



Intraspecific kleptoparasitism and counter-tactics in the archerfish (*Toxotes chatareus*)

Bradley Duane Davis and L.M. Dill*

Evolutionary and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6

*Corresponding author's e-mail address: ldill@sfu.ca

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Abstract

The mechanics of the archerfish's remarkable ability to spit down aerial prey is well studied. Relatively unknown, however, are the social consequences of this hunting method. To explore how physical factors and behavioural choices affect the use and success of intraspecific kleptoparasitism in socially foraging archerfish, 10 tagged, juvenile archerfish (*Toxotes chatareus*) were presented in groups of 3, 5, and 7 with single crickets of 3 sizes overhanging the water by either 15 or 30 cm. Video review revealed all spits, jumps, attempted thefts, and consumptions. Kleptoparasitism attempts were common, resulting in a 43.6% loss rate to the fish that successfully brought down the prey. Group size affected the probability of kleptoparasitism asymptotically: loss rate increased as group size increased from 3 to 5 members, but with no further increase at 7 members. As observed with other kleptoparasitic species, the rate and success of kleptoparasitism increased with both prey size and prey height (analogous to handling time). Several counter-kleptoparasitism behaviours were observed, including jumping to grab prey directly, aggression, spitting technique, and positioning.

Keywords

archerfish, *Toxotes chatareus*, social foraging, kleptoparasitism, social behaviour.

1. Introduction

For organisms that live and forage amongst others it is an inevitable consequence that their behaviour both depends on and affects the behaviours of others. Individuals actively respond to this interdependence of payoffs and penalties while foraging, resulting in alternative foraging strategies and counter behaviours. Food stealing is an explicit example: an individual reduces costs by exploiting the foraging efforts of others. Food stealing is a

common form of the larger concept of kleptoparasitism — the direct, parasitic exploitation of another's resource (Giraldeau & Caraco, 2000).

Kleptoparasitism has been reported throughout the animal kingdom: in birds (Brockmann & Barnard, 1979), spiders and insects (Higgins & Buskirk, 1988; Field, 1992), large carnivores (Packer & Ruttan, 1988), primates (Di Bitetti & Janson, 2001), and marine invertebrates (Zamora & Gomez, 1996; Morrissette & Himmelman, 2000). Despite this, the majority of kleptoparasitism research focuses on avian subjects (Iyengar, 2008). Aquatic examples, especially piscine ones, are rare. Nilsson & Bronmark (1999) found that prey handling time for northern pike (*Esox lucius*) increases with prey size and this extra time increases the risk of kleptoparasitism (as well as predation and cannibalism). As a consequence, pike target smaller prey than predicted based on maximizing energy intake. In a second example, surgeonfish (*Acanthurus coeruleus*), western buffalo bream (*Kyphosus cornelii*), and several other tropical reef fish attempt to steal from territorially guarded algae gardens, even forming 'gangs' to make raids more successful (Foster, 1985a, b; Hamilton & Dill, 2003). Iyengar (2008) provides a few more piscine examples and a review of the state of kleptoparasitism research in general.

Vulnerability to kleptoparasitism is affected by various characteristics of one's foraging and food-handling behaviours (Brockmann & Barnard, 1979; Giraldeau & Caraco, 2000). High-quality food items and/or ones that require difficult or lengthy handling are particularly attractive to kleptoparasites (Giraldeau & Caraco, 2000). Cheetahs (*Acinonyx jubatus*), for example, hunt high-quality prey that are difficult to catch and as a consequence are frequently kleptoparasitized by larger savannah predators looking to avoid hunting effort (Hunter et al., 2007). Additional vulnerability arises when food processing requires a temporary reduction in control of the food item (Giraldeau & Caraco, 2000). Gulls (*Larus canus*), for example, open cockles by dropping them onto hard surfaces, leaving themselves open to theft as others swoop in to steal (Norris et al., 2000). Lastly, the more conspicuous the hunting or food-handling behaviours, the easier it is for potential thieves to identify exploitation opportunities. It has been noted, particularly in birds, that kleptoparasitism is more extensive in open habitats where visibility is high (Paulson, 1985; Giraldeau & Caraco, 2000).

Each of these characteristics of vulnerability to kleptoparasitism can be identified in the social foraging behaviours of the archerfish (*Toxotes*

chatareus), which, therefore, represent an ideal study species to expand our understanding of kleptoparasitism and social foraging. Native to mangroves, estuaries and freshwater streams of Southeast Asia (Schuster, 2007), the seven species of archerfish (genus *Toxotes*) are known for their remarkable ability to spit water at, and thereby knock down, insects and other small prey that rest or fly above the water (Lüling, 1963; Bekoff & Dorr, 1976; Dill, 1977; Timmermans & Vossen, 2000). By rapidly closing its gill covers an archerfish forces water through a tube formed by the roof of its mouth and a grooved tongue (Milburn & Alexander, 1976; Timmermans & Souren, 2004). Although their eyes never break the surface of the water, archerfish can accurately predict the true position of a target, despite refraction, across a wide range of shooting angles (Dill, 1977; Timmermans, 2001; Ben-Simon et al., 2009; Temple et al., 2010). Furthermore, the force of a shot can be adjusted for the distance, size, and velocity of the target (Schlegel et al., 2006; Schuster et al., 2004, 2006). Archerfish very rapidly and accurately predict the trajectory of a dislodged prey even when the prey is knocked down by another fish (Rossel et al., 2002; Wöhl & Schuster, 2006, 2007). As is evident, much research has been devoted to the remarkable individual abilities of archerfish hunting terrestrial prey via spitting. Published descriptions of archerfish sociality, however, are unfortunately brief. Unknown are the effects this unique hunting technique has on individual behaviours within a group and the relative success of individuals foraging within that group.

Spitting is effectively a solitary hunting method. Yet juvenile archerfish, who can spit when only 2.5 cm in length, forage socially in small schools. Observations (by LMD) of introduced archerfish in freshwater lakes in North Queensland, Australia show juveniles advancing from cover in small groups (4–6 individuals) to hunt prey on overhanging vegetation. With all members of a foraging group eager to consume a discovered prey item, the archerfish that spits a prey item down from its perch is not always the fish that consumes it: kleptoparasitism is common (Lüling, 1963; Goldstein & Hall, 1990; Rossel et al., 2002).

The social foraging behaviours of archerfish exhibit each of the characteristics that affect vulnerability to kleptoparasitism. First, terrestrial prey consumed by juvenile archerfish are large, attractive food items. Second, leaving cover, cruising to find prey, and performing the choreographed steps necessary to successfully hunt via spitting involves searching and handling effort, and leaves the fish exposed to predation risk. Individuals should try to avoid

some of these costs, when possible, by hanging back in or near cover and stealing from coforagers. Third, direct control over a prey item does not occur until ingestion. Lastly, spitting is conspicuous. Both potential thieves and watchful researchers recognize and exploit the distinctive approach and tipping movements that betray a spitter's intent (Dill, 1977). Further attention is drawn with each spit needed to bring down a prey. Selection should promote behaviours that mitigate one's vulnerability to kleptoparasitism (Nilsson & Bronmark, 1999) and such behaviours may be evident in archerfish.

At prey discovery there is a clear distinction between the role of a spitting fish and of a kleptoparasite. A fish inclined to spit chooses if, when, at what angle, and with what force to shoot at a prey. In this way the spitting fish retains some control over the availability of prey items and their probability of ingestion. However, because the most likely projection of a targeted prey item is away from the spitter, a second tactic, theft, is available to the alert bystander. These roles are mutually exclusive at any given moment but a fish is not confined to one role. The distinct foraging roles observed in this system warrant a framework of kleptoparasitism rather than one of scramble competition. Within this framework, the fish that knocks down a prey item is considered the 'owner' and any other fish that consumes it is considered a thief.

Studying archerfish foraging behaviours in a social context expands our knowledge of this unique fish and provides an ideal system to broaden our understanding of the factors that affect the use and success of kleptoparasitism. In the present study, juvenile archerfish were observed foraging while we manipulated factors potentially affecting a spitter's vulnerability to theft. The objectives of our study were to describe the behaviours of socially foraging archerfish, to discover ways in which archerfish may alter their behaviour in response to the behaviours of others or to a change in environmental context, and to test the following hypotheses: if group size, prey height, and prey size are increased then the prevalence and success of kleptoparasitism will increase for each. Given the limited size of the study population, it was not our intent to look at all possible interactions between these variables.

2. Methods

2.1. General methods

Imported, wild caught, juvenile *Toxotes chatareus*, 7.12 ± 0.10 cm mean fork length \pm SE (SE is given for all subsequent reported means) at tagging

and 8.70 ± 0.11 cm mean fork length after study ($N = 10$), were acquired from a local aquarium importer (provenance unknown) and housed together in a filtered 275 litre aquarium. After two weeks of acclimation, each fish was anaesthetised using a clove oil and ethanol solution in an aqueous bath (1.36 ml/l water) and tagged for individual identification with two 2.5 mm diameter, coloured plastic beads sutured through the musculature just anterior to the dorsal fin. After a 2–3 day recovery tagged fish were maintained in the experimental pool (see below) for up to 11 days prior to the start of observations. The tagging procedure and the beads had no observable effect on the behaviour of the fish.

Tagged fish were put into a continuously filtered 3.05 m diameter circular pool filled to a depth of 60 cm. The pool was sectioned into quadrants with removable opaque dividers (Figure 1). Anchored driftwood and rooted plastic plants provided cover. Water temperature was kept at 27–28°C by heating the room. The pH was kept at 6.5–7.5 and hardness at 6.5 HD. Fluorescent lights maintained a 12 h:12 h light/dark cycle. Prior to the start of the experiment the fish were fed brine shrimp flakes, krill, and live white cloud mountain minnows (*Tanichthys albonubes*).

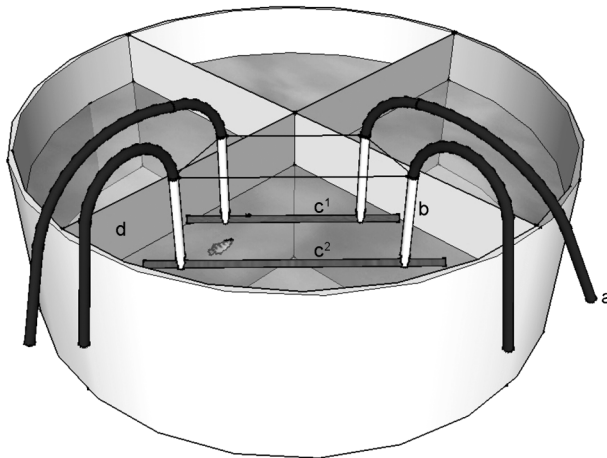


Figure 1. The circular observation pool and a prey presentation apparatus. For each trial a cricket was placed into one of four black tubes below the pool's edge (a) and delivered through a PVC pipe (b) to either the 61 cm dowel (c^1) or the 104 cm dowel (c^2) via compressed air. Opaque dividers (d) between quadrants lifted to form new groups of fish for observations. Items not shown include: rigging suspending the prey presentation apparatus, the second identical apparatus, the video camera, and plant cover submerged in each quadrant.

Observations were conducted between 22 August and 18 October 2007. During observations, groups of fish were presented with live crickets (lab-reared, 2–4 weeks old, 1.0–1.6 cm in length) on overhanging wooden dowels. Trials occurred sequentially with one cricket per trial; multiple trials were conducted each testing day. No more than 5 crickets per fish per day were presented. This was well short of the number required to cause satiation: in preliminary observations fish consumed 30–40 crickets in succession if available. In order to maintain equal sustenance across fish, all fish received brine shrimp flakes and each fish received individualized portions of frozen krill inversely proportional to their prey intake during testing. This feeding attempted to equalize daily rations and occurred after experimental observations. All fish were food-deprived overnight and until testing.

2.2. Prey presentation apparatus

Two identical prey presentation apparatuses were constructed out of 3.2 cm diameter PVC piping, 2 cm diameter wooden dowels, and black tubing (Figure 1). For each apparatus, two parallel dowels (one 104 cm in length and one 61 cm in length) separated by 26 cm were hung parallel to the water surface and perpendicular to the radius of the pool. Five centimetres from the ends of each dowel ran a vertical, 40 cm long PVC pipe. Each pipe was attached such that a cricket could fall through it, land on the dowel, and crawl out onto it in either direction through one of two small semicircles cut out of the pipe. Flexible, black plastic tubing ran from the top of each PVC pipe to outside and below the pool's edge. A cricket could be inserted into one of the 4 black tubes and be delivered unseen to a dowel rod via a short burst of compressed air. The two apparatuses hung over separate quadrants of the pool, allowing two groups of fish to be tested each day. The height of the apparatuses could be adjusted as desired to position the dowels at either 15 (Height 1) or 30 cm (Height 2) above the water.

Every attempt was made to prevent the fish from being able to predict the arrival of a cricket in space and time. Spatially this was achieved by numbering the pipes 1–4 and using a random number generator to choose which pipe each cricket was sent down, and by allowing crickets to emerge from the pipe in either direction. The interval between cricket presentations was varied haphazardly, ranging from immediate presentation of the next cricket to delays of over 5 min between crickets. Once delivered, crickets took anywhere from less than 1 s to over 3 min to emerge from a PVC pipe

and crawl out onto the dowel where they could be seen. This variability in emergence time further reduced the predictability of prey arrival. The behaviour of the crickets after emergence onto the dowel was unpredictable and included small infrequent movements, sporadic rapid movements, and constant movement. The time between the cricket's emergence and the first shot ranged from less than 1 s to over 30 s in rare cases.

2.3. Trials

Archerfish group size, prey height, and cricket size were varied while all fish behaviours, including spits, jumps, consumptions, attempts to steal, and aggressive behaviours, were recorded for later review with a Canon HV20 high definition video camera situated above the pool. Verbal and written accounts were also recorded. Each cricket defined a trial: this included all events occurring between a cricket's delivery and eventual consumption after being knocked onto the water by a spit or a jump. On occasion a cricket would voluntarily jump into the pool or would fail to catch on the dowel when sent down the pipe and would fall into the pool. Although its consumer was noted, these events were infrequent and were removed from the data set before analysis.

The 10 tagged fish were allowed to school together in 1 or 2 quadrants between observational sessions. Smaller groups were formed only for these sessions. The identity of members in the groups of 3, 5, and 7 fish were varied from test day to test day through haphazard subsampling, disallowing assortments that matched a recent or reoccurring assortment. Haphazard subsampling was necessary to avoid the excessive handling that using random or predetermined groups would have required.

In total, with prey presented at Height 1 (15 cm), 77 trials (crickets) were observed using groups of 3 fish (G3), 188 using groups of 5 fish (G5H1), and 116 using groups of 7 fish (G7) (Table 1). In addition, with prey presented at Height 2 (30 cm), 99 trials were observed using groups of 5 fish (G5H2). Trials of each type interspersed haphazardly across observation days, except that most of the G5H2 trials were clumped within the G5H1 trials. Theft rates did not differ between early and late G5H1 trials ($\chi_1^2 = 0.64$, $p = 0.423$). In addition, no order effects were found within any treatment group when testing across quartered data for changes in theft rate ($\chi_3^2 \leq 2.62$, $p \geq 0.453$) or spitting efficiency (number of spits per cricket) (Jonckheere–Terpstra tests, 4 levels, $Z \geq 1.356$, $N = 77, 188, 116$, and 99 , $p \geq 0.175$).

Table 1.

Trial counts for each treatment group.

	Group size	Prey height (cm)	Total number of trials	Cricket size			Prey downed via	
				1	2	3	Spit	Jump
G3	3 fish	15	77	39	34	4	64	13
G5H1	5 fish	15	188	106	67	15	157	29
G7	7 fish	15	116	69	36	11	84	34
G5H2	5 fish	30	99	58	29	12	99	0
Total			480	272	166	42	404	76

The experimental variable cricket size was varied haphazardly and the three sizes were presented to the four treatment groups in roughly the same proportions ($\chi^2_6 = 6.64$, $p = 0.355$). In 272 of the 480 total trials a lighter coloured, 1 cm (size 1) cricket was used; a 1.3 cm (size 2) cricket was used in 166 trials, and in 42 trials a darker, 1.6 cm cricket (size 3) was used (Table 1). The sizes of the crickets consumed were taken into account when maintaining equal satiation across fish after observations.

2.4. Observations of social foraging

For each observed spit or jump, the identity of the performing fish and its success in dislodging the cricket were recorded. It was assumed that every spit or jump was an attempt to knock down the cricket. Once a cricket was dislodged all attempting thieves were recorded (fish who made a deliberate movement towards the falling or fallen prey dislodged by another fish). Because many spits were unsuccessful, an individual could spit at a cricket, and then attempt to steal it if another fish successfully knocked it down. Throughout this paper, the terms ‘theft’ and ‘proportion stolen’ refer only to successful consumptions by thieves; ‘attempted thefts’ may be either successful or unsuccessful. Finally, the identity of the successful consumer of each cricket was recorded.

2.5. Analysis

Despite careful video review, the consumer’s identity was inconclusive in 5 of the 480 trials. These five trials were removed from analyses regarding rates of loss to kleptoparasitism. Information regarding spitting, jumping,

aggression, and theft attempts was available, however, so these trials were included in analyses of this nature.

The effects of group size, prey height, prey size, and the presence of aggression on spitting frequencies, jumping frequencies, kleptoparasitism, and probabilities of success in consuming the prey were determined. The effects of group size were examined by comparing results across the three group sizes at Height 1 (G3, G5H1, G7 trials), and the effects of prey height by comparing the trials with 5 fish at 15 cm and 30 cm (G5H1 vs. G5H2 trials). The effects of prey size were explored by comparing trials using different crickets sizes within and across groups. In a group of N fish, the number of attempting thieves varied from zero to $N - 1$; thus, comparisons across multiple numbers of attempting thieves were made by grouping the data by the number of attempting thieves, regardless of group size.

Spit count and jump count data were nonparametric, so Mann–Whitney U and Jonckheere–Terpstra tests were used when comparing spitting or jumping rates between two or more groups. Chi-square tests were used to compare the categorical data between groups, such as proportion of prey stolen and proportion of trials with aggression.

For testing for significant effects and interactions across multiple categorical variables, log-linear models were constructed. For example, a log-linear model was constructed to test if cricket theft was dependent on prey height, on the number of attempting thieves, and on the interaction between prey height and thief number. Using a log-linear model allowed a comparison of theft rates across prey heights while accounting for the disparate number of attempting thieves between these groups of data.

It must be noted that the data compared in this study are not strictly independent. Ten fish were repeatedly subsampled into groups for trials. Due to the necessary haphazard manner in which groups were formed, a few individuals were significantly underused or overused in each of the four treatment groups (G3, G5H1, G7, and G5H2): of the 40 fish-group combinations, 5 fish were underused and 2 were overused (chi-square tests, $p < 0.05$). However, regardless of their relative representation, all fish participated equally across foraging trials within each treatment group (proportion of trials performing a spit/jump/theft attempt, $\chi^2_9 \leq 9.36$, $p \geq 0.404$). Furthermore, to test if individuals behaved differently depending on group composition, the behaviour of each fish was compared when in the presence and absence of each of the other 9 fish, and in each of the different fish assemblages in which

it was observed. These tests indicate that individual fish do not significantly alter their behaviour based on membership in the coforager assemblage (see Appendix A for details).

3. Results

3.1. Spitting, jumping, and kleptoparasitism

In the 480 trials observed, 1489 spits, 160 jumps and 1466 attempted thefts were recorded (Table 2). The following section presents rates of spitting, jumping and stealing; this is followed by results on how each of these behaviours vary with prey height, prey size, and group size.

All fish performed all three foraging behaviours — spitting, jumping, and stealing. It took from 1 to 38 spits to knock down a cricket in those trials where no fish jumped. It took on average 3.02 ± 0.232 spits to knock down crickets perched at 15 cm; 4.36 ± 0.403 spits at 30 cm. These distributions are highly skewed: at Height 1 it took up to 38 shots to knock down one cricket, yet 42.7% of the time one shot was sufficient (Figure 2). At Height 2, one spit was sufficient only 20.0% of the time, reflecting the greater difficulty in spitting down crickets at the greater height.

Kleptoparasitic attempts occurred frequently: 97.7% of all trials had at least one. Successful thefts were also common: over all trials, 43.6% of crickets were ingested by a fish other than the fish that knocked it down. Crickets that were stolen took significantly more spits to knock down than crickets that were not stolen (3.65 ± 0.251 vs. 3.06 ± 0.286 spits/cricket, Mann–Whitney $U = -3.85$, $N_1 = 267$, $N_2 = 208$, $p < 0.001$). Figure 3 shows the relationship between the probability of theft and the number of

Table 2.
Observation counts for each treatment group.

	Spits sum	Spits per trial			Jumps sum	Jumps per trial		
		\bar{x}	Mode	SE		\bar{x}	Mode	SE
G3	272	3.53	1	0.521	28	0.36	1	0.080
G5H1	568	3.02	1	0.287	62	0.33	1	0.050
G7	217	1.87	1	0.154	70	0.60	1	0.092
G5H2	432	4.36	1	0.403	0	–		
Total	1489				160			

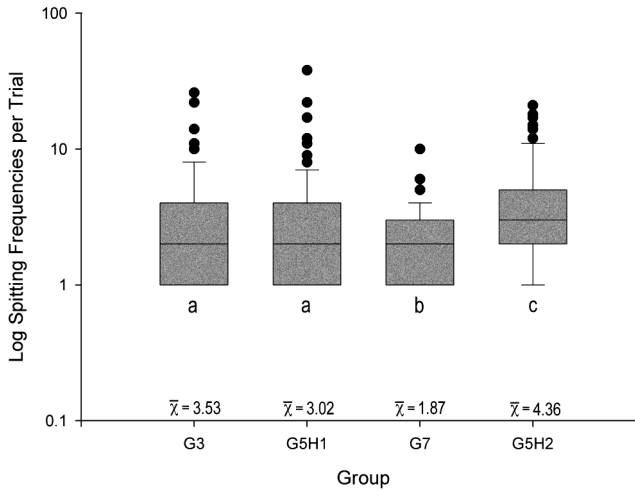


Figure 2. Box plots of spits per trial (across all fish) for each treatment group presented on a log scale. Closed dots represent the most extreme data points. Plots not sharing the same letter differ significantly at $p < 0.05$ (Mann–Whitney U -test).

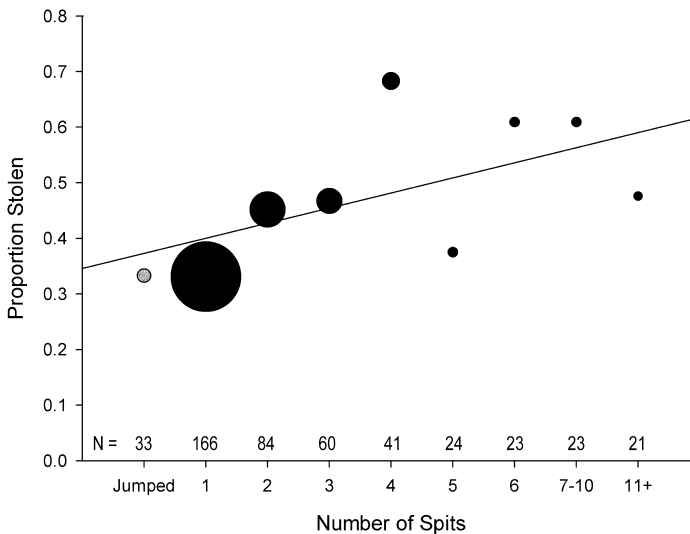


Figure 3. The proportion of crickets stolen (dot centre height), binned by the number of spits needed to knock the crickets down. The gray dot represents crickets knocked down by a jump. Dot sizes correspond to sample sizes, which are written along the bottom. The solid line is a linear regression across all solid dots ($R^2 = 0.339$).

spits needed to knock down the cricket. The greater variability and smaller sample sizes at the higher spit counts resulted in a non-significant linear regression (trials with jumping removed, $F_{1,396} = 2.449$, $p = 0.118$). However, if the number of potential thieves is added as a covariate, the probability of kleptoparasitism was found to increase significantly with spit number (trials with jumping removed, $F_{2,395} = 21.187$, $p < 0.001$).

Jumping from the water to grab a cricket off a dowel was observed much less frequently than spitting and did not occur at Height 2; successfully jumping to grab a cricket 30 cm above the water would be a remarkable feat for a 7 cm fish. Thirty-nine percent of trials at Height 1 included a jump, with a frequency of 1.39 ± 0.064 jumps per trial. Since spitting and jumping were alternative tactics, trials with a jump had fewer spits compared to trials without a jump (2.66 ± 0.169 vs. 3.03 ± 0.474 , Mann–Whitney $U = -1.73$, $N_1 = 266$, $N_2 = 115$, $p = 0.042$, 1-tailed).

On any given trial, a spit had a 33.0% chance of knocking down a cricket perched at 15 cm. A jump had a 47.5% chance of dislodging a cricket, which proved significantly more efficient than spitting (Mann–Whitney $U = -6.38$, $N_1 = 160$, $N_2 = 1057$, $p < 0.001$). Jumping resulted in a statistically insignificant decrease in thefts when compared to spitting (all H1 trials, 32.9% vs. 41.1% stolen, $\chi_1^2 = 1.70$, $p = 0.193$). The directionality of this result was consistent, however, within each group (Figure 4). Jumping as a hunting technique, therefore, was significantly more successful than spitting at dislodging low perched prey and potentially more successful in securing ingestion in the midst of potential thieves.

3.2. Prey height

The effects of prey height were assessed by comparing G5H1 trials to G5H2 trials, with trials with a jump removed from the former. In G5H1 trials fish spat on average 2.78 ± 0.224 times per cricket; in G5H2 trials fish spat on average 4.36 ± 0.403 times per cricket, a significant increase (Mann–Whitney $U = -4.26$, $N_1 = 141$, $N_2 = 99$, $p < 0.001$).

On average, in groups of five, more fish attempted to steal the higher perched crickets than crickets perched at 15 cm (3.20 ± 0.095 vs. 2.87 ± 0.082 fish/trial, Mann–Whitney $U = -3.09$, $N_1 = 99$, $N_2 = 188$, $p = 0.002$). Correspondingly, a significantly greater proportion of prey were stolen in G5H2 trials than in G5H1 trials (59.9% vs. 44.1%, $\chi_1^2 = 5.09$, $p = 0.024$; Figure 4). To test if crickets were more easily stolen at 30 cm

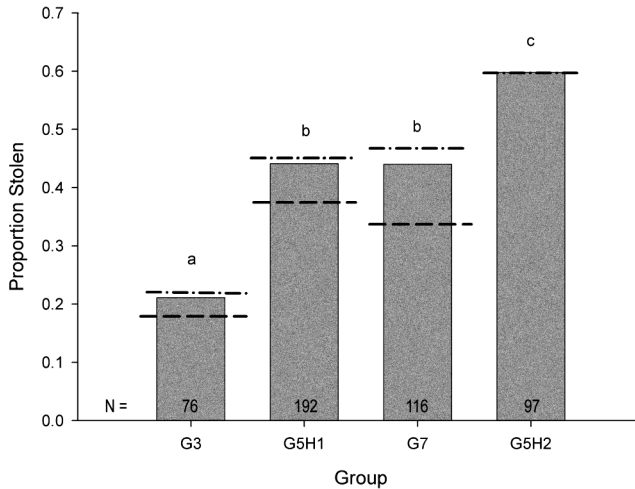


Figure 4. The proportion of crickets stolen within each treatment group. Bars not sharing the same letter differ significantly at $p < 0.05$ (pairwise chi-square tests). Sample sizes are written along the bottom. The horizontal lines represent the proportion of crickets stolen after being knocked down by a spit (dash dot lines) or by a jump (dashed lines). No jumps were observed in G5H2 trials.

independent of the greater number of fish attempting to steal, a log-linear model was constructed comparing theft rates between heights at each number of potential thieves. The 3-way higher order effect was non-significant ($\chi_3^2 = 2.48$, $p = 0.479$), but two partial associations were significant (Figure 5): the proportion stolen increased as the number of attempting thieves increased (partial $\chi_3^2 = 32.88$, $p < 0.001$), and the proportion stolen at 30 cm was greater than at 15 cm (partial $\chi_1^2 = 5.47$, $p = 0.019$). Thus, significantly more crickets were stolen when knocked down from 30 than from 15 cm even when the number of fish who attempted to steal was the same.

3.3. Prey size

The number of spits per cricket varied with increasing cricket size, but not significantly (2.82 ± 0.179 , 3.50 ± 0.379 , and 3.36 ± 0.479 for cricket sizes 1–3, respectively, Jonckheere–Terpstra test, 3 levels, $Z = 0.833$, $N = 480$, $p = 0.405$). The number of jumps per trial increased significantly with cricket size (H1 trials only, 0.346 ± 0.056 , 0.482 ± 0.057 , and 0.667 ± 0.205 for sizes 1–3, respectively, Jonckheere–Terpstra, 3 levels, $Z = 3.168$, $N = 381$, $p = 0.002$).

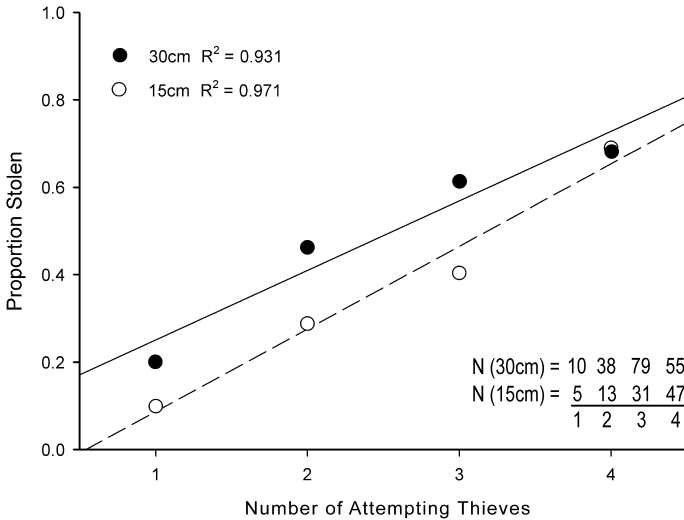


Figure 5. The proportions of prey stolen at 15 cm and 30 cm (open and closed circles, respectively), across the number of attempting thieves. Data exclude trials with jumping. Dotted and solid lines show linear regressions for the two prey heights. Sample sizes are shown in the table at bottom right.

Across all trials, as cricket size increased, the number of fish attempting to steal increased, although this change fell short of statistical significance (3.00 ± 0.082 , 3.01 ± 0.098 , and 3.62 ± 0.177 fish per trial for cricket sizes 1–3, respectively, Jonckheere–Terpstra, 3 levels, $Z = 1.627$, $N = 480$, $p = 0.104$). This trend held true within each treatment group and was statistically significant in two (G3 and G5H2 trials, respectively, Jonckheere–Terpstra, 3 levels: $Z = 1.978$, $N = 77$, $p = 0.048$ and $Z = 2.314$, $N = 99$, $p = 0.021$). In addition, the size of a cricket affected its probability of being stolen, with theft increasing significantly as cricket size increased (all H1 trials: 34.1%, 43.1%, and 60.0% stolen of sizes 1–3, respectively ($\chi^2_2 = 8.56$, $p = 0.014$; Figure 6). The trend of increasing probability of theft with increasing prey size held true within each treatment group.

To test if larger crickets were stolen more often independent of the number of attempting thieves, a log-linear model was constructed comparing theft rates between size 1 crickets and size 2 plus size 3 crickets (sizes 2 and 3 were pooled due to their smaller sample sizes). The three-way higher order effect was non-significant ($\chi^2_{10} = 2.76$, $p = 0.986$), but two partial associations were significant: the proportion stolen increased as the number of attempting thieves increased (partial $\chi^2_5 = 36.21$, $p < 0.001$), and a greater proportion

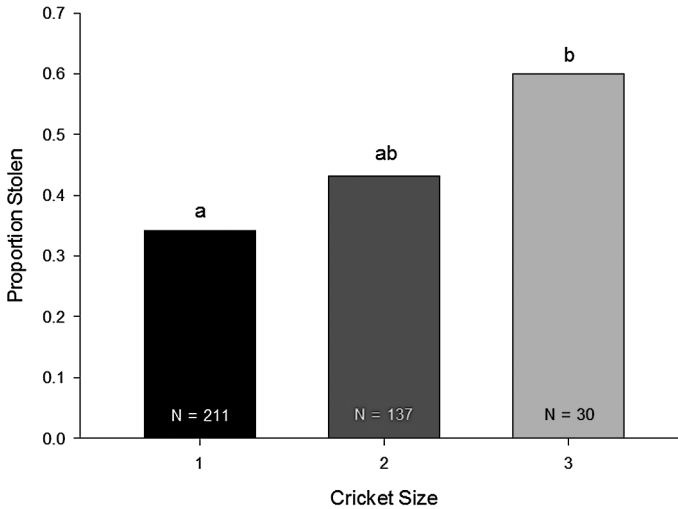


Figure 6. The proportion of crickets stolen across the three cricket size classes. Bars not sharing the same letter differ significantly at $p < 0.05$ (pairwise chi-square tests). Data include only Height 1 trials. Sample sizes are written along the bottom.

of size 2–3 crickets were stolen than size 1 crickets (partial $\chi^2_2 = 6.21$, $p = 0.045$). Thus, larger crickets were stolen significantly more often regardless of the number of fish attempting to steal (Figure 7).

3.4. Group size

The effects of group size were assessed by comparing trials across the three group sizes (3, 5, and 7 fish) with prey at Height 1. The number of spits per trial decreased with increasing group size (3.53 ± 0.521 , 3.02 ± 0.288 and 1.87 ± 0.154 spits/trial for G3, G5H1, and G7, respectively; Jonckheere–Terpstra test: $Z = -2.827$, $N = 381$, $p = 0.005$). This can be at least partially explained by the fact that jumping, an alternative tactic, increased significantly with group size (29%, 30% and 59% of trials with group sizes 3, 5, and 7, respectively, Jonckheere–Terpstra test: $Z = 2.812$, $N = 381$, $p = 0.005$). With trials with jumping removed, the decrease in number of spits per trial with increasing group size was no longer significant (3.56 ± 0.584 , 3.27 ± 0.329 , 2.17 ± 0.176 spits/trial for groups of 3, 5, and 7, respectively, Jonckheere–Terpstra test: $Z = -0.818$, $N = 266$, $p = 0.413$). Thus, it appears that group size had a significant effect on the occurrences of jumping and less if any effect on the number of spits per trial.

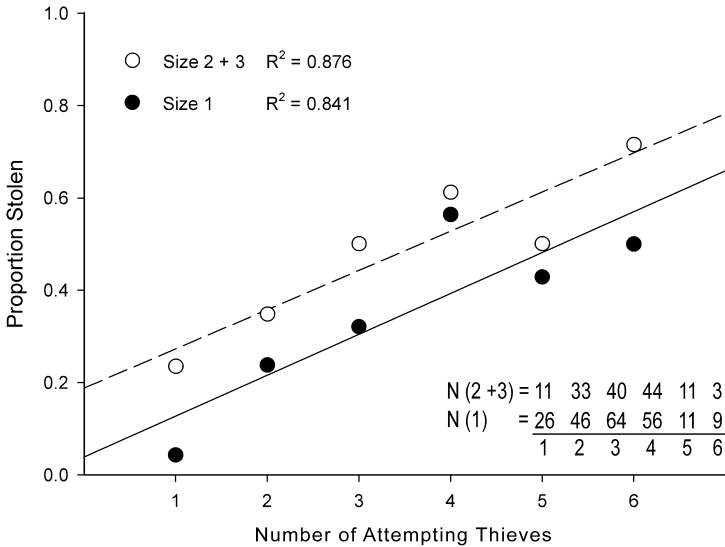


Figure 7. The proportions of crickets stolen, binned by the number of attempting thieves. Closed circles represent size 1 crickets; open circles represent size 2 and 3 crickets combined. Data include all Height 1 trials without jumping. Dotted and solid lines represent linear regressions for the two cricket size classes. Sample sizes are shown in the table at bottom right.

Naturally, as the size of the group increased the mean number of fish that attempted to steal each cricket increased (1.48 ± 0.073 , 2.87 ± 0.071 , and 4.27 ± 0.111 for group sizes 3, 5 and 7). Controlling for group size by dividing by the number of fish available to steal ($N - 1$), shows that on average fish attempted to steal with roughly the same probability across group sizes (0.740, 0.718, and 0.711 for group sizes 3, 5 and 7, respectively; all pairwise Mann–Whitney $U \leq -1.769$, $p \geq 0.077$; Jonckheere–Terpstra test for an effect across treatment groups: $Z = -1.74$, $N = 381$, $p = 0.082$).

Overall kleptoparasitic pressure increased with group size (average number of attempting thieves per trial divided by group size: 0.494, 0.574, and 0.610 for groups of 3, 5, and 7, respectively, Jonckheere–Terpstra test, $Z = 2.380$, $N = 381$, $p = 0.017$). Correspondingly, thefts increased with increasing group size, though not linearly. Groups of 3 fish had the lowest proportion of crickets stolen (G3 vs. G5H1 and G7, respectively, $\chi_1^2 = 12.20$, $p < 0.001$ and $\chi_1^2 = 10.60$, $p = 0.001$; Figure 4). The probability of theft for G5H1 trials was the same as for G7 trials (44.1% vs. 44.0%, $\chi_1^2 = 0.004$, $p = 0.984$) despite having on average 1.4 more attempting thieves per trial in

the latter. Jumping was more prevalent in G7 trials and although this reduced the overall theft rate, removing trials in both groups where the cricket was knocked down by a jump did not affect the result (45.2% vs. 47.6% stolen in G5H1 and G7 trials, respectively; $\chi^2_1 = 0.12$, $p = 0.731$).

4. Discussion

Kleptoparasitism is clearly a major source of direct conflict within groups of juvenile archerfish. Attempted in over 97% of the trials, kleptoparasitism resulted in loss rates as high as 60%. Our results show that the use and success of kleptoparasitism was affected by environmental factors (such as prey height and prey size), contextual factors (such as group size), and by behavioural factors (such as jumping).

4.1. Prey height

Prey height was shown to significantly affect archerfish foraging behaviours and the probability of kleptoparasitism. One or two spits brought down most prey perched 15 cm above the water. Efficiency declined when prey were raised to 30 cm; here 1 to 2 spits were sufficient only one third of the time as greater force and accuracy were required. This additional force made spitting at more distant prey more conspicuous (Schlegel et al., 2006). Once dislodged, prey items at 30 cm travelled further before hitting the water, allowing thieves more time to spot the prey and to move towards it. These factors made attempting to steal higher prey more attractive and successful: both with and without accounting for the increase in number of attempting thieves, crickets at 30 cm were stolen more frequently than those perched at 15 cm.

4.2. Prey size

Attempting to steal another's prey is worthwhile only if the rewards outweigh the costs of kleptoparasitism and the costs of forgoing your own discovery opportunities (Giraldeau & Caraco, 2000). Thus, large prey are more attractive to thieves as the costs are similar, but the rewards much greater. Here, as with prey height, prey size had a significant effect on the use and success of both spitting and stealing tactics. The greater spitting force needed to dislodge larger insects (Schlegel et al., 2006) drew greater attention and afforded thieves more time as the dislodged prey flew further from its perch. In addition, the larger, darker crickets were more conspicuous than the smaller,

lighter crickets. Both with and without accounting for the differences in the number of attempting thieves, larger prey were stolen more frequently than were smaller prey.

Other studies exploring factors that affect kleptoparasitism support the results found here with archerfish (Fuchs, 1977; Barnard & Thompson, 1985; Fischer, 1985; Nilsson & Bronmark, 1999; Ha & Ha, 2003). Steele & Hockey (1995) found that the most important factor determining the rate and success of intraspecific kleptoparasitism in kelp gulls (*Larus dominicanus*) was prey size and handling time. The risk of theft was directly proportional to the size of the prey's shell and the number of times a gull needed to drop a shell before it broke. With archerfish, kleptoparasitism was positively correlated with both prey size and the number of spits needed to knock down the cricket — an archerfish equivalent to handling time. Studies of intraspecific piscine kleptoparasitism are rare, but the findings of a study of northern pike complement those found here (Nilsson & Bronmark, 1999). Pike, like many piscine predators, required longer handling times to consume larger prey, and as handling time increased, the risk of losing the prey item to conspecifics increased as well.

4.3. Group size

In natural conditions where resources are limited, the size of the foraging group can affect individual behaviours and foraging success (Giraldeau & Caraco, 2000). Often when group size increases, the prevalence of kleptoparasitism increases as individuals take advantage of the collective search effort around them (Giraldeau & Caraco, 2000). Archerfish in relatively small groups of 3 to 7 fish forage on discrete, sequentially arriving prey and at prey discovery all foragers turn their focus towards this prey item. With one fish being a successful spitter, $N - 1$ individuals are potential kleptoparasites. Here the ratio of thieves to non-thieves is much higher with archerfish than with many other examples of intraspecific kleptoparasitism. Thus, rather than a system in which foraging groups find and share divisible patches within a landscape, archerfish represent a system similar to what Bélisle (1998) describes with parasitic jaegers (*Stercorarius parasiticus*). Small groups of jaegers chase and steal food items from common terns (*Sterna hirundo*), but only one jaeger enjoys the spoils. With jaegers and archerfish, as group size increases, additional foragers are better represented as more mouths to feed rather than as more eyes to search. This should be kept in mind when comparing the effects of group size between this and other systems. Nevertheless,

simple comparisons can be made regarding the probability of theft and the number of foragers.

Our data show that the probability of kleptoparasitism increased with group size, at least initially from 3 to 5 fish. Beyond 5 fish loss rate plateaued: loss rate did not continue to rise as five or more fish attempted to steal, but competition between thieves did. In small groups it was easier for a fish to discover and shoot down a prey item before others in the group were aware of the prey's arrival. With each fish that became aware of a prey item, the more likely its presence was to be revealed to others. In small groups there were simply fewer eyes observing and fewer movements to observe, making thieving more difficult. Furthermore, the spitter retains at least partial control of when and where prey will fall and in less crowded waters has a clearer path to the fallen prey. In larger groups when a handful of fish rushed to steal a falling prey, a moment of chaos occurred at the water's surface making it difficult for the spitter to track its prey, resulting in a greater probability of theft. In groups of 7 fish, however, each thieving fish beyond 3 increased competition while generating negligible increase to the overall probability of kleptoparasitism: the spitter retained a minimum probability of success due to the spitter's advantage and thieves likely interfered with each other. Thus, as group size increased, loss rate approached a maximum, suggesting that the maximally effective number of thieves may be 3 or 4 fish.

4.4. Counter-kleptoparasitism behaviours

If kleptoparasitism costs are small, foragers may tolerate kleptoparasites. More often, however, strong competition for resources encourages the evolution of counter-measures, be it through retaliation, compensation, or evasion (Barnard, 1984). A high rate of intraspecific kleptoparasitism of large food items within archerfish foraging groups appears to have led to the evolution of several anti-kleptoparasitism behaviours. The behaviours observed in this study were solely evasive measures intended to improve chances of consuming the prey. No retaliatory behaviours were observed.

Some fish attempted to reduce competition through aggressive guarding: a dominant fish was often seen to lunge at an approaching subordinate's flank forcing it from a patrolled area beneath one of the four pipes. Aggressive behaviours were performed exclusively prior to prey discovery since attention turned towards the prey after discovery. No individual could monopolize the entire area beneath the cricket apparatus, or even a small area absolutely.

Because the location of prey arrival was random, an aggressive fish was no more likely to be nearer the cricket than a fish under another part of the apparatus, but was more likely than a fish in cover. In each trial the presence or absence of an aggressive behaviour was recorded for each fish. Six of the 10 fish showed aggression in at least one trial. However, due to strong hierarchical dominance no two fish showed aggression in the same trial. An aggressive behaviour occurred prior to prey discovery in 53.4% of all trials. Statistics regarding aggression are presented in Appendix B. The prevalence of aggression varied between group sizes but with no obvious trend. Aggression had no effect on spitting or jumping frequency per trial.

Aggression did reduce the number of fish attempting to steal. The resulting reduction in loss rate, however, was consistent whether or not the aggressive fish was a spitter. Thus, aggression appears to have reduced competition for all spitters. The effect of aggression on overall theft rate depended on the size of the group and the perching height of the prey. Aggression had no effect on the probability of theft when crickets perched at 30 cm above the water. At this height it took more spits to knock down prey and prey fell further before hitting the surface of the water. This afforded potential thieves more time to get into position and attempt to steal, even if an aggressor had initially kept them back prior to prey discovery. With prey at 15 cm, aggression decreased the probability of theft only in groups of 3 or 5 fish. With the higher forager density in groups of 7 fish aggression may simply have been ineffectual.

The prevalence of aggressive behaviours between socially foraging juvenile archerfish in the wild is unknown. This study suggests that aggression and guarding may only be profitable in the wild if group sizes are small, prey arrival is predictable to some extent, and prey are perched less than 30 cm above the water.

Jumping, spitting technique, and forager positioning further illustrate how archerfish assess the risk of kleptoparasitism and alter their behaviour. When presented with prey at 15 cm the archerfish had the option to jump out of the water to grab a cricket off its perch. Jumping was more successful at dislodging the prey than spitting, suggesting that jumping may have been more accurate or the fish more discriminating when jumping. Observations indicate that archerfish were more likely to jump at crickets that were clearly available near the side or underside of the dowel, while spits were fired

at all manner of perched prey. As an alternative to spitting, jumping lowered the probability of being kleptoparasitized and its prevalence increased significantly as group size increased. Jumping circumvented kleptoparasitic opportunity and, thus, carried the biggest payoff when used amidst a crowd. Presumably jumping was not used more regularly because of its much higher energetic cost. Decisions relating to jumping may be evidence that archerfish are keenly aware of the presence of competitors. Perhaps the best example of this awareness occurred when a fish jumped out of the water to catch a falling cricket mid-air. Although only observed a handful of times, this act was only performed by a fish in a cluster of three or more fish waiting under a falling prey item. Solitary archerfish were more patient.

Spitting technique demonstrates another counter-tactic to kleptoparasitism. Recall that the more spits needed to knock down a cricket, the more likely it was to be stolen. It follows that an archerfish should have spat as efficiently as possible via a strong direct shot. However, our observations suggest that fish spat with much less force than they were capable of, since they were capable of spitting at targets up to two meters away (BDD personal observation). By minimizing the force needed to knock it down, spitters minimized the distance the cricket was launched, its time in the air, and its conspicuousness, thereby reducing risk of being kleptoparasitized. Minimizing risk of theft, therefore, may have involved a tradeoff between haste and control.

Positioning throughout a foraging event undoubtedly affected the foraging success of each fish. The spitter may be at both an advantage and a disadvantage during a foraging event. The immediate advantage is knowing when and where spits will be directed. Yet, immediately afterwards this fish is likely not where the prey will fall and is not poised for burst speed. Thieves, however, most often positioned themselves with the prey between themselves and the spitter. Although the launch trajectory of the prey was partially erratic, thieves held the best odds of being nearest the landing spot of the projectile meal. Although not a focus in this study, forager positioning affected the success of both spitting fish and thieves and deserves further attention.

Strong kleptoparasitic pressure has led to the evolution of behavioural counter-measures in a wide range of taxa. Northern pike, as mentioned earlier, choose to eat smaller prey in order to avoid being kleptoparasitized (Nilsson & Bronmark, 1999). Female shield bugs (*Parastrachia japonensis*) protect their drupes (food resources) from conspecific females by guarding

them when other females approach the burrow (Hironaka et al., 2007). In the presence of conspecifics or gulls, crows (*Corvus c. corone* and *Corvus brachyrhynchos*) drop hard-shelled food items (bivalves or walnuts, respectively) onto hard surfaces in order to break them open from lower heights than when alone (Whiteley et al., 1990; Crisol & Switzer, 1999). Strong selective pressures from kleptoparasitism can even lead to the evolution of different morphological or life-history traits: gall-stealing thrips (genus *Kop-tothrips*) appear to have evolved soldier morphs and early dispersing larvae as strategies to thwart would-be thieves (Crespi & Abbot, 1999).

4.5. Archerfish sociality

Living and foraging socially carries costs, including increased risk of disease, increased conspicuousness, and indirect competition (Giraldeau & Caraco, 2000). Direct competition, explicitly observed as intraspecific kleptoparasitism in archerfish, is a key cost of social foraging. Since no published study explores archerfish sociality in the wild, explanations of why archerfish forage socially despite the costs are at this point speculative. In reference to archerfish sociality, Goldstein & Hall (1990) proposed that losing prey to coforagers is akin to a variable ratio schedule of reinforcement and that this helps maintain spitting behaviour. Although this suggests why archerfish do not refuse to spit when in a group, it does not explain why they forage in groups in the first place.

There are at least two plausible reasons why they might do so. First, as is common among fish, juveniles may school to reduce predation risk through earlier predator detection, predator confusion, or risk dilution (Bertram, 1978; Foster & Treherne, 1981). Keenleyside (1995) suggested that pronounced vertical body striping such as found on juvenile archerfish may have evolved to facilitate schooling. As they mature, adults may simply outgrow the need for sociality and become top predators themselves, too large for piscivorous birds. Notably, their stripes become less obvious as they mature.

Second, sociality in juvenile archerfish may be a consequence of the distribution of quality foraging habitats. Simon & Mazlan (2010) showed that while insects constituted roughly the same proportion of the diets of all size classes, juvenile archerfish consumed a less diverse range of prey species. Larger archerfish showed greater prey diversity and an ability to capture teleost fishes (including other archerfish in some cases). Juveniles likely forage in smaller patches: quality foraging patches, with overhanging vegetation

and adjacent cover, are likely limited and spatially clumped. This may force juveniles to forage near each other, providing opportunities for kleptoparasitism and driving selection for counter-tactics.

In contrast to archerfish, many social birds demonstrate aggregation economies, where the per capita intake rate is higher in a group than for solitary individuals because the limiting factor for consumption is the number of searching eyes (Clark & Mangel, 1986; Ranta et al., 1993; Giraldeau & Caraco, 2000). Individuals forage more efficiently in larger groups up to the point of ‘overflocking’. This economy is unlikely with archerfish as prey cannot be shared once discovered and foraging rate is likely limited by prey arrival rather than primarily by search efficiency. Social groups of archerfish likely represent dispersion economies where additional group members decrease individual foraging success (Fretwell & Lucas, 1970; Giraldeau & Caraco, 2000). Since spitting is essentially a solo hunting behaviour, highly vulnerable to kleptoparasitism, non-economic forces such as predation or patch structure must encourage sociality. Ultimately, speculations on archerfish sociality cannot be confirmed without additional field research.

In the present study we have shown that archerfish kleptoparasitism is affected by the perch height and size of prey and by the size of the foraging group. In addition, fish alter their behaviours to increase their probability of success, whether as a spitter or a thief. Future studies into archerfish foraging patch structure, group stability, social behaviour, and forager positioning in natural conditions should further our understanding of archerfish sociality, the evolution of this unique hunting method, and of kleptoparasitism in general.

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Appendix A

To test if individuals behaved differently depending on group composition, the behaviour of each fish was compared when in the presence and absence of each of the other 9 fish and in each of the different fish assemblages in which it was observed. Behaviour was broken down into the proportion of trials as a spitter and as a potential thief (compared separately). Since this process required using well over a 100 chi-square tests on the data for each treatment group (G3, G5H1, G7, and G5H2), depending on the number of different assemblages of fish used, both a Bonferroni correction and a Step-up False Discovery Rate (FDR) correction (Benjamini & Hochberg,

1995) were applied to account for multiple testing. These correction methods agreed across all results.

For the G3, G5H2, and G7 data, no fish spat or attempted to steal significantly more or less frequently when in any one assemblage of fish compared to any other or when in the presence or absence of any one of the other 9 fish. For groups of 5 fish with prey at 15 cm, no fish behaved differently in any unique assemblage of coforagers. Of all the tests performed, only one proved significant: one fish spat significantly more often in the presence of another specific fish than in its absence (G5H1 trials; $\chi_1^2 = 13.9$, $p < 0.001$). Although this result was statistically significant, it is difficult to deduce a reasonable biological explanation for it considering all relevant behavioural data. Thus, barring this unexplained result, fish did not significantly alter their behaviour based on their coforagers' identities.

Appendix B

The presence of aggression in a trial had no effect on spitting frequency per trial (all trials, Mann–Whitney $U = -0.01$, $N_1 = 223$, $N_2 = 257$, $p = 0.991$) or jumping frequency (Mann–Whitney $U = -0.03$, $N_1 = 223$, $N_2 = 257$, $p = 0.978$). Since crickets were presented randomly with respect to size, and aggression occurred prior to prey arrival, the proportion of trials with aggression did not differ between cricket sizes (0.511, 0.560, 0.595 for prey sizes 1–3, respectively; all pairwise $\chi_1^2 \leq 1.03$, $p \geq 0.309$).

The prevalence of aggression varied between group sizes, but with no obvious trend. Groups of 7 fish showed the highest prevalence of aggression (significantly higher when compared with G5H1 and G5H2 trials: $\chi_1^2 = 4.59$, $p = 0.032$ and $\chi_1^2 = 4.00$, $p = 0.046$, respectively). No difference in the prevalence of aggression was found between G5H1 trials and G5H2 trials ($\chi_1^2 = 0.03$, $p = 0.874$).

The assumed function of aggression is to reduce competition. This was achieved: the average number of fish that attempted to steal divided by the number that potentially could ($N - 1$) was significantly less in trials with aggression (all H1 trials, 0.785 without aggression vs. 0.667 with; Mann–Whitney $U = -2.89$, $N_1 = 223$, $N_2 = 257$, $p = 0.004$). Over all Height 1 trials, proportionately fewer thefts occurred when aggression was observed, although results within each group size were mixed (Table B1).

Just as at 15 cm, fewer fish attempted to steal prey at 30 cm when aggression was observed (3.00 fish with aggression vs. 3.39 fish without;

Table B1.

Within experimental groups, the proportions of crickets stolen for trials with an observed aggressive behaviour compared to those with no aggression.

	Proportion stolen with aggression		Statistical significance	
	Present	Absent	χ^2	p
G3	0.159	0.281	1.66	0.197
G5H1	0.347	0.532	6.39	0.011
G7	0.458	0.409	0.27	0.604
Total at H1	0.346	0.453	4.47	0.035
G5H2	0.596	0.600	0.02	0.966

Results of Chi-square tests for statistical significance are also shown.

Mann–Whitney $U = -2.05$, $N_1 = 48$, $N_2 = 51$, $p = 0.040$). Despite this, aggression had no observable effect on the probability of theft with prey at 30 cm (Table B1).

Fish who showed aggression prior to prey arrival had greater success as a spitter than when not aggressive (Height 1 trials only, 31.6% stolen when aggressive vs. 52.9% when not aggressive; $\chi_1^2 = 10.80$, $p = 0.001$). Yet, the loss rate was the same regardless of whether or not it was the aggressor who spat (31.6% stolen in trials with the aggressor as the spitter vs. 32.7% stolen with another fish as spitter; $\chi_1^2 = 0.032$, $p = 0.858$). Thus, aggression appears to have reduced the loss rate for all spitters not just for the aggressor.