SPITTING AT THE DINNER TABLE: ARCHERFISH (*TOXOTES CHATAREUS*) KLEPTOPARASITISM AND SOCIAL FORAGING

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ABSTRACT

Juvenile archerfish forage in small groups by spitting down overhanging insects and by kleptoparasitizing prey downed by others. To explore factors affecting the use and success of kleptoparasitism, countermeasures, and behavioural tactics within a producer-scrounger framework, ten archerfish (*Toxotes chatareus*) were presented in groups of three, five, and seven with crickets of varying sizes and heights. Matching observations across taxa, kleptoparasitism increased with increasing group size, prey size, and handling time. Although some predictions of producer-scrounger theory were met (tactic preference and tactic use reflecting tactic success), the assumption of negative frequency dependent kleptoparasitism success was not, and the theory did not account for important factors found to affect tactic economics, including positioning, non-autonomous "producing", and a frequency dependent "finder's share". This study confirms universal factors affecting kleptoparasitism and illustrates the difficulty of applying general theory to unique and complex systems. Suggestions for improving future social foraging studies are discussed.

Keywords:

Toxotes chatareus; archerfish; social foraging; kleptoparasitism; behaviour; producer-scrounger; social foraging theory

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GLOSSARY

Kleptoparasitism   The direct, parasitic expropriation of another's resource.

Producer   An individual within a foraging group that expends time and energy generating opportunities to exploit previously unavailable resources essential to survival and reproduction.

Scrounger   An individual within a foraging group that searches for and joins the food discoveries of others.

Opportunist   An individual within a foraging group that concurrently searches for food and for the food discoveries of others, but is restricted to either producer or scrounger upon food discovery/production.

Spitter   An archerfish that attempts to dislodge a prey item via a spit or a jump.

Terminal Spitter   An archerfish that spits or jumps at a prey item and does not attempt to steal (most often because it successfully downed the prey item).

Unsuccessful Spitter   An archerfish that spits or jumps at a prey item unsuccessfully, and then attempts to steal the prey downed by another fish.

Lurker   An archerfish that does not spit or jump, but attempts to steal (defined by making a deliberate movement towards a prey felled by another fish).

Non-Participant   An archerfish that does not spit, jump, or attempt to consume the prey.

CHAPTER 1: INTRODUCTION

1.1　Introduction to Social Foraging Research

Competition with other organisms is ubiquitous to all life and is a central focus of behavioural ecology. Competition is greatest for resources that are essential and limited, such as habitat space, access to mates, or, of interest here, food. When competition occurs between individuals of a single species the study of competition becomes a study of social behaviour. Thus, research on social behaviour not only seeks to answer why animals are social, but also questions of why and how individuals make decisions, what factors are involved, and importantly, how these decisions affect the behaviour and fitness of those around them.

Living and foraging socially can provide significant benefits, such as reduced predation risk (Powel 1974; Foster & Treherne 1981; Dehn 1990; Lima & Dill 1990), or increased foraging efficiency (Barnard & Sibly 1981; Pitcher et al. 1982; Foster 1985). Yet, foraging in close proximity to conspecifics also increases the potential for direct competition as individuals try to maximize their own energy intake rate, often at the expense of others. A prime and widespread example of this is kleptoparasitism—the direct expropriation of resources from another individual. Barnard (1984) suggested that kleptoparasitism is second only to true parasitism as the most common form of exploitation in nature.

Kleptoparasitism occurs throughout the animal kingdom, yet the vast majority of studies use avian subjects and very few studies explore

kleptoparasitism with aquatic species, including fish (Brockmann & Barnard 1979; Iyengar 2008). This may be due to the difficulty of observing fish in the wild and to the fact that many carnivorous fish eat small prey that are quickly consumed with little handling, which makes kleptoparasitism difficult. These foraging characteristics are not universal to all aquatic species, however, and research on kleptoparasitism should reflect its prevalence and diversity across habitats.

Two studies of piscine kleptoparasitism serve to illustrate the two principal approaches to kleptoparasitism and social foraging research. These studies will introduce the overarching questions this research field hopes to answer and introduce the research methods used to address them in this thesis.

Large northern pike (*Esox lucius*) are known to kleptoparasitize and even cannibalize conspecifics that catch, manipulate, and attempt to consume piscine prey. Nilsson and Bronmark (1999) showed that in order to avoid greater risk of kleptoparasitism, northern pike eat smaller prey than what is expected to maximize their energy intake. This and similar research is concerned primarily with determining what conditions promote or discourage the evolution of kleptoparasitism and counter-behaviours. Nilsson and Bronmark contribute by showing that for pike kleptoparasitism risk increases as prey items require greater handling effort. Across the animal kingdom, many characteristics of foraging have been shown either to promote or discourage kleptoparasitism, including: the quality of the food items, the difficulty or length of handling required, the degree and duration of direct control over the food item, and the

conspicuousness of the foraging behaviours (Brockmann & Barnard 1979; Giraldeau & Caraco 2000).

As Nilsson and Bronmark demonstrate, the first approach to kleptoparasitism and social foraging research uses observational studies to ascertain what characteristics of social foraging affect the rate and success of kleptoparasitism, and what counter-tactics are employed. This approach is often also comparative: researchers gain better understanding of how natural selection favours particular traits by comparing the behaviour and ecology they observe to that of other species. Lagging behind predator-prey interactions and parasitology, the study of kleptoparasitism has many stones unturned. These stones include: quantitative measurements of the costs and benefits this form of competition has on both parasites and hosts, comparisons of facultative versus obligative kleptoparasitism, comparisons of the prevalence of kleptoparasites across taxa, the universality of factors affecting the use and success of kleptoparasitism, and if or how these factors interact.

The second approach is suggested by the work of Klimley et al. (2001), who showed that white sharks (*Carcharodon carcharias*) hunt in relative close proximity in order to "eavesdrop" and scavenge on successful seal captures of conspecifics, thereby increasing their feeding rate and avoiding some of the costs of hunting. It is evident that the foraging tactics of one white shark (be it searching for prey or stealing from others) can influence the foraging economics not only of that individual, but also of its coforagers and the foraging group as a whole. Thus, although Klimley and his co-authors did not analyze their data in

this way, a second method of studying kleptoparasitism is through the use of social foraging theory, which attempts to model the economic interdependence of individuals in a foraging group and thereby predict both the efficiency of the group and the behaviours of individuals as they attempt to maximize their fitness (Giraldeau & Caraco 2000).

Unlike the empirical and comparative method, foraging theory tries to find universal rules for how individuals should behave given specific sets of needs and constraints. Traditionally, optimal foraging models explore what foraging strategy maximizes an individual's intake in a given environment (MacArthur & Pianka 1966). The predictions are then used either to explain animal behaviour and decision-making or are scaled up to understand dynamics at the population or community level. The realization that an individual's foraging success depends not only on its own behavioural tactic, but also on the tactic employed by those around them, has shifted focus from models based on optimal foraging theory towards models based on the concept of an evolutionarily stable strategy (ESS) (Maynard Smith 1982). Here concepts of optimality and stability are combined in a game-theoretical equilibrium (Giraldeau & Caraco 2000).

In a continuing process of improvement, social foraging theory is not complete. Ongoing inquiries include: if and how individuals adjust their time and effort between tactics, especially as payoff structures change; the plasticity and genetic basis of tactic preference; how differences in phenotype, dominance, predation pressure, and group size affect individual foraging decisions and economics; how social foraging models can illuminate decision-making

processes; and how the interdependence of tactics affect social learning and the selective advantage of sociality. Social foraging theory is a top-down, largely model-based approach. Nevertheless, empirical behavioural studies are essential to inform the theory and ascertain its utility.

1.2   Project Overview

Both of these approaches were used in this thesis to study intraspecific kleptoparasitism and social foraging behaviours in archerfish. Native to Southeast Asian mangroves and estuaries, archerfish (genus *Toxotes*) forage by spitting down insects from overhanging vegetation (Schuster, 2007). Doing so socially in small groups affords abundant opportunities for individuals to steal prey items downed by others via scramble kleptoparasitism.

In this laboratory study, small groups of archerfish were presented with crickets for foraging. Controlling and adjusting variables such as group size, prey size, and prey height, while directly measuring the use and success of spitting and kleptoparasitism, allowed quantitative measurements of factors affecting theft and the plasticity of this and counter-tactics. Comparisons were then made to observations of other species. In addition, I tested how well current social foraging theory explains archerfish behaviours by testing specific predictions of the producer-scrounger model (i.e., how individual behaviours should react to changing payoffs). Although there exists an extensive body of literature modelling social foraging behaviour (e.g., Barnard & Sibly 1981; Thompson et al. 1974; Vickery et al. 1991; Giraldeau & Caraco 2000), empirical studies lag behind mathematical advances and nearly all use avian subjects with few exceptions

(non-avian studies: Carbone et al. 1997; Di Bitetti & Janson 2001; Hamilton & Dill 2003; Bicca-Marques & Garber 2005). Thus, in addition to expanding our knowledge of a unique fish species, archerfish represent a non-traditional study system that can increase our understanding of kleptoparasitism and assess the utility and applicability of current social foraging theory.

In addition to these merits, there are several benefits to using archerfish as a study system. Wild caught archerfish are keen, intelligent fish, quick to learn, and they acclimate well to captivity. Their social structure consists of small, manageable groups. Archerfish do not have fixed foraging roles but rather display high behavioural plasticity. Behaviours (including spits, jumps, thefts, and aggression), individual consumption success, and intake rates over time are easily observable as they occur near the surface of the water or above it. Furthermore, variables such as group size, dominance structures, production rates, and payoffs can be manipulated within the laboratory environment. Thus, the archerfish study system offers great flexibility and control to investigate both social foraging theory and universal characteristics of kleptoparasitism.

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CHAPTER 2: INTRASPECIFIC KLEPTOPARASITISM AND COUNTER-TACTICS IN ARCHERFISH

2.1   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 inherent vulnerabilities of spitting to intraspecific kleptoparasitism affect the behavioural choices of socially foraging archerfish, 10 tagged, juvenile archerfish (*Toxotes chatareus*) were presented in groups of 3, 5, and 7 with crickets of 3 sizes overhanging the water by 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 successful spitters. Group size affected the probability of kleptoparasitism asymptotically: loss rate increased as group size increased from 3 to 5 members, but with no increase thereafter. As observed with other species, the rate and success of kleptoparasitism increased with both prey size and prey height (analogous to handling time).

2.2   Introduction

The seven species of archerfish (genus *Toxotes*) are native to Southeast

Asian mangroves, estuaries and freshwater streams (Schuster 2007). Archerfish

are known for their remarkable ability to hunt by spitting down insects and other

small prey that rest or fly above the water (Lüling 1963; Bekoff & Dorr 1976; Dill

1977; Timmermans & Vossen 2000). Spitting is accomplished by rapid closure of

the gill covers, which forces a jet of water through a tube formed by the roof of

the 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 direction and distance of a target across a

wide range of shooting angles (Dill 1977; Timmermans 2001). The force of a shot

can also be adjusted for the distance, size, and velocity of a target (Schlegel et

al. 2006; Schuster et al. 2004, 2006). Once the prey has been dislodged, the fish

are able to very rapidly and accurately predict the trajectory of the falling prey,

even when it was spat 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. Little, however, has been published on archerfish

behaviour in a social context; unknown are the effects this unique hunting

technique has on the behaviours and successes of archerfish forging in a group.

Juvenile archerfish can spit when only 2.5cm in length and do so socially

in small schools (Lüling 1963; Allen 1978; Timmermans & Maris 2000).

Observations of introduced archerfish in freshwater lakes in N. Queensland,

Australia (LM Dill, personal communication) show juveniles advancing from cover

in small groups (4-6 individuals) to hunt prey on overhanging vegetation. As they mature, archerfish disperse into more open water and no longer aggregate. Little is known about the relative importance of terrestrial prey in the diet of archerfish, adult or juvenile. Previous speculations contend that spitting is both unlikely and likely to be a significant contributor to an archerfish's diet (Lüling 1963 and Timmermans 2000, respectively).

Spitting is essentially a solo hunting method and yet juvenile archerfish forage socially. Since all individuals in the group are keen to consume the discovered prey, the fish that spits the insect down is not always the fish that consumes it (Lüling 1963; Goldstein & Hall 1990; Rossel et al. 2002). This presents a conflict between the spitter and its coforagers.

Food stealing, as seen in archerfish, is a common form of kleptoparasitism—the direct, parasitic exploitation of another's resource (Giraldeau & Caraco 2000). Kleptoparasitism has been formally recognized for many decades and 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, and especially piscine examples, are rare. Nilsson and Bronmark (1999) found that prey handling time for northern pike increases with prey size. This extra time increases the risk of predation, cannibalism, and kleptoparasitism and causes

pike to target smaller prey than predicted if maximizing their energy intake. In a second example, surgeonfish, western buffalo bream, 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 examples and a review of the state of kleptoparasitism research in general.

An organism's vulnerability to kleptoparasitism is affected by several characteristics of its 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, for example, hunt high-quality food that is difficult to catch and as a consequence they are frequent victims of kleptoparasitism as larger savannah predators look 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, 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 an organism's hunting or food-handling behaviours, the easier it is for potential thieves to recognize opportunities to exploit them. It has been noted that kleptoparasitism, particularly in birds, 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 spitting behaviour of socially foraging archerfish. Archerfish are

carnivorous predators that consume prey as large as their gape width. Terrestrial prey pursued by juvenile archerfish are large, attractive food items. Second, leaving cover, finding a prey, and successfully spitting it down involves searching effort, handling effort, and likely increased predation risk. Individuals should try to avoid some of these costs by stealing from coforagers. Third, when hunting via spitting, a temporary loss of control is unavoidable and direct control over the prey occurs only at 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 by each additional spit needed to down the prey. Behaviours that mitigate vulnerability to kleptoparasitism should be selected for. Maximal accuracy, for example, seems an essential skill to thwart potential thieves and flighty prey. Alternatively, jumping to grab prey within reach may avoid the temporary loss of control inherent in spitting.

In the present study, juvenile archerfish were observed foraging while some of the potential factors affecting a spitter's vulnerability to theft were manipulated, specifically group size, prey height, and prey size. The objectives are to describe the behaviours of socially foraging, juvenile archerfish, to observe how the three variables mentioned affect the prevalence and success of spitting and stealing, and to discover ways in which archerfish may react to this competition by altering their behaviour.

2.3   Methods

2.3.1   General Methods

Imported, wild caught, juvenile *Toxotes chatareus* (N=10), 7.1 cm mean fork length at tagging and 8.7 cm mean fork length after study, were acquired from a local aquarium store and housed together in a filtered 275 L glass tank. After two weeks of acclimation, each fish was tagged for individual identification with two 2.5 mm diameter, coloured plastic beads sutured through the musculature just anterior to the dorsal fin. The beads caused no observable hindrance to the fish.

Tagged fish were put into a continuously filtered 3.05 m diameter circular pool filled 2/3 full to a depth of 60 cm. The pool was sectioned into 4 quadrants with liftable opaque dividers. Driftwood and 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 12h light/dark cycle. Prior to the start of the experiment the fish were fed brine shrimp flakes, krill, and feeder fish.

Observations were conducted between 22 August and 18 October 2007. All fish were food-deprived overnight prior to testing each day. During observations, groups of fish were presented with live crickets (lab-reared, 2-4 weeks old, 1.0-1.6 cm in length) sequentially on overhanging wooden dowels. No more than 5 crickets per fish per day were presented, well short of the number required to cause satiation. In order to maintain equal sustenance and satiation

levels across fish, each was fed brine shrimp flakes and krill after observations according to their consumptions during testing.

2.3.2 Prey Presentation Apparatus

Two identical prey presentation apparatuses were constructed out of 3.2 cm diam. PVC piping, 2 cm diam. wooden dowels, and black tubing. For each apparatus, two level and parallel dowels (one 104 cm and one 61 cm) were separated by 26 cm and hung perpendicular to the radius of the pool. Five cm from the ends of each dowel was attached a 40 cm long PVC pipe; each pipe ran vertically up from the dowels and was attached such that a cricket could fall through the PVC pipe, land on the dowel, and crawl out onto it in either direction. 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 and allowed two groups of fish to be tested each day. The height of the apparatuses could be adjusted as desired—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 time and space. Spatially this was achieved by randomly choosing which of the four pipes each cricket was sent down, and by allowing the cricket to emerge from the pipe in either direction. The interval between cricket presentations was varied but not randomized, ranging from immediate presentation of the next cricket to delays of over 5 min between crickets. Once

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delivered, crickets took anywhere from less than 1 sec to several minutes to emerge from the PVC pipe and crawl out onto the dowels to where they could be spotted by the foraging fish. This added an additional element of unpredictability to prey arrival.

2.3.3   Trials

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 held above the pool on a tripod. Simultaneous verbal accounts were also recorded. Each cricket defined a trial: this included all events occurring between a cricket's delivery and eventual consumption as a result of being knocked onto the water by a spit or a jump. On occasion a cricket would jump or fall into the pool; although its consumer was noted, these events are not considered trials and were removed before analysis.

The 10 tagged fish were allowed to school together when not being tested. Groups of 3, 5, and 7 fish were haphazardly subsampled for observations. The members of each group were varied by subsampling daily and by disallowing assortments matching a previous assortment. Haphazard subsampling avoided the excessive handling that using random or predetermined groups would have required.

In total, 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). Additionally, at Height 2 (30cm), 99 trials were observed using groups of 5 fish (G5H2). Most Height 1 trials were performed before the Height 2 trials. Sixty-six G5H1 trials were run after the Height 2 trials in an attempt to reduce or at least observe possible order effects when comparing groups of 5 fish at both heights (Fig. 2.1).
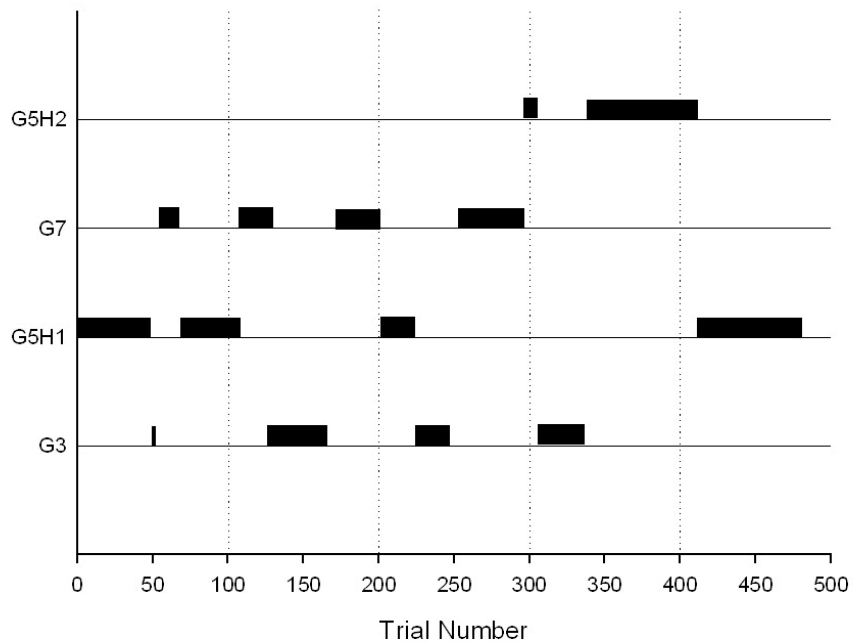
Figure 2.1   The chronological sequence of group variants (G3, G5H1, G7, G5H2) used across the 480 trials.

Cricket size also varied haphazardly between trials. The majority of trials, 272 of 480, were conducted with lighter coloured, 1 cm (size 1) crickets; 166 trials were conducted with 1.3 cm (size 2) crickets, and 42 trials with darker, 1.6 cm (size 3) crickets. The sizes of the crickets consumed were taken into account when maintaining equal satiation across fish after observations.

2.3.4　Observations

For each observed spit or jump, the identity of the fish, and its success in dislodging the cricket were recorded. It was assumed that every spit was an attempt to knock down the prey. Once a cricket was dislodged all theft attempts were recorded. A theft attempt is defined as a deliberate movement towards the falling or fallen prey dislodged by another fish. The fish that downs a cricket (via spitting or jumping) is considered the "owner" and any other fish that attempts to consume that cricket is considered a potential kleptoparasite. Because many spits are unsuccessful, individuals can spit and then attempt to steal the prey downed by another fish in the same trial. For each cricket, the identity of the successful consumer was recorded.

Despite the unpredictability of prey arrival some fish attempted to reduce competition through aggressive behaviours. This occurred in just over half of all trials. Aggression was easily recognized: a dominant fish lunges at a subordinate's flank, forcing it from the immediate area. The juveniles used in this study were unable to guard the entire foraging space under the prey presentation apparatus. The most common use of aggression was to patrol a foraging area beneath one dowel rod. Aggression was recorded on a presence/absence basis for each fish in each trial.

2.3.5　Analysis

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 with those with 5 fish at 30 cm (G5H1 versus G5H2 trials). Although the G5H2 trials were clumped within the G5H1 trials (Fig. 2.1), no order effects were apparent. Regardless of how the G5H1 trials were divided, no significant differences were found between the early and later G5H1 trials. The effects of prey size were explored by comparing trials using different crickets sizes within and across groups, and the effects of aggression, by comparing trials with and without observed aggressive behaviours.

Despite careful video review, the consumer's identity was undeterminable in 5 of the 480 trials. Information regarding spitting, jumping, aggression, and theft attempts was discernable and thus these trials were included in analyses of this nature. These five trials were removed from analyses regarding rates of loss to kleptoparasitism.

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.

2.4 Results

2.4.1 Spitting, Jumping, and Kleptoparasitism

In the 480 trials (crickets) observed, 1489 spits, 160 jumps, and 1466 attempted thefts were recorded (Table 2.1). The following section presents the use of spitting, jumping, and stealing; this is followed by results on how each of these behaviours vary with prey height, prey size, group size, and aggression.

Table 2.1   Trials and counts of behaviours.

	Total Trials	Cricket Size			Aggression		Theft		
		1	2	3	No	Yes	No	Yes	Not Known
G3	77	39	34	4	33	44	60	16	1
G5H1	188	106	67	15	95	93	104	82	2
G7	116	69	36	11	44	72	65	51	0
G5H2	99	58	29	12	51	48	39	58	2
TOTAL	480	272	166	42	223	257	268	207	5

	Hunting Method		Spits	Spits/trial			Jumps	Jumps/trial		
	Spat Down	Jumped Down	Sum	Mean	Mode	S.D.	Sum	Mean	Mode	S.D.
G3	64	13	272	3.53	1	4.573	28	0.36	1	0.705
G5H1	157	29	568	3.02	1	3.942	62	0.33	1	0.684
G7	82	34	217	1.87	1	1.66	70	0.60	1	0.995
G5H2	99	0	432	4.36	1	4.014	0	0.00	0	0.000
TOTAL	402	76	1489				160			

All fish performed all three foraging behaviours—spitting, jumping, and stealing. On average it took 3.03 spits (SD = 3.78) to down a cricket 15 cm above the water (averaging over all Height 1 trials where no fish jumped), and 4.36 spits per cricket (SD = 4.014) at 30 cm. These distributions are highly skewed: at Height 1 it took up to 38 shots to down one cricket, yet 42.7% of the time one shot was sufficient (Fig. 2.2). At Height 2, one spit was sufficient only 20.0% of

the time, reflecting the greater difficulty in spitting down crickets at the higher height.
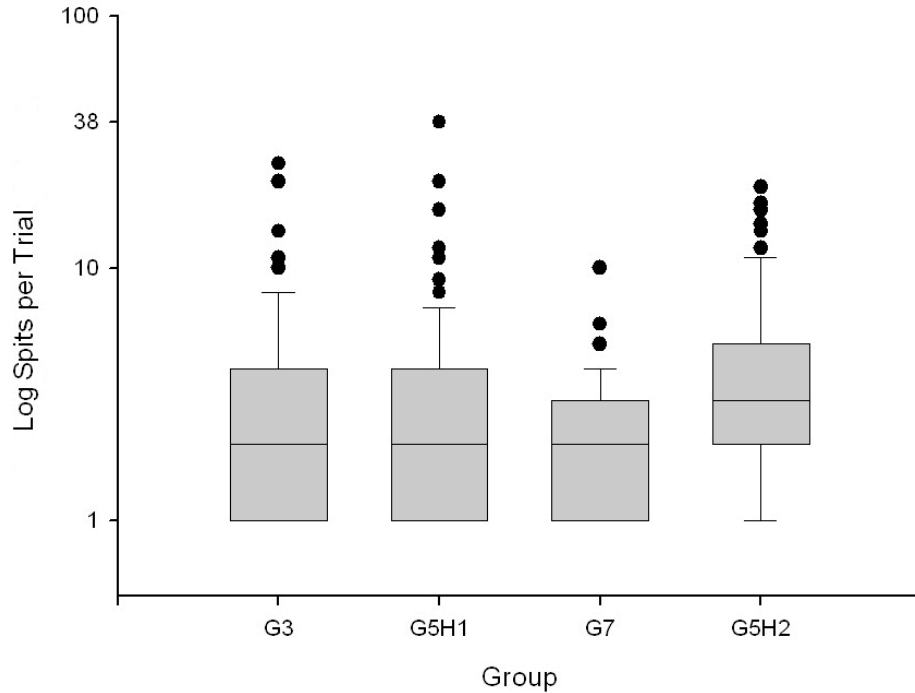
Figure 2.2   Box plots of spits per trial (across all fish) for each treatment group presented on a log scale.

Jumping up to grab a cricket off a dowel was much less frequent and only occurred at Height 1. Archerfish jump via a C-start motion from just below the surface of the water; thus, 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 at least one jump. Of these trials, the number of jumps per trial was low (mean = 1.39, SD = 0.69). Because jumping and spitting are alternative tactics, trials with jumps show a reduced number of spits (Mann-Whitney U, Z = -1.728, 1-tailed, p = 0.042). Kleptoparasitic attempts were very common: 97.7% of all

trials had at least one. Successful thefts were also common: over all trials, 43.6% of prey were stolen.
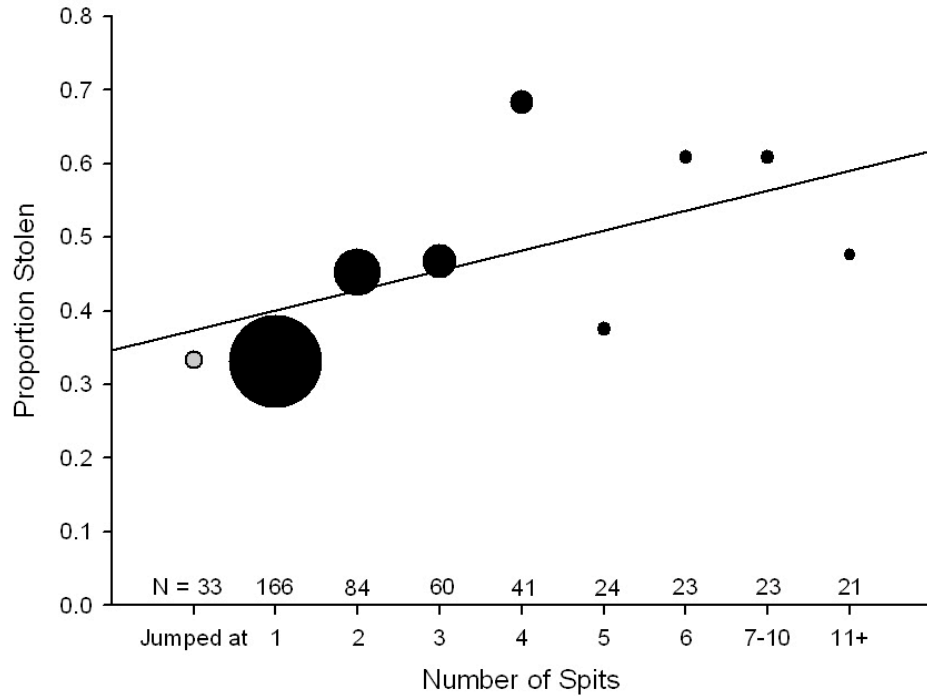
Figure 2.3 **The proportion of crickets stolen (dot centre height), binned by the number of spits needed to down them. The gray dot represents crickets downed by a jump. Dot sizes correspond to sample sizes, which are written along the bottom. The solid line is a linear regression across all solid points (R^2 = 0.339).**

Crickets that were stolen took significantly more spits to knock down than crickets that were not stolen (3.65 vs. 3.06 spits/cricket, Mann-Whitney U, Z = -3.852, p < 0.001). As more shots are needed to down a prey, the greater the probability that it is stolen (Fig. 2.3); this suggesting that it benefits the spitter to dislodge its prey quickly and with as few shots as possible.

On any given trial, a spit had a 33.0% chance of downing a cricket at 15 cm. A jump, however, was significantly more efficient, having a 47.5% chance of

dislodging the cricket (Mann-Whitney U: Z = -6.375, p < 0.001). Archerfish may be more accurate when jumping, or simply more discriminating. Observations suggested that archerfish are more likely to jump at crickets that are clearly available on the side or underside of the dowel. Spitters seemed less fussy.

Jumping also resulted in fewer thefts than spitting (all H1 trials: 32.9% stolen when downed by jumping; 41.1% stolen when downed by spitting) although this failed to reach statistical significance (χ^2 = 1.70, p = 0.193). The directionality of this result was consistent within each group (Fig. 2.4). Therefore, jumping as a hunting technique was significantly more successful in dislodging the prey and possibly more successful in securing consumption in the midst of potential thieves.
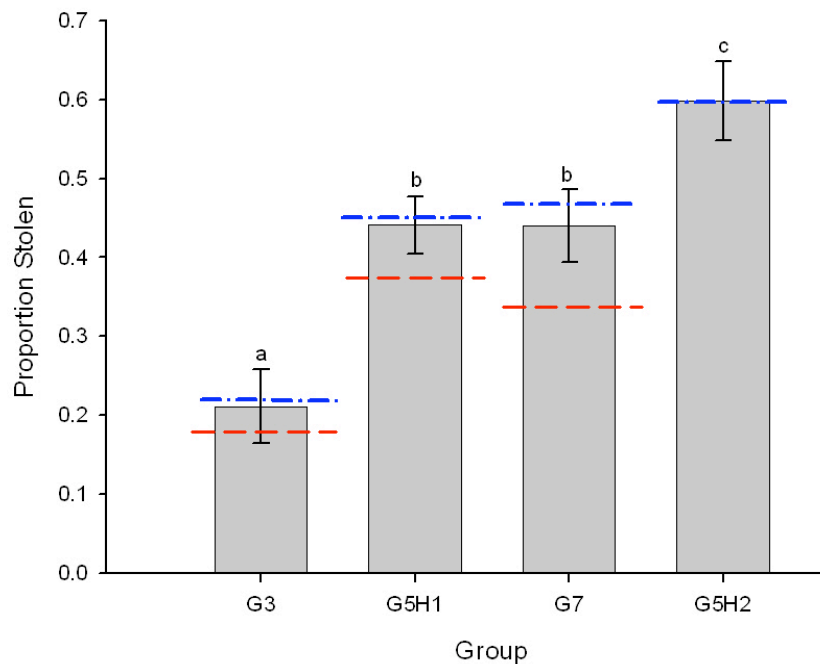
Figure 2.4 **The proportion of crickets stolen within each treatment group (± one SE of proportions). Blue dash dot lines and red dashed lines represent the proportion of crickets stolen when downed by spitting and jumping, respectively. No jumps were observed in G5H1 trials.**

2.4.2 Prey Height

The effects of prey height are assessed by comparing G5H1 trials to G5H2 trials. Trials with jumping were removed from G5H1 data before comparisons between groups were made. In groups of 5 fish and prey at 15 cm, fish spat on average 2.78 times per cricket (SD = 2.66). At Height 2 the fish spat on average 4.36 times per cricket (SD = 4.014). Thus, when prey height is doubled, archerfish took significantly more spits to knock the prey down (Mann-Whitney U, Z = -4.259, p < 0.001). This is unsurprising since dislodging more distant prey is more difficult, requiring greater muzzle velocity and accuracy.

On average, more fish tried to steal prey felled from 30 cm than from 15 cm (3.20 vs. 2.87 fish/trial for G5H2 and G5H1, Mann-Whitney U test: Z = -3.091, p = 0.002). It follows that significantly more prey were stolen in G5H2 trials than in G5H1 trials (59.9% versus 44.1%, χ^2 = 5.09, p = 0.024; Fig. 2.4). To test if crickets are more easily stolen at Height 2 independent of the greater number of attempting thieves, a loglinear model was constructed comparing theft rates between heights at each thief number. The 3-way higher order effect was non-significant (χ^2 = 2.482, df = 3, p = 0.479), but two partial associations were (Fig. 2.5): the proportion stolen increased significantly as thief number increased (Partial χ^2 = 32.876, df = 3, p < 0.001), and the proportion stolen at 30 cm was significantly greater than at 15 cm (Partial χ^2 = 5.47, df = 1, p = 0.019). Thus, crickets were stolen significantly more often when knocked down from 30 than from 15 cm even when the same number of fish attempted to steal.
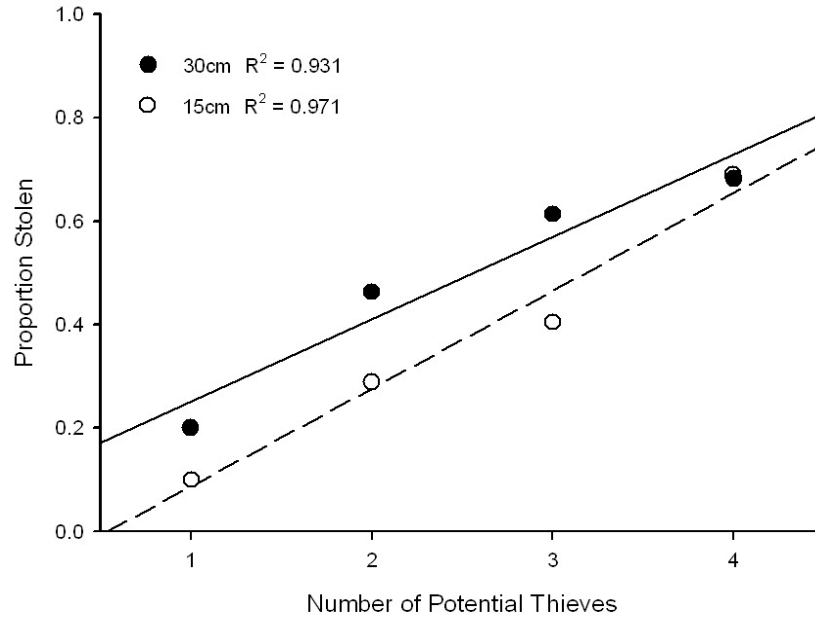
Figure 2.5   **The proportions of prey stolen at 15 cm and 30 cm (open and closed dots, respectively), across the number of potential kleptoparasites. Data exclude trials with jumping. Dotted and solid lines show linear regressions for the open and closed dots, R^2 = 0.931 and R^2 = 0.971, respectively.**

2.4.3   Prey Size

The three cricket sizes were presented to all four groups in roughly the same proportions (χ^2 = 6.64, *df* = 6, p = 0.355; Fig. 2.6). Considering only trials where the cricket was downed by a spit, the number of spits per trial increased insignificantly with increasing cricket size (sizes 1-3 respectively: 2.82, 3.50, 3.36; Jonckheere-Terpstra, 3 levels, N = 401, p = 0.225). Across trials at Height 1 (15 cm), the number of jumps per trial increased with cricket size and this proved significant (sizes 1-3 respectively: 0.346, 0.482, 0.667; Jonckheere-Terpstra, 3 levels, N = 381, p = 0.002; Fig. 2.7). Post hoc tests indicate that fish jumped at size 2 and size 3 crickets significantly more than at size 1 crickets (proportion of trials with a jump: χ^2 = 9.46, p = 0.002 and χ^2 = 3.84, p = 0.050, sizes 2 and 3

respectively; Fig. 2.7). No significant difference in jumping was found between size 2 and size 3 crickets ($\chi^2 = 0.179$, p = 0.894).
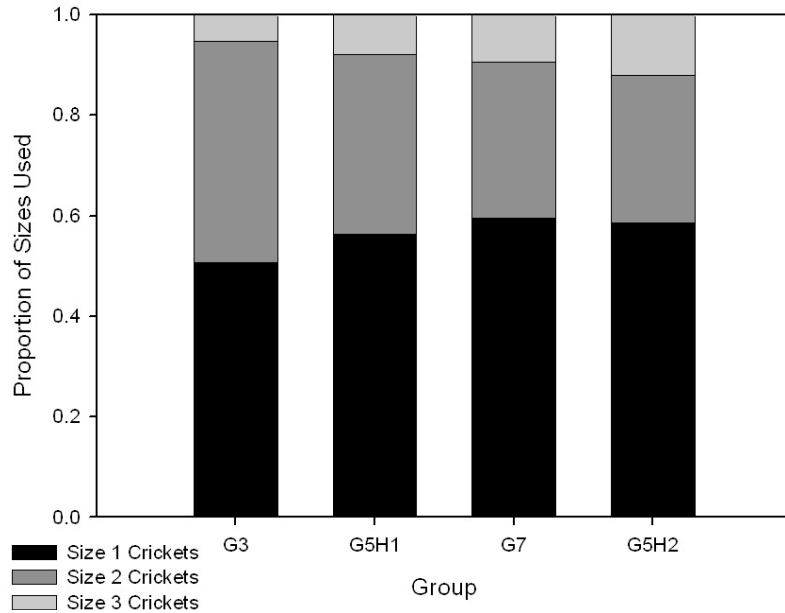
Figure 2.6   The proportion of cricket size classes (Sizes 1, 2, and 3) used in each treatment group.
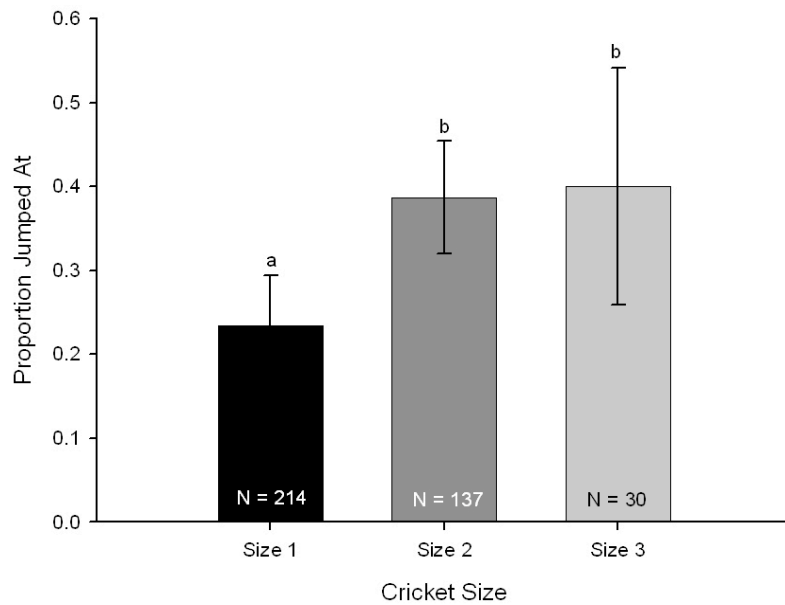
Figure 2.7   The proportion of crickets of the three size classes jumped at (± one SE of proportions). Data include only Height 1 trials. Sample sizes (N) are shown in the bottom of each bar.

Across all groups, there were no significant differences between the numbers of fish attempting to steal crickets of the varying sizes (3.00, 2.41, and 2.74 thieves/trial for sizes 1-3 respectively; pairwise Chi-Square tests: $\chi^2 \leq 1.23$, $p \geq 0.267$). Despite this, the size of the cricket did have a significant effect on its probability of being stolen, with larger sizes stolen more often (Height 1 trials: 34.1%, 43.1%, 60.0% stolen of sizes 1-3 respectively; Fig. 2.8). Comparing directly between size classes, size 3 crickets were stolen significantly more often than size 1 crickets ($\chi^2 = 2.84$, $p = 0.006$); differences between size 1 and size 2, and between size 2 and size 3 were not quite significant ($\chi^2 = 2.83$, $p = 0.093$ and $\chi^2 = 2.84$, $p = 0.092$ respectively). The trend of increasing probability of theft with increasing prey size held true within each experimental group.
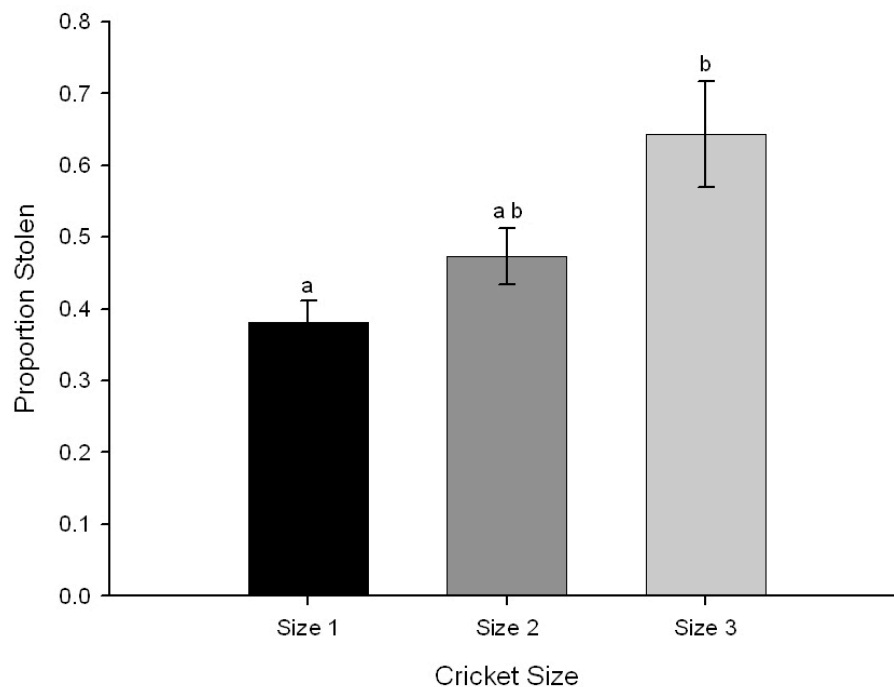
Figure 2.8 **The proportion of the three size classes of crickets stolen (± one SE of proportions). Data include only Height 1 trials.**

To test if larger crickets are stolen more often independent of the number of thieves they attract, a loglinear model was performed comparing theft rates between size 1 crickets and size 2 plus 3 crickets (sizes 2 and 3 were pooled to increase statistical power). The 3-way higher order effect was non-significant (χ^2 = 2.763, df = 10, p = 0.986), but two partial associations were significant: the proportion stolen increased significantly as thief number increased (Partial χ^2 = 36.205, df = 5, p < 0.001), and a greater proportion of size 2 and size 3 crickets were stolen than size 1 crickets (Partial χ^2 = 6.211, df = 2, p = 0.045). Thus, larger crickets are stolen significantly more often regardless of the number of fish attempting to steal (Fig. 2.9).
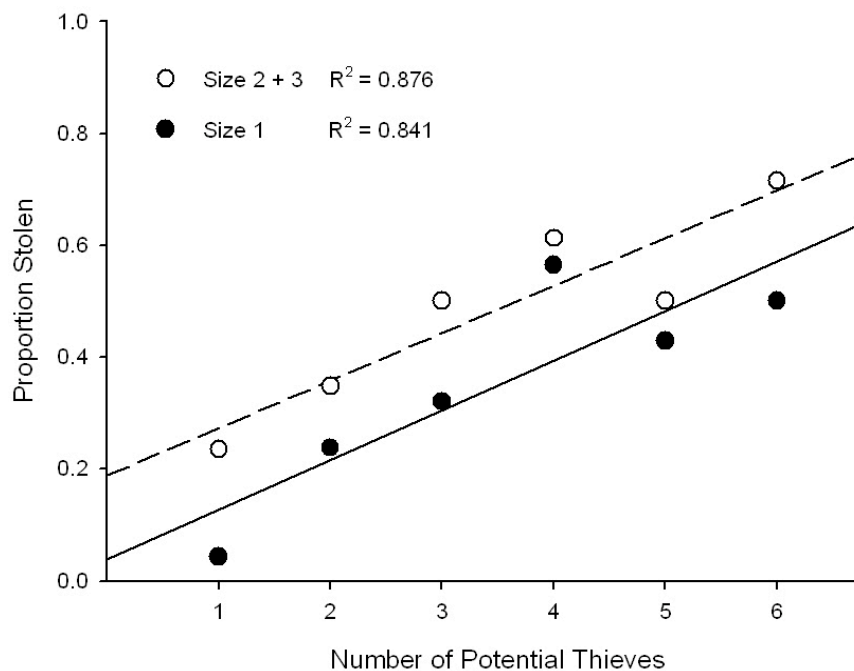
Figure 2.9 **The proportions of size 2 and 3 crickets stolen (open dots) and size 1 crickets (closed dots) stolen in relation to the number of potential thieves. Data includes all Height 1 trials without jumping. Dotted and solid lines represent linear regressions for the open and closed dots, R^2 = 0.835 and R^2 = 0.841, respectively.**

2.4.4 Group Size

The effects of group size were assessed by comparing trials with prey at 15 cm above the water across the three group sizes (3, 5, and 7). The number of spits per trial decreased with increasing group size (3.53, 3.02, and 1.87 spits/trial for G3, G5H1, and G7 respectively; Jonckheere-Terpstra Test, N = 381, p = 0.005). This can be at least partially explained by the fact that jumping, an alternative tactic, increased with group size, occurring in 29% of G3 trials, 30% of G5H1 trials, and 59% of G7 trials (Jonckheere-Terpstra Test, N = 381, J-T = 2.812, p = 0.005). If trials with jumping are removed, the number of spits per trial decreases insignificantly with increasing group size (3.56, 3.27, 2.17 spits/trial for G3, G5H1, and G7 respectively; Jonckheere-Terpstra Test, N = 266, p = 0.413). Thus, it appears that group size has a significant effect on the probability of jumping and less of an effect on the number of spits per trial.

Comparisons of the number of attempting thieves per trial across group sizes cannot be made directly. In groups of 7, 4.27 fish per trial attempted to steal, which is much higher than either G3 (1.48 fish/trial) or G5H1 (2.87 fish/trial) because there are more fish available to steal. Controlling for group size by dividing by the number of fish available to steal (G − 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 G3, G5H1 and G7 respectively; Mann-Whitney U: G3 vs. G5H1, Z = -1.371, p = 0.170; G5H1 vs. G7, Z = -0.742, p = 0.458; G3 vs. G7, Z = -1.769, p = 0.077; Jonckheere-Terpstra Test for an effect across groups: N = 381, J-T = -1.74, p = 0.082).

Since on average each forager attempts to steal with similar effort, overall kleptoparasitic pressure increases with group size (average number of attempting thieves per trial/G: 0.494, 0.574 and 0.610 for G3, G5H1 and G7 respectively; Jonckheere-Terpstra Test, N = 381, p = 0.017). With overall kleptoparasitic effort increasing with group size it is no surprise that thefts increased as well. As expected, groups of 3 fish had the fewest crickets stolen (Chi-Square tests: χ^2 = 12.2, p < 0.001 and χ^2 = 10.6, p = 0.001, for G3 vs. G5H1 and G7 respectively; Fig. 2.4). However, the probability of theft for G7 trials (44.0%) was the same as for G5H1 trials (44.1%), despite having on average 1.40 more attempting thieves per trial (χ^2 = 0.004, p = 0.984). Recall that capturing prey via a jump reduces kleptoparasitism success and jumping was more prevalent in G7 trials. Removing trials where the cricket was downed by a jump yielded a more expected trend, but the difference was still non-significant (47.6% and 45.2% stolen in G7 and G5H1 trials respectively; χ^2 = 0.119, p = 0.731).

2.4.5 Aggression

At least one aggressive event was observed in 53.4% of all trials. Six of the 10 fish performed an aggressive act and no two fish showed aggression in the same trial due to strong hierarchical dominance. Aggression had no effect on spitting frequency per trial (all trials, Mann-Whitney U, Z = -0.012, p = 0.991) or jumping frequency (Mann-Whitney U, Z = -0.027, p = 0.978).

No relationship between aggression and cricket size is predicted 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; pairwise Chi-Square tests: $\chi^2 \leq 1.03$, p = ≥ 0.309).

The prevalence of aggression varied between groups, but with no obvious trend with group size (Fig. 2.10). Groups of 7 fish showed the highest proportion of trials with aggression (significantly higher when compared with G5H1 and G5H2 trials, which showed the lowest prevalence of aggression: $\chi^2 = 4.59$, p = 0.032 and $\chi^2 = 4.00$, p = 0.046 respectively). In addition, no measurable difference in aggression was detected between groups of 5 with prey at 15 or 30 cm ($\chi^2 = 0.025$, p = 0.874).
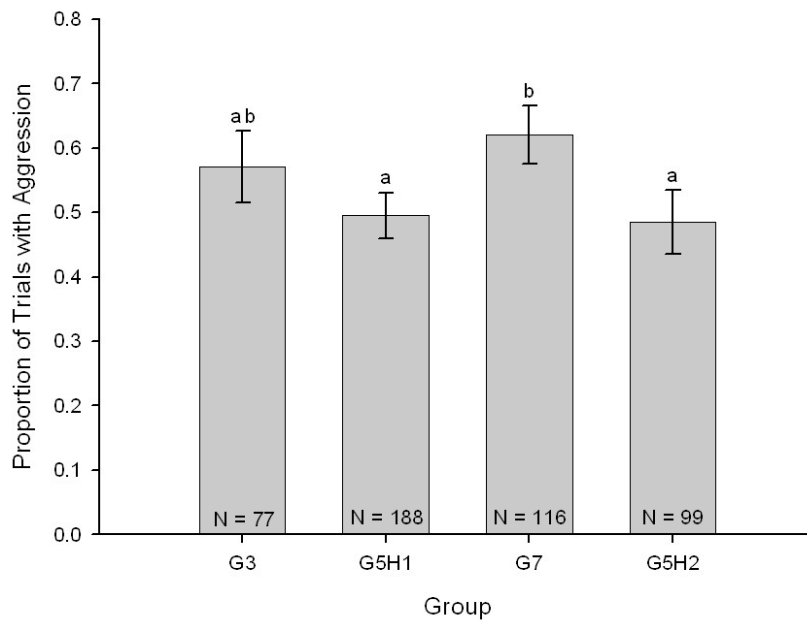
Figure 2.10 The proportion of trials with at least one aggressive event, separated by each group size-height combination (± one SE of proportions). Sample sizes are shown in the bottom of each bar.

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 could potentially steal (G – 1) was significantly less in trials with aggression (all H1 trials, 0.785 without aggression versus 0.667 with; Mann-Whitney U, Z = -2.889, p = 0.004; Fig. 2.11).
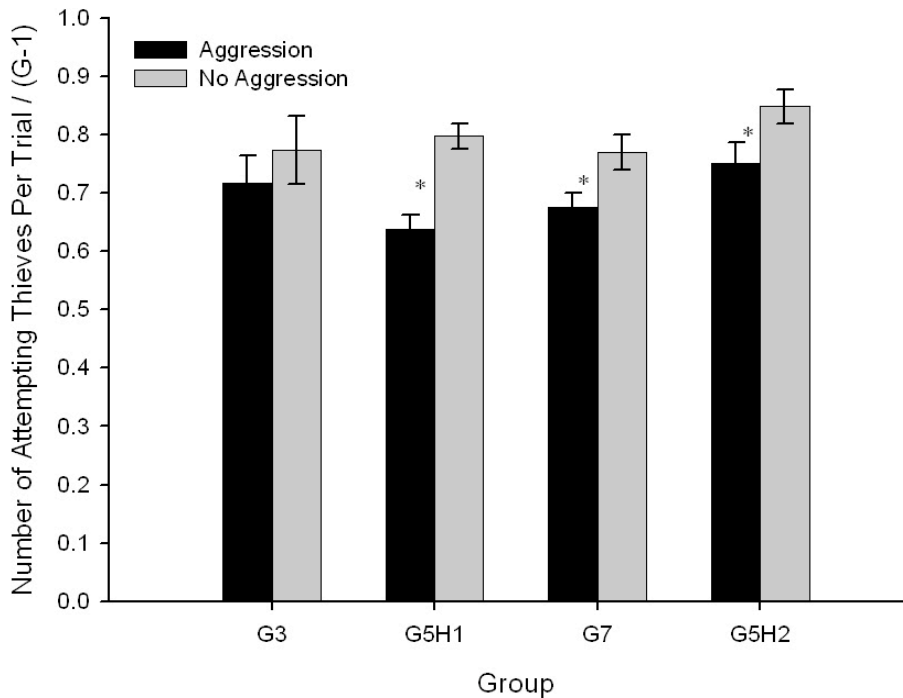
Figure 2.11 **Black and gray bars represent the mean number of attempting thieves per trial divided by the number of potential thieves (G – 1) (± one SE) for trials with and without aggression, respectively. Data for each group size-height combination are shown separately. Asterisks indicate significant within treatment group differences (p < 0.05).**

Over all Height 1 trials, significantly fewer successful thefts occurred when aggression was observed (34.6% vs. 45.3% stolen with and without aggression, respectively; χ^2 = 4.47, p = 0.035; Fig. 2.12). The effect is proportionally largest in G3 trials, though the Chi-Square test was non-significant (15.9% vs. 28.1%

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stolen with and without aggression respectively; $\chi^2 = 1.66$, p = 0.197). The effect

is significant for G5H1 trials, the group with the greatest sample size (34.7% vs.

53.2% stolen with and without aggression, $\chi^2 = 6.39$, p = 0.011). Conversely, in

groups of 7 fish, aggression significantly reduced the number of attempting

thieves, but did not affect the probability of theft (45.8% vs. 40.9% stolen with

and without aggression, respectively; $\chi^2 = 0.27$, p = 0.604).

Just as at 15 cm, with prey raised to 30 cm fewer fish attempted to steal

when aggression was observed (3.00 fish with aggression vs. 3.39 fish without;

Mann-Whitney U, Z = -2.049, p = 0.040). Despite this, aggression had no

observable effect on the probability of theft at 30 cm (59.6% vs. 60.0% stolen

with and without aggression; $\chi^2 = 0.018$, p = 0.966; Fig. 2.12).
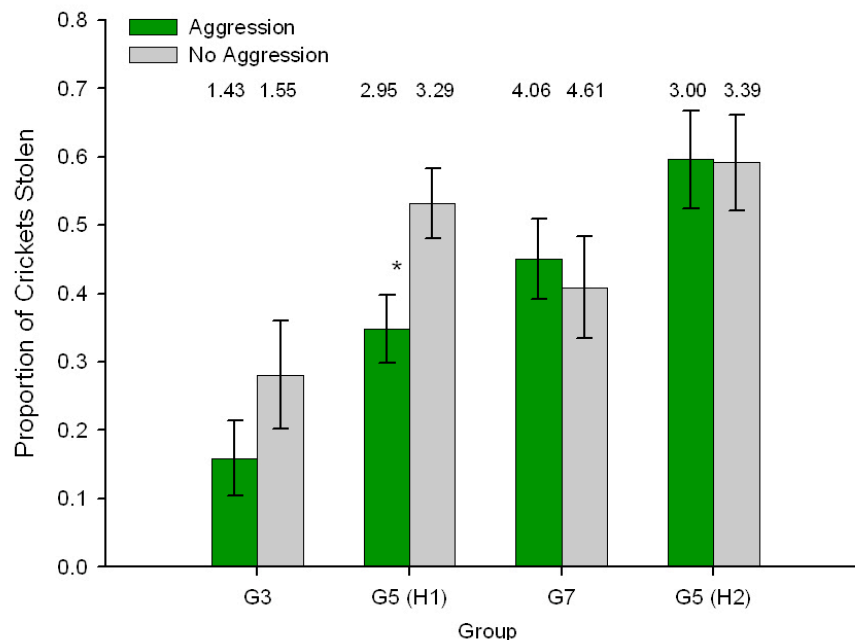
**Figure 2.12 The proportion of crickets stolen for trials with aggression (dark green bars)
and without aggression (light gray bars) across each treatment group (± one
SE of proportions). The asterisk indicates a significant within group difference
(p < 0.05). The mean numbers of attempting thieves per trial for each group are
presented across the top.**

2.5   Discussion

Always alert, at least one fish attempted to steal the cricket in over 97% of
the trials. With loss rates observed as high as 60%, kleptoparasitism is certainly
a major source of direct conflict within groups of juvenile archerfish. All archerfish
in this study demonstrated spitting and stealing tactics. The use and success of
kleptoparasitism was affected by both physical factors (such as prey height and
prey size) and behavioural factors (such as group size and counter-tactics).

2.5.1   Prey Height

Prey height was shown to significantly affect archerfish foraging
behaviours and the probability of kleptoparasitism. At 15 cm spitting was efficient:
the majority of the time the prey was downed on the first or second shot.
Efficiency declined when prey were raised to 30 cm; here 1 to 2 spits were
sufficient only one third of the time. Greater force and accuracy were required to
down crickets at 30 cm than at 15 cm. In addition, once dislodged, the greater
height means prey items travel further before hitting the water, allowing more
time for thieves. These factors make stealing higher prey more attractive: even
when accounting for the increase in number of attempting thieves, more crickets
were stolen at 30 cm than at 15 cm.

2.5.2   Prey Size

As with prey height, prey size has a significant effect on the use and
success of both spitting and stealing tactics. 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 than small prey as the costs are

likely similar, but the reward is not. The greater spitting force needed to dislodge

larger insects (Schlegel et al. 2006) draws greater attention and gives more time

to thieves as the dislodged prey flies further from its perch. In addition, the larger,

darker crickets used in this study were more conspicuous when falling than were

the smaller, lighter crickets. All this made larger crickets more attractive and

easier to steal. Even when accounting for the differences in the number of

attempting thieves, larger prey were more likely to be kleptoparasitized than were

smaller prey.

Other studies exploring factors that affect kleptoparasitism support the

results found here with archerfish (Fuchs 1977; Fischer 1985; Barnard &

Thompson 1985; Nilsson & Bronmark 1999; Ha & Ha 2003). For example, Steele

and 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 is positively correlated with both prey

size and the number of spits needed to down a prey. The time needed to knock

down the prey plus the time it takes for the prey to hit the water is effectively the

archerfish's handling time. The more spits needed, the larger the prey, or the

farther the item has to fall, the greater the likelihood of theft.

Studies of intraspecific piscine kleptoparasitism are rare, but the findings of a study of northern pike (*Esox lucius*) complement those found here (Nilsson & Bronmark 1999). Pike, like many piscine predators, require longer handling times to consume larger prey, and as handling time increases, the risk of losing it to conspecifics increases as well.

2.5.3   Group Size

In natural conditions where resources are limited, the size of the foraging group often greatly affects individual behaviours and foraging success. As group size increases, the prevalence of kleptoparasitism often increases as individuals can take advantage of the increased collective search effort around them (Giraldeau & Caraco 2000). Archerfish in relatively small groups of 3 to 7 fish, however, forage on discrete, sequentially arriving prey. At prey discovery, foragers focus to obtain the prey; with one successful spitter, $G - 1$ individuals are potential kleptoparasites. Thus, the ratio of thieves to non-thieves is much higher with archerfish than with many other examples of intraspecific kleptoparasitism. Rather than a system with foraging groups finding and sharing divisible patches in a landscape, archerfish may 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 abundance of kleptoparasites.

My data show that the probability of kleptoparasitism increased with group size, at least initially from 3 to 5 fish. Beyond 5 fish, however, loss rate plateaued. Loss rate was already relatively high in the smallest group; thus, a quick plateau is reasonable since loss rate cannot surpass 100 percent. A plateau at 5 fish may suggest that the optimal number of thieves is 3 or 4 fish. Loss rate does not continue to rise as five or more fish attempt to steal, but competition does. In groups of three or more, when a downed prey attracts only one thief, this often means that the spitter downed it quickly, not allowing time for additional thieves to be involved. In this scenario the spitter's advantage (control of when and largely of where the prey will fall) and a clear path to the fallen prey give the spitter a distinct advantage. However, when a handful of fish rush to steal a falling prey, confusion is generated at the water's surface making it difficult for the spitter to track the prey. This makes successful consumption more random across group members and thereby increases the theft rate. Beyond 3 thieves, however, additional thieves increases competition while providing minimal additional benefits: spitter confusion is not significantly increased, the spitter retains a minimum probability of success due to the spitter's advantage, and the thieves may begin to interfere with each other. Thus, as group size increases, loss rate increases until approaching a maximum, assuming all other parameters such as prey size and prey height are constant.

2.5.4   Aggression

In an effort to reduce aggression, this experiment was designed to mimic natural foraging conditions (including random prey arrival), while still maintaining adequate control of prey presentation and video recording. Juvenile, wild-caught fish of a restricted size range were used since pilot studies showed that aggression increased with age. Despite these efforts, some fish showed aggressive behaviours. Nevertheless, no fish could guard the entire foraging area beneath the cricket apparatus, or even a small area absolutely. Because of uncertainty in prey arrival, the two most common pre-discovery foraging tactics were to either wait near edge cover, being alert to both immediate and distant foraging opportunities, or to cruise throughout the quadrant in hopes of being the first at the scene when a prey arrives.

Aggression was lowest in groups of 5 and highest in groups of 7. Several factors might help explain this, although a significant caveat is offered. In groups of 3, aggression is likely the most effective and efficient. Thefts dropped by 43.4% in groups of 3 when aggression was observed, the largest proportional drop. In groups of 7 the efficiency of aggression was lowest, but the density of fish in the quadrant was the highest and the opportunities for aggression were highest. Thus, the level of aggression observed at each group size may have been a function of both its effectiveness and the number of opportunities to perform it. Consider, however, that since each of the 10 fish had a different penchant for aggression and each fish was not used equally across groups, the levels of aggression in each group may have been a product of unequal presences of aggressive fish. Groups of 7, for example, had the highest

probability of simply having an aggressive fish in the group. Interpretations of the frequency of aggression across groups should be mindful of this caveat.

In this system, aggression reduced competition by reducing the average kleptoparasitism effort of other individuals in the group. At the smaller group sizes, G3 and G5H1, aggression noticeably decreased the probability of theft, which is intuitive given that aggression lowered the per-fish theft effort. In groups of 7, however, the probability of theft was the same whether aggression was present or not. At this higher forager density, aggression may simply be ineffectual at reducing the success of kleptoparasites. Furthermore, in the absence of an aggressor, the additional thieves are not expected to increase the loss rate if the plateau in thefts observed across group sizes is true.

Aggression also did not affect the probability of theft when crickets were presented at 30 cm. Here, aggression is likely ineffectual because of the additional time thieves had to be an effective forager. When a cricket was spotted at 30 cm, it took more spits to knock it down and it fell further to hit the surface of the water. All this gave subordinates time to get in and attempt to steal, even if the aggressor had initially kept it back.

The relevance of this laboratory observed aggressive behaviour to natural scenarios is unknown since the prevalence of aggressive behaviours between social juveniles in the wild is unknown. This study suggests, however, that aggression and guarding may be unprofitable in the wild if group sizes are large or prey arrival is highly unpredictable and/or at least 30 cm above the water.

2.5.5   Counter-Kleptoparasitism Behaviours

If kleptoparasitism costs are small, hosts 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 social groups appears to have led to the evolution of several anti-kleptoparasitism behaviours. The behaviours discovered here are solely evasive measures as archerfish try to improve their chances of consuming the prey before others do. Already discussed, aggression is an example of an anti-kleptoparasitism behaviour. Archerfish aggression remains an evasive measure rather than retaliation since it is exclusively preformed prior to prey discovery.

Jumping, spitting technique, and forager positioning are several other behaviours that illustrate how archerfish assess the risk of kleptoparasitism and alter their behaviour to reduce it. Fish chose to jump from the water to grab a cricket off its perch rather than spit it down more often in groups of 7 than in the smaller groups. Since hunting by jumping had a lower probability of being kleptoparasitized than did spitting, it makes sense to jump when surrounded by potential thieves; the more potential thieves around, the greater the benefit of jumping. Jumping, in this way, can be seen as an anti-kleptoparasitism behaviour. Presumably jumping was not used more regularly because of its much higher energetic cost.

Spitting technique demonstrates another counter-tactic to kleptoparasitism. Recall that as more spits were needed to down a cricket the more likely it was to be stolen. Intuitively, it follows that an archerfish should spit

as efficiently as possible with a strong direct shot. Personal observations, however, suggest that archerfish spit with surprisingly lesser force than they are capable of. By minimizing the force needed to down the prey, the spitter minimizes the distance the prey is launched and thereby reduces the risk of losing it. A cricket that falls just off its perch falls close to the spitter, takes a shorter time to fall, and is a less conspicuous projectile. Thus, minimizing the risk of theft may involve a conflict between haste and tidiness. This may provide at least a partial explanation of why archerfish exhibit less efficient spitting than might be expected.

Potential thieves also perceive the competition around them. This is perhaps best demonstrated in the observation that fish sometimes jump out of the water to catch a falling prey before it even hits the water's surface. On seven or eight occasions a fish was observed gaining an edge by meeting the cricket in the air. This behaviour was observed only when at least three fish were waiting where the prey would hit the water. Solitary archerfish were more patient.

As a last example, positioning before a foraging event undoubtedly affects one fish's advantage over another. The spitter may be at both an advantage and a disadvantage during a foraging event. As mentioned above, the immediate advantage is knowing when and where spits will be directed. Yet, immediately after a spit the spitter is not poised for burst speed, as are the thieves. In addition, thieves frequently positioned themselves with the prey between them and the spitter. The trajectory of the prey after a spit is often erratic; but, by positioning themselves this way, thieves hedge their bets to be nearest the

landing spot of the projectile meal. Although forager positioning was not a focus in this study, it is undoubtedly affects the probability of success of both tactics and deserves further attention.

In a wide range of taxa, strong kleptoparasitic pressure has led to the evolution of behavioural, morphological, and life-history counter-measures. Northern pike, as mentioned above, 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 draping themselves over their offspring and drupes in an effective guarding manner when other females approach the burrow (Hironaka et al. 2007). Though effective, this behaviour incurs a high cost as her matricidal nymphs attack persistently to suck her hemolymph until she lets go. 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. In the presence of conspecifics or gulls, the crows drop these items from lower heights than when alone (Whiteley et al. 1990; Crisol & Switzer 1999). Pied babblers (*Turdoides bicolor*) facultatively reduce their reaction to the alarm calls of cooperatively breeding but kleptoparasitic drongos (*Dicrurus adsimilis*) when their group size is large enough to be self-sufficient in predator vigilance (Ridley & Raihani 2006). And finally, strong selective pressures from kleptoparasitism can lead to the evolution of different morphological or life-history traits: gall-stealing thrips (genus *Koptothrips*) evolved soldier morphs or early dispersing larvae as strategies to thwart would-be thieves (Crespi & Abbot 1999).

2.5.6 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. Realizing that intraspecific kleptoparasitism occurs in archerfish, Goldstein and Hall (1990) asked if spitting could be maintained through a reinforcement schedule. The authors proposed that losing prey to coforagers is akin to a variable ratio schedule of reinforcement and that this helps maintain spitting. Although this suggests a reason 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). The pronounced vertical body striping of the juveniles may have evolved to enhance schooling (Keenleyside 1955). 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 grow.

Second, sociality in juvenile archerfish may be a consequence of the distribution of quality foraging habitats. Although unexplored, it is reasonable that a greater proportion of a juvenile archerfish's diet comes from spitting (as

compared to adults), as they are too small to compete in open water. Quality hunting patches, with overhanging vegetation and adjacent cover, are likely limited and spatially clumped. Thus, their distribution 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 as 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 is unlikely with archerfish as prey cannot be shared once discovered and foraging rate is likely limited by prey arrival rather than 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 field research. Future research into archerfish foraging patch structure, group stability, social behaviour, diet, and life history is needed to fully understand archerfish sociality and the factors that affect kleptoparasitism in natural conditions.

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CHAPTER 3: DO ARCHERFISH PLAY A PRODUCER-SCROUNGER GAME?

3.1 Abstract

Juvenile archerfish forage socially while spitting down insects from overhanging vegetation. Observations of frequent kleptoparasitism suggested that archerfish might represent a non-traditional producer-scrounger (PS) system: spitting fish being "producers" and non-spitting kleptoparasites being "scroungers". In order to demonstrate the basic PS assumption of negative frequency dependence of tactic payoffs and test if tactic proportions adjust to changing payoffs as the PS model predicts, archerfish were presented in groups of 3, 5, and 7 with crickets overhanging the water by 15 or 30 cm. Results indicate that although some predictions were met (including tactic specialization and greater kleptoparasitism with increasing group size), kleptoparasitism success was not frequency dependent, at least at low frequencies. Several characteristics of archerfish social foraging are not well captured by current social foraging theory. This study illustrates potential difficulties with applying general theory to unique and complex systems. Suggestions for improving future social foraging studies are discussed.

3.2 Introduction

Ethologists have long recognized that exploitation of resources by individuals is altered as a consequence of foraging socially (Krebs & Davies 1993). On the one extreme this can encourage sociality as individuals take advantage of the collective foraging effort around them. More eyes searching for food or more hunters pulling down large prey allow individuals to enjoy greater foraging success than when foraging alone (Barnard & Sibly 1981; Pitcher et al. 1982; Foster 1985). Such groups are known as aggregation economies and economic benefits are considered a major driver for sociality (Pulliam & Caraco 1984; Giraldeau & Caraco 2000).

On the other extreme, sociality can result in an economic disadvantage if individuals suffer strong indirect or direct competition. Such groups are known as dispersion economies; greater competition caused by close proximity means individuals suffer reduced foraging success as group size increases (Fretwell & Lucas 1970; Giraldeau & Caraco 2000). Clearly in these groups there must be one or more important non-economic reasons for sociality to persist, such as protection from predation or foraging patch structure (Foster & Treherne 1981; Lima & Dill 1990).

Social foraging theory attempts to explain the economic interdependence of the consequences and payoffs of individuals' behaviours within a foraging group. The recognition that group size affects the rate of food discovery and individual foraging efficiency led to "information sharing" models (Thompson et al. 1974; Clark & Mangel 1984; Packer & Ruttan 1988). These models assume that

all individuals simultaneously search for food and search for opportunities to join food discoveries of coforagers. Upon a discovery, all individuals converge to exploit the patch. Since an individual's consumption rate is greater in groups than when alone (but see Ruxton et al. 1995), the optimal group size (which provides the greatest per capita foraging intake) is unstable in groups with open membership: individuals will continue to join the group until the intake rate returns to that of a solitary forager (Caraco & Wolf 1975; Clark & Mangel 1984, 1986; Vickery et al. 1991).

Kleptoparasitism—the direct expropriation of resources from another individual—is a prime example of direct competition and is found extensively throughout the animal kingdom (Brockmann & Barnard 1979; Iyengar 2008). A second theoretical framework for social foraging developed out of the observation that some individuals use kleptoparasitism as a primary foraging tactic. These "scroungers" are parasitic to "producers" who search for and/or make food available for consumption. Producer-scrounger (PS) models explore the stability of foraging groups with frequency-dependent games (Maynard Smith 1982) considering individual payoffs with various proportions of producers and scroungers (Barnard & Sibly 1981; Vickery et al. 1991; Ranta et al. 1993; Giraldeau & Caraco 2000). The PS model assumes that at any moment individuals play either producer or scrounger, often specializing in one tactic over time. Tactic incompatibility—the inability to produce and scrounge concurrently— is an assumption of PS models and a major distinction from information-sharing models. The second major PS assumption is negative frequency dependence of

the scroungers' payoffs (Giraldeau & Caraco 2000), i.e., scroungers do best when rare, potentially better than producers as they can take advantage of the collective production of food while avoiding the associated costs. As a group fills with scroungers, however, payoffs decrease until it pays more to be a producer. Producers receive a "finder's share" portion of the patch before scroungers arrive; thus, their payoffs do not fall as steeply at high levels of competition. Assuming frequency dependent tactic successes, PS models can predict stable mixtures of producers and scroungers (where both tactics obtain equal payoffs), which vary with group size, finder's share, and food density/distribution (Vickery et al. 1991; Ranta et al. 1993; Giraldeau & Caraco 2000).

Archerfish are known for their remarkable ability to hunt by spitting down insects and other small prey from overhanging vegetation (Lűling 1963; Bekoff & Dorr 1976, Dill 1977). They inhabit brackish waters of South Asian mangroves and estuaries and forage socially when young (Lűling 1963; Timmermans & Maris 2000). Foraging for terrestrial prey involves discovering a prey item, and then one or more fish attempting to knock it down with jets of water while other fish position themselves to steal the prey once felled. Each fish must choose either to spit (produce the prey) or attempt to steal (scrounge prey downed by another). Since an archerfish cannot both spit and steal at the same time (i.e., tactics are incompatible) and some individuals appeared to prefer one tactic (preliminary observation), this suggested that archerfish might represent an atypical example of a producer-scrounger system.

Although there is a considerable body of producer-scrounger theory, relatively few empirical tests of the model have been conducted and nearly all use avian subjects (Giraldeau & Caraco 2000); no study to date uses a piscine subject species. Archerfish offer an opportunity to test the assumptions and predictions of a producer-scrounger model in a unique and novel system. This laboratory study was designed to explore if archerfish social foraging represents a producer-scrounger system and test the predictions of the model. By presenting groups of individually tagged archerfish with insects, observations of individual foraging behaviours and successes allowed an examination of how well the producer-scrounger model describes archerfish social foraging behaviour and the economics of each tactic.

Showing that the assumption of negative frequency dependence of tactic payoffs holds for archerfish is key to determining the appropriateness of the model. This assumption was explored by comparing each tactic's payoffs across the frequencies of fish using that tactic. In addition, evidence that some individuals spit or steal consistently more often than others could indicate that archerfish have individualized foraging roles. Although consistent tactic preference is not a defining assumption of PS models it is another feature that distinguishes them from information sharing models.

Concurrent with testing if archerfish meet PS assumptions, two predictions of the model were tested. First, the model predicts that decreasing the finder's share should make scrounging more profitable and thereby increase the proportion of scroungers within the group (Vickery et al. 1991; Giraldeau &

Caraco 2000). With archerfish, raising the height at which the prey is presented makes spitting more difficult and thieving easier as the additional height gives more time to rush in and steal; thus, the probability of consumption for the fish that spits down the prey decreases (shown in Chapter 2). Thieving as a tactic should, therefore, become more frequent. According to the second prediction, as group size increases there will be more individuals producing food and thus more opportunities to kleptoparasitize; therefore, the finder's share should decrease and the proportion of kleptoparasites should increase (Barnard & Sibly 1981; Vickery et al. 1991; Giraldeau & Caraco 2000; Coolen 2002). I studied archerfish in groups of 3, 5, and 7, to test this prediction.

3.3   Methods

3.3.1   General Methods

The general methods, including the fish used, the housing apparatus and conditions, and the tagging procedure are described in detail in the "General Methods" section of Chapter 2. Not included there is a complete description of the fish identification system. Each of the ten fish had two individually identifying, coloured beads sutured just anterior to the dorsal fin. The fish will be referred to individually as Fish A, B, C, D, E, G, H, I, J, and K. Note that there is no Fish F; this fish lost its beads immediately after tagging and was retagged as fish K.

The experimental design, setup, apparatus, and details of the observations, including the definition of a trial and behaviours recorded, were also described in detail in Chapter 2.

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3.3.2 Terms and Definitions

Although hunting via spitting is a very different behaviour from other systems, it is analogous to manipulating a prey item in preparation for consumption. Archerfish "produce" by spitting at a prey item in attempt to knock it down and make it available on the water's surface for consumption.

Archerfish forage for indivisible prey and only one forager eats for each food "patch" (prey) discovered. This means that the expected payoff for each tactic at a prey discovery is the probability of consumption. Similarly the "finder's share" or "producer's share" is simply the spitter's probability of consuming the prey. These probabilities can be determined by considering the success and failure rates over a large number of identical scenarios. Prey discreteness is not unique to archerfish, however, and there are many analogous systems (e.g., Crisol & Switzer 1999; Nilsson & Bronmark 1999; Morand-Ferron et al. 2007).

Careful consideration of the assumptions of a producer-scrounger model and the features of archerfish behaviour suggested not confusing systems by using the traditional "producer" and "scrounger" terminology. Consequently, throughout this paper the terms used for archerfish tactics are "spitter" and "lurker", referring to individuals that attempt to down prey via a spit or jump, or do no attempt to knock it down but rather attempt to steal, respectively (Table 3.1).

A fish becomes a spitter if it attempts to down the cricket at any point in the trial. This tactic is categorized further as either "terminal spitters" or "unsuccessful spitters" based on whether the individual only spat/jumped in a trial or also attempt to steal, respectively. By definition, each prey is felled by a terminal spitter, for this individual cannot steal the prey it felled. Although rare, it

was possible for a terminal spitter to not knock down a prey in a trial. This occurred when a fish spat at a cricket but then lost sight of it and shifted its attention elsewhere. By not returning to attempt to consume the cricket when it was felled by another fish, this fish only played spitter and thus was a terminal spitter. Terminal versus unsuccessful spitters do not represent separate tactics, but rather this categorization is useful for tracking the fate of each prey item.

"Non-participating" is considered a tactic, but without a measureable payoff. Often non-participants are simply too far from the action to attempt rushing in to steal the prey. Because it almost always appears that every fish is aware of the action, not pursuing the prey may be a strategic choice.

Table 3.1   **Producer-scrounger terms modified to suit archerfish. For each trial, each fish falls into one of four mutually exclusive and comprehensive categories: terminal spitter, unsuccessful spitter, lurker, and non-participant.**

Producer-Scrounger Terms		Archerfish Terms	
Term:	Defining Action:	Term:	Defining Action:
Producer:	Searches for and locates/prepares food, making previously unavailable food open for consumption.	Spitter:	Attempts to dislodge a prey via spitting or jumping.
		Terminal Spitter:	Spits or jumps, does not attempt to steal (most often successfully downs the prey and attempts consume it).
Opportunist:	Concurrently searches for food and for food discoveries, but is restricted to either producer or scrounger upon food discovery/production.	Unsuccessful Spitter:	Spits or jumps unsuccessfully, then attempts to steal (makes a deliberate movement towards a prey felled by another fish).
Scrounger:	Searches for and joins food discoveries of others.	Lurker:	Does not spit or jump, but attempts to steal (makes a deliberate movement towards a prey felled by another fish).
		Non-Participant	Does not spit, jump, or attempt to consume the prey.

3.3.3   Analysis

The frequency dependence of payoffs for each tactic and the effects of prey height, group size, aggression, and individual differences on tactic use and

success were determined. The frequency dependencies of each tactic's payoff were examined by comparing the successes of each tactic across trials binned by the number of fish using that tactic. For example, lurker success was compared across trials when no other fish played that tactic all the way up to when 5 other fish used that tactic (up to 6 fish can play lurker in the largest group size used, 7 fish). These analyses were performed over all trials with prey at 15 cm excluding those in which the cricket was downed by a jump. Pooling across group sizes assumes that non-participants do not affect the probability of consuming the cricket for the other two tactics. Thus, the effective group size is the number of active participants.

The effects of prey height were explored using groups of 5 fish and by comparing trials with prey at 15 cm to those at 30 cm (G5H1 versus G5H2 trials). The effects of aggression were examined by comparing trials with and without observed aggressive behaviours. The effects of group size were resolved by comparing results across the three group sizes at Height 1 (G3, G5H1, G7 trials).

Despite careful video review, the consumer's identity was unable to be determined in 5 of the 480 trials. Nevertheless, information regarding spitting, jumping, aggression, and theft attempts was discernable so these trials were included in analyses of this nature. These five trials were removed from analyses regarding theft rates and tactic or individual success.

Many results required measuring tactic success (i.e., the probability of consumption). In these cases each fish playing a tactic was considered an observation of that tactic. Tactic success was measured by dividing the number

of observations of that tactic by the number of successful consumptions for all fish playing that tactic. Chi-Square tests were used to compare success rates between tactics, between heights, and so on. Chi-Square tests were also used for comparison of theft rates, tactic use rates, and all proportional data. All non-proportional data (such as counts of spits or fish per trial) remained non-normal despite transformations. Thus, Mann-Whitney U and Kruskal Wallis tests were used to compare means of two or more groups.

3.4   Results

3.4.1   Prey Height

Loss rate was higher for crickets downed from 30 cm than from 15 cm (54.1% versus 40.6% successful with trials with jumps excluded, χ^2 = 4.35, p = 0.037; Fig. 3.1). Thus, terminal spitters suffered lower payoffs when spitting at more distant prey.

In Chapter 2 I did not distinguish between crickets stolen by lurkers or by unsuccessful spitters and thus, simply measuring theft rates is an incomplete measure of the success of spitting and lurking tactics. Unsuccessful spitters showed a significant increase in tactic success with increased prey height (16.6% vs. 30.2% at 15cm and 30cm; χ^2 = 6.52, p = 0.011; Fig. 3.1). Lurkers, however, did equally well at both prey heights (29.3% vs. 29.2% at 15 and 30 cm; χ^2 = 0.005, p = 0.982; Fig. 3.1). Because of this, the disparity in theft rates between prey heights shown in Chapter 2 appears due to the greater success of unsuccessful spitters rather than greater success of lurkers.
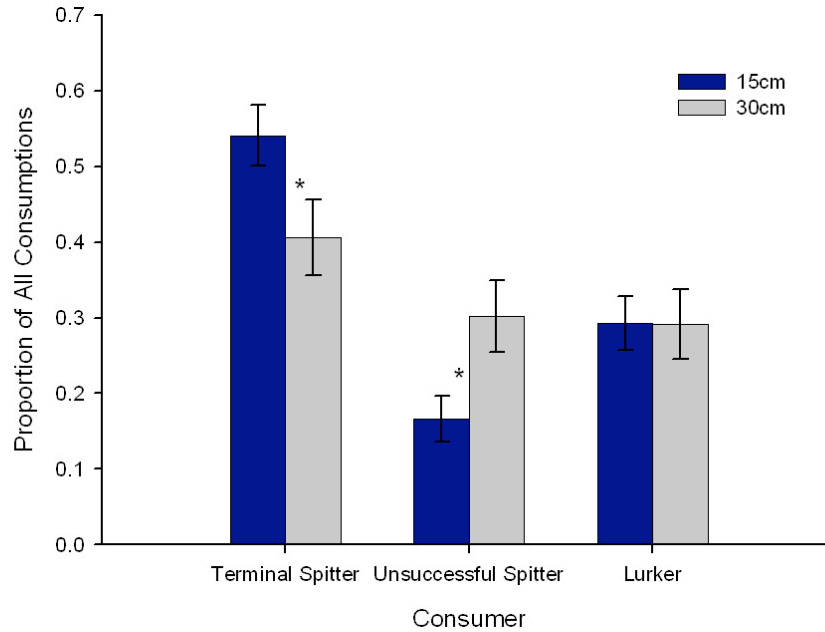
Figure 3.1   Tactic successes (proportion of all consumptions) at two prey heights (± one SE of proportions). Data include only trials with fish in groups of five and where a spit downed the cricket. The asterisks indicate significant within group differences (p < 0.05).

The number of spitters (terminal and unsuccessful combined) significantly increased with prey height (1.50 vs.1.72 spitters/trial at 15 and 30 cm, Mann-Whitney U: Z = -3.246, p = 0.001; Fig. 3.2). Since it is assumed that every spit is an attempt to down the cricket and spitting has less success at the greater prey height, the increased number of spitters per trial may be a surprise. However, as shown in Chapter 2, the additional height means fish require significantly more spits to knock the cricket off its perch. The greater difficulty in spitting gives greater opportunity for others to attempt a shot. Successful spitting is still more valuable than lurking (see Figure 3.14 later in text) and thus it is reasonable that fish should take the opportunities and that the number of spitters increases with height.
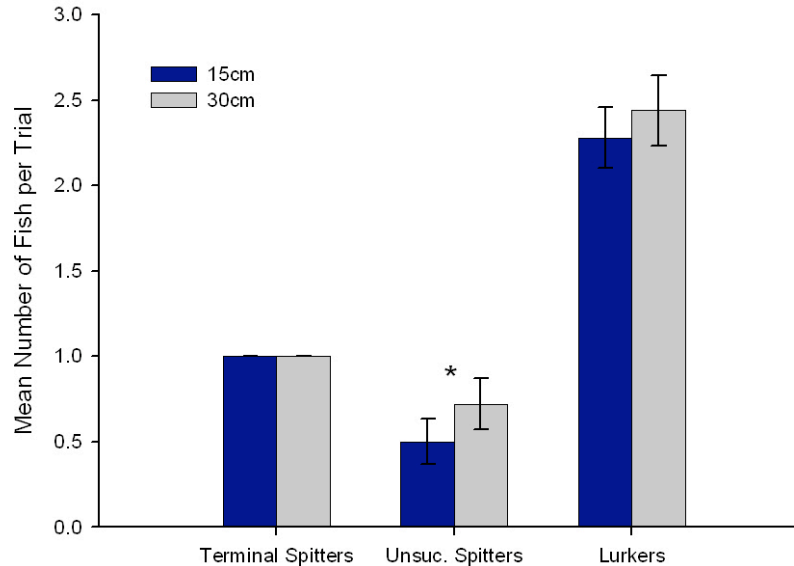
Figure 3.2 **The mean number of fish performing the three active tactics per trial at each prey height (error bars represent 95% CI). Data include only trials with 5 fish and crickets downed by a spit. The asterisk indicates a significant within group difference (p < 0.05).**

The number of lurkers per trial increased with prey height, though not significantly (2.28 versus 2.44 lurkers/trial for 15 and 30 cm respectively, Mann-Whitney U: Z = -1.074, p = 0.283; Fig. 3.2). With both spitting and lurking increasing with prey height, it is unsurprising that overall participation increased significantly (3.89 vs. 4.22 fish/trial for 15 and 30 cm respectively: Mann-Whitney U: Z = -3.054, p = 0.002). It is probable, therefore, that the increase in lurking observed is an artefact of the increased opportunity that the extra height provides to join the active foragers after prey discovery, rather than a tactical switch.

A better test of a tactical switch from spitting to lurking is to look at the ratio of participating individuals playing lurker to those playing spitter. Doing so shows a similar relative proportion of spitting and lurking effort for the two prey heights: dividing the number of lurkers in each trial by the number of spitters gives means of 2.04 for 15 cm prey and 1.78 for 30 cm prey (Mann-Whitney U: Z

= -1.485, p = 0.138). This indicates that although overall participation increased at Height 2 (meaning more lurkers per trial), the relative use of spitting and lurking tactics did not change.

3.4.2 Group Size

Group size affected the success of spitting more than of lurking. As group size increased, the payoffs to each spitter declined significantly (2x3 contingency table: χ^2 = 21.1, *df* = 2, p < 0.001; Fig. 3.3), but lurking success changed little (2x3 contingency table: χ^2 = 2.83, *df* = 2, p = 0.242). The number of spitters per trial increased slightly with group size, but not significantly so (1.32, 1.47, and 1.55 for G3, G5H1, and G7; Kruskal Wallis test: χ^2 = 4.133, *df* = 2, p = 0.129).
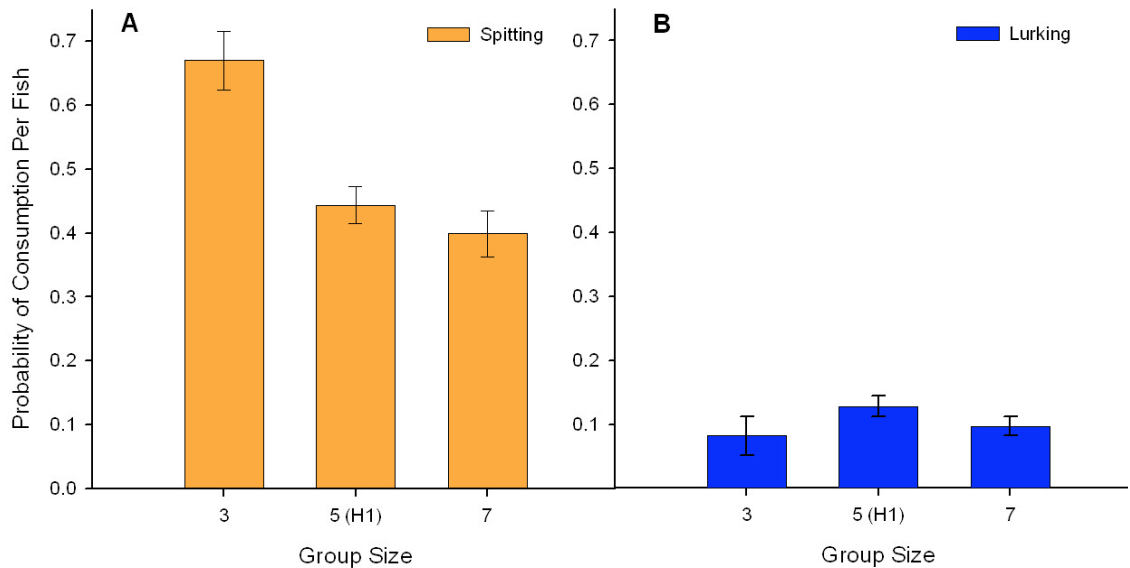
Figure 3.3 **The probability of consuming the cricket for (A) each spitter (orange bars) and (B) each lurker (blue bars) in each group size (± one SE of proportions).**

Looking just at absolute numbers, the number of lurkers per group increased dramatically (1.13, 2.35, and 3.71 mean fish/trial for G3, G5H1, and

G7, respectively; Kruskal Wallis test: χ^2 = 162.488, *df* = 2, p $\ll$ 0.001). The ratio

of lurkers to spitters increased as well (0.84, 1.50, and 2.35 for G3, G5H1, and

G7, respectively; Kruskal Wallis test: χ^2 = 70.372, *df* = 2, p $\ll$ 0.001). However, to

quantify lurking effort per fish while accounting for the changing group size, the

number of lurkers in each trial was divided by the number of fish available to lurk,

i.e., the group size (G) minus one. This reveals what proportion of fish available

to lurk chose to do so. Comparing across group sizes, lurking increased only

slightly with group size, and non-significantly (0.57, 0.59, and 0.62 for G3, G5H1,

and G7, respectively; Kruskal Wallis test: χ^2 =0.327, *df* = 2, p = 0.849; Fig. 3.4).

Unlike between prey heights, the expected window of opportunity to join a prey

discovery should be similar between groups foraging at a fixed prey height (15

cm). Thus, participation level differences due to different prey heights should not

confound comparisons of the number of lurkers/(G-1) between group sizes.
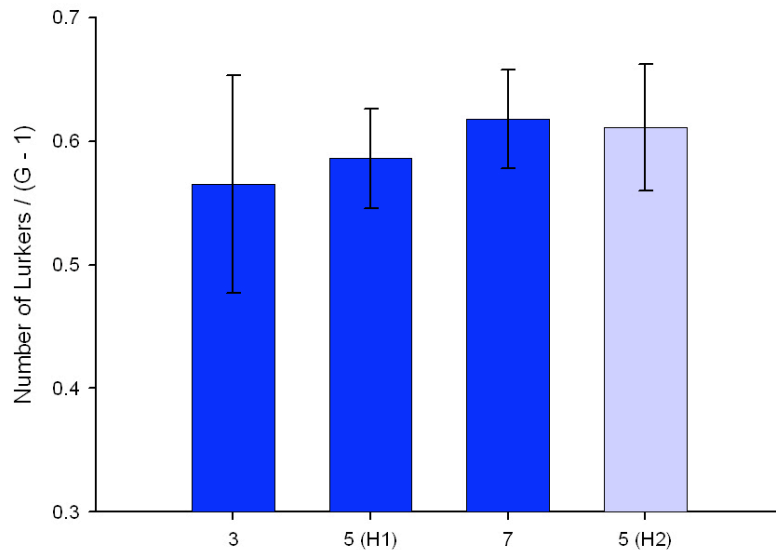
Figure 3.4 **The mean proportions of fish available to lurk that did so in each trial (± 95% CI). Data with prey at Height 2 (30 cm) are included (light blue bar) for comparison with trials with 5 fish and prey at Height 1 (15 cm).**

3.4.3   Aggression

Aggression was observed in 257 of the 480 trials conducted (53.5% of trials). Six of the ten fish used in this study displayed aggressive behaviours in at least one trial during the experiment. Recorded on a presence/absence basis for each trial, the prevalence of aggressive behaviours ranged from 4.2% of trials for Fish G to 37.3% of trials for Fish D (Fig. 3.5). A strong dominance hierarchy prevented more than one fish from displaying aggression in the same trial.
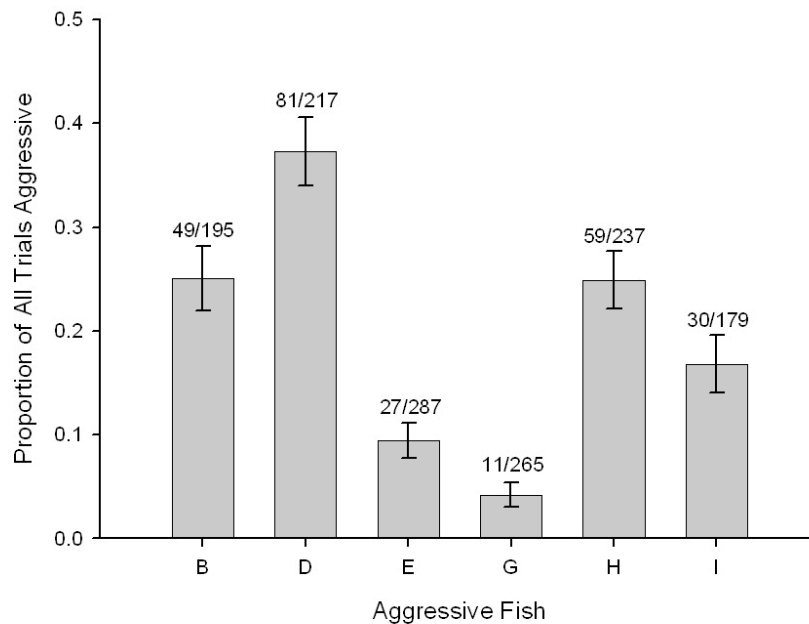
Figure 3.5   The proportion of trials that the six aggressive fish showed aggression (± one SE of proportions).

The main effect of aggression was to reduce participation of coforagers (all groups: 3.90 vs. 4.29 participants/trial with and without aggression, respectively; Mann-Whitney U, Z = -3.274, p = 0.001). Aggression significantly reduced the number of fish that spat (across all groups: 1.51 vs. 1.67 spitters/trial with and without aggression; Mann-Whitney U, Z = -2.618, p = 0.009), and

65

moderately reduced the number of lurkers (across all groups: 2.40 vs. 2.61

lurkers/trial with and without aggression; Mann-Whitney U, $Z = -1.674$, p =

0.094). The above trends held true within each group with one exception: in trials

with 3 fish lurking slightly increased in the presence of aggression. The reduction

in competition caused by aggression often led to fewer crickets being stolen

(details and statistics presented in Chapter 2; Fig. 2.12).
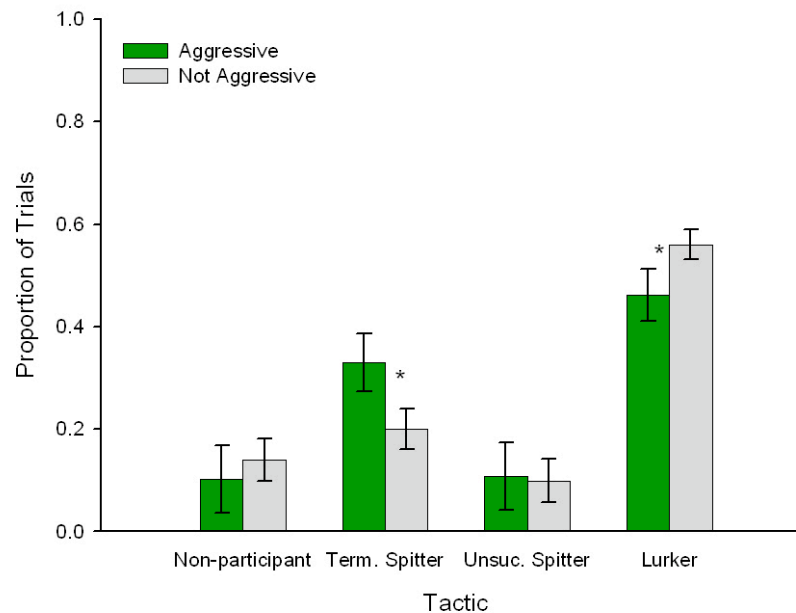
Figure 3.6   The proportion of trials at Height 1 that the aggressive fish played each tactic (± one SE of proportions), when aggressive (dark green bars) and when not aggressive (light gray bars). Asterisks indicate significant within group differences (p < 0.05).

Because aggression reduces participation, the aggressor is given greater

opportunity to spit. In general at Height 1, individuals were more likely to use a

spitting tactic rather than a lurking tactic when aggressive (Fig. 3.6). Only Fish E

did not spit more when aggressive. Excluding Fish E, aggressive fish were

significantly more likely to play spitter rather than lurker when aggressive than

66

when not (spat in 45.6% of trials when aggressive vs. 35.5% when nonaggressive, χ^2 = 5.00, p = 0.025).

Individuals benefited from greater success at the spitting tactic when aggressive than when not aggressive (Height 1 trials only, 31.6% stolen with aggression vs. 52.9% without aggression; χ^2 = 10.80, p = 0.001). Yet, within trials with aggression, the loss rate was the same regardless of whether the aggressor spat or not (31.6% stolen in trials with aggressor as a spitter vs. 32.7% stolen with aggressor not spitting; χ^2 = 0.032, p = 0.858). Thus, aggression appears to reduce competition for all spitters regardless of whether the aggressive individual was one of them.

3.4.4 Frequency Dependence of Tactic Payoffs

The frequency dependence of tactic payoffs were determined for spitting and for lurking by comparing the tactic success for individuals across data grouped by the number of individuals using that tactic. Across Height 1 trials at all group sizes, up to 6 fish played lurker, and up to 5 fish spat (out of a possible 7). Thus, the data were split into 6 groups based on lurker number to test for a frequency dependence on lurking payoffs, and into 5 groups based on spitter number to detect a frequency dependence on spitting payoffs. Pooling across groups provided sufficient sample size but assumed that only active participants (spitters and lurkers) influenced tactic successes. The analyses excluded trials at Height 2, trials where the cricket was downed by a jump, and the few trials where the consumer was unknown.
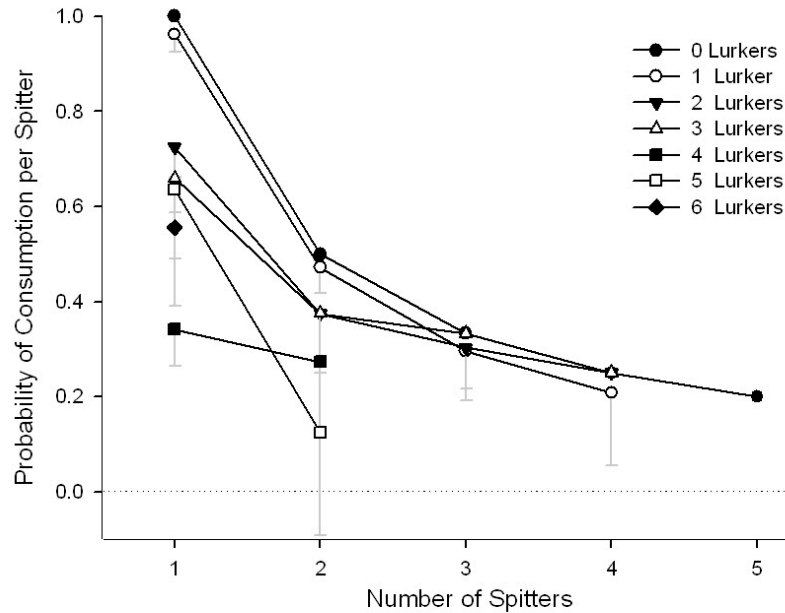
Figure 3.7 Spitter success (probability of consumption) plotted against the number of spitters present per trial. For visual comparison the data are split by lurker number as well, although for analysis the data were binned only by spitter number. Data include all Height 1 trials where the cricket was spat down and the consumer was known. Error bars (bottom halves shown) represent one SE of proportions.

The payoff to spitters shows strong negative frequency dependence (Fig. 3.7). A spitter's payoff was found to decrease rapidly as the number of spitters increased (2x5 Chi-Square contingency table, $\chi^2 = 20.1$, *df* = 4, p < 0.001). Unsurprisingly, Figure 3.7 shows that a spitter's payoff also declines as additional lurkers join the group (2x7 contingency table: $\chi^2 = 57.3$, *df* = 6, p ≪ 0.001). Thus, both additional spitters and additional lurkers negatively affect a spitter's payoff.

In contrast to spitters, the payoff to lurkers showed no overall frequency dependence, negative or otherwise, at least up to 6 lurkers (Fig. 3.8). Pairwise comparisons between lurking successes when alone or with up to 5 additional lurkers yielded no significant result ($\chi^2 \leq 2.28$; p ≥ 0.131) and a 2x6 Chi-Square contingency table indicated no overall deviation from parity ($\chi^2 = 4.70$, *df* = 5, p =

68

0.454). In addition, simple blocked Chi-Square tests yielded no support for a

possible Gaussian distribution or other non-linear shape.
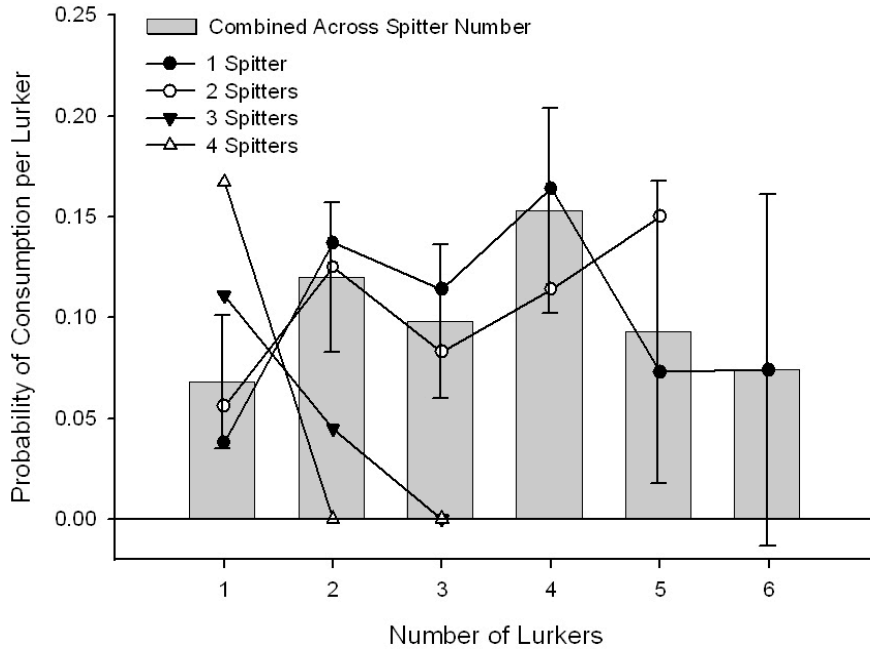
Figure 3.8   **Lurker success (probability of consumption) per trial plotted against lurker number and split by the number of spitters per trial (± one SE of proportions). Data include all trials at Height 1 where the cricket was spat down and the consumer was known.**

3.4.5   Spitting Efficiency of Individuals

Chapter 2 showed that it took the foraging group significantly more spits to

down a cricket at 30 cm (4.36 spits) than at 15 cm (2.78 spits). Spitting aptitude,

however, varied between individuals. Assuming that each spit is an attempt to

knock down the prey, spitting efficiencies can be determined by averaging the

number of spits each fish took to successfully knock down the cricket. Mann-

Whitney U tests were used to compare the efficiency of each fish to the

combined efficiency of the remaining 9 fish. Data at each prey height were

compared separately and Bonferroni corrections were applied to account for multiple testing: with one comparison for each fish, a p-value below 0.005 was required to claim statistical significance.

At Height 1, individuals varied from needing on average only 1.39 spits to up to 3.06 spits to knock down the cricket (Fig. 3.9). The average across fish was 1.89 spits/cricket. Only one fish showed a significantly different spitting efficiency: Fish J required significantly more spits to down its prey (3.06 spits/cricket; Mann-Whitney U: Z = -4.23, p < 0.001).
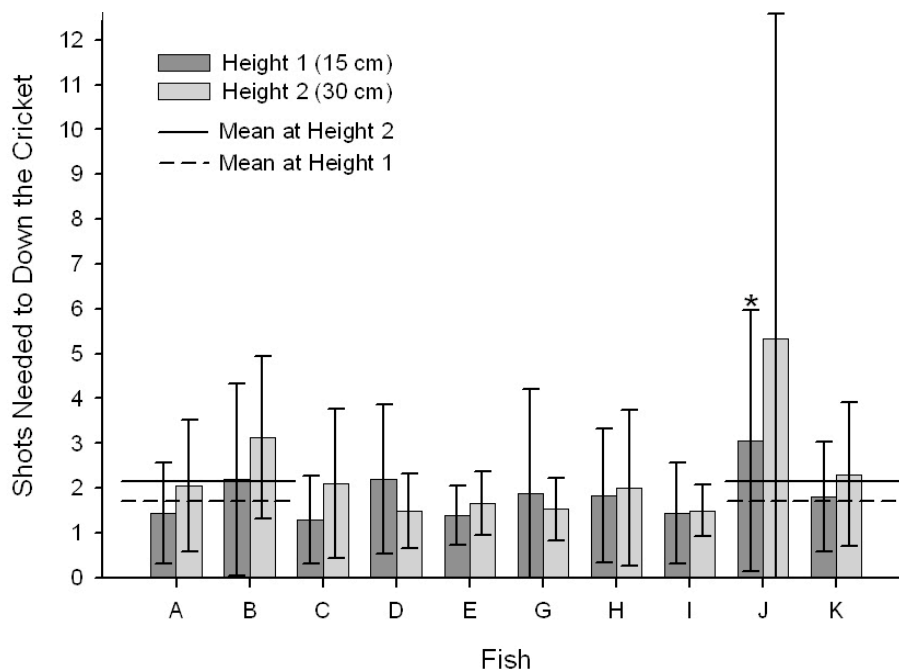
Figure 3.9   The mean spitting efficiency of each fish, i.e., the mean number of shots needed to successfully down a cricket, at Height 1 (dark gray bars) and height 2 (light gray bars)(± one SD). The asterisk represents a significant deviation from the mean of the remaining fish at prey Height 1 (p < 0.005).

At Height 2, individuals varied from needing on average only 1.50 shots to 5.33 shots to knock down the cricket (Fig. 3.9). The average across fish was 2.18

shots/cricket. Due to a lower sample size and higher variability, no fish's efficiency reached the $p < 0.005$ criteria. Fish J consistently undershot the target by roughly one centimetre (personal observation), causing it to take consistently more spits to down the cricket than the average fish.

3.4.6   Tactic Use

All recorded behaviours were classified into one of three exclusive tactics: spitter, lurker, and non-participant. Spitters were further subdivided into terminal and unsuccessful spitters for analytical purposes. I examined whether any of the ten fish performed any of the four behavioural categories significantly more or less often than the others in each of the four treatment groups and over all groups combined. In addition, to more directly measure the tactic preference of each fish, I compared the proportion of trials each fish was a spitter (terminal and unsuccessful combined) versus a lurker while excluding trials in which the fish did not participate. Since expected rates of tactic use were previously unknown and incalculable, I compared the proportional tactic use of each fish to the combined proportion of the remaining nine fish—again comparing each fish to the average of the rest. To account for multiple testing, Bonferroni corrections were applied: with one comparison for each fish, a p-value below 0.005 was required to claim statistical significance.

Rather than reporting complete statistics on how each fish used each tactic in each group, I will present statistical results just for the comparisons of spitting (terminal and unsuccessful combined) to lurking for each group as well as comment on the notable results of the tests for each tactic separately (refer to

Figure 3.10 for a complete visual presentation of all proportion data and statistical significance).

In groups of 3 fish, when comparing the proportion of trials as a spitter to trials as a lurker for each fish, only Fish G showed significant deviation from the rest, spitting significantly more than lurking (χ^2 = 11.1, p = 0.001).

In groups of 5 fish with prey at Height 1, comparing spitting to lurking in participatory trials revealed 8 of the 10 fish in the 0.05 to 0.005 range of p-values (only fish B, p = 0.499, and Fish K, p = 0.129, showed middling rates of spitting and lurking). Only Fish G, however, had a statistically significant deviation from the rest (Fish G spat significantly more than lurked: χ^2 = 24.2, p < 0.001). Notably, comparisons of rates of just lurking revealed that 6 of the 10 fish in this group had significantly extreme rates of lurking.

Unlike G5H1 trials, groups of 7 fish showed less evidence for individual differences in tactic use polarity. Although Figure 3.10 Part C shows Fish A, B, and C with significant deviations from the average rate of lurking, these results are likely created in large part by significantly disparate proportions of inactive trials. When comparing just the proportions of participatory trials as a spitter to trials as a lurker, no fish reached the p = 0.005 cut-off for statistical significance.

Comparing the proportion of trials spitting to lurking for each fish in groups of 5 and prey at 30cm, Fish G and Fish J showed significant preferences to spit rather than lurk (χ^2 = 8.33, p = 0.004 and χ^2 = 8.16, p = 0.004, respectively) with no other fish deviating significant from the rest. This result is representative of the results when comparing each behavioural category separately.
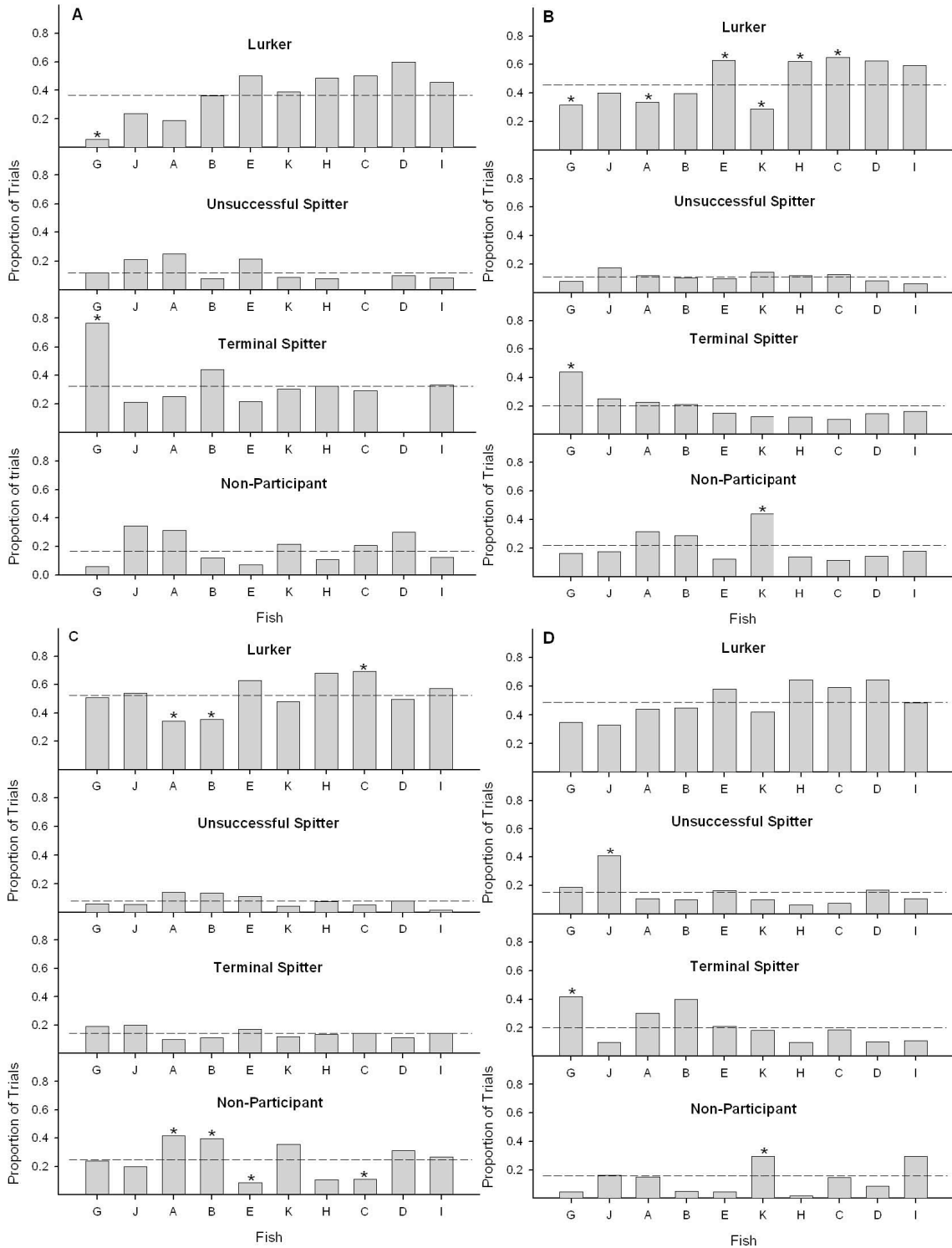
Figure 3.10 Tactic uses for the ten fish in G3 (A), G5H1 (B), G7 (C), G5H2 (D) trials. The dashed line represents the proportion for all fish combined; asterisks indicate a significant deviation for that fish from the rest (p < 0.005). Fish are presented in order of their preference for spitting across all trials, greatest preference being at the far left.
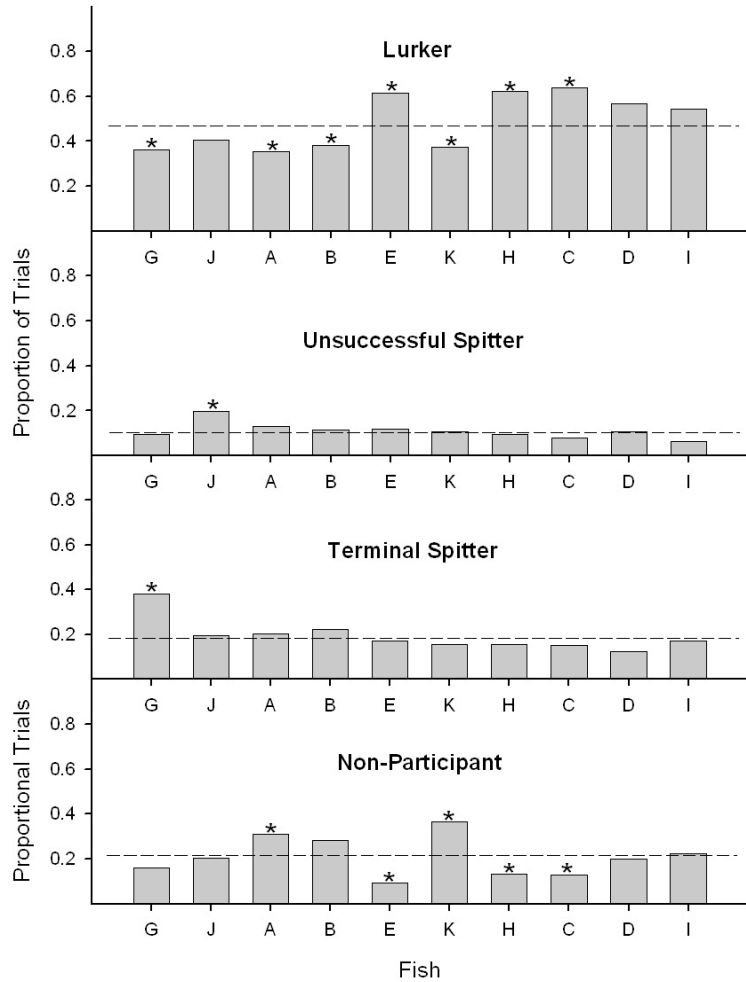
Figure 3.11 Tactic uses for fish across all treatment groups combined. The dashed line represents the proportion for all fish combined; asterisks indicate a significant deviation for that fish from the rest at p < 0.005. Fish are presented in order of their preference for spitting across all trials, greatest preference being at the far left.

Combining across all treatment groups yielded the greatest power to detect significant differences in individual tactic preferences, assuming these preferences do not change between groups. Comparing spitting and lurking directly, 6 of the 10 fish showed a significant preference for one tactic (Fig. 3.11). Fish A, G, and J had significantly more trials as a spitter (χ^2 = 8.69, p = 0.003; χ^2 = 34.1, p < 0.001; and χ^2 = 10.5, p = 0.001, respectively), and Fish C, D, and H significantly more as a lurker (χ^2 = 16.1, p < 0.001; χ^2 = 7.76, p = 0.005; and χ^2 =

74

9.90, p = 0.002, respectively). Only Fish K showed moderate levels of spitting and lurking (Fish K: χ^2 = 0.383, p = 0.536; all other fish: χ^2 ≥ 4.05, p ≤ 0.044). Thus, over all recorded trials, most fish showed a significant preference for either spitting or lurking.

3.4.7 Success of Individuals

The success (consumptions/trials) for each individual was compared to the combined success for the rest of the fish for each treatment group and for all groups combined. Accounting for multiple testing, a p-value below 0.005 was required to meet statistical significance.

In groups of 3, only Fish G's success rate significantly differed from the others: Fish G consumed significantly more crickets/trial (χ^2 = 8.14, p = 0.004). This is unsurprising given that Fish G was a significantly more frequent spitter and that spitting had greatest success in groups of 3 fish. In groups of 5 fish at 15 cm prey height, Fish J consumed significantly more crickets/trial (χ^2 = 8.51, p = 0.004) and Fish K, significantly less (χ^2 = 8.35, p = 0.004). Personal observations suggest that Fish J makes up for its reduced spitting aptitude with talent and hustle as a kleptoparasite. No fish consumed significantly more or less crickets than their coforagers in groups of 7 fish or in groups of 5 fish at 30 cm prey height.

Looking across all groups, only Fish K showed significant deviation in success rate (consuming significantly less prey/trials in: χ^2 = 8.36, p = 0.004; Fig. 3.12). Fish K's overall lower foraging success was likely due more to its low participation levels than its spitting or lurking aptitude.
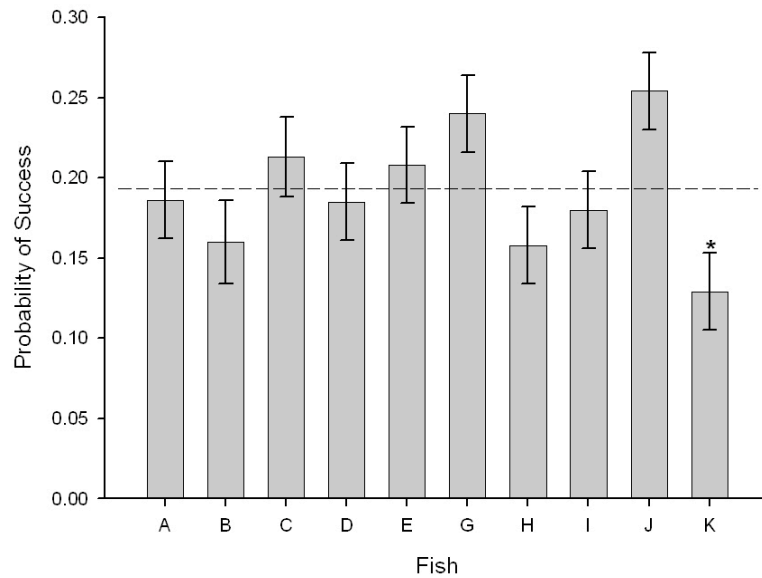
Figure 3.12 The probability of success for each fish over all trials, measured as the number of successful consumptions over the number of trials in which it was present (± one SE of proportions). The asterisk indicates a significant difference from the rest (p = 0.004).

Plotting the relative use of spitting and lurking against the relative success of using these tactics for each fish in each treatment group yielded no clear patterns. No consistent assertion can be made regarding whether fish did or did not choose to use tactics based on their individual success at using them.

3.4.8 Effect of Group Assemblage on Individual Behaviour

Tactic use by a fish may depend on the identity of one or more of the other fish present in their group. For example, Fish A may have a tendency to spit, but may switch to lurking when in the presence of Fish G, a more ardent spitter. 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 lurker (compared separately). Since this process required using well over a hundred Chi-Square tests on the data for each group type (G3, G5H1, G7, and G5H2) depending on the number of different assemblages of fish used, both a Bonferroni correction as well as a Step-up False Discovery Rate (FDR) correction were applied to account for multiple testing. Because the null hypothesis was that fish behave differently in different group compositions, the Step-up FDR was in this case a more conservative method as it makes a significant result more likely than with the Bonferroni method. Nevertheless, for all of the following results both correction methods agreed.

For groups of 3 and of 7 fish, no fish spat or lurked significantly more or less when in any one assemblage of fish compared to the other assemblages; furthermore, no fish behaved significantly differently when in the presence or absence of any one of the other 9 fish. This was the case for groups of 5 fish with prey at 30 cm as well. For groups of 5 fish with prey at 15 cm, no fish behaved differently in any one assemblage of coforagers. Of all tests performed, only one result proved significant: when comparing tactic uses and the presence/absence of individual fish, Fish A spat significantly more often in the presence of Fish B than in Fish B's absence (G5H1 trials; χ^2 = 13.9, p = 0.00019). Although this result is statistically highly significant, it is difficult to deduce a reasonable biological explanation for it. Thus, barring this unexplained result, fish do not significantly alter their behaviour based on their coforagers' identities.

3.4.9 Tactic Success

The relative successes of terminal spitting, unsuccessful spitting, and lurking were compared within each experimental group by comparing the proportion of all crickets consumed by each tactic (Fig 3.13 A). The relative success of individuals using a tactic is measured by comparing the ratio of successful consumptions for the tactic to the number of observations of individuals using it (Fig 3.13 B).
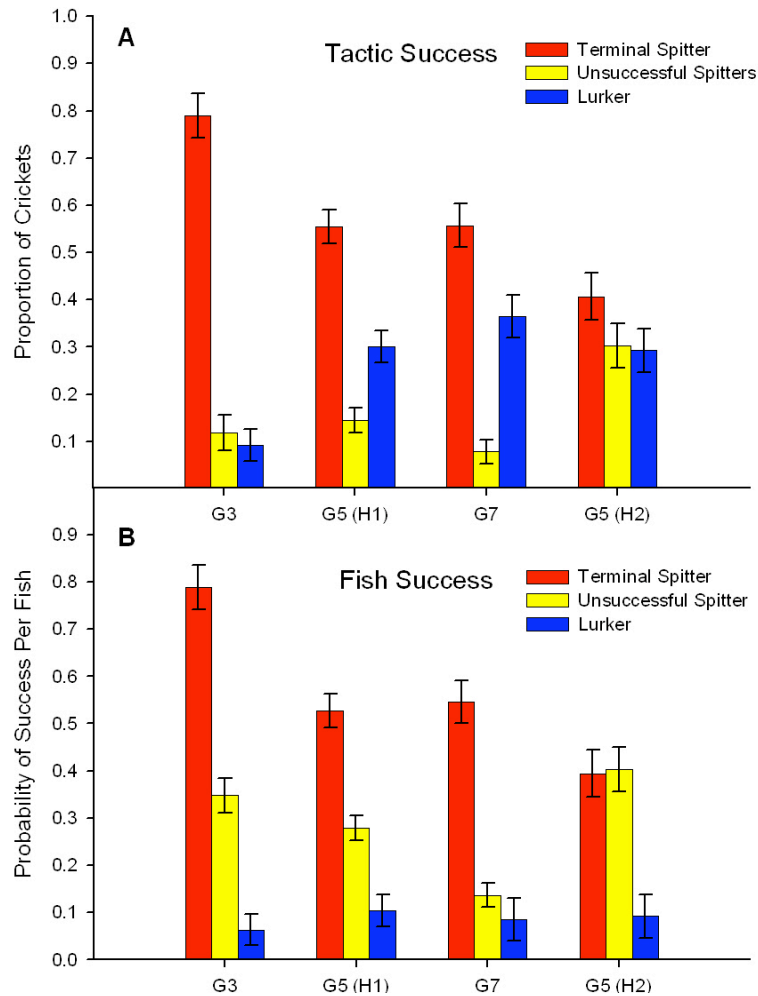
Figure 3.13 The relative success of each tactic across each treatment group (± one SE of proportions). (A) The proportion of crickets obtained by each tactic. (B) The ratio of successful consumptions to the number of observations of individuals using each tactic, i.e., the probability of success for each fish using that tactic.

Within groups of 3 fish, the most successful tactic was terminal spitting, followed by unsuccessful spitting, and then lurking (pairwise Chi-Squares; $\chi^2 \geq$ 10.5, p < 0.001). This success distribution was observed within groups of 5 fish at Height 1 as well (pairwise Chi-Squares; $\chi^2 \geq$ 10.2, p $\leq$ 0.001). Within groups of 7 fish, terminal spitting was the most successful tactic compared to either unsuccessful spitting or lurking (pairwise Chi-Squares; $\chi^2 \geq$ 30.9, p < 0.001). Unsuccessful spitting and lurking were roughly equally successful (χ^2 = 0.846, p = 0.358). In groups of 5 at Height 2, terminal spitters and unsuccessful spitters had equal success (χ^2 = 0.075, p = 0.784) and both of the spitting categories were significantly more successful than lurking ($\chi^2 \geq$ 26.6, p < 0.001). Thus, as a tactic, spitting was much more successful than lurking in each treatment group. In addition, individuals fortunate to be the terminal spitter enjoyed the highest probability of success in each group, except at Height 2, when they shared equal success with unsuccessful spitters.

3.5 Discussion

Individual archerfish actively foraging in a group ultimately either spit a prey item down or attempt to steal it. Since they are unable to do both at the same time, this represents a system with two incompatible tactics whose payoffs are likely to be dependent on the frequency of tactics within the group—much like that described by a classic producer-scrounger (PS) model. These characteristics of archerfish social foraging led to an experiment to determine if archerfish meet the assumptions and predictions of a PS model.

The results of this experiment will now be presented alongside a discussion of how well the predictions of the PS model are met by archerfish. Although negative frequency dependence is an essential assumption of the model, it is presented last. This is because it indicates most clearly that archerfish deviate from a classic PS system and leads into a discussion of how the archerfish system does or does not fit within current social foraging theory.

3.5.1 Prey Height

Under a PS model, increasing the cost of one tactic should increase the proportion of individuals using the other tactic (Vickery et al. 1991; Giraldeau & Caraco 2000). This was tested in archerfish by presenting crickets at 15 cm and 30 cm above the water. The producer's share should decrease when prey are higher (because spitting down the crickets is more difficult and stealing them is easier), which should increase the proportion of fish playing lurker.

When prey height was raised, thefts significantly increased, terminal spitting success declined (Fig 3.1), and the number of both spitters and lurkers per trial increased (Fig. 3.2). Although unintuitive, the increase in spitters is unsurprising given that prey at 30 cm allows more fish to spit and spitting is still more successful than lurking (Fig. 3.13). Although the number of lurkers increased, this is attributed to an increase in overall participation. The proportion of lurkers did not increase as predicted, despite an increase in thefts. This appears to contradict the PS prediction; closer attention should be paid, however, to the payoff structures of each tactic. The payoff to lurkers changed very little between prey heights (Fig. 3.1). Thus, the significant increase in thefts at 30 cm

prey height is not due to an increase in lurking success, but rather to a significant

increase in the success of unsuccessful spitters as kleptoparasites. This result

was unexpected and is difficult to explain. One possibility is that by arriving

quickly enough and being in a position to spit, unsuccessful spitters are alert and

ready to chase the falling prey. Lurkers may be late, out of position, and unaware

of the exact location of the cricket amidst the crowd. This may give unsuccessful

spitters a small advantage in the ensuing scramble, but it is difficult to imagine

this fully accounting for the observed result.

Although this experiment does not provide evidence that the proportion of

kleptoparasites increases with prey height, as predicted, it cannot be said that

archerfish do not adjust their tactic use according to the present payoff

structures. Had lurking success increased significantly with prey height, this

could have been confirmed more clearly. As it is, the proportional use of the

tactics matched the tactic successes observed, which does not contradict the

theory underlying the PS prediction.

3.5.2   Group Size

According to the PS model, as the size of the group increases and

producers become more abundant, a larger producer's share is required to

prevent the scrounger alternative from becoming more profitable. Larger groups

mean more opportunities to kleptoparasitize and thus more individuals should

exploit these opportunities. Increasing the size of the group while keeping all

things equal should increase scrounging profitability and thus the proportion of

scroungers within the group should increase (Barnard & Sibly 1981; Vickery et al. 1991; Giraldeau & Caraco 2000; Coolen 2002).

Archerfish do indeed show an increase in lurking frequency and proportion with group size and the increase appears to follow a declining curve as predicted by Vickery et al. (1991). This should be examined closely, however, as the magnitude of this result may be misjudged. Since there can only be one successful spitter and foraging involves non-concurrent discoveries, increasing group size will always lead to a proportional increase in lurkers. It is thus unsurprising that the absolute frequency of lurking increases with group size. Per individual lurking effort increased only slightly with group size (Fig. 3.4). This suggests that either there is no significant benefit to increasing one's kleptoparasitic effort in larger groups or that individuals do not change their effort accordingly. Given that lurking success per lurker only increased moderately with group size, the observed lack of change in lurking rate is reasonable.

Thus, as the PS model predicts, both absolute numbers of lurkers and the proportion of lurkers increased with group size. The caveat, however, is that unless fish choose to forgo any chance of getting a meal, lurking will always increase as the group has more and more hungry individuals. The more interesting question is whether lurking use is predicted by lurking success; this appears to be the case, although increases in both were moderate.

3.5.3   Aggression

Most producer-scrounger models predict that dominant individuals should play scrounger within the group because they can use aggression to avoid the

costs of producing, garnering greater resources with less effort (Brockmann & Barnard 1979; Barta & Giraldeau 1998). This makes sense if food patches are found randomly and concurrently within the landscape and if subordinate individuals can be supplanted after food discovery, but before consumption.

This study found, in contrast, that aggressive fish preferred to spit rather than lurk (Fig. 3.6), and that they enjoy greater success at spitting when aggressive than when not aggressive. Vickery et al. (1991) describe factors affecting the profitability of aggression that are appropriate to the archerfish scenario. If a food source is at all defensible, and aggression can increase defensibility, then this should reduce the scroungers' share, profiting an aggressor who plays producer. This was seen with archerfish: aggressive individuals benefit from their ability to reduce competition, making spitting the more successful option. Scroungers could only benefit from aggression if they could supplant others directly from their food. Archerfish, however, cannot commandeer a cricket from another fish once felled and captured.

3.5.4   Individual Differences in Ability and Tactic Preferences

All fish showed roughly equal spitting ability, except Fish J, who required significantly more spits/cricket (Fig. 3.9). Evidence that Fish J's ineptitude influenced its tactic use is difficult to find. Fish J often chose to spit despite most often not successfully downing the cricket. Perhaps compensating for its spitting ability, Fish J was particularly fast and adept at snatching the cricket once fallen. Thus, overall this fish enjoyed a moderately high consumption rate (Fig. 3.12).

In most circumstances PS strategies are not fixed (but see Barnard & Sibly 1981). Instead PS systems involve individuals with flexibility in tactic use and often some tactic preferences (Giraldeau & Lefebvre 1986; Parker & Sutherland 1986). This study shows that although archerfish frequently switch between spitting and lurking, they can and do prefer one tactic to the other. In every treatment group at least some individuals used a tactic significantly more or less than the average of the other fish. Combining data across groups show a nearly universal polarized preference for lurking: only 3 of the 10 fish failed to reach a significant extreme in one direction or the other ($p < 0.005$; Fig. 3.11). Frequent use of both tactics plus consistent polarization provides sufficient evidence that archerfish tactic use is not hard-wired, but is flexible, and that fish chose a tactic based on a combination of the current situation and some inherent tactic preference. Consistent tactic preferences indicate that the social foraging behaviour of archerfish is not described well with an information-sharing model, where individuals share roles equally by providing food and sharing food at the same rate (Giraldeau & Caraco 2000).

3.5.5 Frequency Dependence of Tactic Payoffs

Showing a negative frequency dependence of spitting and lurking payoffs is key to determining if archerfish social foraging fits within a producer-scrounger framework (Vickery et al. 1991; Giraldeau & Caraco 2000). Under this assumption, when scroungers are rare they should be able to take advantage of the collective food production around them and do even better than producers; when abundant, payoffs are worse than for producers. With frequency dependent

tactic success, a stable equilibrium of mixed tactics can be reached where payoffs to both tactics are equal.

The payoff to archerfish spitters does show strong negative frequency dependence (Fig. 3.7). The more fish that attempt spitting, the lower the individual probability of successfully consuming the cricket. In addition, with each lurker added the spitters' payoffs are further reduced, just as predicted for a parasitic relationship of scroungers on producers (Vickery et al. 1991; Giraldeau & Caraco 2000).

Alternately, the payoff to lurkers appears not to have consistent frequency dependence, at least at frequencies below six lurkers (Fig. 3.8). This seems to fly in the face of both PS theory and logic, particularly since these fish must vie for the single prize just like the spitters. Yet, the factors that affect the success of lurking are different than for spitting. Consider how the probability of success for a lurker changes as the number of lurkers increases. A trial with one spitter and just one lurker often means that the spitter knocked down the cricket quickly, not allowing many fish a chance to compete. The expeditious spitter is at a distinct advantage being unhindered in both spitting and retrieving its prey. With prey only 15 cm high, the solitary lurker has a low probability (~7%) of stealing the cricket. His chances actually increase as the number of spitters goes up: additional spitters add stochasticity to the timing and launch angle of the dislodged prey. Additional lurkers also add significant confusion and stochasticity particularly at the point of descent for the prey, decreasing the probability of success for the spitter and distributing success more evenly across foragers. At

four lurkers confusion is significant and the probability of success approaches

parity for all foragers in groups of five or six fish (15-20%). Beyond four lurkers,

the probability of success is already distributed equally, competition becomes

important, and success becomes frequency dependent. Although group sizes

beyond seven fish were not tested, it is certainly unreasonable to imagine that

individual lurker success could be maintained at any level indefinitely.

3.5.6   Tactic Success

In terms of individual payoffs, spitting (on average) is more successful

than lurking in all group sizes and prey heights; i.e., in no treatment group did

lurkers do better than spitters (Fig. 3.13). This is true even when PS theory says

lurkers should do well (when there was one lurker and many spitters). But this is

because the spitters are all attempting to produce the same prey item. Thus, the

lurker cannot take advantage of the collective effort of the spitters and reap

benefits from all of them. Instead, the additional spitters represent more

competition for the same singular prize.

If spitters always do better (on average) than lurkers, it seems fish should

choose to spit more often than is observed, i.e., to just rush in and spit as soon

as possible. However, it takes time and positioning to spit accurately, which may

not be available if another fish is already spitting. It may be better to track the

prey about to be felled rather than try to move in to spit yourself. The positioning

of both spitters and lurkers is likely very important in determining success.

Although unaddressed in this study, this needs more attention as it would shed

additional light on what controls the probability of success for both tactics and why fish chose to spit or steal.

It should be noted that the success of unsuccessful spitters in this study might be overinflating the perceived success of spitting while underestimating the success of kleptoparasitism. While many times the unsuccessful spitter appears to be making the best of a bad job by chasing the cricket once felled by another fish, often fish will back off from spitting when another fish nears, thereby essentially becoming a dedicated lurker. If that fish is successful at getting the prey, that success is counted as a consumption by an unsuccessful spitter, not a lurker. It would have been very difficult to do otherwise, but by not separating the individuals that truly switched tactics from those that simply failed at spitting, lurking success was necessarily lowered. This is an important point when considering the relative success of each tactic.

As a last point on the success of tactics and spatial positioning, consider the spatial positioning of archerfish kleptoparasites. According to PS models, maximally efficient scroungers are expected to position themselves in the centre of the group, with producers at the periphery. In this way scroungers can take quick advantage of the finding events around them (Hirsch 2007). Conversely, archerfish thieves circled the periphery of the group while spitters occupied the space nearest directly under the prey. In this arrangement both tactics maximize their probability of success.

3.5.7 Distinctive Characteristics of Archerfish Social Foraging

In addition to the differences already mentioned between the predictions of a producer-scrounger (PS) model and the results of this study, four distinctive characteristics of archerfish social foraging were discovered that distinguish this system from a traditional producer-scrounger system: the fact that finding and producing food are often not performed by the same individual, the existence of two distinct stages of foraging, the non-autonomous nature of archerfish "producing", and the ability to switch tactics within one "play of the game". Each of these characteristics of archerfish social foraging will be discussed in light of current theoretical frameworks.

3.5.7.1 Definition of Producing

In many social systems, finding a food patch in essence produces it. In other systems, where handling or preparation is required, individuals first find a food item and then must manipulate it to make it available for consumption. Handling or no handling, finding food and making it available to eat often go hand in hand by the same individual. This is not necessarily the case with archerfish. The fish that first spots a prey item may or may not even choose to spit at it, let alone be successful in knocking it down. Nevertheless, their actions often make the prey's presence known to others, who then attempt to spit it down.

This identifies the need to clarify the definition of "producing". Previous studies define producers as individuals that provide a limited resource (Barnard & Sibly 1981), that "search for food" (Koops & Giraldeau 1996; Giraldeau & Caraco 2000), or that are simply "hosts" to scroungers (Vickery et al. 1991). Although

functionally adequate for many studies, these definitions contain ambiguity, which can be problematic in systems where "producing" is socially complex. Functional definitions of "producing" must take into account a potential significant disjunction between finding food and making it physically available for consumption. I propose adopting the definition used by Caraco and Giraldeau (1991) with a small modification: "producers" are individuals that expend "time and energy generating opportunities to exploit [previously unavailable] resources essential to survival and reproduction". The emphasis is placed on attempting to make food available, not on just finding it. Dropping "searching for" or "finding" from the definition has one immediate implication: the term "finder's share" should be reconsidered to reflect systems where the finder is not necessarily the producer, such as with archerfish.

3.5.7.2 Two Foraging Stages

Recognizing this disjunction in the producing of food leads to the second major difference between archerfish and typical producer-scrounger (PS) systems: archerfish social foraging comprises two separate stages characterized by very different degrees of compatibility between foraging tactics.

Stage 1, pre-prey discovery, represents a mixture of opportunists and producers as described by Vickery et al. (1991). With everyone in the group looking for prey and for prey discoveries, the group likely approximates an information-sharing system since compatibility between tactics is very high at this point. Switching between detecting prey overhead and observing other discoveries is as easy as adjusting one's gaze. This low incompatibility leads to

what Vickery et al. (1991) call "overcompensation" and groups primarily composed of opportunists. These conditions mean that all individuals close enough will join a discovery and the success of individuals is dependent on the size of the group and the productivity of the foraging patch. This stage dictates the group's food intake over time, with the maximum intake rate limited by the rate of prey arrival.

Stage 2, post-prey discovery, is characterized by incompatible tactics: individuals cannot spit prey down and simultaneously steal prey spat down by others. Incompatible and recognizable tactics now allow comparisons of individual tactic use and success. The attention of the group is focused around the single indivisible prey item discovered. Only one fish consumes the prey, however, and this indivisibility of the reward limits group size and dictates the foraging economics. It is this stage in which the dynamics of archerfish social behaviour were explored in this study. All recorded behaviours (except aggression) occurred in this stage, and it is this stage that determines individual success and tactic success.

Under a PS model, patch discovery rate is controlled largely by the number of producers. For archerfish this is true in Stage 1. But in Stage 2, consumption rate of the group is independent of the number of producers; the group's success is not tactic frequency dependent. It doesn't matter if there is one spitter or many; there is still only one prize to be eaten. Theoretically it is possible that as the number of spitters increases prey are downed faster and thus the group's overall consumption rate is higher. This study, however, showed

only a small, non-significant decrease in the number of spits needed to down the prey as group size increased.

The two foraging stages are different as described, though they are not independent. Individual tactic preferences likely hold across stages and the behaviours of Stage 1 often carry into Stage 2. For example, individuals that consistently look for prey (produce) in Stage 1, likely choose to spit in Stage 2. But again, the fish that finds a prey is not always the fish that spits it down.

3.5.7.3 Non-autonomous Producing

As alluded to when discussing the definition of producing, archerfish "producers" are not autonomously attempting to produce separate food patches within a landscape. Rather, multiple fish contribute to making the same food item available for consumption (by spitting or jumping at the prey item), though only one actually does so by knocking it down. This differs from typical PS systems where producers search independently for patches of food, even sequentially produce these food patches, and others choose to join when a producer finds/prepares one. In such cases all joining individuals are scroungers. If this approach were taken with archerfish, it would not matter if individuals spat or not. Simply locating a cricket would make an individual a producer, and all subsequent spitters would be scroungers (even though they are attempting to make the food available for consumption). I argue that it does matter who spat, for it is spitting that actually produces the food, not simply its discovery. To determine overall group foraging efficiency, consideration of who spits, who steals, and the conditions that promote one or the other, is unnecessary. But, to

fully understand individual success, the reasons why individuals chose to behave as they do, and the evolution of spitting and archerfish sociality, this information is important.

3.5.7.4 Tactic Switching

The last decidedly atypical aspect of archerfish social foraging that distinguishes it from a classic PS system is the capacity for individuals to switch tactics within one "play of the game". In typical PS systems, for each foraging event individuals are classified as either a producer if they made the food available, or as a scrounger if they joined food patches made available by another. Yet, individuals are not restricted to one tactic over time as individuals can switch tactics opportunistically between foraging events. Even "opportunists", that both produce and scrounge simultaneously pre-food production (with reduced efficiency), are limited to one tactic at each foraging event (Vickery et al. 1991). With archerfish, however, the process of discovering and producing a prey item is not restricted to a single individual. Multiple individuals can attempt to produce a prey (by spitting or jumping), and then switch to scrounging if the prey is knocked down by another fish. Thus, this tactic switching is a direct product of the non-autonomous nature of archerfish "producing".

To resolve this problem, only the terminal spitter could be considered the producer; the unsuccessful spitters that attempt to consume the dislodged prey would be considered scroungers, since they attempt to steal prey made available by another. This, however, neglects the assumed intent and effort of the unsuccessful spitters. Many times two spitters will take turns firing at a cricket

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until it is dislodged. It would be difficult to argue that the tactic employed by these two fish is categorically different and that only the lucky one that downed the prey is the producer. If spits occur nearly simultaneously, the fish themselves may not even know who is stealing from whom.

It seems more appropriate to classify all who behave with intent to down the prey with a spit or a jump as a "producer", which is the working framework of this study. But, we are brought back to the problem of "producers" consuming crickets by kleptoparasitizing the terminal spitter. Deciding whether to classify these individuals as essentially producers or eventually scroungers is difficult and further highlights the difficulty of adapting this system to fit within a PS framework.

As another option, foraging events could be broken down to the level of each spit/jump with just one individual qualifying as the producer. The problem, however, is determining the tactics of the other individuals. The scrounger-defining behaviour, chasing a falling prey, is only observable if the spit in question actually knocks down the prey. It is not possible know if an individual will attempt to steal the prey until it does so. Removing this unknown by looking only at the terminal spit again neglects the intents and efforts in the preceding unsuccessful spits.

3.6 Conclusions

Clearly a producer-scrounger (PS) model does not fully describe the complexities of archerfish social foraging. Although some results were at least consistent with the predictions of PS models (such as tactic use following tactic

success and individual tactic preferences), key findings such as a lack of frequency dependence on lurker payoffs indicated a lack of concordance with the model. Further inquiry revealed some fundamental differences in the structure of archerfish social foraging that are not well accounted for under a producer-scrounger framework, such as the disjunction between finding and producing, the existence of two economically distinct foraging stages, the non-autonomous nature of producing, and the capacity to switch tactics within one play of the game. Current social foraging theory, therefore, can only describe parts of archerfish social foraging behaviour. Information-sharing theory may describe archerfish behaviours prior to prey discovery. Post-prey discovery, a frequency dependent game similar to that of a producer-scrounger model may be suitable, if it accounts for the non-autonomous nature of archerfish producing and the factors affecting lurker success that lead to the lack of frequency dependence.

3.6.1 Suggestions for Future Studies of Social Foraging

Attempting to describe archerfish social foraging behaviour in a producer-scrounger framework illustrates the potential difficulties with applying general theory to unique and complex systems. Nevertheless, these exercises can be useful in assessing both the utility of current theory and in gaining understanding of one's study system. Several lessons of this study can apply to further social foraging studies.

First, in some systems kleptoparasitism success may not strictly decrease with increasing parasite frequency. The payoff for a tactic may be both frequency dependent as well as dependent on additional factors that may themselves be

frequency dependent. Thus, tactic success may not always show strong negative frequency dependence at all frequencies. Archerfish illustrate that although the amount of direct competition is certainly a key determinant of tactic success, there may be other factors, such as positioning, timing, and the physical attributes of producing and scrounging that also affect tactic success and they may do so differently at different tactic frequencies.

Second, careful consideration should to be given to what defines a "producer" in each system, and what behaviours are involved. In addition, patch sharing after a producing event may not be as simple as dividing up what remains after the producer's share. The finder's share is likely not fixed, but dependent on factors such as the number of foragers that join. In addition, those that join likely do not get equal access to the patch: timing, positioning, and patch structure may affect individual shares.

Finally, careful observations of the specific behaviours involved in both producing and kleptoparasitizing for a study species is important. With theory alone and no observational knowledge of how tactics physically interact, understanding of social interactions may be limited or misguided.

3.6.2   Natural Foraging Conditions of Archerfish

Juvenile archerfish forage among overhanging vegetation in mangroves and estuaries. Compared to the laboratory conditions of this study, these natural foraging conditions likely benefit lurkers relatively more than spitters. In nature, prey arrive randomly, at varying heights, and amongst overhanging vegetation that likely adds significant stochasticity to their trajectory once felled. These

conditions would benefit lurkers and lessen the disparity between spitting and lurking success.

If spitting is consistently the most successful tactic (which would encourage its persistence and evolution) then there must either be a cost to spitting or a non-economic benefit to sociality. Otherwise lurkers would disperse to find their own prey and archerfish would not forage socially. If spitting incurs a cost it is not likely to be an energetic one. Although unconfirmed, spitting may incur the cost of increased predation risk from an aerial predator. Lurkers hang back in or near cover, constantly looking up and vigilant of activity above the water. Spitters, on the other hand, are less timid. Spitting requires approaching the prey, watching it for an opportunity to spit, and then tipping at the water's surface to spit. The spitter is necessarily focused on the job at hand and likely exposed to a greater predation risk. This risk could be a trade-off for the greater probability of consuming a meal. Alternatively, there may be a benefit to sociality despite the increased competition: lurkers may provide increased protection from predators through risk dilution or increased vigilance. (Powel 1974; Milinski & Heller 1978; Foster & Treherne 1981; Dehn, 1990).

In nature, groups likely fill quality foraging patches until the payoff to lurking declines to the point where an individual can achieve greater success in a smaller group. Payoffs to lurkers likely dictate naturally occurring group sizes. According to this study, payoff is to lurking is maximal in groups of around five or six fish, though maximal payoffs may be different in natural foraging conditions if spitting success is altered by prey height or complex overhanging vegetation.

3.6.2   Future Work

Further work is certainly needed to discern what micro-conditions influence the choice to spit or to steal. Forager positioning and timing are also likely highly important factors that need more research. In addition, a good understanding of archerfish foraging and social behaviour in natural conditions is lacking. Information regarding the size and stability of natural groups, the ratio of aquatic to terrestrial-derived food in juvenile archerfish diets, the distribution of quality foraging patches, and general life history characteristics of archerfish is needed to better understand the factors that control social foraging and intraspecific kleptoparasitism and the evolution of spitting and archerfish sociality.

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CHAPTER 4: CONCLUSIONS

4.1 Research Summary and Synthesis

Two approaches to studying kleptoparasitism were outlined in Chapter 1: the first descriptive and comparative method explores factors that affect the prevalence and success of kleptoparasitism, and the second uses social foraging theory to investigate how interdependent foraging tactics used within the group affect the success of individuals and the group as a whole. Both approaches were used in this thesis used to explore kleptoparasitic behaviour in socially foraging archerfish.

Food stealing was expected to occur at high levels in archerfish because of the inherent vulnerabilities that hunting via spitting entails. Indeed, this study found loss rates as high as 60%. Chapter 2 provided substantial empirical evidence that vulnerability to kleptoparasitism is variable and is significantly affected by several ecological factors: theft increased as prey size increased, as more spits were required to down the prey (which is analogous to handling time), and as group size increased. These results complement those found with northern pike (Nilsson & Bronmark 1999), kelp gulls (Steele & Hockey 1995), crows (Cristol & Switzer 1999; Ha & Ha 2003), bald eagles (Fischer 1985), flies (Sivinski et al. 1999), and many other species.

Most kleptoparasitism research involves avian subjects or other easily observable terrestrial species (Iyengar 2008). This study showed that several ecological factors have significant effects on kleptoparasitic interactions in

archerfish. Thus, by demonstrating this with a fish species, this further verifies

that these factors are universally applicable across taxa. In addition, this study

quantified the degree and variability of these factors as well as the costs

archerfish thieves imposed on their hosts. And finally, Chapter 2 discussed

several discovered countermeasures to kleptoparasitism: archerfish chose to

jump rather than spit when the risk of theft was highest; the spitting technique

used likely represented a trade-off between reducing the risk of theft and losing

the prey; the positioning of spitters likely reduces the risk of theft even though it

makes spitting more difficult; and aggression, which reduced competition and

thus the risk of theft. Understanding how individuals react to the behaviours of

others is key to understanding the interdependence of individuals within a social

group.

Determining the economic interdependence of tactic payoffs and their

effect on the success of individuals and the foraging group as a whole is a major

goal of social foraging theory (Giraldeau & Caraco 2000). Chapter 3 used social

foraging theory as a framework for understanding archerfish behaviour and used

the archerfish system to measure the generality and utility of the producer-

scrounger (PS) model. The results presented in Chapter 3 show that despite the

apparent potential for archerfish to fit a PS model, an important assumption of

the model was not well met: the success of lurkers (kleptoparasites) was not

negatively frequency dependent at low, but realistic, frequencies. Further

difficulties with fitting archerfish to a PS model arose due to the non-autonomous

nature of hunting via spitting. Archerfish can use more than one tactic within one

play of the game; therefore, determining distinct roles for archerfish within a producer-scrounger framework is difficult. Perhaps most importantly, the model did not encompass the complexity of factors involved in determining individual success and thus could not adequately describe the reasons for using one tactic over the other in each micro-condition.

For archerfish, the foraging success of the group as a whole is likely best described with an information-sharing model. Prior to prey discovery, individuals can easily search for prey and for opportunities to steal at the same time by simply shifting their gaze. The group's productivity is likely dependent on the size of the group and the rate of prey arrival. Yet, because physically incompatible tactics emerge, after prey discovery an information-sharing model can no longer accurately predict individual behaviours or success. Rather, the economics are likely better described with a game-theoretical model. Despite the differences between true PS systems and archerfish as detailed in Chapter 3, archerfish did appear to adjust their use of each tactic according to changes in payoff structures. This result was not discernible as cleanly as hoped, however, because the changes in lurker payoffs between experimental conditions were small.

To date only a few empirical studies demonstrate fulfilment of the assumptions of the PS model: with captive flocks of birds (Coolen et al. 2001 Giraldeau et al. 1994; Mottley & Giraldeau 2000) and with wild birds (Morand-Ferron et al. 2007). Only the latter two demonstrate an equilibrium mixture of producers and scroungers. Producer-scrounger models were developed out of

studies of the behaviour of foraging flocks. When choosing a tactic, archerfish

may have to account for more variables than do flocks of birds foraging on an

open surface. A game-theoretical model suitable for archerfish would have to

account for the interdependence of tactics using tactic frequency, as well as

forager positioning, stochasticity, shifting finder's shares, and known

characteristics of the foraging game (such as group size, prey height, prey size,

and aggression).

If empirical studies are to inform and improve theory, this study provides

several suggestions. Careful consideration should be given to the functional

definition of "producing". With archerfish it was beneficial to focus less on

searching effort and more on the effort to make food available, as the fish that

finds the prey does not necessarily make it available. This is likely not unique to

archerfish. Secondly, tactic frequency is certainly an important economic factor

within a foraging group. However, the success of individual archerfish was not

described well enough using only negative frequency dependency. As listed

above, there are many potentially important factors, each of which may itself be

tactic frequency dependent. It is not realistic to assume, as does the PS model,

that the proportion of tactics within all foraging groups is the only determinant of

tactic success. Social foraging theory applied to novel systems needs to be

flexible enough to consider this and other possibilities.

This thesis should encourage further research into archerfish life history

and behaviour, particularly in the wild. Archerfish remain an excellent laboratory

subject; however, this type of research will remain incomplete as long as so

much about archerfish in their natural conditions remains unknown. Much the same, kleptoparasitism research remains incomplete if not reflecting its prevalence and diversity across the animal kingdom.

The bottom-up approach of exploration through empirical behavioural studies is the brick and mortar of behavioural ecology and is invaluable for expanding the shared body of knowledge. The top-down approach of formally organizing quantitative predictions is also valuable as it provides coherence and generality to this knowledge. The difficulty described in this thesis of adapting current theory to a non-traditional research subject highlights the need to develop more diversely applicable theory. In doing so, we need to be careful to allow math to inform biology without inadvertently forcing the biology to conform to the math.

4.2   Literature Cited

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APPENDIX

Appendix A: DVD of Videos and Photographs

The DVD attached forms a part of this work.

The QuickTime movie files can be opened with QuickTime Player or other capable movie player program. The picture files are JPEGs and can be opened with any picture viewing software.

Movie Files:
- Example – Jump   175.3 MB
- Example – Lurker Attentiveness   170.1 MB
- Example – Kleptoparasitism   478.1 MB
- Example – Kleptoparasitism (in slow mo)   89.7 MB
- Movie Combining All Examples   1.95 GB
- Demonstration of how archerfish can be trained   1.22 GB
- Close-up of a tagged fish   148.5 MB

Picture Files:
- Archerfish laboratory setup (with first   1,004 KB
  generation prey presentation apparatus,
  not the final version with black tubing)
- Fish with Green-Red Tags   204 KB
- Fish with Orange-Orange Tags   264 KB
- Fish with Orange-Yellow Tags   520 KB
- Fish with White-Orange Tags   356 KB