

## AGGRESSIVE INTERACTIONS AND PRELIMINARY EVIDENCE FOR REVERSED SEXUAL DOMINANCE IN *RAMPHOCELUS* TANAGERS

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**Resumen.** – Las interacciones agresivas y evidencia preliminar para la dominancia sexual invertida en el género *Ramphocelus*. – Las aves a menudo compiten agresivamente por los recursos. Entre los passerines, los pájaros más grandes tienden a ser dominantes sobre pájaros más pequeños y los machos tienden a dominar a las hembras. La dominancia sexual invertida es una excepción a estas reglas, en la cual las hembras pequeñas con plumaje apagado dominan a los machos más grandes y brillantes durante encuentros agresivos. En 2002, investigué las interacciones agresivas que involucraron a la Tangara Enmascarada (*Ramphocelus nigrogularis*) y la Tangara de Piquiplateado (*R. carbo*) en la Hacienda Amazonia en Perú del sureste, donde pájaros son acostumbrados a alimentarse en comederos. Encontré que la Tangara Enmascarada fue dominante sobre la Tangara de Piquiplateado durante agresiones interespecíficas al alimentarse de bananas en el comedero. También, las hembras de la Tangara de Piquiplateado dominaron a los machos a pesar de que las hembras eran más apagadas y con menor peso. La dominancia de las hembras de la Tangara de Piquiplateado tal vez representa un ejemplo raro e inexplicado de la dominancia sexual invertida en los passerines.

**Abstract.** – Individual birds often compete aggressively with each other for resources. In passerines, larger birds tend to dominate smaller birds and males tend to dominate females. Reversed sexual dominance is an exception to these trends, whereby smaller females with drab plumage dominate larger and brighter males during aggressive encounters. I investigated aggressive interactions involving Silver-beaked (*Ramphocelus carbo*) and Masked Crimson tanagers (*R. nigrogularis*) at Amazonia Lodge in southeastern Peru, where birds are habituated to feeding stations. I found that Masked Crimson Tanagers were competitively dominant over Silver-beaked Tanagers during interspecific aggressions at banana feeders. Female-plumaged Silver-beaked Tanagers dominated adult males at banana feeders despite being drabber and lacking a weight advantage. Dominance of female Silver-beaked Tanagers may represent a rare and unexplained example of reversed sexual dominance in competitions over resources among passerines. *Accepted 22 February 2008.*

**Key words:** Masked Crimson Tanager, *Ramphocelus carbo*, *R. nigrogularis*, Silver-beaked Tanager, Peru.

### INTRODUCTION

Individual birds often compete for resources

with other individuals belonging to the same or different species. Interference competition, where one individual actively interferes with another's resource access, is often achieved by aggressive interactions between individuals (Ricklefs & Miller 2000). Some birds use interspecific aggression to enforce habitat

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partitioning between individuals of different species (Terborgh & Weske 1975, 1985; Robinson & Terborgh 1995), with heavier species dominating more productive portions of the habitat gradient (Robinson & Terborgh 1995). During aggressive, intraspecific interactions, heavier individuals tend to dominate individuals with less mass, and males dominate females in most passerine species (Piper 1997). North American cardueline finches in the genus *Carpodacus* offer a notable exception to these trends, where smaller and drabber females dominate larger males with ornamental colors and higher androgen levels, a phenomenon known as reversed sexual dominance (McGraw & Hill 2002).

In this paper, I investigate aggressive interactions involving Silver-beaked Tanagers (*Ramphocelus carbo*) and Masked Crimson Tanagers (*R. nigrogularis*) and ask two questions. First, does one species dominate aggressive interspecific interactions? Silver-beaked and Masked Crimson tanagers are closely related species within their genus (Hackett 1996), co-occur in Amazonian forests and riparian habitats, eat similar foods, and sometimes travel together in the same flock (Isler & Isler 1999). The average mass of the Masked Crimson Tanager (31 g) is 11% heavier than that of the Silver-beaked Tanager (28 g, Isler & Isler 1999). The ecological differences between *Ramphocelus* species are poorly understood, though the Masked Crimson Tanager is thought to forage higher off the ground than its congeners (Isler & Isler 1999). Masked Crimson Tanagers frequently occupy forest habitats at the margins of oxbow lakes, whereas Silver-beaked Tanagers more frequently occupy successional forests and scrubs along rivers (Ridgely & Greenfield 2001, Schulenberg *et al.* 2007). The lakeside forests are more productive than younger riparian successional habitats (Emmons & Dubois 2003). If Silver-beaked and Masked Crimson tanagers partition vegetation verti-

cally, as suspected, or along other habitat gradients, then this partitioning might be enforced through aggressive interactions as occurs in other Amazonian birds, whereby the heavier member of a congener pair occupies the more productive vegetation along partitioned habitat gradients (Robinson & Terborgh 1995). If Masked Crimson and Silver-beaked Tanagers partition habitat according to this model, then I predict that the heavier Masked Crimson Tanager should dominate Silver-beaked Tanagers during aggressive interactions, but this has not yet been documented.

Second, I ask do Silver-beaked Tanagers with adult male plumage dominate aggressive intraspecific interactions? Adult male Silver-beaked Tanagers differ strikingly from females and juveniles (which appear similar to females and hereafter are referred to collectively with females as female-plumaged birds) in appearance. Adult male Silver-beaked Tanagers have much darker reddish black plumage and paler silvery bill color compared to females and juveniles, which have browner plumage and dusker bills. If female-plumaged birds dominated adult males during aggressive interactions, then this could provide evidence for reversed sexual dominance in the Silver-beaked Tanager.

## METHODS

I studied *Ramphocelus* tanagers at Amazonia Lodge (12°52'S, 71°22'W; 514 m a.s.l.), in Depto. Madre de Dios, Peru during June 2002. As most birds in this region breed between mid-August and mid-November (Terborgh *et al.* 1990), including the Silver-beaked Tanager (Robinson 1997), the time period of my study likely preceded the majority of breeding activity. Blue-gray Tanagers (*Thraupis episcopus*), Silver-beaked Tanagers, Masked Crimson Tanagers, Black-billed Thrushes (*Turdus ignobilis*), and Russet-backed



FIG. 1. Feeding station with banana visited by *Ramphocelus* tanagers. From left to right; adult Masked Crimson Tanager (*R. nigrogularis*), immature Masked Crimson Tanager, adult male Silver-beaked Tanager (*R. carbo*), female-plumaged Silver-beaked Tanager, and another adult Masked Crimson Tanager. The male Silver-beaked Tanager is opening its beak in a silent gape threat display towards the adjacent female-plumaged Silver-beaked Tanager.

Oropendolas (*Psarocolius angustifrons*) were habituated to fruit and rice feeding stations at the lodge prior to my study through many years of regular (almost daily) feedings by the lodge operators. The feeding station used in this study was a horizontal branch elevated ~ 1.5 m off the ground. Metal nails projected upwards from the feeding station to which bananas were attached. The branch was wide enough for no more than one bird to perch comfortably on each of either side of the banana, but long enough for many birds to perch at the station simultaneously (Fig. 1).

To observe aggressive interactions and determine dominance during feeding visits, I set out single bananas with one or two sections of peel removed, in order to create an environment where aggressive interactions between birds were likely to occur. *Ramphocelus* tanagers use hunched postures and silent open-gape displays during aggressive interactions (Moynihan 1962). Any interactions between tanagers displaying hunched posture or silent gapes were considered events of aggression, as were interactions involving direct contact (fighting) between birds. I

recorded all aggressive encounters and their outcomes into a handheld micro-cassette recorder, and transcribed them immediately following feeding trials. For each aggressive encounter, I classified the bird that fled the spot of the aggression as the loser. I classified the outcome as neutral if neither bird fled at the end of aggressive displays. I recorded the species identity of all birds that interacted aggressively, as well as the plumage (adult male or female/juvenile for Silver-beaked Tanagers). I used chi-square tests to analyze outcomes of interactions. Observation time totaled 5 h over 10 days (mean = 30 min/day  $\pm$  4.5 SE), between 9 and 25 June 2002, with eight of ten feeding trials starting in the morning before 10:00 (EST).

The birds in this study were not individually marked or banded and I could not unequivocally collect multiple observations of aggression for individual birds. As in McGraw & Hill's (2002) study of aggression among a largely unmarked population of House Finches (*Carpodacus mexicanus*), pseudoreplication should not represent a statistical problem in this study because large groups of Silver-

beaked ( $\geq 17$  individuals) and Masked Crimson ( $\geq 9$  individuals) tanagers visited the area around the feeding station in this study and individual birds remained at food resources briefly, suggesting that my observations do not consist of one or few individuals aggressively displacing all others.

I used weight data from Silver-beaked Tanagers specimens (see Appendix 1) collected within Peru at the Louisiana State University Museum of Natural Science (LSUMZ) to determine if males and females differed in mass using two-tailed independent t-tests and assuming equal variances (SPSS, 2004).

## RESULTS

I observed 138 aggressive interactions between Silver-beaked and Masked Crimson tanagers. Masked Crimson Tanagers won 107 of these contests, whereas Silver-beaked Tanagers won 10 contests. Twenty-one contests resulted in neutral outcomes. Of the 117 interspecific contests with non-neutral outcomes, Masked Crimson Tanagers significantly dominated Silver-beaked Tanagers ( $P < 0.001$ ,  $\chi^2_1 = 80.4$ ). I did not record the sex of Silver-beaked Tanagers that won these interspecific contests.

I observed 104 aggressive interactions among Silver-beaked Tanagers. Of these, 19 were between adult males, 41 were between female-plumaged birds, and 44 were between adult males and female-plumaged birds. Of the contests between adult males and female-plumaged birds, female-plumaged birds won 34 contests, adult males won one contest, and nine outcomes were neutral. Of the 35 intraspecific contests among adult males and female-plumaged Silver-beaked Tanagers with non-neutral outcomes, female-plumaged birds significantly dominated ( $P < 0.001$ ,  $\chi^2_1 = 31.1$ ). Adult male Silver-beaked Tanagers had a heavier mean mass of ( $25.7 \text{ g} \pm 0.5 \text{ SE}$ ,  $n = 22$ ) than adult females ( $24.7 \text{ g} \pm 0.7 \text{ SE}$ ,  $n$

$= 20$ ), but this difference was not statistically significant ( $t_{40} = -1.085$ ,  $P = 0.284$ ).

## DISCUSSION

I found that Masked Crimson Tanagers were competitively dominant over Silver-beaked Tanagers during interspecific aggressions at banana feeders. Masked Crimson Tanager dominance over Silver-beaked Tanagers is consistent with Robinson & Terborgh's (1995) model, whereby the heavier member of a congener pair dominates the other, and Masked Crimson Tanager also frequently occupy more productive vegetation along lake margins compared to riparian habitat frequently occupied by Silver-beaked Tanagers. More research is required to determine if interspecific aggression occurs away from banana feeders in these two species.

Female-plumaged Silver-beaked Tanagers dominated adult males during aggressive intraspecific interactions, despite having drabber plumage and no weight advantage. It therefore appears that Silver-beaked Tanagers in this study represented a rare example of reversed sexual dominance in passerines whereby drab plumaged birds dominate ornamentally plumaged males. It would be appropriate if reversed sexual dominance occurs in birds inhabiting the Amazon Basin, itself named after powerful women of Greek mythology.

Future researchers may wish to repeat this study on a marked population, as well as to investigate hypotheses to explain reversed sexual dominance in Silver-beaked Tanagers. Several hypotheses exist to explain reversed sexual dominance in *Carpodacus* finches. First, the male deference hypothesis (Smith 1980, Brown & Brown 1988) suggests that males become more aggressive during courtship, but yield to females to enhance future breeding success. This hypothesis was rejected in a study of hatch-year House Finches (*Carpoda-*

*cus mexicanus*) where females won most aggressive encounters with males outside of the breeding season context (McGraw & Hill 2002). Other hypotheses for greater female ability to defend resources include that females have greater energetic requirements to complete reproduction (Samson 1977) or sole responsibility for defending nest territories (Belthoff & Gauthreaux 1991), and that aggressive behavior among females outside of the breeding season is merely an extension of the same behavior required at other times of the year or provides an unidentified benefit (McGraw & Hill 2002). Future researchers should investigate if reversed sexual dominance in Silver-beaked Tanagers is also observed during the breeding season or not, and if it occurs in other members of the genus.

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APPENDIX 1. Weight data used in this study, coming from the following *Ramphocelus* specimens collected between 1966 and 2001, from nine departments within Peru at the Louisiana State University Museum of Natural Science (LSUMZ).

Adult female *R. carbo* LSUMZ specimens (n = 20): 52453, 79279, 79283, 85528, 88956, 95239, 110946, 110947, 116176, 116177, 116178, 116179, 116182, 116189, 120360, 120361, 156838, 156840, 170231, 173171.

Adult male *R. carbo* LSUMZ specimens (n = 22): 52446, 52448, 52451, 52455, 79280, 79281, 79282, 79284, 88955, 106658, 110943, 110944, 116180, 116181, 116184, 116185, 116186, 116187, 116188, 116190, 120362, 156839.