

# Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution

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Familiarity is thought to stabilize dominance hierarchies and reduce aggressive interactions within groups of socially living animals. Though familiarity has been widely studied in shoaling fish, few studies have investigated changes in prey competition as a function of time spent together within groups of initially unfamiliar individuals. In this study, we created shoals of three-spined stickleback (*Gasterosteus aculeatus*) and monitored changes in foraging rates and related competitive behaviors within shoals over a 4-week period in experimental series where prey was spatially and temporally concentrated or dispersed. Prey share was unequal under both prey distribution modes, and disparity in prey share was not seen to change as trials progressed. Interestingly, the contest rate for prey items fell over time when individuals were competing for dispersed prey but not when prey were concentrated. We found no evidence that fish showed association preferences for either group members that had consumed a greater or lesser proportion of prey during trials. Though the intensity of competition may be reduced by increased group stability in nature, this is likely to be strongly dependent on the way prey resources are distributed through space and time. *Key words:* flock, foraging, scrounging behavior, shoal, threespine stickleback. [*Behav Ecol* 17:959–964 (2006)]

Group living is widespread in nature, and animals may actively aggregate for a variety of reasons. Individuals that forage together bear lower per capita vigilance and predation risk costs and stand to gain from potentially higher prey detection rates compared with those foraging alone. A detriment of social foraging is the increased potential for competition with conspecifics for prey once it is discovered because animals are often compelled to compete among themselves in order to maximize their share of it. Competition can be costly in terms of time and energy expenditure or risk of injury or predation, and selection should favor the adoption of behaviors that most efficiently minimize the intensity or duration of conflict while simultaneously preserving the benefits of sociality (Giraldeau and Caraco 2000).

These costs can be reduced if individuals are able to discriminate between their group mates in a competitive context on the basis of recent associations and interactions and moderate their own behavior accordingly when interacting with others of higher or lower competitive standing. This allows disputes to be settled without the need for intense or prolonged agonistic conflict (Barnard and Burk 1979). Research has revealed that species in many taxa possess the capacity to recognize familiar individuals and to change certain behaviors when interacting with them (Barnard and Burk 1979; De Vries 1998; Dugatkin and Earley 2004), and a great deal of work on familiarity has been carried out on shoaling fish.

This work (reviewed by Griffiths 2003; Ward and Hart 2003; Griffiths and Ward forthcoming) has shown that individuals in many species prefer to associate with familiars over unfamiliar. It has revealed that in some species familiar groups forage more efficiently than groups composed of unfamiliar (Swaney et al. 2001), that they are more cohesive and may therefore be less susceptible to predation (Chivers et al. 1995), and that information diffuses more rapidly between members (Laland and Williams 1997; Lachlan et al. 1998). Familiarity is also considered to be an important factor in reducing aggression within groups of foraging fish (Seppa et al. 2001); however,

despite the large literature on familiarity effects in general, relatively few studies have specifically examined the role of familiarity in relation to prey competition.

One study, a detailed analysis of the effects of individual recognition on social behavior in sea trout (*Salmo trutta*) by Höjesjö et al. (1998), revealed that food intake and growth were higher and that dominance hierarchies were more stable in familiar than in unfamiliar groups. Similarly, Seppa et al. (2001) revealed greater growth rates and lower mortality in familiar groups of Arctic char (*Salvelinus alpinus*). Utne-Palm and Hart (2000) studied prey resource share and aggression within pairs of three-spined sticklebacks (*Gasterosteus aculeatus*) as a function of time spent together and showed that in longer established pairs the disparity in prey share and levels of foraging-related aggression were lower.

Our study aimed to identify temporal changes in kleptoparasitic prey competition as familiarity developed within groups of initially unfamiliar fish. Kleptoparasitism, in this study, took the form of contest competition, with aggressive interaction between the captor and challenger for prey items. Contest competition is distinct from both scramble and exploitation competition (Ward et al. forthcoming), although both of these can also be used alongside kleptoparasitic foraging strategies. We selected contest competition for the focus of our study as it is costly to the kleptoparasite in terms of lost foraging time and potentially heightened predation risk through lower vigilance and greater conspicuousness, costs that are balanced against the benefit of usurping another's foraging effort. Using three-spined stickleback, we created shoals of 5 fish and monitored foraging rates and related competitive behaviors in each individual over a 4-week period.

We looked at 2 different prey distributions, concentrated and dispersed, determined by the spatiotemporal presentation of prey. The concentrated distribution treatment considered prey that was presented simultaneously in a spatially focused patch. This is ecologically relevant because foraging effort is often mediated by fine-scale habitat structure (Webster and Hart 2004, 2006), and many models of optimum foraging assume such patchy prey distribution (Charnov 1976; Stephens and Krebs 1986). The dispersed distribution treatment considered prey that was presented sequentially and in differing locations. In nature, drifting prey can assume a discrete and

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unpredictable spatiotemporal distribution and is known to form a substantial proportion of the diet of many stream-dwelling fishes (Flecker 1992) such as those used in our study.

We predicted that levels of kleptoparasitism should be greater when prey distribution is spatially and temporally dispersed compared with when prey is concentrated because the value of competing for a given item is greater given that no other prey are present at that moment. We also predicted that levels of kleptoparasitism and the disparity in prey share between individuals should fall over time and that individuals should make adaptive decisions about which shoal mates they associate with based on their relative competitive abilities.

## METHODS

### Fish collection and housing

Two hundred subadult three-spined sticklebacks measuring 25–30 mm in standard length were collected from a 350-m-long reach of Stonton Brook, Leicestershire, UK, in September 2004 using dip nets. They were transported by road for 40 min to the laboratory, where they were divided equally between 16 chemically and visually isolated holding tanks (40 × 25 × 25 cm, water depth 20 cm) with a 1-cm-deep fine-sand substrate. Fish were fed frozen chironomid larvae once per day. The water temperature and light:dark regimens were held at 11 °C and 12:12 h, respectively, over the duration of the study. Fish were held under these conditions for 6 weeks.

### Experimental groups

Thirty-six experimental groups composed of 5 fish each were created, with individuals within each experimental group drawn from different holding tanks. Twelve groups were used in concentrated prey trials, 12 in dispersed prey trials, and 12 in a control experiment designed to control for prey delivery rate predictability in the dispersed prey trials. In each group, fish were size matched to within <1 mm standard length, and every individual was given an identification tag (described below). Experimental groups were each housed within their own chemically and visually isolated tanks (22 × 15 × 15 cm, 1 cm fine-sand substrate).

Fish were tested in foraging trials on every fourth day over a 28-day period as described below. On the days in which the fish were not tested, they were fed frozen chironomid larvae once per day. These were provided in excess and were distributed evenly within the tank. This ensured that all fish were able to feed to satiation on the days that they were not tested because we had predicted that differences in foraging ability would result in different levels of prey intake during trials. If prey were limited over the course of the whole study (rather than only on the days of testing), then we might expect to see differences in nutritional status between individuals leading to differences in foraging and competitive motivation that could affect our results. This method of feeding was used in both the concentrated and dispersed prey trials. Providing excess prey and conducting tests at 4-day intervals thus ensured that hunger levels were standardized between trials.

### Tagging procedure

In order to be able to recognize individuals within experimental groups, we gave each fish an identification tag. We used fluorescing Visible Implant Elastomer tags, a purpose-designed product manufactured by Northwest Marine Technology Inc. (Shaw Island, WA). Fish were first cooled in 6 °C water for

several minutes. This was performed in place of anesthesia, which can cause high levels of stress and mortality in such small fish (MW Webster, personal observation). A tag measuring approximately 3 × 0.4 mm was implanted into the dorsal surface of each fish using a 0.4-mm-diameter needle. Tags were positioned in front of, alongside, or behind the first dorsal spine, and yellow or green tags were used, producing a unique mark for each group member. Immediately after tagging, fish were transferred to aerated 11 °C water to recover. No fish died following this procedure. The tissues of the dorsal musculature were sufficiently transparent for the tags to be visible when fish were viewed side on, and all fish were seen to retain their tags over the duration of the study.

### Competition for dispersed prey: experimental arena

Trials took place in an experimental tank (40 × 25 × 25 cm, water depth 20 cm, 1-cm-deep fine-sand substrate), the sides and rear of which were nontransparent, to minimize outside disturbance. Observations were made via a vision slit in an opaque screen to remove observer effects. One side of the tank contained a row of 5 equally spaced 5-mm holes at the waterline. These served as prey introduction points, through which prey items could be introduced over the course of a trial via a 5-cm<sup>3</sup> syringe. Twenty-five 5-mm-long sections of chironomid larvae were used as prey. These were introduced sequentially, as described below. Fish of the size used in this study have been seen to consume up to 10 5-mm chironomid sections within 5 min (MM Webster, unpublished data), so competition for prey should be expected to persist even when an individual has consumed its expected share of 5 prey items.

### Competition for dispersed prey: experimental procedure

Food was withheld for 18 h before the trial began. Experimental groups were transferred from their respective tank to the holding unit, where they were allowed to acclimatize for a settling period of 5 min before the holding unit was removed and the trial began. Individual prey items were added through the prey introduction points, and 10 s were allowed to elapse between the ingestion of one prey item before the introduction of the next. Prey was introduced through a different point each time, in a predetermined random order. We recorded the number of prey items consumed by each individual and the number of contested prey items. Tests were repeated every fourth day for 28 days after experimental group formation.

### Competition for dispersed prey: control for prey delivery rate predictability

A fall in the contest rate for prey over time in the dispersed prey experimental series could be attributed either to changes in behavior as a function of the time the shoal had spent together or to learning of the prey delivery rate by test fish. That is, if over time fish were to learn that multiple prey would be presented over the course of the trial, then the value of competing for singular items may be diminished. In order to separate these effects, we conducted a control experiment in which 12 groups of 5 fish were housed under the same conditions as those in the dispersed prey competition experiment but were not tested until day 28, the final day of testing. If the contest rate in these groups was not significantly lower than that seen on day 4, the first day of testing in the dispersed prey competition groups, we could not rule out experience of the prey delivery rate as a causal factor of any fall in the contest rate for prey over time in the distributed prey competition experiment. We used the same apparatus and procedure as described above, with fish in this control experiment being

deprived of food for 18 h as they were in the dispersed prey competition experiments every fourth day, the exception being that testing was only conducted on day 28 rather than on every fourth day. We recorded the number of prey items eaten by each individual and the number of contests that occurred.

#### Competition for concentrated prey: experimental arena

Trials took place in an experimental tank (40 × 25 × 25 cm, water depth 20 cm, 1-cm-deep fine-sand substrate) with non-transparent side and rear walls. Observations were made via a vision slit in an opaque screen. Twenty-five 5-mm-long sections of dead chironomid larvae were distributed equally within a 12-cm-square, 1-cm-tall colorless Perspex dish set into the substrate. The dish also contained substrate material and was situated centrally on the bottom at one end of the tank. Prey items were immobile and were placed on the surface of the substrate in the dish. At the opposite end of the observation tank, 21 cm from the prey patch, a holding unit was situated. This consisted of a 7-cm-square, 22-cm-tall tower constructed from perforated colorless Perspex. This was used to hold experimental groups prior to testing, allowing them to acclimate, and facilitated visual and chemical assessment of the experimental arena.

#### Competition for concentrated prey: experimental procedure

Test fish were deprived of food for 18 h prior to the commencement of trials in order to increase foraging motivation. Experimental groups were transferred from their respective tank to the holding unit, where they were allowed to acclimatize for a settling period of 5 min. After the settling period, the holding tower was removed and the fish released into the arena. Fish were allowed to explore the arena and the trial began when a fish detected and engaged the first prey item. Trials ran for 5 min or until all prey had been consumed, whichever occurred first, and we recorded the number of prey items eaten by each individual and the number of contests that occurred. Trials were repeated every fourth day for 28 days after experimental group formation.

#### Kleptoparasitic prey contests

Kleptoparasitic prey contests occurred when an individual attempted to obtain a prey item from the jaws of the fish that had originally captured it. This behavior had 2 components, the pursuit of the initial captor by the challenger, followed by the seizure of the prey by the challenger, resulting in either the retention and ingestion of the prey by the captor or it being yielded to the challenger. The prey items used in this study were of sufficient size to require a period of handling before ingestion, thus providing the opportunity for kleptoparasitism to occur.

#### Relative competitive ability and association preference

At the end of the experimental period, 3 days after the final foraging trial and 31 days after group formation, we sought to determine whether individuals could identify shoal mates with respect to their relative competitive ability and whether they displayed association preferences based on this. Within each experimental group, for both prey distribution treatments, we determined the mean proportional prey share consumed by each individual over the whole study period. Based on prey share rankings, we found that within each group 2 individuals consumed substantially more prey than did the other 3 group members on average (see Results). We randomly selected one of these 3 fish as a focal fish in each group. This individual was then presented with a standard binary

choice between shoaling with either the 2 fish that obtained higher prey shares than it did or the 2 individuals with which it shared a similar amount of prey over the course of the study (Metcalf and Thomson 1995).

Binary choice experiments were conducted in a 39-cm × 17-cm × 18-cm-deep, 15-cm water depth, binary choice arena with a 1-cm-deep fine-sand substrate. At either end of the arena was a 6-cm-wide stimulus compartment in which the stimulus fish were housed. The focal fish was held in a 7-cm × 7-cm × 22-cm-tall holding tower prior to the commencement of the trial. The walls of the holding tower and the stimulus compartments were constructed from colorless perforated Perspex, allowing visual and chemical exchanges to occur. We conducted trials in the absence of prey as we sought to determine whether the focal individual displayed an associated preference based on condition-independent individual recognition, rather than through the use of overt cues from the stimulus fish such as prey-handling ability or aggressive behavior. Focal fish were hunger motivated through 18 h of food deprivation prior to each trial. After a 5-min settling period, the tower was raised, the focal fish released, and the trial commenced. Each trial ran for 3 min, and we recorded the proportion of time the focal fish spent within 5 cm of either stimulus group compartment.

#### Statistical analyses

Nonnormality in the distribution of our data precluded the use of parametric statistics, so we used the Friedman test, a non-parametric repeated measures analysis, and performed post hoc analyses using equal groups paired comparisons as described by Langley (1979). This test was used to compare differences in the coefficient of variance of prey share and contest rates for prey between days of testing within the 2 prey distribution treatments.

We calculated the coefficient of variance of prey share for each group on each day. We compared these between days, as described above. If the coefficient of variance were to increase over days of testing, this would indicate that prey share was becoming less equal within groups. Conversely, if it decreased, this would imply that prey share was becoming more equal. The mean prey share of each individual in each group over the whole study period was determined. We calculated the coefficient of variance of mean prey share for each group and compared this with a null expected value of zero using Wilcoxon signed-rank tests. A value of zero would be obtained if prey share were equal within groups because the standard deviation would also be zero.

Next, we determined the daily contest rate by dividing the number of contested prey items within each group by the total number consumed on each day of testing. We compared differences in overall contest rates for prey within days of testing between prey distribution treatments and between the dispersed prey treatment and the control experiment using Mann–Whitney *U* tests.

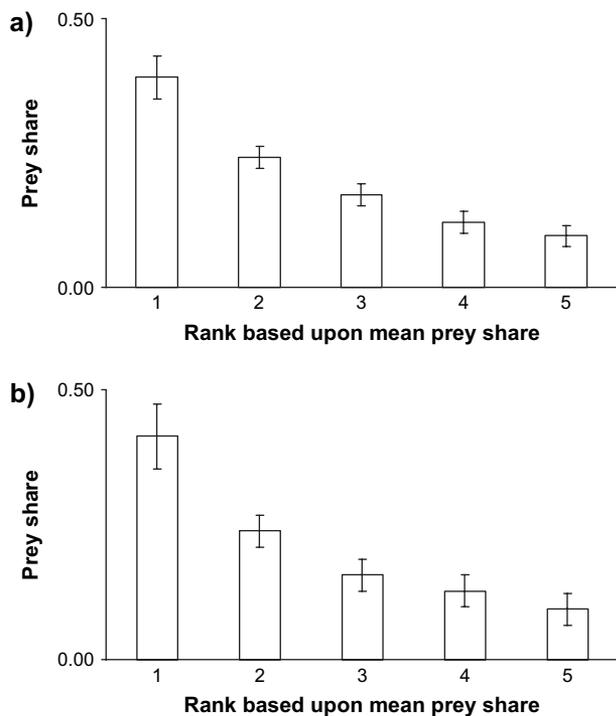
Finally, we calculated the shoaling preferences of lower ranked fish for better or similar-ranked individuals by converting the amount of time allocated to each stimulus shoal to a proportion of the total time spent shoaling, subtracting one from the other, and comparing this with a null expected value of zero using Wilcoxon signed-rank tests.

## RESULTS

### Prey resource share

#### *Dispersed prey*

The mean share of prey consumed by each individual over the duration of the study was not equal (Wilcoxon signed-rank test

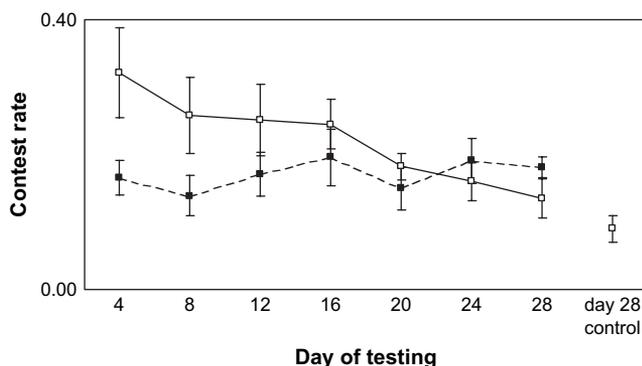


**Figure 1** Differences in mean proportional prey share ( $\pm$  standard error) between highest and lowest prey consumers in dispersed prey (graph a) and concentrated prey (graph b) trials over the duration of the study period.

comparing the coefficient of variance of mean prey share with a null expected value of zero:  $Z = -3.590$ ,  $P = 0.001$ , Figure 1a). A Friedman test of the coefficient of variance of prey share between days of testing revealed no changes in prey share within groups over time ( $\chi^2_{(1,6)} = 4.224$ ,  $n = 12$ ,  $P = 0.646$ ).

#### Concentrated prey

The mean share of prey consumed by each individual over the duration of the study was also unequal in the concentrated prey trials, both for mean prey share (Wilcoxon signed-rank test:  $Z = -3.061$ ,  $P = 0.002$ , Figure 1b). These prey



**Figure 2** The mean contest rate ( $\pm$  standard error), the number of instances of kleptoparasitism per prey item consumed, decreased significantly over time in dispersed prey trials (open square, solid line) but not in concentrated prey trials (filled square, broken line). A control experiment on day 28 in the dispersed prey trials revealed this to be a function of the time that fish spent together rather than a response to the experimental procedure.

share patterns did not change over time (Friedman test:  $\chi^2_{(1,6)} = 6.072$ ,  $n = 12$ ,  $P = 0.415$ ).

#### Contest rate for prey

##### Dispersed prey

The prey contest rate decreased significantly over the 28-day study period (Friedman test:  $\chi^2_{(1,6)} = 14.706$ ,  $n = 12$ ,  $P = 0.023$ , Figure 2), with post hoc analyses revealing that it was significantly lower on day 28 than on days 4, 8, and 12 (equal groups paired comparisons:  $P = 0.010$ ,  $P = 0.050$ ,  $P = 0.050$ , respectively).

##### Control for learnt prey predictability

The contest rate seen on day 28 in the control experiment was significantly lower than that seen on day 4 in the drift competition experiment (Mann-Whitney  $U$  test:  $Z_{(1,11)} = -3.376$ ,  $P < 0.001$ ) but not significantly different to that seen on day 28 in the drift competition experiment (Mann-Whitney  $U$  test:  $Z_{(1,11)} = -0.072$ ,  $P = 0.467$ ).

##### Concentrated prey

The prey contest rate did not differ significantly between days of testing in trials where fish foraged for concentrated prey items (Friedman test:  $\chi^2_{(1,6)} = 5.245$ ,  $n = 12$ ,  $P = 0.513$ , Figure 2).

#### Differences in contest rate between dispersed and concentrated prey trials

The contest rate on day 4 was significantly higher in the dispersed prey trials than in the concentrated prey trials (Mann-Whitney  $U$  test:  $Z_{(1,11)} = -2.288$ ,  $P = 0.022$ ). Thereafter, contest rate was not seen to differ between treatments (Mann-Whitney  $U$  tests—day 8:  $Z_{(1,11)} = -1.450$ ,  $P = 0.160$ ; day 12:  $Z_{(1,11)} = 1.040$ ,  $P = 0.298$ ; day 16:  $Z_{(1,11)} = -0.579$ ,  $P = 0.563$ ; day 20:  $Z_{(1,11)} = -1.265$ ,  $P = 0.172$ ; day 24:  $Z_{(1,11)} = -0.752$ ,  $P = 0.452$ ; days 8–28:  $Z_{(1,11)} = -1.082$ ,  $P = 0.139$ , Figure 2).

#### Relative competitive ability and association preference

Fish that were given a choice between shoaling with 2 shoal mates that had consistently consumed more prey than they had during experimental trials and 2 that had consumed a similar amount to them showed no shoaling preference for either. This was the case both for fish from groups where prey had been dispersed during trials (Wilcoxon signed-rank test:  $Z = -0.786$ ,  $n = 12$ ,  $P = 0.432$ ) and when it had been concentrated during trials (Wilcoxon signed-rank test:  $Z = -1.060$ ,  $n = 12$ ,  $P = 0.289$ ).

#### DISCUSSION

Decreasing rates of kleptoparasitic prey competition were thought to be a benefit of associating and foraging with familiar individuals, but this study reveals that changes in contest rate as a function of developing familiarity are determined by prey distribution. The rate of kleptoparasitic prey contests in dispersed prey trials declined as the experimental series progressed, but this was not the case in the concentrated prey trials where the contest rate remained low and stable over time. A control experiment revealed the fall in contest rates in the dispersed prey trials to be a function of the time that fish spent together, rather than a response to exposure to the experimental protocol. Individual prey intake within groups was not equal, and disparity in prey share did not change over the course of the study, even in dispersed prey trials where the contest rate was seen to decrease.

Prey contest rates were initially greater when prey was spatially and temporally dispersed compared with when it was concentrated. This is unsurprising because the benefits of kleptoparasitism and aggressive prey competition are predicted to increase within groups of foragers as rates of prey detection fall (Amat and Obeso 1991; Sirot 2000; Broom and Ruxton 2003). Furthermore, though foragers often obtain prey both by searching for it themselves and by observing other foragers in order to steal their captures (Ha RR and Ha JC 2003), producer–scrounger models assume that they cannot engage in both types of behavior simultaneously (Barnard and Sibly 1981; Vickery et al. 1991, and empirical work by Mottley and Giraldeau 2000, but see Smith et al. 2002). Under such circumstances, where conventional foraging and kleptoparasitism are simultaneously incompatible, the overall prey detection rate of a group of a given size will fall as the proportion of speculative kleptoparasites increases (Coolen 2002). Consequently, the prey returns of kleptoparasites will also diminish. As such, the contest rate for prey should remain relatively low and relatively constant when food resources are spatially and temporally concentrated, though this is likely to be affected by prey patch depletion, something we did not examine in this study. Conversely, when the prey is spatially and temporally dispersed, prey detection rates at a given point in time will be lower, increasing the relative value of competing for singular prey items. Additionally, it is conceivable that foragers rely on social information to a greater extent than when prey is more predictable and may therefore switch more frequently between searching the prey patch and observing conspecifics, so increasing the opportunity to detect and kleptoparasitize their prey captures (Rafacz and Templeton 2003). Again, this is something that we did not explicitly test in this study, and further research in this area could be useful.

The stable contest rate level seen in the concentrated prey trials and attained over time in the dispersed prey trials may represent a food return–predation risk trade-off baseline. The fall over time in the dispersed prey trials may be attributed to the development of familiarity between individuals, and previous studies have demonstrated lower levels of aggressive interaction within groups that are composed of familiar individuals (Höjesjö et al. 1998; Utne-Palm and Hart 2000; Seppa et al. 2001). Competition is costly, using time that could otherwise be invested engaging in other behaviors. It has also been shown to increase the risk of predation to the individuals taking part, both when competing for prey (Jakobsson et al. 1995; Slotow and Paxinos 1997) and, for example, during mating opportunities (Candolin 1997; Kelly and Godin 2001). Familiarity promotes greater rates of foraging and social learning (Laland and Williams 1997; Lachlan et al. 1998; Swaney et al. 2001), and as familiarity develops within a group, this may outweigh the benefits to be gained from kleptoparasitizing others, leading to a decrease in aggressive interaction.

Our study revealed no evidence of individual recognition through shoaling preference of intermediately ranked prey consumers. Metcalfe and Thomson (1995) previously found that intermediately ranked European minnows (*Phoxinus phoxinus*) displayed a preference for shoaling with poorer competitors, presumably because it afforded the choosing individual a potentially greater prey share. Interestingly, it has recently been shown that fish can recognize others using self-referent matching of chemical cues pertaining to recent prey and habitat use (Ward, Hart, and Krause 2004; Ward et al. 2005), whereas hierarchies can develop and persist through winner and loser effects, which allow individuals to assess their chances of winning or losing contests based respectively on their past victories or losses (Barnard and Burk 1979; Hollis et al. 1995). Neither of these mechanisms assumes the capacity of a group member to recognize conspecifics individually.

In any case, research has demonstrated that hierarchies based on dominance relating to individual likelihood to initiate, escalate, or win agonistic encounters do not always correlate with resource share (Soma and Hasegawa 2004).

The inequality in prey share can be explained by factors such as phenotypic variation in foraging behavior, individual physiological state, and predation risk versus prey return trade-offs. For example, individuals consuming more of a prey resource may simply be consistently better foragers, perhaps because they are consistently faster swimmers who therefore prevail in scramble competition, because they are more vigilant for or more efficient at handling prey, or because they are driven to forage at a greater rate due to higher metabolic demands (McCarthy 2001). Related to this, they may have greater innate tendencies to take risks when foraging. Some individuals are known to consistently engage in such behavior to a greater extent than others across a range of different contexts (Bell and Stamps 2004; Ward, Thomas, et al. 2004; Bell 2005). Further to this, more danger prone or bold individuals were seen by Ward, Thomas, et al. (2004) to be better foraging competitors than their danger averse or shy opponents. The bold–shy axis phenomenon could account for the prevalence of both of these behavioral phenotypes in nature because the seemingly disadvantaged shy individuals are thought to trade off a greater share of a contested resource in favor of lower mortality through reduced predation risk (Huntingford 1976).

Familiarity reduces kleptoparasitic prey competition under some foraging modes but not under others. In order to build on this finding, we need to study these effects in groups of free-ranging animals in the field, where environmental perturbations and dynamic group composition contribute further levels of complexity. It has been suggested that environmental heterogeneity serves to limit the formation of prey share hierarchies in the field (Slovan et al. 2001, 2002), whereas individual variation in hunger, a constant in this study, also influences the motivation of individual animals to forage and aggressively compete for prey (Hart and Gill 1992; Gill and Hart 1994, 1998). Empirical field studies designed to address these issues should eventually allow us to better model and predict resource share inequality, associated social interactions, and their interplay with environmental pressures in wild populations.

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