168:811–818.
- Hausmann, F., C. P. Catterall, and S. D. Piper (2005). Effects of edge habitat and nest characteristics on depredation of artificial nests in fragmented australian tropical rainforest. *Biodiversity and Conservation* 14:2331–2345.
- Howlett, J. S., and B. J. Stutchbury (1996). Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. *The Auk* 113:1–9.
- Jørgensen, S. E., B. Fath, S. Bastianoni, J. C. Marques, F. Muller, S. N. Nielsen, B. D. Patten, E. Tiezzi, and R. E. Ulanowic (2007). *A New Ecology: Systems Perspective*. Elsevier, Amsterdam, The Netherlands.
- Lloyd, J. D. (2004). Nest-site preference and maternal effects on offspring growth. *Behavioral Ecology* 15:816–823.
- Loiselle, B. A., and W. G. Hoppes (1983). Nest predation in insular and mainland lowland rainforest in Panama. *The Condor* 85: 93–95.
- Lokemoen, J. T., and R. O. Woodward (1992). Nesting waterfowl and water birds on natural islands in the Dakotas and Montana. *Wildlife Society Bulletin* 20:163–171.
- Losos, J. B., and R. E. Ricklefs (Editors) (2010). *The Theory of Island Biogeography Revisited*. Princeton University Press, Princeton, NJ, USA.
- MacArthur, R. H., and M. Wilson (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Major, R. E., and C. E. Kendal (2008). The contribution of artificial nest experiments to understanding avian reproductive success: A review of methods and conclusions. *Ibis* 138: 298–307.
- Marini, M. Å., and C. Melo (1998). Predators of quail eggs, and the evidence of the remains: Implications for nest predation studies. *The Condor* 100:395–399.
- Martin, T. E. (1987). Artificial nest experiments: Effects of nest appearance and type of predator. *The Condor* 89:925–928.
- Martin, T. E. (2001). Abiotic vs. biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology* 82:175–188.
- Martin, T. E., R. D. Bassar, S. K. Bassar, J. J. Fontaine, P. Lloyd, H. Mathewson, A. Niklison, and A. Chalfoun (2006). Life history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* 60:390–398.
- Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- Martin, T. E., J. Scott, and C. Menge (2000). Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B* 267:2287–2293.
- Mayfield, H. F. (1975). Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- Moore, R. P., and W. D. Robinson (2004). Artificial bird nests, external validity, and bias in ecological field studies. *Ecology* 85:1562–1567.
- Ocampo, D., and G. A. Londoño (2011). Nesting of the Fulvous-breasted Flatbill (*Rhynchocyclus fulvipectus*) in southeastern Peru. *Wilson Journal of Ornithology* 123:618–624.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9.
- Robinson, S. K. (1985). Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *The Auk* 102:506–519.
- Roldán-Clarà, B., J. B. LaPergola, L. Chapa-Vargas, and S. Calmé (2013). Nest survival in the Neotropical Black Catbird (*Melanoptila glabrirostris*). *Journal of Ornithology* 154:491–499.
- Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer 2014. A classification of the bird species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>
- Schmidt, K. A., J. R. Goheen, R. Naumann, R. S. Ostfeld, E. M. Schauber, and A. Berkowitz (2001). Experimental removal of strong and weak predators: Mice and chipmunks preying on songbird nests. *Ecology* 82:2927–2936.
- Sieving, K. E. (1992). Nest predation and differential insular extinction among selected forest birds of central Panama. *Ecology* 73:2310–2328.
- Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* 36:575–594.
- Stutchbury, B. J. M., and E. S. Morton (2001). *Behavioral Ecology of Tropical Birds*. Academic Press, San Diego, CA, USA.
- Weatherhead, P. J., and G. Blouin Demers (2004). Understanding avian nest predation: Why ornithologists should study snakes. *Journal of Avian Biology* 35:185–190.
- White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.
- Willms, M. A., and R. D. Crawford (1989). Use of earthen islands by nesting ducks in North Dakota. *Journal of Wildlife Management* 53:411–417.
- Wright, S. K., G. V. Byrd, H. M. Renner, and A. L. Sowls (2013). Breeding ecology of Red-faced Cormorants in the Pribilof Islands, Alaska. *Journal of Field Ornithology* 84:49–57.
- Zoellick, B. W., H. M. Ulmschneider, B. S. Cade, and A. W. Stanley (2004). Isolation of Snake River islands and mammalian predation of waterfowl nests. *Journal of Wildlife Management* 68:650–662.

APPENDIX

TABLE 4. We detected 36 bird species using habitats created by rivers in the Kcosñipata Valley Cusco, Perú. Classification follows Remsen et al. (2013). R/M = resident or migrant. Habit: A = aquatic, T = terrestrial. RA = reproductive activity, as indicated by active or old nests or by carrying of nest material or food; and RA I/E = reproductive activity exclusively on islands or river edges (letter “x” indicates activity). Nest types (as found in the study area or according to literature): C = cup, G = ground, Cv = cavity, D = dome, and Dc = deep-cup bag shape. Habitat (where we observed the species): R = river, C = creek, F = forest, and Oa = open areas far from the river.

Species	R/M	Habit	RA	RA I/E	Nest type	Habitat
<i>Phalacrocorax brasilianus</i>	R	A			C	R
<i>Eurypyga helias</i>	R	A			C	R
<i>Tringa solitaria</i>	M	A			C	R
<i>Hydropsalis climacocerca</i>	R	T	x	x ^b	G	R
<i>Doryfera ludovicae</i>	R	T	x		C	C/F
<i>Chrysuronia oenone</i>	R	T	x		C	R/F
<i>Lochmias nematura</i>	R	T	x		Cv	C/F
<i>Elaenia albiceps</i>	R	T	x	x ^b	C	R
<i>Serpophaga cinerea</i>	R	T ^a	x	x ^b	C	R
<i>Mionectes striaticollis</i>	R	T	x		D	C/F
<i>Rhynchocyclus fulvipectus</i>	R	T	x		D	C/F
<i>Sayornis nigricans</i>	R	T ^a	x	x	C	R
<i>Myiozetetes similis</i>	R	T	x	x	D	R
<i>Myiodynastes chrysocephalus</i>	R	T	x		C	R/Oa
<i>Rupicola peruvianus</i>	R	T	x		C	C/F
<i>Cephalopterus ornatus</i>	R	T	x		C	R/C/F
<i>Stelgidopteryx ruficollis</i>	R	T			Cv	R/Oa
<i>Pheugopedius genibarbis</i>	R	T	x	x	D	R/F
<i>Cyphorhinus thoracicus</i>	R	T	x		Cv	C/F
<i>Cinclus leucocephalus</i>	R	T ^a	x		D	R/C
<i>Myadestes ralloides</i>	R	T	x		D	C/F
<i>Turdus ignobilis</i>	R	T	x		D	C/F
<i>Cissopis leverianus</i>	R	T			C	R/F
<i>Ramphocelus carbo</i>	R	T	x	x ^b	C	R/F
<i>Thraupis episcopus</i>	R	T	x	x	C	R/F
<i>Tangara cyanicollis</i>	R	T	x	x ^b	C	R/F
<i>Coereba flaveola</i>	R	T	x	x ^b	D	R/F/Oa
<i>Saltator maximus</i>	R	T	x	x ^b	C	R/F/Oa
<i>Ammodramus aurifrons</i>	R	T	x	x	D	R/Oa
<i>Sporophila castaneiventris</i>	R	T			C	R/Oa
<i>Chlorospingus parvirostris</i>	R	T	x		C	R/F
<i>Chlorospingus flavigularis</i>	R	T	x	x ^b	C	R/F
<i>Parkesia noveboracensis</i>	M	T ^a	x		C	R/C
<i>Psarocolius angustifrons</i>	R	T	x	x	Dc	R/C/F
<i>Psarocolius atrovirens</i>	R	T	x	x	Dc	R/C/F
<i>Euphonia xanthogaster</i>	R	T	x		D	R/B

^a Always associated with water.

^b Species used in the daily nest survival rate (DSR) analysis.