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Wild Carib grackles play a producer–scrounger game

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Producer–scrounger (PS) game-theoretical foraging models make predictions about the decision of group-feeding animals either to look for food (produce) or for opportunities to exploit the discoveries of other foragers (scrounge). We report the most complete demonstration to date of the applicability of the PS foraging game in a free-living animal, the Carib grackle (*Quiscalus lugubris*) of Barbados. As assumed by PS games, the payoffs obtained by scroungers were negatively frequency dependent. Experimentally, increasing the cost of scrounging led to a decrease in the observed proportion of scroungers, whereas raising the cost of producing increased the proportion of scroungers. Observations of marked birds revealed that group-level changes could be brought about by individual flexibility in tactic use. Despite consistent individual differences in tactic use, most birds used both tactics and could alter their use of producing and scrounging when conditions changed. We found no difference in the payoffs obtained by producers and scroungers, suggesting a symmetrical game equilibrium. Our results call for testing the PS foraging game in a broader range of biological systems that include different types of scrounging behavior (e.g., scramble, stealthful, or aggressive scrounging) as well as the exploitation of different phases of food production (e.g., searching, handling).

Key words: Carib grackles (*Quiscalus lugubris*), field experiments, kleptoparasitism, producer–scrounger games, social foraging theory. *[Behav Ecol]*

The producer–scrounger (PS) game describes the behavior of animals that look for their own food (producers) or search for opportunities to exploit the efforts of other foragers (scrounging) by kleptoparasitism (Giraldeau and Caraco 2000). In this game, the producer and scrounger tactics are incompatible; individuals can be engaged in only one at any one time (Giraldeau and Beauchamp 1999) but may change tactics sequentially. The consequence of tactic incompatibility is negative frequency dependence of scrounger payoffs: as the proportion of individuals engaged in the scrounger tactic increases in a group, the proportion of producers declines, and hence, group production effort decreases. The scroungers must then compete against a larger proportion of scroungers for a smaller number of scrounging opportunities (Barnard and Sibly 1981). If scroungers do better than producers when scroungers are rare, but worse than producers when scroungers are common, then there is a stable equilibrium frequency (SEF; Mottley and Giraldeau 2000) of scroungers at which no individual could do better by switching tactics (Giraldeau and Caraco 2000). In the case of foraging games that must be played repeatedly under changing conditions, the SEF of scrounging is likely attained by individual flexibility in tactic use rather than frequency-dependent selection acting over generations (Giraldeau et al. 1994). Demonstrations of the applicability of the PS game in a social foraging context must therefore provide 3 types of evidence: 1) tactic incompatibility, 2) negative frequency dependence of payoffs to scroungers, and 3) group-level adjustment to variation in ecological factors determining the SEF of scroungers. When these conditions are met, the solution of the game can then be characterized as symmetrical or asymmetrical depending on whether the 2 tactics reap equal payoffs at equilibrium.

To date, demonstrations of this type have been conducted only on captive animals (e.g., Giraldeau et al. 1994; Mottley and Giraldeau 2000; Coolen et al. 2001). In the field, researchers have examined determinants of individual differences in tactic use (e.g., Hansen 1986; Stahl et al. 2001; Bicca-Marques et al. 2005), as well as ecological variables affecting the fraction of each discovered patch that goes to the exclusive use of its finder (i.e., finder's share; Di Bitetti and Janson 2001; Robinette and Ha 2001; Smith et al. 2002). Changes in producing costs have been shown to lead to adjustment in scrounging frequencies in the direction predicted by PS foraging games (Bugnyar and Kotrschal 2002; Barta et al. 2004). However, no field study has yet examined the assumption of negative frequency dependence of scrounger payoffs, such that the general usefulness of the PS game for social foraging (Giraldeau and Caraco 2000) remains to be shown.

In this study, we investigate the applicability of the PS game in a free-living animal, the Carib grackle (*Quiscalus lugubris*). *Quiscalus lugubris* is a generalist group foraging passerine that feeds on clumped food resources in urban areas of Barbados (Jaramillo and Burke 1999). These birds occasionally and spontaneously immerse dry food items in water before consumption, a behavior called "dunking" (Morand-Ferron et al. 2004). Dunked food items require shorter handling times, and dunking, thus, eases the ingestion of hard and/or dry items, making them more profitable (Morand-Ferron et al. 2006). Grackles that engage in dunking within groups often lose dunked items to conspecifics (Morand-Ferron et al. 2004, 2006) that use either stealthful or aggressive kleptoparasitic tactics (sensu Giraldeau and Caraco 2000).

We test the applicability of the PS foraging game in the field via experiments on dunking and stealing of dunked food by Carib grackles foraging on a single food patch of indivisible items. In this case, the scroungers appropriate whole items and exploit the producer's investment in food manipulation

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by dunking. By definition, these tactics meet the assumption of incompatibility because birds cannot simultaneously be engaged in dunking (producing) and kleptoparasitism (scrounging). In a series of field experiments, we ask whether the payoffs to the scrounging alternative are negatively frequency dependent. We also independently manipulate the costs to producers and scroungers to see whether the group can adjust its use of either tactic as predicted by the PS game. We then examine the extent to which banded individuals have fixed or flexible use of tactics. Finally, we compared the payoffs with producers and scroungers to determine whether this system is characterized by a symmetrical equilibrium.

MATERIALS AND METHODS

Field observations

In all, 278 Carib grackles were caught, identified with unique color band combinations, and released on the grounds of the Bellairs Research Institute of McGill University, in St James, Barbados, between January 2002 and May 2004. Experimental trials were conducted on a paved terrace located in the grounds of the institute. Each trial lasted 60 min and started when the observer placed approximately 200 pellets of dry dog food (0.7 cm in diameter, 21% protein, "Atlantic Marketing," St Michael, Barbados) in a clump on the ground 30 cm away from a puddle of water. A maximum of 4 trials were conducted per day (total = 85 trials). Both the food pile and the puddle were replenished whenever they were approximately half depleted. The experimenter (J.M.-F.) observed and video recorded all trials from a distance of approximately 15 m. Sightings of banded birds were narrated into the camera microphone in order to insure correct identification of color combinations on data collection from the video recordings. During the second half of the study, a second observer (M.V.) noted the payoffs obtained by producers and scroungers.

Experimental manipulations

To vary the scrounging cost, we changed the shape of the puddle, keeping its surface approximately constant. We used a circular (50 cm diameter, 1963 cm^2) puddle for the low scrounging cost condition and a rectangular (100 × 20 cm; 2000 cm^2) puddle in the high scrounging cost condition. The assumption here is that the rectangular puddle, having a larger perimeter for a given surface than a circle, allowed for larger interindividual distances for the same number of birds at the puddle, thereby increasing costs to scroungers by reducing their success rate (Vines 1980). To avoid order effects, we recorded data for 5 consecutive days in the low scrounging cost followed by 5 consecutive days in the high scrounging cost condition and again 5 more consecutive days in the low scrounging cost condition. The shape of the puddle affected scrounging costs as expected: 48.4% of attempts were successful in the low cost condition, whereas this proportion fell to 36.8% in the high cost condition (2-sample *t*-test on arcsine-transformed proportions with all data from low scrounging cost conditions pooled: $t = 3.2$, degrees of freedom [df] = 35, $P = 0.003$).

To vary the producing cost, 2 days before the start of trials, we placed a 1.5-m-high × 4-m wire mesh fence between the food and the puddle to manipulate the distance a producer had to travel in order to dunk. In the low producing cost condition, the birds could walk directly from the food to the puddle (distance = 30 cm) through an opening in the fence. In the high producing cost condition, the opening was shut, forcing the birds to fly over or walk around the fence. The wire mesh fence was present in both conditions. Birds had access to the pellets and puddle for 5 successive days in the low producing cost condition and another 5 successive days in the high producing cost condition. Between the two 5-day blocks, they were given a 1-day period of familiarization to the closed fence. As in the scrounging cost experiment, a second 5-day block of low producing cost trials was added after the high cost ones to control for order effects. The fence affected the costs of producing in the way we expected. Travel time between the food pile and puddle was shorter in the low versus high producing cost condition (2.39 ± 1.29 s vs. 6.60 ± 1.18 s, respectively; 2-sample *t*-test on log-transformed travel times with all data from low producing cost conditions pooled: $t = -12.3$, df = 30, $P < 0.001$).

Negative frequency dependence of scrounger payoffs

The experimenter scanned videocassettes looking for successful stealing and consumption of a dunked item, noting when possible the identity and sex of a banded scrounger and only its sex when unbanded (Jaramillo and Burke 1999). We calculated a bird's latency to a successful scrounging event from landing or from its last successful feeding event. There was no effect of the type of starting point on latencies ($F_{1,23} = 0.02$, $P = 0.88$), and so both categories were pooled for the rest of the analyses. The relative frequency of scroungers for a given scrounging event was estimated from 10-s scan samples in which we counted the number of birds engaged in dunking (producer) and attending the puddle (i.e., located 15 cm or less from the puddle) without food (scroungers), excluding the focal scrounger. These scans were repeated from the time the focal scrounger either landed or swallowed its previous food item up to and including the scrounging event. For each scrounging event, we calculated the mean ratio of scroungers to producers plus scroungers. We extracted scrounger payoffs and frequencies from videocassettes of a randomly chosen condition (second series of low scrounging cost condition). In order to ensure that the results could be generalized, we repeated the analysis on the first series of observations in the low producing cost condition and obtained similar results (not shown).

The payoff to a focal scrounger is the inverse of its latency to scrounge, estimated from the second set of low scrounging cost trials. Twenty-five of the 41 data points for this measure were taken on birds that were not banded. To deal with difficulties related to unidentified birds and the likely codependence of trials collected on the same day, we used generalized linear mixed models for autocorrelated data. We modeled the variation in log-transformed payoffs to scroungers using the %GLIMMIX macro in SAS version 8.2 (Kuss 2002). We included the proportion of scroungers and group size as fixed factors and individual and trial as random factors. The identity of unmarked birds was coded in 2 ways: once assuming that all unmarked individuals were different individuals and once considering all unmarked females as one individual and all unmarked males as another individual. We obtained similar results with both analyses and so present only the latter as this coding system assumes more pseudoreplication than was probably the case and is thus more conservative.

Varying producing and scrounging costs

We used analyses of covariance with group size as a covariate (Coolen 2002) to examine the effect of experimental manipulations on the proportion of scroungers in groups (calculated from 10-s scan samples; see above) using log-transformed values.

Individual flexibility in tactic use

A total of 60 banded birds were observed producing and/or scrounging at our experimental site (range = 1–393 acts per individual). We included in these analyses only marked individuals that engaged in at least 2 acts in each of the conditions we compared. We pooled the 2 data sets from the low scrounging cost conditions and from the low producing costs conditions, respectively, in order to increase statistical power. Here we defined an individual's proportion of scrounging acts as the number of kleptoparasitic attempts (unsuccessful and successful) over the total number of acts (unsuccessful and successful kleptoparasitic attempts plus the number of items dunked, whether these were lost to conspecifics or successfully eaten) for each condition. In order to examine individual flexibility in tactic use, we ran a repeated-measures analysis of variance (ANOVA) on the arcsine square-root transform of the proportion of scrounging acts per condition for each individual (test of within-subjects effects). We analyzed only the data collected when varying scrounging costs ($n = 25$) as power for the data collected when varying producing costs was very low ($n = 8$, power = 0.075 with $\alpha = 0.05$). Individual differences were assessed with the between-subject effects test.

To examine individual consistency in tactic use, we ranked individuals according to their proportional usage of scrounging and conducted a Wilcoxon signed-ranks test. We report the correlation between the proportion of scrounging acts by individuals in the low and high scrounging costs conditions.

Comparing payoffs to producers and scroungers

During the second half of the study (varying producing cost), a second observer (M.V.) followed one focal bird at a time and recorded its latency from landing to ingesting a food item, along with the behavior leading to successful ingestion of the item (dunk or steal dunked food). Shorter latencies thus indicate higher payoffs. The observer collected only one data point per focal bird and then switched to observing the next bird landing on the site. We compared average latencies (log transformed) between tactics with an ANOVA controlling for treatment.

RESULTS

Frequency dependence of scrounger payoffs

As predicted, the payoffs to scroungers declined as their proportion increased in the group ($F_{1,23} = 9.28$, $P = 0.006$; Figure 1). This effect held when controlling statistically for variation in group size ($F_{1,22} = 8.83$, $P = 0.007$).

Varying producing and scrounging costs

Experimental manipulations of the cost to scroungers significantly affected the proportion of individuals using the scrounging tactic (ANOVA: $F_{2,43} = 4.14$, $P = 0.017$; Figure 2a). Post hoc comparisons between treatments revealed a near-significant decrease in the proportion of scroungers when the scrounging cost was increased (Tukey, $P = 0.07$), whereas this proportion increased significantly when the scrounging cost was reduced (Tukey, $P = 0.02$).

Variation in the producing cost also influenced the proportion of scroungers (ANOVA: $F_{2,36} = 12.24$, $P < 0.001$; Figure 2b). Scrounging increased when the producing cost was increased (Tukey, $P = 0.005$) and decreased when the producing cost was lowered (Tukey, $P < 0.001$).

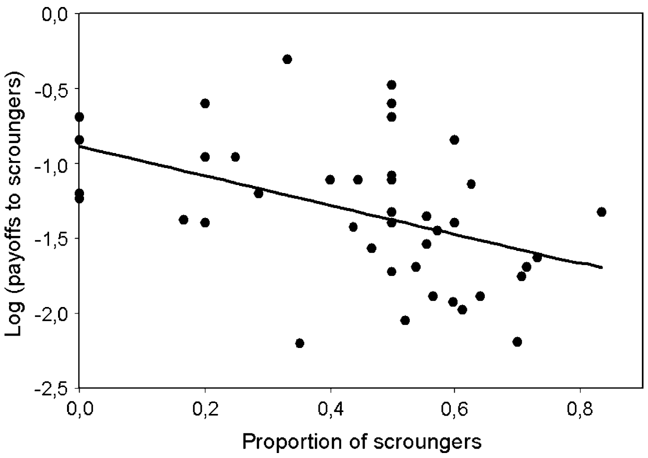

Figure 1
Log-transformed payoffs to scroungers (1/latency to scrounge) as a function of the proportion of scroungers in the group.

Individual flexibility in tactic use

Most birds (22/25 individuals) used both the producing and scrounging tactics, whereas 3 only produced, and none were pure scroungers. Examination of the behavior of these 25 individuals shows that 15 (60%) decreased their use of the scrounging tactic, 7 (28%) increased it, and 3 remained pure producers (Figure 3) in the high compared with low scrounging costs conditions. The alpha probability for an overall

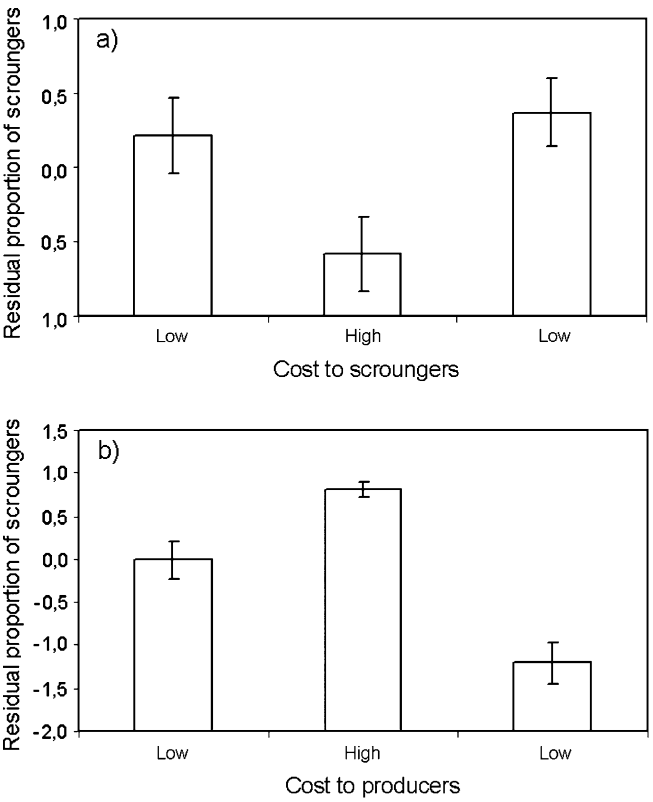

Figure 2
Mean (±standard error) residual proportion of scroungers (a) in the low, high, and low scrounging cost condition, and (b) in the low, high, and low producing cost condition. The residuals are obtained from a log–log regression between the proportion of scroungers and group size on all data.

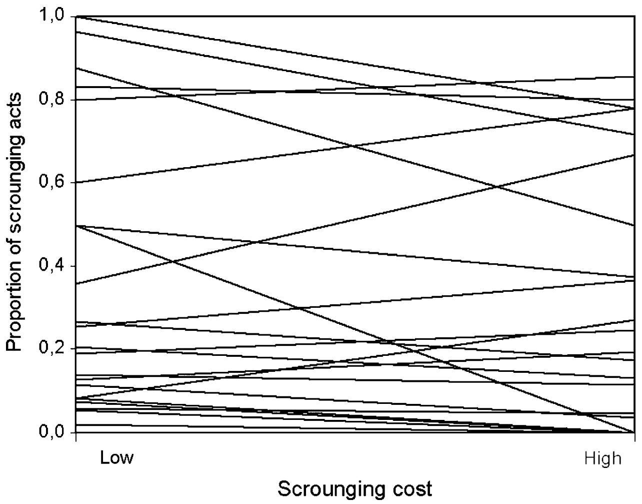

Figure 3
Proportion of scrounging acts by marked individuals in the low (both data sets pooled) and high scrounging cost condition.

decrease in the individual proportion of scrounging acts between the 2 conditions fell just short of the traditional threshold for significance ($F_{1,24} = 4.05$, $P = 0.056$). A test of between-subjects effects revealed significant individual differences in the proportion of scrounging acts ($F_{1,24} = 38.5$, $P < 0.001$).

There were no significant differences in the ranking of individuals according to their proportion of scrounging acts between the low and high scrounging cost condition ($Z = -1.25$, $n = 22$, $P = 0.211$). The within-individual correlation in the proportion of scrounging acts between the 2 conditions was high (Pearson's correlation coefficient: $r = 0.843$; Bartlett $\chi^2 = 24.2$, df = 1, $P < 0.001$).

Comparing payoffs to producers and scroungers

We found no significant difference in the latency to ingest a food item using either tactic (producing: 103.7 ± 74.3 s; scrounging: 129.5 ± 94.5 s; ANOVA: $F_{1,158} = 0.95$, $P = 0.332$).

DISCUSSION

Our study provides, to date, the most complete application of the PS foraging game to a field situation. Specifically, our results indicate that for free-living Carib grackles: 1) payoffs to scroungers were negatively frequency dependent, 2) groups adjusted their use of the producing and scrounging tactics in response to independent manipulation of the costs to each tactic, 3) despite consistent differences among individuals in tactic use, most birds exhibited a capacity for flexible investment, and 4) the payoffs to producers and scroungers were not different. We discuss each of these in turn.

The payoffs obtained by individuals engaged in the scrounging tactic decreased when the relative frequency of scroungers increased in the group. This result confirms the assumption of negative frequency dependence of scrounger payoffs that constitutes one of the basic tenets of PS games, an assumption that has to date only been confirmed in laboratory conditions and in cases where scroungers exploit the producers' searching effort (Giraldeau et al. 1994; Mottley and Giraldeau 2000). We feel that such frequency dependence will likely be more widespread in systems like ours, where scroungers exploit the producers' investment in food handling rather than their searching effort. This is because the incompatibility between producer and scrounger tactics that generates the negative frequency dependence of the scrounger tactic payoff may well be less likely when both tactics involve a form of food searching (Smith et al. 2002; Fernandez-Juricic et al. 2004) than when producing involves food handling and scrounging involves theft of food that has been handled.

The proportional use of producing and scrounging in groups of grackles changed when the costs to each tactic were experimentally manipulated. The changes in the use of strategies were in all cases qualitatively consistent with predictions of the PS foraging game. No study to date has altered the costs of both strategies independently. For instance, some studies on free-ranging birds altered the costs of producing by changing the risk of predation and report results consistent with the PS game (Bugnyar and Kotrschal 2002; Barta et al. 2004). In a study of captive birds, Giraldeau et al. (1994) increased the cost of producing by adding weights to the covers that producers had to remove in order to find food; they report that the proportional use of producing declined when costs increased. In another study of captive birds, Barrette and Giraldeau (2006) increased producing costs by making food patches cryptic and also report reduction in the use of the producer tactic. Earlier laboratory studies have demonstrated that the proportion of scrounging increases when seed distribution reduces the finder's share (Giraldeau and Livoreil 1998; Coolen et al. 2001). That our birds adjusted their tactic use in response to distinct manipulation of producing and scrounging costs suggests that birds can perhaps track several environmental variables to decide on their investment in producing and stealing in the wild.

Group-level adjustment in the grackles' relative frequencies of producers and scroungers apparently results from flexibility in individual production and scrounging effort (Barnard and Sibly 1981; Caraco and Giraldeau 1991; Giraldeau and Caraco 2000). Individual flexibility in tactic use is supported by a generalized (but not universal) near-significant decline in individual use of the scrounger tactic when scrounging costs were increased. However, such a mixed response pattern is not totally unexpected in a frequency-dependent system. If many individuals decrease their use of a tactic when its environmental cost is increased, then the frequency-dependent effects on the tactic's payoffs can actually make it profitable for a few birds to increase their investment in the use of that tactic. Responses to experimental manipulations, therefore, might be less unanimous in frequency dependent than in non–frequency-dependent situations.

Although most grackles engaged in both producing and stealing behavior, there was consistent variation in the proportional use of scrounging by different individuals, such that, on average, birds that engaged in a lot of producing in the high scrounging costs conditions were still producing at relatively high rates in the low scrounging cost condition. Beauchamp (2001) also reported both flexibility and consistency in tactic use in zebra finches (*Taenopygia guttata*). There have been many descriptions of limitations on the use of the producing or scrounging tactic (e.g., dominance, age, body size; Steele and Hockey 1995; Liker and Barta 2002; Bicca-Marques and Garber 2005). We do not know whether such constraints could explain individual differences in tactic use in Carib grackles, but earlier work found that neither the probability of dunking nor of losing food to conspecifics were related to a bird's sex or age (Morand-Ferron et al. 2004, 2006). Published reports of individual flexibility in the use of producer and scrounger tactics suggest a continuum from highly flexible, where individuals seem to be about equally inclined to use both tactics (pigeons, Giraldeau and Lefebvre

1986; nutmeg mannikins, Giraldeau et al. 1994), to strongly phenotypically constrained cases (e.g., Rohwer and Ewald 1981; Liker and Barta 2002).

Individual flexibility is not the only means by which groups can adjust producer and scrounger tactic frequency in response to changing foraging conditions in free-living systems. Groups can change as a result of differential immigration or emigration of individuals committed to one or the other tactic. Rita et al. (1997) suggest that individuals that tend to produce should try to assort themselves with other producers to avoid the cost of foraging with scroungers. However, unless producers invest heavily in keeping scroungers out, scroungers can be expected to join these groups as they would then receive very high payoffs by foraging in a flock composed of a large proportion of producers. It is more likely that scroungers would tend to leave groups in which the frequency of scroungers exceeds the equilibrium and, to the contrary, stay longer within a group where the frequency of scroungers is below the equilibrium. This would be consistent with the prediction of Barnard and Sibly (1981) that groups composed of equilibrium frequencies of producers and scroungers would persist longer. This possible mechanism is not mutually exclusive with individual flexibility in tactic use, and both might contribute to restoring equilibrium frequencies of producers and scroungers after changes in local foraging conditions. We do not know whether this happened in Carib grackles, but it would be an interesting possibility to investigate in future studies.

On average, Carib grackles obtained equal payoffs when using either tactic. Because we do not have information on the identity of focal individuals observed in this analysis, we cannot exclude the possibility that some birds were resampled, which would have resulted in an increased probability of type I error. This should thus not affect our conclusion of no difference between the payoffs obtained by producers and scroungers. Our results are consistent with Barnard and Sibly's (1981) prediction that foragers will reach a SEF of scroungers where the payoffs obtained by the 2 tactics are equal. Such symmetric equilibrium has been observed in captive *Lonchura punctulata* (Mottley and Giraldeau 2000). Field studies often reveal asymmetries in the payoffs obtained by kleptoparasites and honest foragers (e.g., Goss-Custard et al. 1998; Shealer and Spendelow 2002; but see Hansen 1986). However, it is not possible to determine whether these systems represent asymmetric PS games with individuals using the poorest tactic "doing the best of a bad job" because the assumptions of the game have not been tested.

Our study provides the first field application of the PS game to a kleptoparasitic system. It is important to note, however, that the grackle kleptoparasitic system we studied here differs from the scramble kleptoparasitism that has formed the basis of rate-maximizing PS foraging games (Vickery et al. 1991). For instance, whereas in the current models of the PS foraging game individuals have the option between searching for their own food or searching for others that have found food, the grackles in our study had the option of dunking or waiting for another to dunk and then stealing the item. These are more clearly incompatible alternatives. Moreover, whereas in the scramble systems modeled to date each patch is shared between the producer and all the scroungers, in our grackles the food item was either completely eaten by the producer or completely lost to a single scrounger. It is encouraging that our results generally support the PS approach in a system of free-living animals, and it would be important for future work to provide foraging models that more closely correspond to conditions of stealth or aggressive kleptoparasitism of the type exhibited by grackles. We hope that others will be encouraged to study the PS game more extensively in the field.

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