INTERSPECIFIC COLONIALITY IN TWO AMAZONIAN ICTERIDS

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Resumen. – Colonialidad interespecifica en dos ictéridos amazónicos. – El tamaño de la colonia en las aves puede estar relacionado con el éxito de la anidación debido al incremento de la protección y vigilancia de los miembros del grupo. Examiné los patrones de anidación en dos Ictéridos amazónicos y observé la variación entre colonias interespecíficas y colonias monoespecíficas. También comparé la distribución de las colonias en hábitats naturales y hábitats alterados por humanos. El número de nidos fue mayor en colonias interespecíficas así como en hábitats alterados por humanos. En colonias inter-específicas, el número de nidos de ambas especies estaban correlacionados positivamente uno con el otro. Estos resultados pueden sugerir beneficios de la colonialidad interespecífica, como el incremento de protección de nidos.

Abstract. – Colony size in birds may be related to nest success due to increased protection and vigi-lance from group members. I examined nesting patterns in two Amazonian icterids and looked for varia-tion between interspecific colonies and monospecific colonies. I also compared the distribution of colonies in natural and human-altered habitats. Nest numbers were higher in interspecific colonies as well as in human-altered habitats. In interspecific colonies, nest numbers of both species were positively correlated with each other. These results may suggest benefits to interspecific coloniality, such as increased nest protection. *Accepted 25 May 2012.*

Key words: Russet-backed Oropendola, *Psarocolius angustifrons*, Yellow-rumped Cacique, *Cacicus cela*, colony, defense, interspecific, Icteridae, nesting, Peru.

INTRODUCTION

The formation of colonies in birds may be an important behavioral adaptation to increase nesting success (Clark & Robertson 1979). Birds that nest in groups derive benefits from other group members in the form of increased vigilance and nest defense (Robin-son 1988). However, little is known about how factors such as predation may influence interspecific nesting aggregations and colony sizes (Clark & Robertson 1979, Wiklund 1982, Richardson & Bolen 1999).

Interspecific colony defense and vigilance has been suggested for two colonial Icterids, the Yellow-rumped Cacique (*Cacicus cela cela*) and the Russet-backed Oropendola (*Psaro-colius angustifrons angustifrons*) (Robinson 1985a, b). Both species construct large pendant nests in isolated trees (Hilty & Brown 1986). Nests of the two species are often placed in adjacent trees suggesting that they may derive benefits from being close to nesting colonies of the other species (Robinson 1985b, Hilty & Brown 1986, Robinson 1988, Schulenberg *et al.* 2007). Robinson (1985a, 1988) notes vari-ous instances where caciques and oropendo-las either actively defend the other's nests, or provide indirect protection via alarm calls.

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Thus, both species may benefit from increased defense by forming interspecific colonies (Haemig 2001).

Several studies have found decreased nest predation with higher nest numbers, including caciques in southeastern Peru and southeastern Brazil (Clark & Robertson 1979, Robinson 1985a, Raveling 1989, Wiklund & Anderson 1994, Duca & Marini 2008). However, many of the studies on caciques and oropendolas have not examined the potential for human influence on colony size and distribution.

Nesting colonies of both species are often located along river edges but they are also common along clearings adjacent to plantations and towns (Canaday 1997, Schulenberg et al. 2007). Nesting in completely natural sites may result in greater risk than nesting in human-altered habitats (Skutch 1966, Gering & Blair 1999) because of a decrease in nest predators near human settlements (Snow & Snow 1963).

Caciques return to sites where they were previously successful in rearing young and will not return to those sites where they were not successful, thus, the safest sites accumulate larger numbers of nests (Robinson 1985a). In this paper I compare the habitat characteristics and structure of monospecific and interspecific icterid colonies in the Peruvian Amazon. I also discuss some potential benefits of forming interspecific colonies and nesting in human-altered habitats.

STUDY SITES

I conducted this study in and around the Madre Selva Biological Station, 145 km east of Iquitos, Region Loreto, in northeastern Peru (3°37'2"S, 72°14'8"W). This station lies on the south bank of the Rio Orosa, a tributary of the Amazon River (Project Amazonas 2010). Along the Rio Orosa, there are small towns and indigenous villages, which pro-

vided opportunities to sample human-altered habitat as well as natural sites. I also took samples on the outskirts of Iquitos (3°44'53"S, 73°14'50"W) and along the Amazon River between Madre Selva and Iquitos. I conducted surveys for nesting colonies between 5 June 2010 and 20 August 2010, which coincides with the breeding season of both species (Robinson 1985a).

METHODS

I searched for active colonies of both species in a variety of ways. Along the Rio Orosa, I sampled colonies by kayak and foot. Local residents sometimes helped in directing me towards colonies. Along the Amazon River, I stood atop a *colectivo* waterbus, which stayed near the shore and moved slow enough to sample colonies. In the countryside surrounding Iquitos, I searched for colonies by *moto-taxi*, a three-wheeled motorcycle with a rear bench seat. I used 8x32 binoculars to make observations when conducting surveys.

Colonies were defined as a group of active nests in the same tree or adjacent trees during breeding season (Fraga 1989, Webster 1994). Active nests were identified by the color and quality of nest fibers. All nest trees contained within a contiguous open habitat and not separated by forest were considered part of the same colony. Schäfer (1957) notes that oropendola colonies often contain nest trees separated by 100–200 m. In my study, the largest maximum distance (i.e., two extreme ends of a colony) between any two nest trees was 90 m but the average was much lower (see Results). Interspecific colonies were defined using the same criteria but included both species. I limited surveys to mornings (6:00–9:00 h) and late afternoons (16:00–19:00 h) when birds were most likely to be attending nests (Webster 1994).

When a colony was located, I counted the number of clustered and isolated nests. For

caciques, clustered nests were defined as those within 1 m of at least two nests, while isolated nests were more than 1 m from any nest (following Robinson 1985a). Cacique nest clusters were often very apparent, with nests often touching. For oropendolas, I defined clustered nests as those within 1.5 m of each other, while isolated nests were those that were separated by more than 1.5 m (following Webster 1994, for related *Psarocolius montezuma*). I estimated distances between adjacent oropenodola nests using the length of their nests (about 1 m) as a proxy when it was not clear. I based this on one fallen nest that I measured, but Fraga and Kreft (2007) recorded a similar mean nest length of 1.1 m for *Psarocolius angustifrons alfredi* in Bolivia. Typically, oropendola nests were obviously isolated (see Discussion). All oropendolas in this study were of the black-billed form, *P. a. angustifrons*, as distinguished from the complex of pale-billed forms (Jaramillo & Burke 1999).

In order to assess nest site quality and make comparisons with previous literature I collected data for the following variables: estimate of tree height, number of occupied trees in the colony and estimate of distance between nest trees of the same colony. Additionally, I recorded presence or absence of wasp colonies on nest trees. I also looked for patterns between colonies in isolated trees and non-isolated trees. A tree was considered isolated if its branches did not reach another tree, which may deter some primates and other mammalian predators (see Robinson 1985a). These characteristics may be important determinants of colony site selection (Robinson 1985a, Fraga 1989).

Human-altered habitats were areas that were obviously manipulated by people including small villages and agricultural fields. Natural habitats were defined as areas that were not cleared, burned or altered by humans, but rather were formed by non-human disturbances. These included oxbow lakes, tree-fall gaps, sandbars, cocha edges, river edges, and islands.

I applied a Shapiro-Wilks test to assess normality of my datasets. I compared colony sizes, clustering, and tree characteristics between colony types using Welch's *t*-test or Mann-Whitney U-test depending on the distribution of the data. Relationships between nest numbers, distances of nest trees, and tree heights were tested using a Spearman rank correlation test. Distribution of colonies between habitat types was assessed using a chi-squared test. All statistical tests were conducted using program R version 2.11.1.

RESULTS

I found 43 active colonies of which 15 contained only oropendola nests, 11 contained only cacique nests, and 17 contained nests of both species. In the 43 colonies, I observed a total of 207 oropendola nests and 366 cacique nests spread over 68 trees. The mean number of nests varied between habitat and colony type (Fig. 1).

Interspecific colonies had higher nest numbers than monospecific colonies (Welch's *t*-test for unequal variances, $t = 3.582$, df $= 25.836$, $P = 0.001$). Cacique nest numbers within interspecific colonies did not differ from those within monospecific colonies ($P = 0.089$). However, there were more clustered cacique nests in interspecific colonies than monospecific colonies ($U = 50.5$, $P < 0.001$). There was no difference in number of clustered oropendola nests between interspecific and monospecific colonies ($P = 0.300$). Within interspecific colonies, the number of cacique nests was positively correlated with the number of oropendola nests ($r_s = 0.687$, n $= 17$, $P = 0.002$; Fig. 2).

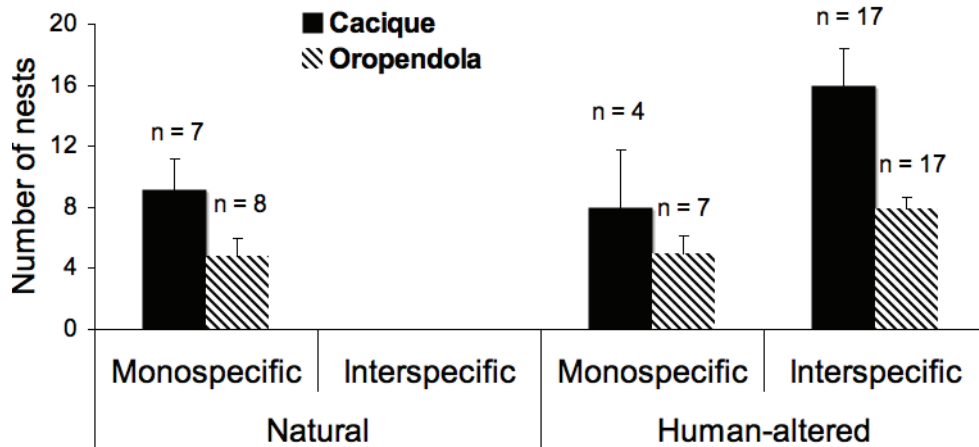Interspecific colonies contained more nest trees than monospecific colonies ($U = 60$, $P <$

FIG. 1. Mean colony size (number of nests ± SE) of Yellow-rumped Caciques and Russet-backed Oropendolas based on colony type (monospecific or interspecific) and habitat type (natural or human-altered) in northeastern Peru, summer 2010. Interspecific colonies were not found in natural habitats.

0.001). With the exception of one cacique colony, all monospecific colonies were composed of a single tree. In interspecific colonies, there were 14 instances where both species nested in the same individual tree. Sixty of 67 nest trees were isolated, but there was no difference in nest numbers between isolated and non-isolated trees ($P = 0.3433$). Tree height did not correlate with nest numbers ($r_s = 0.0867$, n = 43, $P = 0.5804$). The mean distance between trees of the same colony was 29.4615 m ± 6.5765, but distance also did not correlate with nest numbers ($r_s = 0.2444$, n = 13, $P = 0.4208$). I did not identify species of nest trees, which may also influence colony size and site selection (Fraga 1989). I found only four colonies near wasp nests, all were monospecific cacique colonies in natural habitats.

Interspecific colonies were found exclusively in human-altered habitats ($\Phi^2 = 15.756$, df = 1, $P < 0.001$). In monospecific colonies, the number of nests did not differ between human-altered and natural habitats for caciques ($U = 8$, $P = 0.2942$) or oropendolas ($U = 25$, $P = 0.7697$).

DISCUSSION

Nest numbers were higher in interspecific colonies and human-altered habitats. Furthermore, nest numbers of the two species were positively correlated when they nested together. Two plausible explanations for these results are food availability and protection. However, both species forage in markedly different microhabitats and substrates (Robinson 1988), so it is unlikely that food resource is a reason for coloniality, or that interspecific competition for food resources is a limiting factor to colony size.

If larger colony sizes are indeed beneficial to nesting success, then interspecific coloniality may be a tactic employed by both species to achieve it. Interspecific nesting may enhance site quality by increasing the total number of vigilant or defensive birds. This is consistent with Robinson's (1985a) observation that as nest numbers increased, so did the number of caciques defending the colony against Black Caracaras (*Daptrius ater*).

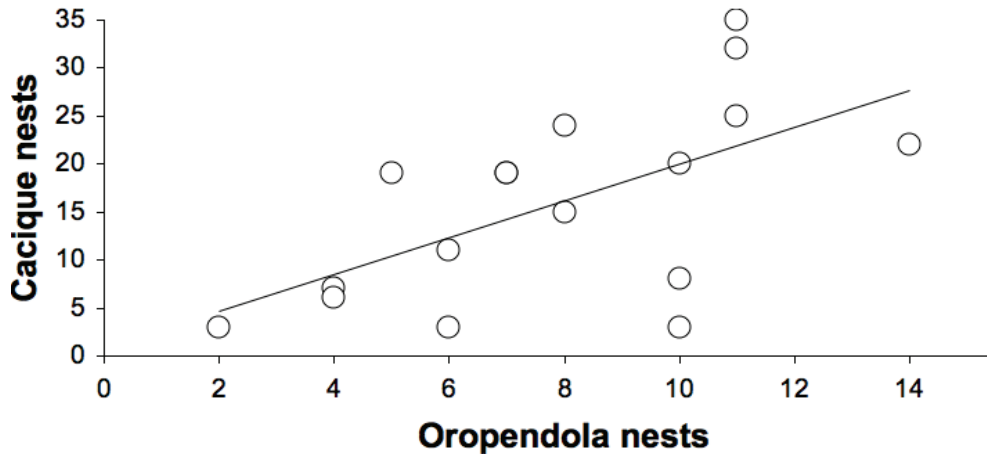Caciques and oropendolas may provide mutual protection (Robinson 1988, Haemig

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FIG 2. Relationship between number of Yellow-rumped Cacique and Russet-backed Oropendola nests in interspecific colonies in northeastern Peru, summer of 2010.

2001). Wiklund (1982) observed larger Field-fare (*Turdus pilaris*) colonies in association with nesting Merlins (*Falco columbarius*). Higher nest success and nest densities have been observed for other passerines in association with a protective species (see Clark & Robertson 1979 and Richardson & Bolen 1999). However, these situations represent commensal relationships where only one species benefits at no additional cost to the protective species. Caciques and oropendolas show a different pattern in that reciprocal protection is provided (Robinson 1988). Reciprocal protection may help explains the positive correlation of cacique and oropendola nests (Picman *et al.* 1988, Haemig 2001).

In this study, I did not measure nest success to complement nest numbers. However, Robinson (1985a) pointed out that Yellow-rumped Caciques are faithful to nest sites where they were previously successful and thus larger colony sizes may be indicative of higher nest success. Further work is needed to compare nesting success between interspecific and monospecific colonies.

Population densities could also explain such results. Indeed, populations of oropen-dolas or caciques were not measured here, so the potential for density to influence colony size remains plausible. However, if population densities between human-altered and natural habitats are different one might expect colony sizes to reflect this. So, since monospecific nest numbers between the two habitat types did not differ for either species, population densities may not be drastically different between the two habitat types (Fig. 1). This same observation also suggests that both natural and human-altered habitats are comparable as suitable nesting sites and that neither appears to be more limited than the other.

Caciques and oropendolas are closely related and have similar nesting ecologies partly due to shared predation risks. Therefore, there may be a tendency for association due to similar nesting requirements, which may then be promoted by interspecific defense (Whittam & Siegel-Causey 1981). In one interspecific colony, I observed several caciques defending a nest from an Orange-backed Troupial (*Icterus croconotus*), a noted nest pirate (Robinson 1985b). Caciques from trees as far as 20 m away mobbed the troupial as it attempted to enter a nest. Interestingly,

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the oropendolas were not present, but their nests may have benefited from the aggressive behavior of the caciques. This is consistent with the observation that cacique colonies are seldom vacant since foraging is accomplished in small groups rather than the entire flock as in oropendolas (Robinson 1988). Oropendolas are large enough to singly mob primates (Leak & Robinson 1988). Yet, caciques do not mob primates, thus they may benefit from the boldness of the larger oropendolas (Robinson 1985a).

The number of clustered cacique nests was higher in interspecific colonies. This may indicate higher demand for space near oropendolas. Robinson (1985a) found higher clustering in cacique colonies near wasp colonies. In my study, only four monospecific colonies were found to be in association with a wasp nests. Clustering patterns did not differ between monospecific and interspecific colonies in oropendolas. Since oropendola nests are much larger than cacique nests, they are more susceptible to branch breakage when clustered (Webster 1994). It seems that *P. a. angustifrons* may not exhibit the clustering behavior apparent in caciques. Similarly, *P. a. alfredi*, did not cluster their nests in Bolivia (Fraga & Kreft 2007).

Interspecific coloniality was observed when there were multiple isolated trees in a large open area surrounded by forest or river. However, I only found this situation in human-altered habitats, and perhaps it is less common in more natural habitats. Larger colony sizes in human-altered habitats may be attributed to; presence of a protective species (Wiklund 1982), greater number of isolated nest trees (Fraga 1989), greater number of already established nests (Brown & Rannala 1995), and lower number of terrestrial predators as a result of land clearing (Snow & Snow 1963). Such attributes were found in concert only in human-altered habitats. Caciques and oropendolas may be attracted to these habitats as a variety of beneficial nesting characteristics may result from human alteration.

All interspecific colonies were located within human-altered habitats. Thus, it is difficult to determine which is a stronger influence on nest numbers, characteristics of human-altered habitats or simply the presence of interspecifics. However, when looking at monospecific nest numbers in natural habitats vs. human-altered habitats, there was no difference in nest numbers for either species. This result suggests that in the absence of interspecifics, nesting sites in natural and human-altered habitats are comparable. Thus, the presence of interspecifics appeared to have a stronger effect on nest numbers than did nesting in human-altered habitats.

ACKNOWLEDGMENTS

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