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AGONISTIC BEHAVIOR OF BREEDING PURPLE GALLINULES *PORPHYRULA MARTINICA*: POTENTIAL ECOLOGICAL CORRELATES

COMPORTAMIENTO AGONISTA DE GALLITOS AZULES *PORPHYRULA MARTINICA* EN ESTADO REPRODUCTIVO: CORRELACIONES ECOLOGICAS POTENCIALES

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ABSTRACT

Purple gallinules *Porphyrula martinica* are territorial birds that breed in natural ponds with abundant aquatic vegetation as well as in rice fields. Observations of the aggressive behavior during the breeding season conducted on a rice field and on a naturally flooded savanna (estero), in the Central Llanos of Venezuela, showed that purple gallinules exhibit three types of agonistic behaviors towards conspecifics: replacements, chases and fights. Replacements are brief interactions involving two individuals in which one bird flies or walks toward another, with the result of the later moving away. Chases are pursues on vegetation or during flight, and fights are strong interactions involving mutual pecking and kicking. Fights were significantly longer in duration that replacements and chases in both sites but they were shorter in the rice field than in the natural pond. Replacements and chases were more frequent than fights in both breeding sites. Average overall interaction frequency (all types of aggressive interactions) was lower in the rice field than in the natural pond (0.83 and 2.04 h^{-1} respectively). Differences detected between sites do not mirror encounter probability because this was probably higher in the rice field than in the natural pond, as estimated from bird density in both sites (rice field: 31 ± 2.1 bird/ha, natural pond: 11.5 ± 0.9 bird/ha). Differences in frequency and duration among the three types of aggressive behaviors and between sites suggest some ecological correlates of aggression in breeding purple gallinules that must be analyzed.

Keywords: rice field, aggression, competition, resource defense, economic defense, fight

RESUMEN

Los gallitos azules *Porphyrula martinica* son aves territoriales que nidifican en cuerpos de agua naturales con abundante vegetación acuática y en arrozales. Observaciones de su comportamiento agresivo durante la época reproductiva realizadas en un arrozal y en un estero, en los Llanos Centrales de Venezuela, mostraron que los gallitos azules expresan tres tipos de conductas agresivas hacia sus coespecíficos: sustituciones, persecuciones y peleas. Las sustituciones son interacciones cortas que involucran a dos individuos, en las que un ave vuela o camina hacia otro, que resultan en la huida del segundo del sitio que ocupaba. Las persecuciones ocurren sobre la vegetación flotante o al vuelo, y las peleas son interacciones más fuertes que involucran picoteo mutuo, pateo y forcejeo. Las peleas duraron significativamente más que los otros tipos de interacciones en ambos sitios, pero duraron significativamente más en el estero que en el arrozal. Las sustituciones y las persecuciones fueron más frecuentes que las peleas en ambos sitios. La frecuencia global de interacción (todos los tipos de interacciones agresivas) fue menor en el arrozal que en el estero (0,83 y 2,04 h^{-1} respectivamente). Esta diferencia no refleja la probabilidad de encuentro entre individuos en cada sitio porque ésta probablemente fue mayor en el arrozal que en el estero, según estimaciones de la densidad de aves en ambos sitios (arrozal: 31 ± 2,1 bird/ha, estero: 11,5 ± 0,9 bird/ha). Las diferencias en la frecuencia y la duración de las interacciones en cada sitio sugieren algunas correlaciones ecológicas de la agresión en los gallitos azules que deben ser analizadas.

Palabras clave: arrozal, competencia, defensa del recurso, defensa económica, pelea

INTRODUCTION

The term agonistic behavior includes all of the possible competitive interactions between two or more individuals, whether submissive or aggressive, from ritualized displays to actual fights (Grier and Burk 1992). Agonistic behaviors are associated with access to or protection of valuable resources and result in the spacing out of individuals (Davies 1978). Intraspecific agonistic behaviors displayed during the breeding season are often related to territorial defense (Davies and Houston 1984), mate acquisition or defense (Eens and Pinxten 1995), defense against brood parasitism (Møller 1987), offspring protection (Hotta 1994) or intra-sexual competition for parental care (Sandell and Smith 1997).

Competing individuals are predicted to adjust the level of aggressive behaviors in relation to the relative costs and benefits derived from aggression (Brown 1964). The intensity (i.e., duration, frequency or amplitude) of aggressiveness is often correlated with resource abundance, distribution or quality, and also with the number of potential competitors (Davies and Houston 1984, Milinski and Parker 1991). Specifically, models of economic resource defense predict that aggressiveness should increase as the spatial clumping of resources increases from low to moderate, but decrease as temporal clumping increases (Brown 1964, Emlen and Oring 1977). Aggressiveness should also increase as resource quality varies in space or as the number of competitors decreases (Davies and Houston 1984, Milinski and Parker 1991). These predictions have empirical support (e.g., Gill and Wolf 1975, Carpenter 1987, Robb and Grant 1998).

Purple gallinules are widely distributed from southern North America to northern Argentina (Blake 1977). They are very common in natural ponds and rice fields in the seasonally-flooded savannas (llanos) of Venezuela during the wet season, when they breed. Purple gallinules arrive at the llanos at the onset of the wet season (May-June), breed and depart at the beginning of the dry season (December) (Thomas 1979). Despite their abundance, little is known about their natural history and general behavior in the savannas of northern South America (McKay 1981, Lira and Casler 1982, Tárano *et al*. 1995). Purple gallinules have been observed to reproduce cooperatively (i.e., have helpers at the nest) in permanent ponds in Costa Rica (Krekorian 1978, Hunter 1985) and observations suggest that they also form cooperative groups in Venezuelan seasonal savannas (Tárano 1990). In Costa Rica, reproductive groups consist of one breeding pair plus up to eight non-breeding helpers, that defend the territory, feed and protect the chicks (Krekorian 1978, Hunter 1985). However, aggressive behaviors involved in territory defense have not been described and potential ecological correlates of these behaviors have not been analyzed either.

The main purpose of this observational study was to describe the agonistic behavior of the purple gallinules, during the breeding season, at two sites in the Central Llanos of Venezuela: a naturally flooded savanna (estero) and a rice field. Naturally flooded savannas and rice fields are floristically and physiognomically different, thus, this study might also help elucidate potential ecological correlates of aggressive behaviors in this marsh bird.

METHODS

I conducted the study in a natural pond (2.34 ha) at Hato Masaguaral and in two contiguous plots at a rice field (0.28 and 0.41 ha respectively) at Hato La Esperanza. Both ranches are located in the Central Llanos of Venezuela in Guárico State (8°34'N, 67°35'W) about 10 Km apart. I observed the birds during their breeding season, from October to mid December 1988. Purple gallinules do not move between habitats while they are breeding.

Aggressive interactions

I observed the birds from 700 to 1100 h and from 1500 to 1800 h, from two 6-m high scaffolds, one at each site, using a 16-36 x zoom telescope. Observation periods lasted three to four hours straight through and observation time did not vary among days. Observations were performed every two days on each site alternatively. I estimated bird density through direct counts of individuals twice during each observation period, one at the beginning and one at the end. I averaged these two counts to obtain daily estimations of bird densities. With these figures I estimated average bird density for each site (results are means ± standard errors). I estimated the area of the naturally flooded savanna (estero) occupied by birds by using a scale map drawn from aerial photographs and a planimeter. The rice plot was irregularly shaped and was divided into two triangles and a rectangle whose perimeter

were measured in the field. Although vegetation structure and distribution varied between the rice field and the naturally flooded savanna and may affect detection probability, birds were easily observed because they spent a lot of time feeding, preening and resting on emergent and floating vegetation.

I recorded all instances of aggressive behaviors and registered their duration (time from the beginning to the end). Interactions always involved vocalizations that made their recording and localization easy and reliable. In addition, the areas occupied by several breeding pairs could be observed simultaneously because they were contiguous. I also recorded the number of birds involved on each interaction. I classified aggressive interactions in relation to their level of escalation. I calculated interaction frequencies (interactions/h) for each type of aggressive behavior for each observation period and with these figures, I estimated average interaction frequency for each aggressive behavior and for all aggressive behaviors as a whole for each site (results are means ± standard errors).

Statistical analysis

I compared average duration of all types of aggressive behaviors between and within sites with a two-way ANOVA, after testing for variance suppositions (Bartlett´s test). I used a G-test of independence to examine whether the frequency of each type of aggressive behavior was independent of the site (Sokal and Rohlf 1995). I also compared overall average interaction frequency (all types of interactions included) for observation period at the naturally flooded savanna and at rice field using the Mann Whitney U-test. Analyses were performed with Statgrafics 6.0.

RESULTS

I observed breeding purple gallinules during 33.3 hours in 24 days in the naturally flooded savanna and during 47.4 hours in 23 days in the rice field. Average bird density was higher in the rice field than in the natural savanna (31 ± 2.1 bird/ha and 11.5 ± 0.9 bird/ha respectively), thus encounter probability was probably higher in the former than in the latter. I recorded 88 interactions in the natural savanna and 32 in the rice field and measured the duration of 55 interactions in the former and of 31 interactions in the latter. Most interactions occurred between two individuals at both sites.

I identified three types of aggressive interactions. These were, in order of escalation, as follows:

Replacement: One bird flied or walked toward another, with the result of the later moving away. During replacements the approaching bird usually tried to land beside or above the standing bird. The approaching bird often produced vocalizations. Replacement occurred while the birds perched on floating or emergent vegetation. Most replacements involved only two individuals (88%), the substitute and the substituted, but ocassionaly one bird could be replaced sucessively by two (10%) or three individuals (2%). The substituted bird often remained near the substitute.

Chase: One bird pursued another, vocalizing and flapping its wings. Chases usually occurred on floating vegetation, but might also occur at flight. Chases typically involved two individuals (74%) but occasionally one (18%), two (5%) or more birds (3%) could join the pursuer.

Fight: One bird approached another and both engaged in mutual chases, pecks and kicks, while emitting loud vocalizations. Two birds usually initiated fights (52%) but one (21%), two (16%), three or more (11%) additional individuals might join them.

The three types of aggressive interactions were observed in both breeding sites. Two-way analysis of variance showed a significant difference in the duration of interactions between sites (Table 1: $F_{1,82} = 3.92$, $P = 0.05$) and also a significant difference in duration between the three types of interactions (Table 1: $F_{2,82} = 8.22$, $P = 0.001$). All types of interactions were significantly longer in duration in the naturally flooded savanna than in the rice field, and fights were significantly longer than chases and replacements.

The relative frequency of replacements, chases and fights was not significantly different between breeding sites (G-test, G = 4.072, ns): replacements and chases (the mildest interactions) were more frequent than fights (the strongest interaction) in both sites (Figure 1). However, average interaction frequency was lower in the rice field than in the natural pond (0.83 ± 0.18 and 2.04 ± 0.59 h^{-1} respectively), the difference being

Table 1. Duration in seconds of the three types of aggressive interactions observed in the naturally flooded savanna and in the rice field. Results are means ± SD, sample size in parenthesis.

	Type of interaction		
	Replacements	**Chases**	**Fights**
Naturally flooded savanna	0.21 ± 0.14 (23)	0.21 ± 0. 17 (17)	0.57 ± 0.58 (15)
Rice field	0.13 ± 0.10 (17)	0.15 ± 0.11 (7)	0.26 ± 0.21 (7)

significant (U-test, two-tailed, U = -1.92, n_1= 24, n_2= 23, P = 0.03).

DISCUSSION

Purple gallinules showed diverse aggressive behaviors towards conspecifics during the breeding season. Interactions varied in their level of escalation from relatively short and safe interactions (replacements and chases) to relatively long and risky interactions. The frequency of aggressive interactions varied between breeding sites probably in relation to differences in payoffs of aggression.

Under a cost-benefit approach, costly interactions are expected only if gains are high enough to overcome their cost, for example when defending high quality foods, or protecting the nests or the chicks (Brown 1964, Parker 1974, Maynard Smith and Parker 1976). Purple gallinules prey upon the eggs of conspecifics and heterospecifics (McKay 1981), thus, breeding pairs or other group members are expected to show intense aggressive behaviors, i.e., fights, when other birds are in the vicinity of their nests or chicks. On the other hand, within a group, reassurance of dominance, immediate access to food resources or preferred perches can be achieved at low cost through relatively mild interactions such as replacements and chases. Similarly, territory boundaries can be patrolled at low cost through chases, and fights can be a secondary option when intrusion persists. Observations at the naturally flooded savanna, where territory limits were identified, support all of these predictions. First, substituted birds usually remained visible and close to the initiator (substitute). Second, chases usually resulted in one bird crossing out a territory boundary, and the pursued bird usually disappeared amidst emergent vegetation, while the pursuer returned to its original position. Third, fights usually occurred at the boundaries of territories or in the vicinity of the nests, and involved several individuals more often than replacements and chases. Observations at the naturally flooded savanna indicate that purple gallinules breed cooperatively in the llanos, and breeding groups consist of one breeding pair and 0 to 2 helpers (Tárano 1990). Thus birds involved in fights might have been from two breeding groups. Fights were the longest, in duration, although the less common interaction in both sites. The relatively lower frequency of fights might be related to their potential higher fitness costs (Jakobsson *et al.* 1995).

The results of this study suggest some ecological correlates of aggressive behaviors in purple gallinules that must be investigated. The naturally flooded savannas are physiognomically and floristically more complex and diverse than rice fields. Although plant richness in rice fields is high (up to 74 species from 19 families, Anzola 1981), rice fields are dominated by one species (*Oryza sativa*) both in terms of relative cover (> 90%) and absolute frequency. Whether spatial heterogeneity in the naturally flooded savanna

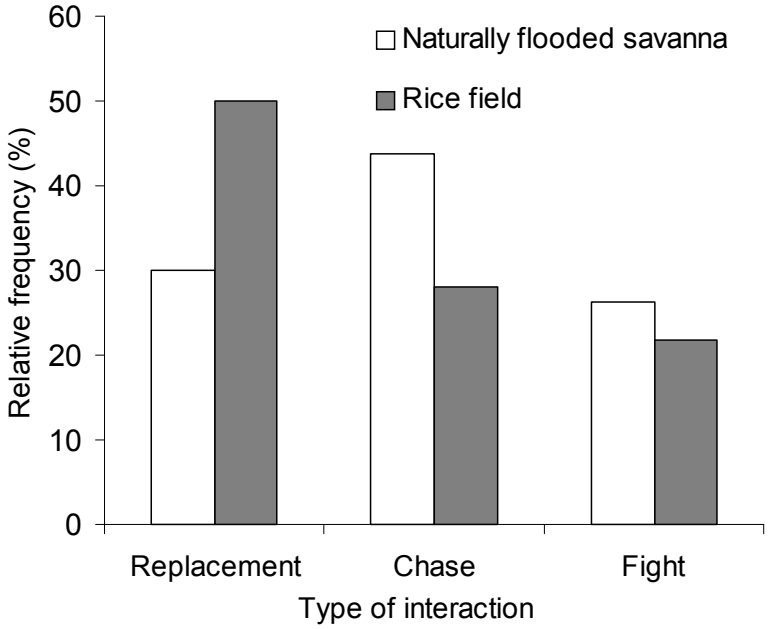

Figure 1. Relative frequency of three types of aggressive interactions in the naturally flooded savanna and in the rice field.

corresponds to differences in relative abundance and/or quality of valuable resources for breeding purple gallinules, and whether these differences correlate with interaction frequency remains to be addressed in future studies. The correlation between individual aggression and patchy or irregular resource distribution, or local differences in resource abundance has been demonstrated in several vertebrates (Zahavi 1971, Gill and Wolf 1975, Sullivan 1988, Grant and Guha 1993, Larsson and Hemborg 1995, Thresher 1997, Robb and Grant 1998).

The rice field and the naturally flooded savanna also differed in the number of potential conspecific competitors. Bird density in the rice field was more than twice as high as that in the natural pond. Differences in vegetation structure between sites could be expected to affect density estimates. Specifically since vegetation density is higher and plant distribution is more uniform in the rice field than in the natural pond, detection could be impaired in the former. However, my estimates are similar to those found by other researches during walk counts. For instance, Lira and Casler (1982) reported minimum densities of 15 bird/ha in a rice field at Portuguesa State in Venezuela, and McKay (1981) reported minimum densities of 20-27 birds/ha in Colombian rice fields. The number of individuals may affect interaction frequency in several ways. When many individuals occupy an area, the probability of encountering another individual at specific sites increases. As a result, interaction frequency may also increase. However my results run in the opposite direction: interactions were more frequent in the natural savanna than in the rice field.

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