

## KLEPTOPARASITISM OF AMERICAN COOTS BY GADWALLS AND ITS RELATIONSHIP TO SOCIAL DOMINANCE AND FOOD ABUNDANCE

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**ABSTRACT.**—Kleptoparasitism of American Coots (*Fulica americana*) by Gadwalls (*Anas strepera*) was recorded from October 1991–February 1992. We used these data to test whether frequency and rate of kleptoparasitism were related to variation in food abundance and dominance status of Gadwalls. Overall, 30% ( $n = 423$ ) of Gadwalls observed were kleptoparasitic; the relative frequency and rate of kleptoparasitism varied monthly. The proportion of individuals engaged in food stealing and the rate of kleptoparasitism were greatest for subordinate sex/pair status classes of Gadwalls. When comparing diurnal time-activity budgets, kleptoparasitic Gadwalls spent less time feeding (56 vs. 68%) and more time searching for food (37 vs. 24%) than did individuals not participating in kleptoparasitism. Eurasian watermilfoil (*Myriophyllum spicatum*) was the primary food of Gadwalls and American Coots. As this aquatic macrophyte declined in abundance over the winter as a result of the effects of herbivory and natural senescence, so did numbers of coots and Gadwalls. When coot and Gadwall numbers were held constant statistically, the rate of kleptoparasitism was inversely related to milfoil cover. Food-stealing behavior of Gadwalls was influenced by social dominance and food abundance; it was mediated by host/parasite numbers. Results suggest that kleptoparasitism is an alternative foraging strategy used by subordinate Gadwalls that do not have access to good feeding areas. Received 17 January 1994, accepted 1 April 1994.

FOOD STEALING, or kleptoparasitism, has been reported in many species of birds (Brockmann and Barnard 1979). It is especially prevalent in seabirds including gulls (*Larus* spp.; Hatch 1970, Schnell et al. 1983, Carroll and Cramer 1985, Rice 1985, Hesp and Barnard 1989), skuas (*Stercorarius* spp.; Andersson 1976, Furness 1977), and boobies (*Sula* spp.; Duffy 1980, Tershy and Breese 1990). Waterfowl (Anatidae) are hosts to at least 47 species of kleptoparasites, but only 3 species of ducks have been reported as kleptoparasites, despite the fact that waterfowl frequently occur in mixed species flocks (Brockmann and Barnard 1979). Gadwalls (*Anas strepera*) and American Wigeons (*A. americana*) are frequent parasites on American Coots (*Fulica americana*) and Eurasian Coots (*F. atra*) in areas of distributional overlap (Knapton and Knudsen 1978, Ryan 1981, Amat and Soriguer 1984).

Kleptoparasitism can be important for meeting energy requirements, but benefits depend on cost of attack and profitability of food items

(Thompson 1986). For example, kleptoparasitic Eurasian Curlews (*Numenius arquata*) acquired 3.6 times more net energy than conspecifics that did not steal food (Ens et al. 1990). American Wigeons stealing food from American Coots gained access to a food source that was unavailable to wigeons because of water depth (Knapton and Knudsen 1978).

Kleptoparasitism can have negative effects on host species. Nettleship (1972) reported lower fledging success of Common Puffins (*Fratercula arctica*) in areas where they were heavily kleptoparasitized by Herring Gulls (*L. argentatus*). Kleptoparasitized Eurasian Coots dived more often and, therefore, spent more energy than nonparasitized coots (Amat and Soriguer 1984).

Several factors may promote kleptoparasitism (review in Brockmann and Barnard 1979). Food stealing is more likely to occur when food items are large, visible and/or require long handling times to consume. Shortages in the quantity or quality of food may also stimulate kleptoparasitic behavior (Amat and Soriguer 1984, Amat 1990). Subordinate individuals with reduced access to food resources may be more likely to engage in food stealing than dominants (Brockmann and Barnard 1979). Occurrences of klep-

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toparasitism may also depend on there being a sufficient number of hosts that do not defend food resources aggressively.

Wintering Gadwalls and American Coots frequently occur together at sites with abundant aquatic vegetation; both feed on a diet of leafy vegetation. In Louisiana, for example, vegetative material comprised over 95% of diets of Gadwalls, and they foraged for 61% of the diurnal period (Paulus 1982, 1984). American Coots potentially have a broader foraging niche than Gadwalls because coots feed either by diving or on the surface. Although diving has been reported in Gadwalls (Kear and Johnsgard 1968), we did not observe this behavior.

We studied kleptoparasitic behavior of Gadwalls on American Coots during the winter and evaluated three factors which may influence its occurrence. First, food availability may differ for individual Gadwalls within a population; dominant individuals, for example, frequently have greater access to preferred food resources than subordinates (Gauthreaux 1978). In winter, paired Gadwalls are dominant to unpaired individuals, and males are dominant to females (Paulus 1983, Hepp and Hair 1984). If asymmetries in social status among Gadwalls influence acquisition of food, birds in subordinate classes (females and unpaired birds) should initiate kleptoparasitic behavior more frequently than dominant classes (males and paired birds). Second, we also examined diurnal time-activity budgets of Gadwalls and predicted that kleptoparasitic individuals would spend more time searching for food and less time feeding than birds that do not steal food. Third, we measured the abundance of Eurasian watermilfoil (*Myriophyllum spicatum*), the dominant macrophyte at the site (Bates et al. 1991) and the primary food of Gadwalls and American Coots, several times during the fall and winter. If kleptoparasitism is influenced by variation in food quantity, the frequency and rate of kleptoparasitism should increase with decreasing amounts of Eurasian watermilfoil. If these predictions are supported, kleptoparasitism can be considered an important foraging strategy (i.e. "making the best of a bad situation") used by subordinate Gadwalls that do not have access to high-quality feeding areas.

#### STUDY AREA AND METHODS

Guntersville Reservoir is a 27,480-ha impoundment on the Tennessee River in northeastern Alabama (Fig.

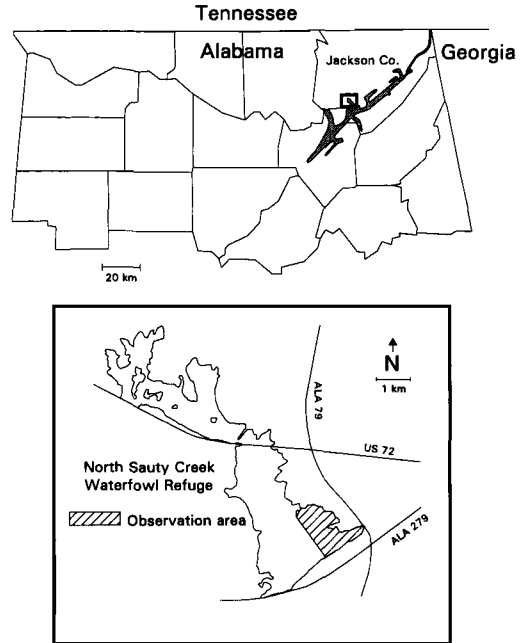


Fig. 1. Location of Guntersville Reservoir, Alabama and North Sauty Creek Waterfowl Refuge (NSCWR). Cross-hatched region within NSCWR delineates study area.

1). In 1990, aquatic macrophytes were present in 2,550 ha of Guntersville Reservoir, and Eurasian watermilfoil accounted for 90% of total coverage (Bates et al. 1991). Other plant species included American lotus (*Nelumbo lutea*), chara (*Chara* spp.), southern naiad (*Najas guadalupensis*), spinyleaf naiad (*N. minor*), spikerush (*Eleocharis* spp.), and pondweed (*Potamogeton* spp.). The study was conducted on the North Sauty Creek Waterfowl Refuge (NSCWR), which has a water surface area of approximately 1,154 ha.

**Behaviors.**—Diurnal time-activity budgets were recorded for Gadwalls from 17 October 1991 to 26 February 1992. Observations were from a blind overlooking a 72-ha section of the NSCWR using a 15–60× spotting scope (Fig. 1). Aerial photographs taken in September 1991 showed that milfoil covered approximately 54 ha (75%) of the study area and was the only submerged vegetation present. Behaviors were recorded during three periods: (1) 0.5 h before sunrise to 1100 CST; (2) 1100 to 1500; and (3) 1500 to 0.5 h after sunset. Each time block was divided into 1-h observation periods (i.e. 0600–0659, 0700–0759, etc.) and randomly sampled two to three times per month. We used focal-animal sampling to record behaviors (Altmann 1974). We defined activity categories as: feeding (dabbling or diving), swimming (movement between foraging and food-stealing bouts), resting (loafing and sleeping), comfort movements

(preening, stretching, and bathing), alert, courtship (displays and copulations), and aggression (bill threats, chasing, and biting). Individuals were chosen by pointing the spotting scope in a randomly selected direction and observing the appropriate sex (also determined randomly) closest to the center of the field of vision. Individuals were then observed for 5 min and their behavior recorded every 15 s ( $n = 20$ ). During each 5-min observation, all occurrences of kleptoparasitism, sex and pair status of the focal individual, and outcome of the event were noted. Sex was determined using plumage and bill characteristics (Bellrose 1980), and pair status was determined using the criteria outlined by Hepp and Hair (1984). We defined rate of kleptoparasitism as the number of times a Gadwall successfully stole food from a coot during a 5-min period.

*Food abundance, herbivory, and waterbird numbers.*—Five permanent plots (25 m<sup>2</sup>) were randomly distributed in the observation area at the NSCWR. To estimate vegetative cover of aquatic plants for use as an index of food abundance, two permanent transects were established in each plot; water depth, vegetation depth, and percent cover and species composition of vegetation were recorded for two subplots (1 m<sup>2</sup>) placed randomly along each transect. Percent cover was recorded as no cover or one of 10 classes from 1–10% through 91–100%. Permanent plots were sampled on seven occasions from October through February.

Biomass and waterbird herbivory of milfoil were examined using 61-cm-tall, 1-m<sup>2</sup> exclosures constructed of 2.5 × 5 cm mesh welded wire with enclosed tops ( $n = 24$ ). They were placed in milfoil-vegetated areas of the NSCWR on 12–13 October 1991 using steel fence posts to hold them in position. Sides of exclosures were immersed about 40 cm to prevent foraging by waterbirds, while permitting underwater access by other aquatic herbivores. Coots rarely dived while foraging from October through mid-December and none were observed inside exclosures (LeSchack 1993). Exclosures were selected randomly and sampled on 15 November ( $n = 13$ ) and 14 December ( $n = 11$ ). A similar number of control plots (1 m<sup>2</sup>), randomly located 3 m from each exclosure, also was sampled. Vegetation from half (0.5 m<sup>2</sup>) of each exclosure and control plot was clipped to a depth of 30 cm, which was about the maximum depth that Gadwalls could reach when tipping up to feed. Wet vegetation samples were placed in nylon mesh bags, and excess moisture was removed by spinning for 5 min in a washing machine. After spinning, wet mass was measured (nearest 1 g) using a digital scale. Differences in biomass between control plots and exclosures was used to estimate the effects of waterbird herbivory.

Population counts of Gadwalls and American Coots were conducted at the NSCWR observation area every week, except during inclement weather, using a 15–60 × spotting scope (LeSchack 1993).

*Analysis.*—Effects of month, sex, and pair status on

frequency and rate of kleptoparasitism of Gadwalls were tested with likelihood-ratio tests ( $G$ -tests) and analyses of variance (ANOVA), respectively. After an ANOVA, we used Tukey's studentized range test for multiple comparisons.

We computed the proportion of each 5-min sample period that an individual spent feeding and swimming by dividing the frequency of each of these activities by the maximum frequency possible during the sample period ( $n = 20$ ). Proportions were arcsine transformed (Sokal and Rohlf 1981), and we used an ANOVA to examine differences in time spent feeding and swimming by kleptoparasitizing and nonkleptoparasitizing Gadwalls. Data collected in October and November were excluded from these analyses because kleptoparasitism was recorded infrequently ( $n = 3$ ) during these months.

To determine whether rate of kleptoparasitism was correlated with food abundance and the numbers of coots and Gadwalls, we placed data in the following seven time periods (with the sampling date of the 25-m<sup>2</sup> permanent plots the midpoint of each period): 15 October–2 November, 3–21 November, 22 November–10 December, 11–23 December, 24 December–12 January, 13 January–12 February, and 13–26 February. Mean values of kleptoparasitism rate and population size were computed for each period. We used the median value of the four 1-m<sup>2</sup> subplots to estimate cover class of individual 25-m<sup>2</sup> plots. Median cover class of the 25-m<sup>2</sup> plots ( $n = 5$ ) was computed for each time period. Spearman's rank correlations of median cover class, average population size, and average rate of kleptoparasitism were computed.

Wet mass of milfoil in exclosures (ungrazed) and control plots (grazed) was compared using an ANOVA after log transformation made means and variances independent. The Statistical Analysis System was used for data summaries and analyses (SAS Institute 1988); level of significance was set at the 0.05 probability level.

## RESULTS

Gadwalls were observed for 117 h during 1,402 focal-animal observations from 17 October 1991 to 26 February 1992. Kleptoparasitism occurred during 30% ( $n = 423$ ) of the observations (Table 1). Gadwalls kleptoparasitized American Coots by taking food that had been brought to the surface after diving. Coots responded aggressively and prevented Gadwalls from stealing food only five times (<1%) during the study. Food stealing rarely occurred in October and November (Table 1). The rate of kleptoparasitism varied among other months ( $F_{2,950} = 32.10$ ,  $P < 0.001$ ) and was greatest in December (Table 1). The proportion of Gadwalls initiating klep-

TABLE 1. Frequency and mean rate of kleptoparasitism of American Coots by Gadwalls by month. Mean values with different letters are significantly different ( $P < 0.05$ ; Tukey's studentized range test).

| Month    | $n^a$ | Frequency <sup>b</sup> | Rate of kleptoparasitism ( $\bar{x} \pm SE$ ) <sup>c</sup> |
|----------|-------|------------------------|--|
| October  | 116   | 1                      | 0.01 $\pm$ 0.01  |
| November | 330   | 2                      | 0.01 $\pm$ 0.00  |
| December | 318   | 179                    | 1.58 $\pm$ 0.11 A  |
| January  | 318   | 142                    | 1.07 $\pm$ 0.08 B  |
| February | 320   | 99                     | 0.66 $\pm$ 0.07 C  |

<sup>a</sup> Numbers of Gadwalls observed each month for 5 min.

<sup>b</sup> Numbers of Gadwalls observed that were kleptoparasitic.

<sup>c</sup> Numbers of kleptoparasitic events per 5-min observation period.

toparasitism also varied ( $G = 42.29$ ,  $df = 2$ ,  $P < 0.001$ ) by month; 76% ( $n = 321$ ) of kleptoparasitism acts occurred in December and January (Table 1).

*Sex and pair status.*—Interaction of sex with pair status accounted for a significant amount of variation ( $F_{1,950} = 26.53$ ,  $P < 0.001$ ) in the rate of kleptoparasitism. Unpaired females had a higher rate and frequency of kleptoparasitism ( $G = 100.55$ ,  $df = 3$ ,  $P < 0.001$ ) than any other sex-pair status class (Table 2). The rate of kleptoparasitism by unpaired males was greater ( $P < 0.05$ ) than that of paired males and paired females, but the kleptoparasitism rate of paired males and paired females did not differ statistically ( $P > 0.05$ ; Table 2).

TABLE 2. Frequency and mean rates of kleptoparasitism by sex and pair status of Gadwalls. Within each group, mean values with different letters are significantly different ( $P < 0.05$ ; Tukey's studentized range test).

| Group                  | $n^a$ | Frequency <sup>b</sup> | Rate of kleptoparasitism ( $\bar{x} \pm SE$ ) <sup>c</sup> |
|------------------------|-------|------------------------|--|
| <b>Sex</b>             |       |                        |  |
| Female                 | 699   | 211                    | 0.83 $\pm$ 0.06 A  |
| Male                   | 703   | 212                    | 0.68 $\pm$ 0.05 B  |
| <b>Pair status</b>     |       |                        |  |
| Unpaired               | 644   | 268                    | 1.14 $\pm$ 0.07 A  |
| Paired                 | 758   | 155                    | 0.42 $\pm$ 0.04 B  |
| <b>Sex/pair status</b> |       |                        |  |
| Female unpaired        | 215   | 119                    | 1.76 $\pm$ 0.14 A  |
| Female paired          | 484   | 93                     | 0.41 $\pm$ 0.05 C  |
| Male unpaired          | 429   | 149                    | 0.83 $\pm$ 0.07 B  |
| Male paired            | 274   | 62                     | 0.45 $\pm$ 0.06 C  |

<sup>a</sup> Number of focal individuals observed for 5 min.

<sup>b</sup> Number of Gadwalls observed that were kleptoparasitic.

<sup>c</sup> Number of kleptoparasitic events per 5-min observation period.

TABLE 3. Mean percent time spent feeding and swimming by nonkleptoparasitizing and kleptoparasitizing Gadwalls by month. Mean values with different letters within a month and an activity are significantly different ( $P < 0.05$ ; Tukey's studentized range test).

| Activity        | Gadwalls (%)          |                    |
|-----------------|-----------------------|--------------------|
|                 | Nonkleptoparasitizing | Kleptoparasitizing |
| <b>December</b> |                       |                    |
| $n$             | 139 <sup>a</sup>      | 179                |
| Feeding         | 66.8 $\pm$ 2.4 A      | 50.5 $\pm$ 1.8 B   |
| Swimming        | 24.9 $\pm$ 2.0 B      | 41.8 $\pm$ 1.6 A   |
| <b>January</b>  |                       |                    |
| $n$             | 176                   | 142                |
| Feeding         | 67.1 $\pm$ 1.8 A      | 58.9 $\pm$ 1.7 B   |
| Swimming        | 25.6 $\pm$ 1.4 B      | 35.4 $\pm$ 1.6 A   |
| <b>February</b> |                       |                    |
| $n$             | 221                   | 99                 |
| Feeding         | 70.2 $\pm$ 1.7 A      | 61.7 $\pm$ 2.1 B   |
| Swimming        | 21.7 $\pm$ 1.4 B      | 32.4 $\pm$ 1.9 A   |

<sup>a</sup> Number of focal individuals observed for 5 min.

*Time-activity budgets.*—The percentage of time spent feeding and swimming differed significantly for kleptoparasitizing and nonkleptoparasitizing Gadwalls. Individuals that did not steal food from American Coots spent more time feeding and less time swimming (i.e. searching for food or hosts) in December, January, and February than individuals that were kleptoparasitic (ANOVA, all  $P < 0.001$ ; Table 3).

*Food abundance, population size, and kleptoparasitism.*—Eurasian watermilfoil was the only species of aquatic macrophyte in 1-m<sup>2</sup> samples ( $n = 160$ ) of the 25-m<sup>2</sup> permanent plots. The median cover class of milfoil, an index of food abundance, was relatively high from October to early December (periods 1–3), then declined from mid-December through the end of the study (Fig. 2). Numbers of Gadwalls and American Coots were positively correlated with amount of milfoil cover ( $r_s = 0.86$ ,  $df = 6$ ,  $P = 0.01$ ; Fig. 2). When combined numbers of Gadwalls and coots were held constant using partial correlation, the rate of kleptoparasitism was inversely correlated with median cover class of Eurasian watermilfoil ( $r_s = -0.86$ ,  $df = 6$ ,  $P = 0.03$ ).

Waterbird herbivory had a significant impact on Eurasian watermilfoil abundance. Milfoil wet mass (grams  $\cdot$  [0.5 m<sup>2</sup>]<sup>-1</sup>) declined 75% from 153 g in November to 39 g in December ( $F_{1,44} =$

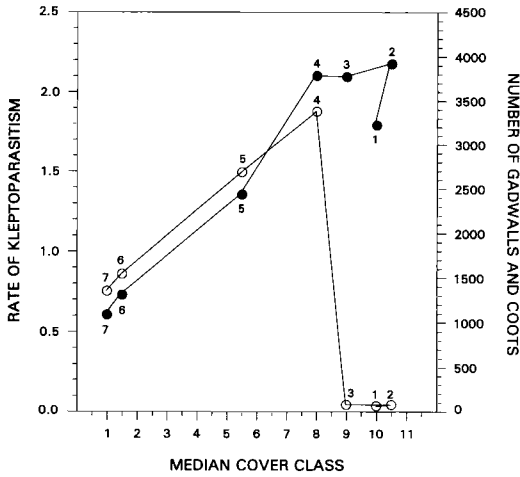


Fig. 2. Relationships of average rate of kleptoparasitism and combined numbers of Gadwalls and American Coots with median vegetation cover-class values during seven time periods on North Sauty Creek Waterfowl Refuge. Open circles are rate of kleptoparasitism and closed circles are numbers of Gadwalls and American Coots. Numbers above and below data points correspond to time periods: (1) 15 October–2 November, (2) 3–21 November, (3) 22 November–10 December, (4) 11–23 December, (5) 24 December–12 January, (6) 13 January–12 February, and (7) 13–26 February.

61.87,  $P < 0.001$ ); however, wet mass was greater in exclosures (ungrazed) than in control (grazed) plots in both November (200 vs. 107 g, respectively;  $F_{1,24} = 12.77$ ,  $P = 0.002$ ) and December (58 vs. 19 g, respectively;  $F_{1,20} = 11.18$ ,  $P = 0.003$ ). Besides herbivory, other factors like plant senescence caused milfoil mass to decline even in exclosures.

DISCUSSION

Winter can be energetically demanding for birds of temperate climates. In some species of ducks, for example, individuals in good physical condition survive better in winter than those in poor condition (Haramis et al. 1986, Hepp et al. 1986, Conroy et al. 1989). Acquisition and maintenance of energy during the winter, therefore, is vital. Wintering Gadwalls spend most of the day feeding on a low-quality diet of leafy vegetation and algae (Paulus 1982, 1983, LeSchack 1993). For some herbivores, keeping a high level of food intake is important for maintaining a positive energy balance (Sibly

1981). Kleptoparasitism by herbivorous Gadwalls under certain conditions may be important for helping to meet daily energy requirements.

*Aggression, dominance status, and kleptoparasitism.*—The proportion of Gadwalls initiating kleptoparasitism at the NSCWR was three times greater (30 vs. 10%) than that reported by Amat and Soriguer (1984) for Gadwalls in Spain. Our study showed that American Coots responded less aggressively to Gadwalls than did Eurasian Coots (<1 vs. 21%, respectively; Amat and Soriguer 1984). Because Eurasian watermilfoil is lower in nutritional quality (i.e. kcal/g) than many species of aquatic macrophytes (Paulus 1982), and was the only species present at the NSCWR, coots may have been less aggressive because there was little advantage to defending a low-quality food. In Amat and Soriguer's (1984) study, Eurasian Coots had access to several species of submerged plants and aggressively defended the resource from kleptoparasites.

In Gadwalls, males are dominant to females, and paired individuals are dominant to unpaired individuals (Paulus 1983, Hepp and Hair 1984). Kleptoparasitism of American Coots occurred more frequently and at higher rates by Gadwalls in subordinate classes. Food stealing was performed most often by unpaired females, followed by unpaired males, and lastly by paired males and females. Amat and Soriguer (1984) found that female Gadwalls kleptoparasitized Eurasian Coots more than males, but they did not distinguish between paired and unpaired birds. If dominant individuals exclude subordinates from better-quality feeding sites (Gauthreaux 1978), stealing food might help subordinates meet daily energy demands when food is not abundant. The fact that kleptoparasitizing Gadwalls spent less time feeding and more time swimming and searching for food than individuals that did not steal food suggests that food was limited at the NSCWR.

*Food abundance, population size, and kleptoparasitism.*—It has been suggested that reductions in quality (Amat and Soriguer 1984) and accessibility (Knapton and Knudsen 1978) of plant foods cause kleptoparasitic behavior in Gadwalls and American Wigeons, respectively. Eurasian watermilfoil cover was extensive at the NSCWR from mid-October until early December. Numbers of Gadwalls and American Coots during this time were high, but food resources were abundant and kleptoparasitism was low.

In late December and early January, Gadwall and coot numbers remained relatively high, but milfoil declined and kleptoparasitism increased to high levels. Milfoil and numbers of Gadwalls and coots declined through the end of February. Despite reduced food resources, however, kleptoparasitic behavior decreased during this time, indicating that densities of hosts and parasites influenced food stealing behavior. The rate of kleptoparasitism in our study could be demonstrated to be inversely correlated with milfoil cover only when variation in population size of Gadwalls and coots was controlled statistically.

Kleptoparasitism of American Coots by Gadwalls was promoted by several factors. First, diving coots brought milfoil to the surface making it available to potential kleptoparasites. Second, coots did not respond aggressively toward Gadwalls which permitted the theft of their food. Finally, the rate and frequency of kleptoparasitism increased as food abundance declined, but only when suitable numbers of Gadwalls and American Coots were present.

Our three predictions for the occurrence of kleptoparasitic behavior in Gadwalls were supported: (1) food stealing became prevalent only when food abundance began to decline; (2) kleptoparasitism was performed most frequently by subordinate classes of Gadwalls; and (3) Gadwalls that stole food spent less time feeding and more time swimming and searching for food than those that did not steal food. Therefore, we propose that subordinate classes of Gadwalls "made the best of a bad situation" by using kleptoparasitism as an alternative foraging strategy to compensate for a reduction in food resources.

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