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ALLOPARENTAL CARE IN THE PURPLE GALLINULE

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Purple Gallinules (*Gallinula martinica*) occupy lowland fresh-water marshy habitats throughout the Americas (Wetmore 1965). Their breeding range extends from central Ohio in the United States to northern Argentina and Uruguay in South America (A.O.U. 1957). With the exception of Gross and van Tyne's (1929) excellent description of the nest, eggs, and nesting behavior of the Purple Gallinule on Barro Colorado Island, Panama, and a description of its nesting behavior in Ohio (Trautman and Glines 1964), little is known about the ethology of this species. Available information characterizes the Purple Gallinule as monogamous, with the parents setting up feeding territories and sharing care of the precocial chicks (Gross and van Tyne 1929, Meanley 1963, Trautman and Glines 1964). Alloparental care ("helpers") in this species is not mentioned in the literature although some zoologists (Gerald Collier and Paul Fromer, pers. comm.) have suspected it. "Alloparental" is a neutral term used to describe the behavior of members in a social group other than the parents which assist in the care of offspring (Wilson 1975).

Approximately 80 species of birds in 32 different families are known to exhibit cooperative breeding in which helpers feed nestlings and occasionally fledglings (Skutch 1961, Harrison 1969, Fry 1972, Grimes 1976, Rowley 1976, Woolfenden 1976, Zahavi 1976). In addition, some helpers aid in nest and/or territory defense (Ligon 1970, Parry 1970, Brown 1972, Zahavi 1974, Woolfenden 1975), and nest sanitation (Skutch 1961, Ligon 1970, Fry 1972). Nest building, incubation, and brooding by helpers have been recorded less frequently but do occur in "mutual helpers" such as the anis (*Crotophaga*; Vehrencamp 1977) and in some other groups such as bee-eaters (Meropidae; Fry 1972) and swallows (Hirundinidae; Skutch 1961).

Alloparental care is currently of sociobiological interest because it is used as evidence of kin selection and altruism (Wilson 1975). The controversy over kin selection versus individual selection (Hamilton 1964) can be resolved only when additional studies of alloparental care document the filial relationship of helpers to breeders and the effect of helpers on reproduction.

The objectives for this study of Purple Gallinules in Costa Rica were: (1) to establish whether they have alloparental care, and to learn the status or condition of the helpers; (2) to describe the types of assistance provided, and quantify the relative contributions made by various members of the social unit, including the chicks; and (3) to gain information about Purple Gallinule social structure and data that might serve for evaluating the effect of helpers on the reproductive success of the breeders.

STUDY AREA

This study was conducted on the shallow 7-acre pond (2.83 ha) located on the grounds of the Centro Agronomico Tropical de Investigación y Ensenañza (CATIE) near Turrialba, Costa Rica. The pond, its flora and fauna, and the climate of the area were described in detail by Jenni and Collier (1972).

The distribution of vegetation on the pond varied from year to year due to CATIE's management practices. During my study, three distinct zones of vegetation existed, each characterized by one or more conspicuous plant species (Fig. 1). The first consisted of papyrus (*Cyperus papyrus*) which attained a height of 3.5 m and grew on the north and east sides of the pond. The second zone was made up of semiaquatic grasses and sedges, 0.3–2 m high, which covered the west and the east ends of the pond. The grasses (*Leersia hexandra*) and sedges (*Eleocharis geniculata*) also covered mud islands (5–20 m diam.) at the west and north parts of the pond and a large island (ca. 35 m × 40 m) on the southeastern half of the pond (Fig. 1). The grasses occupied about 35% of the pond area. The third zone, dominated by broad-leaved water lilies (*Nymphaea* sp.) though often mixed with other low lying aquatic plants, covered most of the central and remaining portions of the pond where grasses were not found. The profile of the third zone was low and open, with grassless mud islands scattered throughout. A small area near the center of the pond was open water.

MATERIALS AND METHODS

Observations were conducted for 117 days usually between 06:30–10:30 from 1 October 1976 to 24 February 1977 using a 15–60× zoom telescope and 10 × 50 mm binoculars. The six families studied were observed a total of 238 h. Five hours of observations were made between 13:00–17:00 when weather conditions were cool, and the birds active.

Twenty-nine Purple Gallinules were trapped with self-tripping drop cages (50 × 50 × 24 cm) made of coarse mesh hardware cloth on a wood platform. Platforms were placed in the pond near the shore and next to the grass islands frequented by each family. Captured gallinules were weighed, measured (shield,

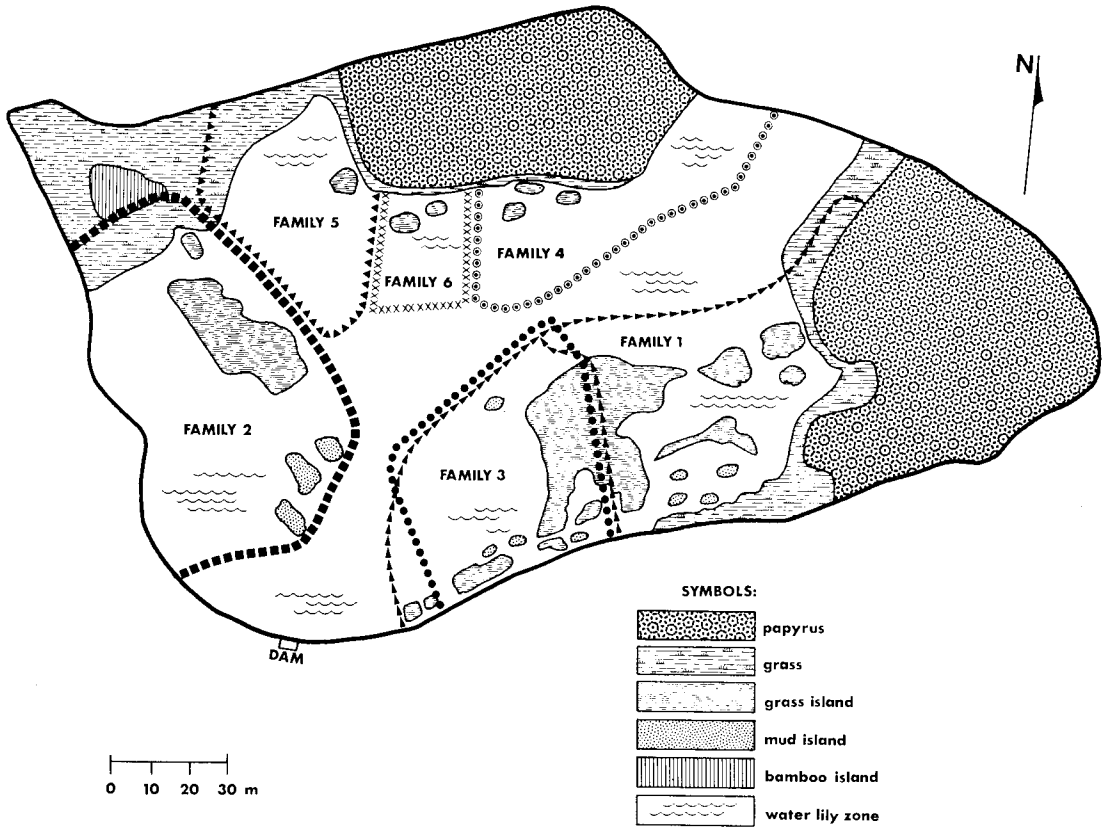

FIGURE 1. The pond at Turrialba, Costa Rica, showing the distribution of vegetation during the study and the approximate location of Purple Gallinule family territories.

beak, and leg) and banded with a USFWS metal band and a unique combination of at least two colored plastic bands using red (R), blue (B), yellow (Y), and orange (O) which were placed on the lower tibiotarsi. With the bird facing the observer the bands were recorded in sequence from top to bottom, from the observer's right to his left. In recording the color code a dash always follows any bands on the right leg and precedes any bands on the left leg. In all cases, observations of families with chicks began before all members, including chicks, were banded.

Three stages in the life history of the Purple Gallinule (chick, juvenile, and adult) generally are recognized. Each stage is associated with a characteristic appearance, but the history of molts and plumages is not known in detail. Nevertheless, the following descriptions, modified from Wetmore (1965), allowed stage identification of the socially interactive birds.

DOWNY CHICKS

Above black, underneath brownish black; crown, sides of head from bill to back of eyes, and throat with filaments of very pale bluish white.

Traces of brown began to appear on the black plumage of some chicks when they were approximately 2 weeks old. When they were 3–4 weeks old, the ventral half of the body was light beige-brown and the dorsum still black with a greenish-olive tint. Juvenile plumage was attained sometime between 5 and 7 weeks of age by some chicks. In this paper, chick status is based on a behavioral criterion rather than plumage condition. Since my use of the term "chick" is based on behavior rather than plumage, it does not always denote young in natal down. I use the term "chick" here to denote any individual receiving food from an adult or older juvenile. Thus, this category included individuals up to 60 days old because they received help from adults even though they wore the juvenile plumage described by Wetmore (1965).

JUVENILE PLUMAGE

Head, neck, sides, and tibia buffy brown; back, rump, and tail dull brown; wings greenish-blue washed with brown; throat, breast, abdomen, and under tail coverts white. I considered individuals to be juveniles (9–24 weeks of age) until they had full adult plumage and markings.

ADULT PLUMAGE

(Sexes alike.) Head, breast, sides, and wings deep blue; back, rump, tertials, and tail dull green; abdomen and tibia black; under tail coverts white.

Fully mature adult Purple Gallinules have a conspicuous light blue frontal plate, and the bill is bright red at the base and yellow over the distal 12–20 mm.

The time and duration of feeding and other pertinent behaviors were recorded with a stopwatch. Each time a chick fed or was being fed by a juvenile or adult, the identity of individuals involved (based on the band combinations) was recorded. When the

TABLE 1. Purple Gallinule families studied and the number of times (numbers in parentheses) banded family members were observed to feed chicks. Feedings of chicks by unbanded adults [UA] are also included. Additional family growth after March 1977 is included in the text.

Family 1	Adult	O-O (46), B-B (23), Y-Y (39)
	Juvenile	R-R (37), B-O (7)
	Chick	B-R, B-Y, R-O
Family 2A	Adult	Y-R (8), BB-O (13), BB-Y (4), UA(s) (2)
	Juvenile	R-Y (7), Y-O (26)
	Chick	Y-B, BB-R
Family 2B	Adult	Y-R (9), BB-O (13), BB-Y (18), R-Y (27), OO-Y (0), Y-O (0), UA(s) (14)
	Juvenile	Y-B (4), BB-R (6)
	Chick	RR-O, OO-R
Family 3	Adult	O-Y (7), RR-Y (5)
	Juvenile	None
	Chick	RR-B, YY-B, YY-R
Family 4	Adult	R-B, O-B, YY-O, O-BB
	Juvenile	None
	Chick	3 unbanded
Family 5	Adult	4 unbanded
	Juvenile	2 unbanded
	Chick	3 unbanded
Family 6	Adult	2 unbanded
	Juvenile	2 unbanded
	Chick	3 eggs

bands could not be seen or the individuals involved had no bands, the birds were designated as chick, juvenile, or adult and the performed behavior described. Territory defense, conspicuous postures, and food items were recorded and described.

RESULTS

FEEDING OF CHICKS BY FAMILY MEMBERS

Three families of Purple Gallinules were studied in detail and less detailed observations were made on an additional three families. Families studied in detail ranged in size from five individuals in Family 3 to ten banded individuals in Family 2B (Table 1). Family size and the number of individuals banded are the same except for Family 2 in which at least one individual was not banded. Four families had easily distinguishable juveniles; the other two lacked juveniles (Table 1). Alloparental feeding occurred in all families with both juveniles and chicks (3 of 6 families).

Family 1, located in the southeastern part of the pond (Fig. 1), consisted of eight individuals, including three chicks. All members of the family fed the chicks (Table 1). The two juveniles in Family 1 fed the chicks 70 times or 13% of the observed feeding instances (Table 2). The three adults accounted for 26% of the feeding instances observed. On the average, each juvenile of Family 1 fed the chicks about as frequently as did each adult (Table 2).

The weights of the adults and juveniles in Family 1 captured on 14 and 15 October were: BB (306 g), O-O (263 g), Y-Y (228 g), and juvenile R-R (215 g). Juvenile B-O weighed 230 g on 25 October. The base of the bill of both B-B and O-O was bright red, which is typical of fully mature adults, but the base of Y-Y's bill was light red. The base of Y-Y's bill had become bright red by 2 February 1977. The lighter weight and the bill coloring of Y-Y compared to other adults at capture indicate that it had recently acquired adult plumage. The similarity in weight of Y-Y and the juvenile B-O, which was caught 10 days after Y-Y, also supports this conclusion.

Data for Family 2 are presented in two parts because there were two pairs of chicks. Y-B and BB-R hatched on 23 November 1976 (±1 day), and these chicks along with the adults and juveniles who fed them are designated Family 2A. The second pair of chicks (RR-O and OO-R) was sighted 28 January 1977 when they were estimated to be 2 or 3 weeks old. These chicks with the adults and juveniles who fed them are designated as Family 2B. Both pairs of chicks are presumed to have been in the same family for two reasons. First, all of the chicks foraged over and frequented the same areas within Family 2's territory (Fig. 1). Second, the two chicks of the second brood were fed by the two chicks of the first brood and also by four of the six individuals which fed the first pair of chicks (Table 1).

I saw two juveniles, three marked adults, and an unmarked adult feed the chicks of Family 2A during the 9 weeks they were watched. Because I also saw at least two, possibly three, unmarked adults in this area concurrently, the chicks may have been fed by two different unmarked adults (Table 1).

The two juveniles of Family 2A (R-Y, Y-O) accounted for 9% of the total feeding instances of the two chicks, while the four (or five) adults accounted for 18%. On the average, the juveniles of Family 2A fed the chicks frequently as did the adults (Table 2).

When the chicks of Family 2B were seen on 28 January, the chicks of Family 2A were 67 ± 1 days old and in juvenile plumage. The next day, these two juveniles fed the new chicks whose age at that time I estimated to be between two and three weeks. All together, the chicks of Family 2B were fed by the two juveniles, and at least five adults. One of these adults (R-Y) had recently acquired adult plumage and had been a juvenile when observations were made on Family 2A. An unbanded adult fed the chicks 14 times (Table 1) during the three weeks I observed Family 2B. Again, the chicks may have been fed by more than one unbanded adult because several unbanded adults were present in this area. One adult which was caught and banded (OO-Y) on 20 February 1977, fed the juvenile Y-B (chick of Family 2A), who in turn fed this food to two new downy chicks on 11 April 1977 (L. Reeves, pers. comm.). This third pair of chicks, members of Family 2C, frequented the same areas as other chicks in Family 2, and was fed by OO-Y, the adult R-Y, the juvenile Y-B, and an unbanded adult (Reeves, pers. comm.). Thus, the number of gallinules in this family is not known but could be 13 or 14.

In Family 2B the new juveniles (Y-B, BB-R) accounted for only 5% of the total feeding instances for the chicks (RR-O, OO-R), while adults accounted for 41%. The percentage of feedings contributed per individual by adults (8.2%) was three times that by each juvenile (2.5%) (Table 2).

Family 3 consisted of two adults and three chicks when observations began. Its area of activity included the western half of the large grass island. Previously, this area had been occupied exclusively and defended by Family 1; but on 19 January 1977, O-Y and two unbanded adult gallinules, one of which carried nesting material in its bill, were observed on the western shore of the grass island. From that time onward, Family 1 was seen only on the eastern half of the island and in other areas to the east of the island (Fig. 1). I never saw fighting between Families 1 and 3.

TABLE 2. The percentage of feeding instances that self-feeding and allo-feeding in chicks was observed in two families of Purple Gallinules. Families 2A and 2B refer to the first and second pairs of chicks produced by Family 2. The numbers of chicks, juveniles, and adults are shown in parentheses.

Family	1	2A	2B
Total feeding instances	550	469	210
Total chick	61 (3)	73 (2)	54 (2)
Total juvenile	13 (2)	9 (2)	5 (2)
Per juvenile	6.5	4.5	2.5
Total adult	26 (3)	18 (4)	41 (5)
Per adult	8.7	4.5	8.2

Both adults fed the chicks, providing food to the three chicks with about the same frequency (Table 1). The body weights of the adults were 275 g (O-Y) and 256 g (RR-Y). On the basis of its heavier body weight, I assume that O-Y was the male and RR-Y was a female. Data from Collier (pers. comm.) and Wetmore (1965) support this assumption.

Three new downy chicks were sighted by Reeves at different times, beginning 29 May 1977, with adults O-Y, RR-Y, and the juvenile YY-R who had recently acquired its juvenile plumage. These chicks were fed by YY-R (Reeves, pers. comm.) which I banded as a chick 22 February 1977.

Families 4–6 lived on the north side of the pond. Distance and vegetation made observations from the south side of the pond and banding difficult (Fig. 1). It was possible, however, to observe care of the chicks by adults and juveniles (when present) in Families 4 and 5 when the chicks were in the third zone of vegetation or on the shore of grass-covered islands. During these periods, I counted the number of chicks, juveniles, and adults present in the area and recorded the number of different individuals observed feeding the chicks. I assumed that Purple Gallinules who fed particular chicks were in the same family because family members excluded individuals of other families from their territories. As family 6 had no chicks when I terminated my observations, but rather a nest containing three eggs, I assumed that adult and juvenile gallinules not chased from areas near the nest were members of this family. Pertinent observations of these families are recorded in Table 1.

FEEDING DURATION

The duration of feeding bouts in which a juvenile helper fed a chick varied from approximately 10 s to 10 min. Brief bouts usually involved a juvenile bringing a single food item to a chick and then leaving. Long bouts occurred when one or more chicks were fed pieces of lily fruit by the helper, while all birds were gathered around the lily fruit. During these bouts, the chicks were sometimes fed more than 10 times from the beak of the helper. Juvenile helpers commonly fed chicks for 2–5 min when they were gathered at a lily fruit.

CHANGES IN THE MODE OF FEEDING WITH TIME

Feeding interactions between helpers and chicks changed considerably as the chicks grew older. I recognize three phases based on my observations of Families 1, 2, and 3. The intervals covered by each phase are approximate as I did not observe the exact date of hatching of most chicks.

Phase 1 lasted from hatching until the chicks were 3–5 weeks old. During this period, the chicks typically followed one or more adults and/or juveniles to a location and waited while family members gathered food nearby or at distances 30–40 m away. Once a family member had food, it either walked or flew to the chick or chicks and fed them by passing the food from its beak to the chick's beak. The chicks pecked at the beak of the juvenile or adult at this time and frequently showed a "begging posture" when the family member approached. In this posture the neck of the chick is stretched forward and lowered below the level of the rump. At the same time the wings are elevated and often vigorously moved up and down synchronously. During this performance, I frequently heard the chick peeping. Chicks received both plant and animal food, including stingless bees (*Trigona sylvestriana* and *T. corvina*), other insects, and pieces of water lily fruit during phase 1.

During phase 2, which began when the chicks were approximately five weeks old and continued until they were about seven weeks old, they more actively solicited food from their elders. Chicks walked or ran to family members feeding on lily fruit out in the pond and were fed from the beak of the helper or parent as it chipped off pieces of the fruit. They also ate fallen fragments of fruit and occasionally quickly swallowed an entire small lily fruit prepared by an adult or juvenile. Chicks began pecking at the lily fruit during this phase but usually were unsuccessful in removing any of it. They never were seen to procure a lily fruit from below the water or mud surface or to successfully prepare one for eating. Before a lily fruit was eaten, adults removed at least a portion of the outer, black, shell-like covering. This often took 1–2 min and sometimes longer. Chicks also took stingless bees, unidentified insects, and spiders from the air and lily flowers, and the seeds of grasses.

The third phase of feeding interaction between chicks and other family members began at seven weeks and continued until chicks were approximately eight weeks old. During this period, adults and juveniles secured lily fruit, sometimes preparing it, and gave it to chicks who quickly swallowed it or took it to another place within the territory to eat. Adults and juveniles exhibited no aggression toward the chicks and made no attempt to retrieve the lily fruit that the chicks carried off. Twice I saw the same adult provide a lily fruit for two chicks in succession before securing one for itself. Beak-to-beak feeding between a chick and an adult or juvenile occurred less frequently during this phase than earlier. At this time I also saw a 45-day-old chick in Family 2A (BB-R) prepare a lily fruit for the first time by removing the outer black covering, and during the following week it prepared more lily fruits. I first saw a chick in Family 1 prepare a lily fruit at approximately 51 days of age. I consider the third phase to have ended when juveniles and adults stopped feeding the chicks from the beak. The chicks in Family 2A were last seen fed from the beak of an adult when they were 57 days old. The last time a juvenile in Family 2A was observed to feed a chick from the beak was when the chick was 54 days old. On the basis of age estimates of the chicks in Family 1, adults stopped feeding chicks from the beak when they were about 59 days old, while juveniles stopped when chicks were about 49 days old. However, I saw chicks in both Family 1 and 2A take a lily fruit from an adult when they were about 60 days old. The chicks became independent at about nine weeks of age.

FOOD EATEN

Lily fruit, which was very abundant because of CATIE's pond, was the food most frequently eaten by Purple Gallinules. Seventy-one percent of the food items positively identified at the time of eating were lily fruits.

In addition, stingless bees (16%), frogs (7%), grass seeds (2%; *L. hexandra* on islands and *Paspalum virgatum* on the shore), spiders, worms, and fish were eaten. Nineteen frogs were taken by Families 1, 2A, and 2B. Each time a frog was caught, most or all members of the family tried to obtain a piece. Two or more individuals often pulled at opposite ends of the frog's body. Individuals who ran off with a piece of the frog were chased by family members who had been unable to secure a portion for themselves. If one bird was successful in obtaining another's piece, the roles of chaser and chased were reversed. On ten occasions this activity persisted for at least 8–23 min, when I ceased watching.

The chicks accompanied members of the family most of the time as they moved through their family territory. Thus, inadvertently or otherwise, helpers assisted the young in recognizing and perhaps preparing food items, especially lily fruit.

ADDITIONAL FORMS OF HELP

Purple Gallinule helpers (both adults and juveniles) also participate in territory and chick defense (see Fig. 1 for the approximate location and size of family territories). Juveniles of Families 1 and 2 performed some form of defense a total of 18 times during the 213 h they were observed. Seventy-two percent of these defensive actions involved territorial defense and 28% chick defense. Forty-four percent (8 of 18) of the defensive actions were directed against conspecific birds and 56% (10 of 18) against birds of other species. Most of the heterospecific defense involved Jacanas (*Jacana spinosa*) while the rest was against Common Gallinules (*Gallinula chloropus*). As all three adults in Family 1, and three adults in Family 2B were observed in some form of defense, I assume that other non-parent adult helpers also participated in defense. The adults, however, have been excluded from these totals because of the difficulty in knowing the exact parentage of chicks. Nest defense also may occur, but data are lacking as is information on the role of helpers in nest building, incubation, and brooding.

On three occasions noisy fights between two or more individuals from each of two families occurred. Other members of both families gathered at the site of the fight so that as many as ten adults could be seen at one time. Twice these conflicts involved Families 2 and 5 where their territories were adjacent. The fighting individuals repeatedly flapped their wings and kicked each other. Another time, the juveniles of Family 1 began fighting two unmarked adult Purple Gallinules near the western border of Family 1's territory (prior to establishment of Family 3). Two adults from Family 1 flew to the site of the fight, the fight soon stopped, and the two intruders left the area.

FAMILY RELATIONSHIP OF HELPERS

Most of the individuals in four of the families studied were banded, and three of the families were sufficiently small and geographically contained to provide evidence regarding the parentage of the chicks and/or the filial relationships among helpers, parents, and chicks. Copulation between adults would be a better indicator of mateship and chick parentage than close association. However, during my study I witnessed copulations only twice. Even when observed, copulation does not prove whose sperm fertilizes the eggs, and thus parentage and filial relationships between family members cannot always be known with certainty. The juveniles and chicks in Family 1 were presumed to be the offspring of the adults O-O and B-B because the third adult in Family 1 (Y-Y) had recently acquired adult plumage. Thus, the juveniles were probably full siblings of the chicks. The two juveniles (R-R and B-O) were never seen to feed individuals other than the chicks. The adults of Family 3, O-Y and RR-Y, were seen with three new chicks in May 1977. These chicks were fed by YY-R, who had recently acquired juvenile plumage. Since YY-R had been one of three chicks in the first brood cared for exclusively by adults O-Y and RR-Y (no juveniles were present in this family when study began) this is the strongest circumstantial evidence possible for demonstrating its sibling relationship to the new chicks. The helpers in Family 4 also may have been sibs of the chicks. Two of the adult-plumaged gallinules in this family weighed less than 200 g and had just acquired their adult plumage.

The parents of the juvenile helpers in Family 2A and 2B are unknown. Three banded adults (Y-R, BB-O, and BB-Y) and at least one unbanded adult fed the chicks of Family 2A (Table 1). These same banded adults, another adult with recently acquired plumage (R-Y), and at least one unbanded adult also fed the chicks of Family 2B (Table 1). Because at least four mature adults of unknown sex fed the chicks of Families 2A and 2B, any combinations involving two of the adults were potential parents of the first and second pair of chicks. Thus, it is not possible to know

which two adults (assuming monogamy in this species) were the parents of the chicks and/or the juveniles that fed the chicks. Because of the small age difference (about 49 days) between the first (Family 2A) and second (Family 2B) pairs of chicks produced by Family 2, some of the helpers may not have been the offspring of the parents of Family 2B.

DISCUSSION

Alloparental care in this population of Purple Gallinules was common. Of the six families studied, five had helpers (Families 1, 2, 3, 4, and 5), and one (Family 6) had potential helpers (two unbanded juveniles) for a clutch of 3 eggs. Both adults and juveniles helped supposed parents feed and defend the young, and defend the family territory. In Families 1 and 2A each juvenile fed the chicks nearly as frequently on the average as each adult.

Scant knowledge exists on the breeding biology of almost all rails, but the Purple Gallinule is the eighth of 132 species of Rallidae for which helpers have been documented. Alloparental behavior has also been observed in: the Tasmanian Native Hen (*Gallinula mortierii*) and the Dusky Moorhen (*G. tenebrosa*; Ridpath 1972a, b), the Purple Swamphen (*Porphyrio porphyrio*; Craig 1975), the Common Gallinule or Moorhen (Grey 1927, McIlhenny 1934, Skutch 1961), the European Coot (*Fulica atra*; Ruthke 1939), the Red-and-White Crake (*Laterallus leucopyrrhus*; Meise 1934), and the Black Crake (*Porzana flavirostra*; Brooke 1975).

Although most of the above findings were based on limited observations, they suggest that helpers may occur regularly, or at least not uncommonly, in these species. They also suggest that alloparental care may be widespread in this family. The kind and amount of help individuals may provide remains to be documented for most of the species discussed above. At present, quantitative information on helpers in the Rallidae is available only for the Tasmanian Native Hen, the Purple Swamphen, and the Purple Gallinule.

Three of the families in my study had only two adults when observations began. An additional family (Family 1) had three adults, one of whom (Y-Y) had recently acquired adult plumage. These observations suggest that the Purple Gallinules at CATIE are monogamous, like those studied elsewhere. But, the possibility of simultaneous polyandry, as exhibited by the Tasmanian Native Hen, cannot be dismissed.

Purple Swamphens in New Zealand also breed in pairs and groups of 3–6 individuals (Craig 1975). Copulation is a group event with most copulations involving more than two adults. In groups, one or more females lay in the same nest at the same time, with the number of eggs being variable. All birds in the group, including the older chicks, care for the young chicks.

All eight Purple Gallinule broods produced at CATIE during this study contained two or three chicks and a nest contained three eggs. Purple Gallinule nests in Panama also contain three or four eggs (Gross and van Tyne 1929). This consistency in clutch and brood size would seem to rule out the type of mating system found in the Purple Swamphen. The large size of Family 2 (Table 1) and the closeness in age of the three separate pairs of offspring produced suggest several other possibilities in the type of mating system in addition to that found in the Tasmanian Native Hen. Some families may contain more than one breeding pair. Polygyny and promiscuity are also possible but seem less likely. The absence of conspicuous sexual dimorphism in this species makes it difficult to determine the sex ratio of large groups. Even though males are heavier than females, weights cannot be judged from a distance, and unless the ages of all adults in a group are known, it is not possible to tell the sex of most individuals because some birds may still be growing. Such information is required to determine the type of mating system and the exact filial relationship of the helpers to the breeders and chicks. Helpers of some chicks at CATIE, for example those of Family 2, could be their "grandparents," "aunts" and/or "uncles."

Studies of alloparental care that have continued long enough to determine the filial relationship of the helpers to the breeders have usually found that the helpers are offspring of the breeders and siblings of the chicks (Rowley 1965, Fry 1972, Ridpath 1972a, Parry 1973, Craig 1975, Woolfenden 1975). Rarely are helpers more distantly related. However, Woolfenden (1975) found that four male Florida Scrub Jays (*Aphelocoma coerulescens*) (uncles) helped care for the offspring of their brothers and their mates. Circumstantial evidence from Families 1, 2, and 3 strongly suggests that some Purple Gallinule helpers are older siblings from earlier broods, but helpers may also have more distant filial relationships.

Evidence that helpers increase reproductive success of their family exists only for the Florida Scrub Jay (Woolfenden 1975), the

Superb Blue Wren (*Malurus cyaneus*; Rowley 1965), and the Kookaburra (*Dacelo gigas*; Parry 1973). Juveniles and non-parent individuals in Purple Gallinule families that care for the chicks provide a substantial amount of food. Thus, the amount of feeding effort expended by breeders with helpers is potentially less than that which would be expended by breeders lacking helpers. This saving in feeding effort could be used for other activities, such as production of an additional brood. Such a benefit was found in the Kookaburra (Parry 1973) in which groups with helpers managed to nest twice during a breeding season, although simple pairs did not. In a territory with abundant food, one pair of Purple Gallinule breeders with helpers might produce two or three broods of chicks in a 5-month period if the amount of time for egg formation and incubation were short enough. At CATIE, a clutch of 3 eggs (Family 6) hatched 22 days after egg-laying commenced. The incubation period was 20 days for the first egg laid and 21 days for the other two eggs, 1–2 days less than that estimated for clutches in Panama (Gross and van Tyne 1929). Thus, the same pair might produce successive broods 50–60 days apart, as hypothesized for Family 2.

The larger number of broods produced in Family 2 as compared to the other families during this study indicates that helpers may increase reproductive success. I do not know whether any egg or chick predation on broods with two chicks occurred before I found them, but no chicks were lost in any of the observed families after they were first seen. In addition, both nests found with three eggs subsequently produced three chicks which survived at least to the juvenile stage. Thus, while additional data are needed, my findings support the view that helpers may increase breeding success by increasing the number of broods produced per year in addition to any influence exerted on the survival rates of chicks.

SUMMARY

Six Purple Gallinule families (*Gallinula martinica*) were studied for a total of 238 h at Turrialba, Costa Rica, from September 1976 through February 1977. Alloparental feeding occurred in four families that had juveniles and chicks. On the average, each juvenile in families studied in detail fed the chicks about as frequently as did each adult. The chicks in Families 1 and 2 were fed by the juveniles and three or more adults in each family. These chicks were last observed being fed by a juvenile when they were 49–54 days old.

Family 2 had two broods during this study. When the two offspring from the first brood were at most 69 days old they were seen feeding the chicks of the second brood. When the feeding began, the offspring from the first brood had juvenile plumage.

In addition to feeding chicks, juveniles also helped the supposed parents defend the family's territory and the chicks from intruders. Forty-four percent of the defensive actions were against conspecific gallinules, the remainder against other birds, mostly Jacanas (*Jacana spinosa*) and Common Gallinules (*Gallinula chloropus*).

Circumstantial evidence indicates that the juvenile helpers in Families 1 and 3 were the older siblings of the chicks. In Family 2, which had four or more adults when observations began, the filial relationships between members of the family are less clear.

Observations suggest that the Purple Gallinules at Turrialba are monogamous, but another type of mating system may also exist. Purple Gallinule helpers may increase the reproductive success of their family by reducing the amount of effort expended by the breeders to care for the chicks. This potential savings in expended energy may be used for production of an additional brood.

Since the Purple Gallinule is the eighth species of rail for which helpers have been documented, the habit may be widespread in this family.

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