

GROUP TERRITORIALITY AND PLURAL BREEDING IN THE PURPLE GALLINULE (*PORPHYRULA MARTINICA*) IN A SEASONALLY FLOODED SAVANNA IN VENEZUELA

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Resumen. – Territorialidad grupal y anidación múltiple en el Gallito Azul (*Porphyryula martinica*) en una sabana estacionalmente inundable de Venezuela. – El sistema reproductivo del Gallito Azul (*Porphyryula martinica*) se examinó en una localidad de los llanos (sabanas inundables) de Venezuela y se comparó con lo reportado para Centro América, donde las condiciones ecológicas son diferentes. Se determinó el tamaño y la estructura de la unidad reproductiva, el tamaño de la nidada, la tasa de interacciones territoriales, el tamaño y la calidad de los territorios y se establecieron las relaciones entre dichas variables. Se identificaron 2 parejas y 11 grupos territoriales, de los cuales, 9 tenían una pareja reproductiva (reproductores sencillos) y 2 tenían más de una pareja (reproductores múltiples), que anidaban por separado. Hubo asociación positiva entre el tamaño del grupo y el tamaño del territorio ($r_s = 0.63, P = 0.029$), y entre el tamaño del grupo y la calidad del territorio estimada a través del área cubierta por plantas consumidas por el gallito ($r_s = 0.85, P = 0.0004$) y del área cubierta por vegetación ($r_s = 0.81, P = 0.001$). Además hubo asociación entre el tamaño del territorio y la tasa de interacciones territoriales totales ($r_s = 0.68, P = 0.031$), pero no con la tasa de interacción *per capita*. Esto sugiere que todos los miembros del grupo comparten la defensa del territorio. Se propone que los beneficios de la cooperación para los no reproductores resultarían del acceso a recursos (ganancias directas). Los grupos y los territorios fueron más pequeños y de mayor calidad en la sabana estacional en Venezuela que en las lagunas permanentes estudiadas en Centro América donde, además, los ayudantes eran juveniles. Las diferencias probablemente se deben a que la riqueza y diversidad vegetal del hábitat es mayor en Venezuela mientras que la densidad poblacional es menor. Esto último probablemente hace posible que una pareja sola o un grupo pequeño defiendan un territorio. Se concluye que las condiciones ecológicas afectan las conductas asociadas a la reproducción en el Gallito Azul, porque se encontraron parejas, reproductores sencillos (con ayudantes) y reproductores múltiples (con o sin ayuandes). Esta diversidad reproductiva no había sido descrita anteriormente en una población de Gallitos Azules.

Abstract. – The reproductive system of Purple Gallinules (*Porphyryula martinica*) was examined in the central llanos (seasonally flooded savannas) of Venezuela and compared with that from Central America where ecological conditions are different. Unit size and structure, clutch size, territorial interaction rate, territory size and quality were determined and the relationships between these variables were established. Two breeding pairs and 11 group territories were identified, of which 9 were single breeders and 2 were multiple breeders that nested separately. Associations between group size and territory size ($r_s = 0.63, P = 0.029$) as well as group size and territory quality, assessed by area covered by food plants ($r_s = 0.85, P = 0.0004$) and by the area covered by plants ($r_s = 0.81, P = 0.001$), were found. A relationship was found between territory size and territorial interaction rate ($r_s = 0.68, P = 0.031$), but not between the former and individual (*per capita*) interaction rate. The latter result suggests that all group members share defense duties. Benefits

of cooperating for non-breeders might derive from access to high quality resources. Group and territory sizes were smaller in the seasonally flooded savanna of Venezuela than in the permanent lagoons in Central America where, in addition, helpers were juveniles. Differences probably result from the habitat being more diverse and richer, while the population density is lower, in Venezuela. The latter probably makes territory defense by pairs or small groups feasible. I conclude that ecological conditions affect behaviors associated with reproduction in Purple Gallinules, because single pairs (no helpers), plural breeders (with and without helpers) and singular breeders (with helpers) were all found in the study. Such diversity within the same population of Purple Gallinules had not been reported before. *Accepted 27 September 2007.*

Key words: Purple Gallinule, *Porphyryla martinica*, cooperative breeding, group size, clutch size, territory size, territory defense, territory quality, non-breeder, helper.

INTRODUCTION

Group territoriality, the defense of a territory by more than two individuals, is uncommon in birds and known only during reproduction (Brown 1987). Group territorial units can be formed by one reproductive pair plus one or more non-reproductive individuals (singular-breeding units) or by two or more reproductive females, either monogamous or not, that lay jointly or in separate nests, with or without additional non-reproductive individuals (plural-breeding units). Differences in group size and structure in different habitats have been observed within and between populations in several species of birds (e.g., Brown & Balda 1977, Stacey & Bock 1978). For example, in the llanos of Venezuela, two subpopulations of Bicolored Wrens (*Campylorhynchus griseus*), less than 2 km apart, one inhabiting mixed habitat of open palm savanna, and the other mixed shrub-woodland and palm savanna, show striking differences in the social system (Austad & Rabenold 1985). The denser subpopulation of the open palm savanna had large groups with helpers of both sexes; the subpopulation of the shrub-woodland and palm savanna had small groups, usually without helpers but mainly males if any present.

Cooperative care of the young by non-reproductive members of the group occurs in most species with group territories (Gaston 1978), and usually relate to delayed breeding and reduced dispersal (Brown 1987); the later

increases intruder pressure and territory defense expenses. Thus, cooperative defense may help offset these costs while reducing abandonment of the young during interactions with intruders (Brown 1964). However, territory sharing entails several costs, resources depletion being the most important (Koenig *et al.* 1992). Therefore, benefits gained through cooperative defense must overcome the disadvantages of sharing resources with additional individuals for group territoriality to evolve (Gaston 1978).

Purple Gallinules (*Porphyryla martinica*) inhabit slow-flowing river margins, lagoons and ponds with aquatic vegetation from southern United States to Uruguay. They have been described as territorial and monogamous with both members of the pair sharing reproductive duties (Gross & Van Tyne 1929). In addition, cooperative breeding has been described for Purple Gallinules occupying permanent lagoons in Costa Rica where they remain year-round (Krekorian 1978, Hunter 1985a). Short-range migrations have been reported in Brazil and Colombia (Blake 1977), United States (Scott & Cutler 1974) and Venezuela (Lira & Casler 1982). In Venezuela, birds arrive at central and southern llanos (flooded savannas) at the beginning of the wet season (May–June) (Thomas 1979), establish territories, and initiate reproduction. They depart in late December (Thomas 1979), at the beginning of the dry season, just after juveniles molt into adult plumage,

but juveniles also travel (pers. observ.). There are no reports of destination localities for these birds. I have observed juveniles arriving in the llanos in June, which suggests that the same Purple Gallinules breed at least twice a year, once in the llanos during the wet season, and another time elsewhere, perhaps in permanent lagoons in northern Venezuela.

Purple Gallinules breeding in Venezuelan llanos seem to face ecological conditions different from those described in Costa Rica. In Costa Rica, they are sedentary and inhabit relatively stable environments (swamps or permanently flooded areas). In Venezuela, they make short-range migrations and move between habitats as flood level and vegetation change throughout the year. I investigated territoriality in relation to reproduction in Purple Gallinules in the central llanos of Venezuela with the aim of determining whether differences in ecological conditions and habits, compared to populations in Costa Rica, affect their behavior. Although this has been tested in several birds (e.g., Craig 1979, Langen & Vehrencamp 1998), Purple Gallinules have been poorly investigated over their distribution range, especially in Venezuela, despite their abundance (but see Tárano *et al.* 1995, Tárano 2003). In Venezuela and Colombia, they are mostly perceived as pests because of their tendency to nest and feed in rice farms (McKay 1981, Elías & Valencia 1984, Gutiérrez 1994, Poleo & Mendoza 2000). Because rice farms are qualitatively similar to the preferred habitats of Purple Gallinules, the latter have occupied these anthropogenic habitats in addition to their natural habitats. However, their behavior in rice farms and natural habitats differs (Tárano 2003).

METHODS

Study site. I conducted field work in Fundo

Pecuario Masaguaral, Guárico State, 50 km south of Calabozo city (08°34'N, 67°35'W), in the central llanos of Venezuela, during one wet season (June–November). The dominant features of the llanos are low relief and open grasslands, interrupted by gallery forests. During the wet season, rain fills the low-lying depressions, locally named “bajíos” and “esteros” (see Ramia 1967 for definitions), resulting in seasonal ponds. Plant communities are complex, and most species develop into dense colonies whose shape and extension vary over the season (Troth 1979). I observed Purple Gallinules in a seasonal pond (bajío) of approximately 2.3 ha, an artificial pond approximately 0.20 ha, which dried out completely during the dry season, and also in a portion of a naturally flooded area which held water throughout the year.

Group structure and territoriality. Observations of territorial behavior took place from 06:30 to 11:00 h and from 15:30 to 18:30 h, 5 days a week, for a total of 134 h. They were performed from 6-m high scaffolds placed at the margins of the ponds, using a 16–36 x zoom telescope. Most birds were color banded (leg bands), or otherwise identifiable by natural marks (e.g., missing feathers, relative size of the yellow tip of the bill, relative size of the frontal shield). Birds were easily observed from a distance since they spent much time walking on vegetation in search of food. Ponds were regularly and thoroughly visited in search of nests or any evidence of breeding activities. Purple Gallinules build several nests before laying eggs in one of them, and also make resting platforms (pers. observ.), both by entwining the soft stems of emergent grasses and sedges several centimeters above the water. Nest location was registered on scale maps of each site and visited regularly to check breeding activity, and to determine clutch size and egg-hatching.

I recorded bird presence in the vicinity of

TABLE 1. Group size and composition, territory size and quality, and interaction rate at the three study sites. Group size of PR2 was two individuals from August to September and three from October. Groups N7 and C1 had two and three reproductive couples respectively, couples laying separate clutches of indicated size.

Site	Group	Goup size	Breeding couples	Clutch size	Territory size (m ²)	Interaction rate (h ⁻¹)	<i>Per capita</i> interaction rate (ind ⁻¹ h ⁻¹)	Total cover (%)	Food plants cover (%)
Seasonal pond	N4	2	1	6	704.24	1.21	0.61	83	42.3
	IPZ1	2	1		636.26			86.6	53.8
	ARB1	3	1	6	652	0.98	0.33	79.3	52.4
	DES	3	1	5	627.69	1.11	0.37	94.4	80.8
	EADY	3	1	6	625.11	1.26	0.42	83.1	61.2
	PLZ1	3	1	5	738.8	3.67	1.22	79.8	47.5
	IEB	4	1	5	731.5	1.63	0.41	89.3	84
	N7	4	2	7	715.55	1.71	0.43	73.7	68.2
					6				
		N502	4	1	5	1371	1.35	0.34	88.5
	CIPZ4	4	1		895	0.41	0.10	67.3	
Flooded area	PR1	3	1	6	1308.08	1.52	0.61	65.1	56.7
	PR2	2.5	1	4	640.6	0.9	0.10	62.8	50.2
Artificial pond	C1	9	3	5	1983.6			82.5	73.93
				5					
				4					

nests, and also all instances of agonistic behavior. I registered the occurrence of interactions on scale maps of each site, as well as the number of birds involved, and the result of the interaction. Interactions usually involved vocalizations, which made recording and locating individuals easy and reliable. From these observations, I estimated territory boundaries, interaction rate, and determined whether gallinules defended territories as a group. Territory boundaries were plotted on scale maps of the ponds and referenced to vegetation distribution. I scanned plotted territories using a leaf area meter (LI-COR LI-3050A) which allowed estimating territory area. The area meter gave a figure in square millimeters that was transformed into square meters by using the map scale. I determined the association between group size and territory size by calculating correlations between these variables (Spearman rank correlation coefficient, $r_s = 0.50$). I also determined whether a relationship existed between territory or group size and average rate of territorial interactions per group (h^{-1}) as well as *per capita* rate of interaction ($\text{ind}^{-1} \text{h}^{-1}$). Average rate of interaction estimated intruder pressure and *per capita* interaction rate estimated the dilution of defense costs with group size, under the assumption that defense costs were shared equally among group members, though this is not always certain.

Territory quality. I estimated territory quality with regards to vegetation according Noon (1981). I established parallel transects, up to 200 m long and 10 m apart on each site. I set a circular sampling plot of 0.5 m^2 every 10 m, where all plants were identified and their relative cover visually estimated. To determine territory composition, I overlapped the map of Purple Gallinule territories with that of habitat composition by considering data from plots completely included in territory boundaries. I performed vegetation surveys twice

during the study, in September and mid-November, and averaged data for each territory. I estimated territory quality using the following criteria: a) plant diversity, b) food plant diversity (see Tárano *et al.* 1995), c) relative cover of food plants, d) vegetation cover (floating and emergent plants), and e) emergent cover. I used the Shannon-Weaver index (H') and Hill numbers N_0 , N_1 and N_2 (Hill 1973), where N_0 is the total number of plant species (richness), N_1 the number of common species [$N_1 = \exp(H')$] and N_2 the number of very common species or the reciprocal of the Simpson index, to estimate plant diversity (either total or only food plants).

RESULTS

I identified 13 breeding territories: 10 in the seasonal pond, 2 in the flooded area and 1 in the artificial pond (Table 1). Territories were occupied either by a breeding pair alone or together with one or two non-breeding individuals in adult plumage (singular breeders) except for groups N7 and C1 that contained two and three breeding pairs, respectively (plural breeders). Group N7 was occupied by two couples that laid eggs almost simultaneously on separate nests. On 8 September, one nest contained five eggs (N7-1) and the other contained three eggs (N7-2). Both nests were lost due to human disturbance, and new nests were built a few meters away from the previous ones. The N7-1 clutch was completed on 25 September (seven eggs), and the N7-2 clutch on 30 September (six eggs). Eggs hatched about 12 December in both nests. Members of both couples defended a common territory against intruders. Nine individuals occupied the artificial pond, including three breeding pairs plus three non-breeding individuals. Clutch size was five, four and five eggs in nests C1-1, C1-2 and C1-3, respectively; eggs hatched on 1 December, 3 and 7 November, respectively.

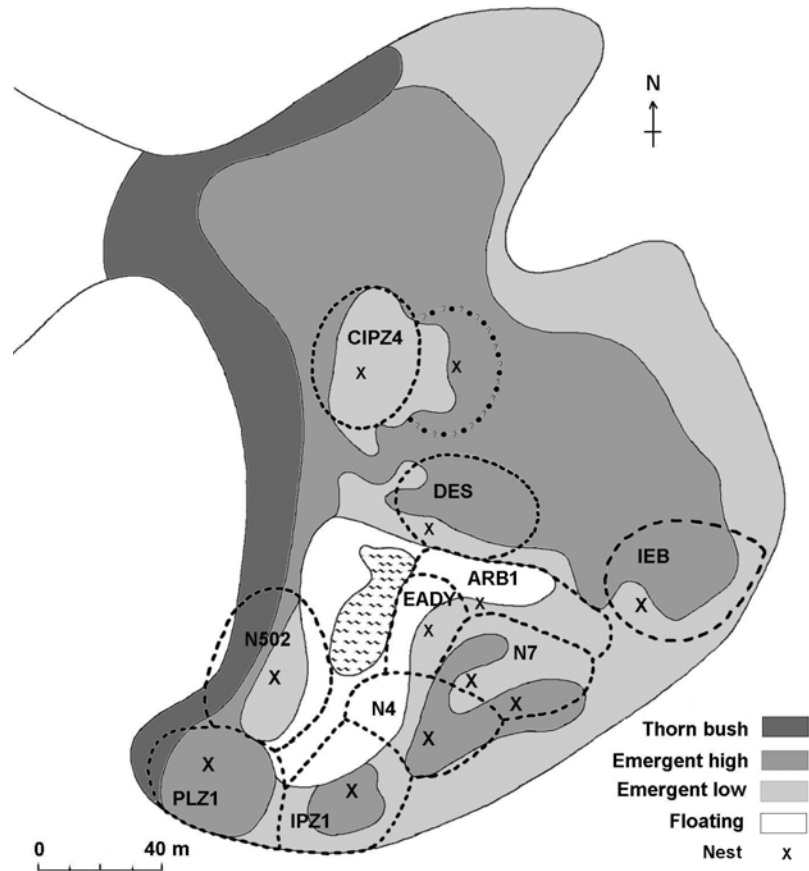


FIG. 1. Territory boundaries and vegetation distribution in the seasonal pond. High emergent plants (1–1.5 m above water) are *Mimosa pigra* (Mimosaceae) (only at the western margin), *Ipomoea carnea* (Convolvulaceae) and *Thalia geniculata* (Maranthaceae). Low emergent plants (0.2 < 1 m) are mainly Cyperaceae (*Eleocharis interstincta*, *E. mutata*, *Cyperus flavicomus*, *Scleria microcarpa*) and Poaceae (*Oryza perennis*). Floating plants (< 0.2 m) are mainly *Eichhornia crassipes* (Pontederiaceae), *Neptunia oleraceae* (Fabaceae), *Ludwigia helminthorrhiza* and *L. sedioides* (Onagraceae), *Salvinia auriculata* (Salviniaceae), and *Nymphoides indica* (Meyantheaceae).

I never observed agonistic interactions among individuals occupying this territory. Interactions with birds nesting outside this pond were rare.

Overall, group and territory sizes were 3.5 individuals (SD = 1.8) and 894.6 m² (SD = 412), respectively (Table 1). Territory and group size remained constant throughout the season except for group PR2, in which one

bird entered in October during the second nesting attempt of the breeding pair, without change in territory size. There was a positive relationship between group size and territory size (Spearman $r_s = 0.63$, $P = 0.029$). The relationship was strongly influenced by C1; however, the relationship remained significant when C1 was removed (Spearman $r_s = 0.52$, $P = 0.05$). Average clutch size was 5.4 ± 0.8

eggs, and larger groups did not have larger clutches.

I recorded 179 interactions (description of territorial interactions in Tárano 2003) and most involved two individuals (70%), one from each territory, but three (17%) or more individuals (13%) could participate. Average group interaction rate was 1.43 h^{-1} (SD = 0.83) and average *per capita* rate was $0.45 \text{ ind}^{-1} \text{ h}^{-1}$ (SD = 0.30). Positive relationships were found between territory size and average interaction rate (Spearman $r_s = 0.68$, $P = 0.031$), but no relationship was found between territory size and *per capita* interaction rate (Spearman $r_s = 0.37$, $P = 0.29$). Both breeding and non-breeding individuals participated in territorial defense, but their relative importance could not be established with certainty. The identity of interacting birds could not be clearly determined when interactions involved chases in flight or occurred on dense floating vegetation which obstructed the view of leg bands or natural marks (e.g., missing feathers). Interactions always ended with birds moving back to their territories; when interactions involved chases or replacements, the resident bird would remain perched on a visible position for a few seconds before going back to its previous activity.

Territories varied in quality according to all the estimators used; territories in the natural pond did not contain open water, contrary to those in the flooded area (Figs 1 and 2). Positive relationships were found between group size and territory quality estimated by both the area covered by plant foods (Table 1, Spearman: $r_s = 0.85$, $P = 0.0004$), and territory area covered by vegetation (Spearman $r_s = 0.81$, $P = 0.001$). There was no relationship between territory quality and interaction rate (either average or *per capita*).

DISCUSSION

Purple Gallinules defended breeding territo-

ries in pairs or in social units of three or more individuals; in the largest units, plural breeding occurred with breeding pairs nesting separately, without interference. This is the first report of plural breeding in the Purple Gallinule. Members of plural-breeding units bred alone (group N7) or with additional non-breeding individuals (group C1). Singular breeders defended their territories alone or together with one or two additional non-breeding individuals.

Krekorian (1978) suspected that Purple Gallinule breeding groups might contain more than one breeding pair, based on large group size and short inter-clutch interval in one group. Later, Hunter (1985a) demonstrated that helpers significantly reduce the reproductive effort of breeders, allowing shorter inter clutch intervals. This observation partly explained Krekorian's previous results. Although other mating systems, besides monogamy, may occur in Purple Gallinules, there is no evidence of such. In Hunter's study (1985a), two of the 11 groups contained three adults, two females and one male, but only one female laid eggs and clutch size was not significantly larger in these groups than in others with only two adults. Plural breeding is somewhat rare among group-territorial bird species (c. 16%) although it is found in many cooperative breeders (review in Brown 1987). In the Rallidae, plural breeding has been observed in the Pukeko (*Porphyrio porphyrio*) (Craig 1977) and in the Dusky Moorhen (*Gallinula tenebrosa*) (Garnett 1980), but in both species joint-nesting occurs. In this study, Purple Gallinule pairs nested separately and behaved monogamously. Small sample size in the present study prevented further analysis of differences between singular and plural breeders, and the effect of non-breeders in both types of units. In general, the effect of non-breeders is harder to estimate in plural breeders, mainly because territory size tends to be large, and

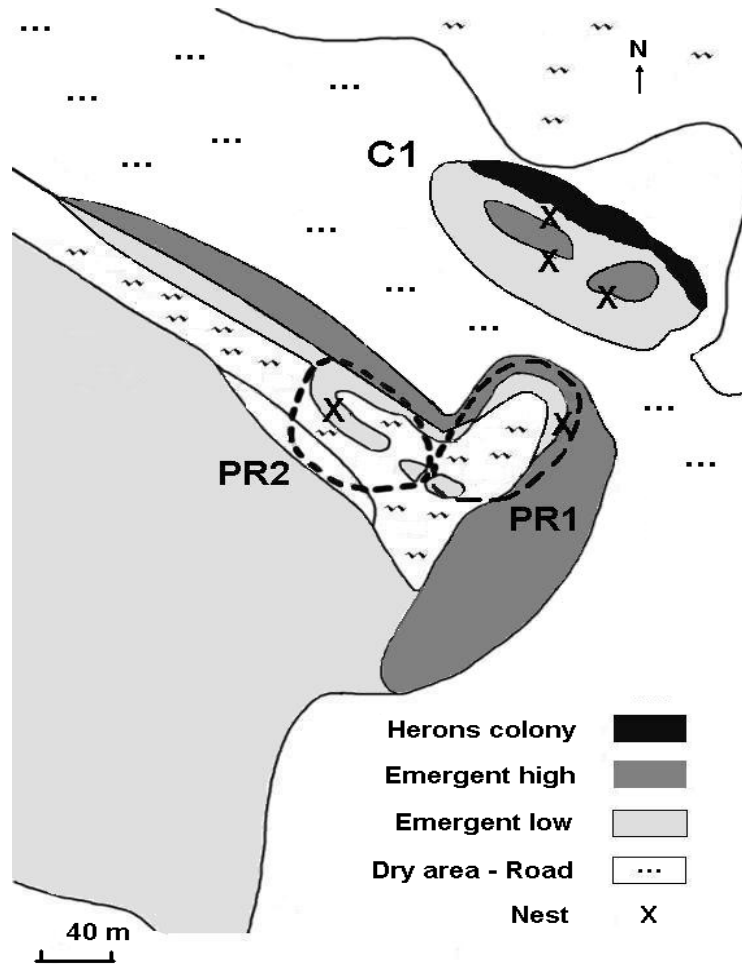


FIG. 2. Territory boundaries and vegetation distribution in the flooded area (territories PR1 and PR2) and the artificial pond (C1). High emergent species (1–1.5 m above water) are *Mimosa pigra* (Mimosaceae) and *Thalia geniculata* (Maranthaceae). Low emergent plants (0.2 < 1 m) are mainly *Eleocharis interstincta* (Cyperaceae), *Hymenachne amplexicaules* and *Oryza perennis* (Poaceae). Floating plants are *Marsilia polycarpa* (Marsileaceae) and *Salvinia auriculata* (Salviniaceae).

usually territory size and reproductive success are correlated, obscuring the effect of group size (Brown 1987).

Independently of the presence of singular and plural breeders, in this study, a positive, although weak, correlation was found between group size and territory size.

Whether the relationship resulted from the beneficial effect of additional group members on territory size, from the inability of breeders to exclude intruders when territory borders were long, or from larger territories being capable of supporting more individuals, was not determined. The positive relationship

between group size and territory quality is hard to interpret as well. Even if one demonstrates a causal relationship between group size and territory size or quality, the net effect of group territoriality on fitness needs further investigation. The presence of additional individuals in a territory, of any quality, undoubtedly reduces territory value to the breeding pair, and also to additional group members (e.g., resource depletion, Brown 1964). Additional group members may also generate other costs to the breeding pairs or the whole group such as predator attraction (Watt & Chapman 1998), cuckoldry, egg destruction or brood parasitism (McRae 1996). Cannibalism of chicks and eggs has been reported for Purple Gallinules (Hunter 1985b), although I did not observe it. However, brood parasitism, may occur, such as that described in the Moorhen (*Gallinula chloropus*) (Gibbons 1986). The clutch of group N502 was monitored from the laying of the first egg (22 August) until the clutch was completed on 28 August (five eggs). A new egg was found on 4 September and disappeared by 9 September. I presume that another female (a group member or not) deposited the egg in the nest and the breeder later expelled it.

In this study, larger territories were under greater intruder pressure, as revealed by higher interaction rates, but individual (*per capita*) defense costs did not increase with territory size. Because group and territory sizes were also correlated, lack of correlation between territory size and *per capita* interaction rate indicates that defense costs were diluted among group members. Defense distribution among breeders and non-breeders could not be determined, but in many group-territorial units, dominants (breeders) usually bear a greater defense cost. Nevertheless, this is not the case for Purple Gallinule groups breeding in Costa Rica. Hunter (1985a) found that non-reproductive individuals participated in 67% of territorial interactions. I do not expect such

an imbalance between breeders and non-breeders in seasonally flooded savannas of Venezuela, because relatedness among group members is probably low or null, since birds migrate at the end of the rainy season and family units are likely dissolved; thus indirect benefits of territorial defense are probably small.

In the present study, group C1 deserves some attention. This group occupied a pond partly isolated from surrounding breeding gallinules. The pond was limited by a dirt road on its southern border and neighboring ponds (containing breeding gallinules) were 10–20 m from the other borders. Birds in group C1 shared this area without interference between breeding individuals or between them and non-breeding birds. Interactions with birds breeding in surrounding areas were extremely infrequent. Only once did I observe the chase of some birds that landed on tall bushes on the eastern borders of the pond. Given the low intruder pressure in this pond, the beneficial effect of additional birds in territory defense seems negligible. This group occupied the largest area of all groups studied. Three independent territories (c. 661 m² each) could have been established in this area and easily defended from each other because at least two borders did not need defense (Fig. 2). In addition, these three potential independent territories would have had similar vegetation cover and plant diversity, comparable to those in the seasonal pond and the flooded area. Thus, there is no indication that birds in the artificial pond formed a single group for reasons related to territory quality (small or poor independent territories) or defendability. While developing a simultaneous project on a rice farm, I witnessed chick predation by the Black-crowned Night-heron (*Nycticorax nycticorax*). Black-crowned Night-herons, Yellow-crowned Night-herons (*Nyctanassa violacea*) and other herons were present in reproductive colonies in bushes surrounding the pond.

Gallinule predators, such as Tiger herons (*Tigrisoma lineatum* and *T. fasciatum*) and the caiman (*Caiman crocodilus*) (J. Thorbjarnarson pers. com.), were also common in this pond. Thus, antipredator defense may have been important in this group.

Group size and composition and territory characteristics in the present study were markedly different from those in Costa Rica: group and territory sizes were smaller in Venezuela but similar to that typically found in group territorial species (one or two helpers). Contrary to what has been observed in Costa Rica, non-reproductive group members in Venezuela were all in adult plumage, and presumably capable of breeding. I propose that these differences relate to habitat quality, population density and bird migratory habits. Qualitatively, territory quality seemed lower for populations studied in Costa Rica. All territories in Hunter's study (1985a, 1987) included a considerable proportion of open water (c. 70–80%); additionally, vegetation diversity was apparently lower compared with what I found in Venezuela. Thus, larger territories may be needed to meet energy demands. Population density seems higher in Costa Rica. Although density data were not available in Hunter's study, by multiplying group density by average group size on each site, I obtained rough estimates for each site (16.7 ind/ha in Costa Rica, 13.5 ind/ha in this study). To these numbers we must add floaters whose numbers are hard to estimate because of their concealed behavior. Estimates in Costa Rica indicated that floaters may comprise as much as 25% of the population (Hunter 1987). I had no data on floater numbers, but they must have been present in the seasonal pond because unidentifiable birds were occasionally chased from one territory to another. Large groups in Costa Rica may be associated with high intruder pressure, due to habitat saturation. In Costa Rica, helpers have a positive effect on fitness of the

breeding pair, through feeding and protection of the chicks, and also an increased chance of maintaining territories longer thus allowing breeders to produce several clutches in a year (Krekorian 1978, Hunter 1985a).

Finally, I conclude that ecological conditions affect behaviors associated with reproduction in Purple Gallinules, because single pairs (no helpers), plural breeders and singular breeders (with one or two helpers) were all found in the study. Such reproductive diversity within the same population of Purple Gallinules had not been reported before.

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REFERENCES

- Austad, S. N., & K. N. Rabenold. 1985. Reproductive enhancement by helpers and an experimental examination of its mechanism in the Bicolored Wren: a facultative communal breeder. *Behav. Ecol. Sociobiol.* 17: 19–27.
- Blake, E. R. 1977. *Manual of Neotropical birds*. Volume 1. Univ. of Chicago Press, Chicago, Illinois.
- Brown, J. L. 1964. Evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160–169.
- Brown, J. L. 1987. *Helping and communal breeding in birds*. Princeton Univ. Press, Princeton, New Jersey.
- Brown, J. L., & R. P. Balda. 1977. The relationship of habitat quality to group size in Hall's Babbler (*Pomatostomus halli*). *Condor* 79: 312–320.
- Craig, J. L. 1977. The behavior of a communal gallinule, the Pukeko (*Porphyrio porphyrio melanotus*). *New. Zeal. J. Zool.* 4: 200–205.
- Craig, J. L. 1979. Habitat variation in the social organization of a communal gallinule, the

- Pukeko, *Porphyrio porphyrio melanotus*. Behav. Ecol. Sociobiol. 5: 331–358.
- Elías, D. J., & P. Valencia. 1984. La agricultura latinoamericana y los vertebrados plaga. Interciencia 9: 223–227.
- Garnett, S. T. 1980. The social organization of the Dusky Moorhen, *Gallinula tenebrosa* (Aves: Rallidae). Aust. Wildl. Res. 7: 103–112.
- Gaston, A. J. 1978. The evolution of group territorial behavior and cooperative breeding. Am. Nat. 112: 1091–1100.
- Gibbons, D. W. 1986. Brood parasitism and cooperative nesting in Moorhen *Gallinula chloropus*. Behav. Ecol. Sociobiol. 19: 221–232.
- Gross, A. O., & J. Van Tyne. 1929. The Purple Gallinule (*Ionornis martinica*) of Barro Colorado Island, Canal zone. Auk 46: 431–447.
- Gutiérrez, T. J. 1994. Estimación poblacional y del daño causado por el Gallito Azul (*Porphyryula martinica*) en arrozales de la Finca Corporación Agrícola del Sur, Guanare, Estado Portuguesa, Venezuela. M.Sc. Thesis, UNELLEZ, Guanare, Venezuela.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54: 427–433.
- Hunter, L. A. 1985a. The effects of helpers in cooperatively breeding Purple Gallinules. Behav. Ecol. Sociobiol. 18: 147–153.
- Hunter, L. A. 1985b. Kin cannibalism in the Purple Gallinule. Wilson Bull. 97: 560–561.
- Hunter, L. A. 1987. Acquisition of territories by floaters in cooperatively breeding Purple Gallinules. Anim. Behav. 35: 402–410.
- Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, & M. T. Stanback. 1992. Ecological factors and the evolution of delayed dispersal in cooperative breeders. Quart. Rev. Biol. 67: 111–150.
- Krekorian, C. O. 1978. Alloparental care in the Purple Gallinule. Condor 80: 382–390.
- Langen, T. A., & S. L. Vehrencamp. 1998. Ecological factors affecting group and territory size in the White-throated Magpie-jays. Auk 115: 327–339.
- Lira, J. R., & C. Casler. 1982. El Gallito Azul (*Porphyryula martinica*). Su presencia en los arrozales de Venezuela. Natura 72: 31–33.
- McKay, W. 1981. Notes on Purple Gallinules in Colombian ricefields. Wilson Bull. 93: 267–271.
- McRae, S. B. 1996. Family values: costs and benefits of communal nesting in the Moorhen. Anim. Behav. 52: 225–245.
- Noon, B. R. 1981. Techniques for sampling avian habitats. Pp. 42–52 in David, E. C. (ed). The use of multivariate statistics in studies of wildlife habitat. USDA Forest Service General Report, RM-87, Fort Collins, Colorado.
- Poleo, Y., & R. Mendoza. 2000. Aves que afectan el cultivo de arroz. FONAIAP Divulga 67: 21–24.
- Ramía, M. 1967. Tipos de sabanas en los llanos de Venezuela. Bol. Soc. Ven. Cien. Nat. 28: 264–288.
- Scott, F. R., & D. A. Cutler. 1974. Fall migration August–November 1974. Middle Atlantic Coast Region. Am. Birds 29: 34–40.
- Stacey, P. B., & C. E. Bock. 1978. Social plasticity in the Acorn Woodpecker. Science 202: 1298–1300.
- Tárano, Z. 2003. Agonistic behavior of breeding Purple Gallinules *Porphyryula martinica*: potential ecological correlates. Ecotrópicos 16: 11–16.
- Tárano, Z., S. Strahl, & J. Ojasti. 1995. Feeding ecology of the Purple Gallinule *Porphyryula martinica* in the central llanos of Venezuela. Ecotrópicos 8: 53–61.
- Thomas, B. T. 1979. The birds of a ranch in the Venezuelan llanos. Pp. 213–232 in Eisenberg, J. (ed.). Vertebrate ecology in the northern Neotropics. Smithsonian Institution Press, Washington, D.C.
- Troth, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Pp. 17–30 in Eisenberg, J. (ed.). Vertebrate ecology in the northern Neotropics. Smithsonian Institution Press, Washington, D.C.

