

## Goldfish in a tank: the effect of substrate on foraging behaviour in aquarium fish

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### Abstract

The welfare of captive animals is influenced by their ability to express natural behaviours. Foraging is one behaviour that may be particularly important in this respect; many species will continue to work for food even when it is freely available. The role of substrate, and in particular particle size, on the foraging behaviour of goldfish (*Carassius auratus*) was examined through three repeated measures experiments. In the first, tanks were set up with five uniform substrates: plastic grid, coarse sand, fine gravel, pebbles, and cobbles. In the second, fish were provided with a choice between coarse sand and fine gravel, fine gravel and pebbles, and pebbles and cobbles. In the third, they were provided with two choices between coarse sand and cobbles, one where the sand contained more food and one where the cobbles did. Our results show that particle size significantly affected the amount of time goldfish spent foraging, and that goldfish exhibited foraging behaviour even in the absence of a substrate they can manipulate. Goldfish foraged longest when provided with coarse sand. Fish foraged significantly longer over smaller particle size substrates when given a choice, although they did not distinguish between the two finest substrates, coarse sand and gravel. Increases in total time spent foraging were achieved through more, rather than longer, bouts. Food density did not significantly alter preference for smaller particle substrates. In general, coarse sand (1.5 mm) was found to be the most appropriate substrate in terms of facilitating natural foraging behaviours. These findings are discussed with respect to the welfare and husbandry of goldfish and aquarium fish in general.

**Keywords:** animal welfare, aquarium fish, foraging, goldfish, husbandry, substrate

### Introduction

The majority of animal welfare standards and legislation pertain to mammals and birds. The welfare of species that are perceived as being either less valuable or more dissimilar to us, such as fish and invertebrates, has historically received disproportionately little attention (Broom 2007). There is a growing interest in the welfare of fish which are kept in ever-greater numbers for aquaculture, research and as pets (eg Lund *et al* 2007; Algers *et al* 2009). Increasingly, fish are being recognised as being on a par with mammals and birds in aspects of their behavioural abilities and responses; there is mounting evidence that they have the capacity to feel pain and to suffer (for reviews, see Huntingford *et al* 2006; Broom 2007; Volpato *et al* 2007). Whilst Rose (2007) cautions against anthropomorphism in considering fish welfare, arguing against their capacity to feel pain as we know it or to experience boredom and other emotions, Volpato *et al* (2007) suggest a precautionary ethical position that, in the absence of conclusive contrary evidence, assumes fish to be sentient and thus capable of suffering.

The need for a greater understanding of the behavioural needs of fish has been highlighted by Huntingford *et al* (2006). Fish have been shown to be capable of complex feats of learning

in a wide range of contexts (eg Brown & Laland 2002; Brown *et al* 2003); from this, we may expect them to suffer in much the same way as other vertebrates if kept in barren or otherwise unstimulating environments (Huntingford 2004).

Volpato *et al* (2007) argue that physiological standards of assessing fish welfare are problematic and propose a preference-based definition. Preference tests, where an animal is given a choice of two or more resources, can provide a useful tool for gathering information on their priorities (Dawkins 1998, 2004). They have been used successfully with fish (eg Anthouard *et al* 1994), and may provide means to identify conditions that may promote better welfare (Huntingford *et al* 2006). They can be used to probe many aspects of fish husbandry, such as stocking density, water depth and flow rates, and lighting and feeding regimes (Volpato *et al* 2007). However, caution should be used in interpreting the results of such tests as animals may not always choose what is best for them. Preferences are only expressed between choices presented, and the most preferred option may be one that is not provided (Brydges & Braithwaite 2008). Here, we use preference tests to examine the effect of substrate particle size on foraging behaviour in goldfish (*Carassius auratus*).

### Substrates

Substrate preferences have been reported for a variety of laboratory and farm animals (Arnold & Estep 1994; van de Weerd *et al* 1996; Beattie *et al* 1998; Sørensen *et al* 2004; Waiblinger & Köning 2004). Substrate may also influence behaviour and physiology. Some behaviours may be performed more frequently or exclusively in conjunction with particular substrates (Arnold & Estep 1994; Sanotra 1995; Beattie *et al* 1998; van de Weerd *et al* 1996; Sørensen *et al* 2004). Animals may also differ in their physiological responses depending upon the substrates on which they are kept (Krohn *et al* 2003; de Leeuw & Ekkel 2004).

Galhardo *et al*'s (2008) study of African cichlids (*Oreochromis mossambicus*) is one of few to examine the importance of substrate to aquarium-housed fish. They find that provision of substrate allows the expression of a fuller range of behaviours, and that when substrate is not provided fish may perform vacuum activities suggestive that behavioural needs are not being met. This is in line with the idea that more complex or enriched environments can accommodate or promote species-typical behaviours and reduce the incidence of abnormal or undesirable behaviours (Shepherdson *et al* 1998; Sørensen *et al* 2004) with a concomitant increase in physical and mental well-being (Gonyou 1994; Kreger *et al* 1998; Baumans 2005).

### Captive husbandry and welfare

Animal husbandry practices that accommodate natural behaviours have been developed over the last 40 years (Gonyou 1994), and the principle is now established in legislation in the UK and elsewhere. The fourth of the Farm Animal Welfare Committee's (FAWC 1993) 'Five Freedoms' states that animals should be 'free to express normal behaviour' by providing sufficient space, proper facilities, and company of the animal's own kind. Knowledge of behaviour in the wild, or at least semi-natural conditions, can be used to inform husbandry practices by showing which otherwise unobserved behaviours should be accommodated.

Boredom and associated stereotypies may be reduced, and activity levels and species-typical behaviours increased through environmental enrichment and the provision of a substrate that can be manipulated (eg Chamove *et al* 1982; Fraser *et al* 1991; Baker 1997; Swaisgood *et al* 2001; de Leeuw & Ekkel 2004). Straw and other substrates have been provided to pigs (*Sus scrofa*) to allow natural rooting behaviour, with positive results for both pig behaviour and physiology (de Jong *et al* 1998; de Leeuw & Ekkel 2004). The significance of foraging behaviour to animals is also indicated by the finding that often most successful environmental enrichment protocols are those that stimulate foraging (Crockett 1998). The reason for this may be not just that food itself is intrinsically motivating but that species may possess an intrinsic behavioural need to forage.

### Behavioural needs

Behavioural needs are behaviours an animal has a strong motivation to pursue (Dawkins 1983, 1988; Dellmeier

1989). Keeping animals in environments where they are incapable of expressing such key behaviours may cause psychological distress, not least because the motivation to perform such behaviours may increase when deprived of the opportunity to do so (eg Dellmeier *et al* 1985; Jensen 1993). The widespread phenomenon of contra-free-loading (Neuringer 1969), where animals work for food when it is also freely available without any effort, has been explained by the idea of specific needs associated with both the end-point and the appetitive phase of a goal-directed activity. Animals may be reinforced by the act of foraging in the same way as they are by its end-point, the acquisition of food. There is some evidence to suggest that barren environments may increase the likelihood of contra-free-loading (see Huntingford *et al* 2006). According to this ethological-needs model, if husbandry practices do not permit the expression of these behaviours, welfare may be compromised which may result in the expression of stereotypies (Hughes & Duncan 1988; Swaisgood *et al* 2001). Barren environments may also result in locomotor stereotypies; natural appetitive foraging being thwarted by lack of opportunity and the drive expressing itself through such stereotypies (Mason 1993). The prevalence of oral stereotypies in both domestic and exotic captive ungulates (eg Appleby & Lawrence 1987; Bashaw *et al* 2001; de Leeuw & Ekkel 2004) may be due to a failure of rapidly consumed captive diets to fulfil a behavioural need to forage (Bashaw *et al* 2001).

### Goldfish

Ornamental fish are the third most popular domestic pet after cats (*Felis catus*) and dogs (*Canis familiaris*) (Iwama 2007); whilst not kept in as many households as dogs and cats, the number of fish kept (excluding pond fish) is far greater (Pet Food Manufacturers' Association 2011). Goldfish are descendants of the Prussian or gibel carp (*Carassius gibelio*) found throughout Europe, Siberia and the Far East (Vasil'eva & Vasil'ev 2000; Komiyama *et al* 2009). Their domestication began in China around 1000 AD (Komiyama *et al* 2009), and today they are perhaps the most familiar aquarium fish. Like other carp, goldfish are group-foraging, benthic fish that root for food in the benthos close to vegetation in shallow water (Magurran 1984; Warburton 1990; Stenberg & Persson 2005). They are notable for their ability to survive large temperature swings, a wide pH range, high turbidity, hypoxia, and heavy metal and organochlorine contamination (Szczerbowski 2002) and have a high tolerance to low salinity (Luz *et al* 2008), however, like most fish, little is known about their welfare requirements. As benthic foragers, goldfish feed by taking particles of substrate into their buccal cavity and removing miobenthic prey (Hinkle-Conn *et al* 1998), as such they may be expected to have a behavioural need to forage through substrate manipulation. The expression of foraging behaviour may be influenced by the particle size of the substrate. Goldfish may have an innate preference for foraging over certain size particles, since particle size affects the miobenthic fauna found within it (eg Ferber & Lawrence 1976; Nel *et al* 1999, 2001), or their foraging

efforts may be influenced by food availability directly (eg Pitcher & Magurran 1983; Lester 1984; Warburton 1990; Stenberg & Persson 2005). This study examines whether in goldfish a behavioural need for foraging exists in the absence of food and the roles of substrate particle size and food availability in facilitating foraging behaviour in this commonly kept species.

## Materials and methods

### Animals and housing

Subjects were 22 comet goldfish, 6–12 cm fork length. For the experiments they were housed singly in experimental tanks, 45 × 30 × 38 cm (length × width × depth), set up with under-substrate filtration powered by air stone uplifts in both rear corners of the tank. The substrate covered the plastic filtration grid to a depth of approximately 3 cm. Water temperature in the unheated tanks matched that of the surrounding room. Tanks were visually isolated from one another to prevent the fish from influencing one another's behaviour. A week before fish were introduced, tanks were filled with tap water treated with conditioner (Tetra AquaSafe®, Tetra GmbH, Germany) to neutralise chlorine. Fish were introduced to the tank a minimum of 24 h before being observed. After observations, goldfish were returned to their communal stock tanks.

### Experimental protocol

For each of the experiments the fish used were observed in each condition. The duration of all foraging bouts for each fish was recorded during two 30-min periods, one in the morning (0900–1200h) and one in the afternoon (1300–1600h). Foraging was defined as 'searching for, selecting and processing food particles from the aquaria substratum, with the body of the fish within four centimetres of the substratum, and the head lowered to 60° or less'. A foraging bout commenced when the fish's mouthparts made contact with the substrate and ceased when the head was raised above 60°. Observations were made 1 m from each tank and commenced 15 min after the observer had positioned themselves to minimise disturbance effects.

Experiment 1 comprised of five aquarium conditions; four tanks each with one of four substrates, plus a fifth tank in which the filtration grid was left bare. The substrates, following the Wentworth scale, were very coarse sand (< 1.5 mm), granules (hereafter, 'fine gravel') (1.5–3 mm), pebbles (10–12 mm) and cobbles (65 mm+). Experiment 2 had three aquarium conditions: in each condition both halves of the tank floor were covered with a different substrate. The three conditions were: coarse sand and fine gravel; fine gravel and pebbles; and pebbles and cobbles. The two conditions in Experiment 3 consisted of two choices between coarse sand and cobbles; one where the sand contained a high density of food and the cobbles a low density and *vice versa*. The low and high food densities were achieved by seeding the substrates with either four or twelve grains of sinking food (TetraFin Gold®, Tetra GmbH, Germany) prior to observation. Two sets of goldfish

were used, ten individuals were observed in Experiment 1 and twelve in Experiments 2 and 3. Fish in Experiment 1 were between 6–8 cm fork length, those in Experiments 2 and 3 comprised six fish of 6–8 cm and six fish 10–12 cm fork length to allow the effect of fish size on foraging to be examined. Fish in Experiments 1 and 2 were fed at 0830h, at least 30 min before the start of observations, those in Experiment 3 were fed at 1600h in addition to the food available as part of the conditions in the experiment. The experimental protocol was approved by the ethics committee at Anglia Ruskin University, UK, prior to commencement of the study.

### Statistical analysis

For each fish, morning and afternoon observations were combined to give 60 min of observation per condition in each of the experiments. The total time each fish spent foraging in each condition was calculated from the raw data. Mean foraging bout length and number of bouts were also calculated per condition for each fish. All statistical modelling was performed using R version 2.10.0 (R Development Core Team 2009). Significance was taken at the  $\alpha = 0.05$  level for all tests.

Generalised linear mixed modelling using the lmer function from the R package lme4 (Bates & Maechler 2009) was used to examine the effect of substrate (all experiments), fish size (Experiments 2 and 3) and food availability (Experiment 3) on the three response variables: total time foraging, mean foraging bout length and number of bouts. Poisson models were used to analyse the number of foraging bouts. For total time foraging and mean bout length, a Gaussian (normal) error structure was defined and data were checked for normality using the Shapiro-Wilk test before modelling. The following corrections were applied to the data (to meet assumptions of normality): Experiment 1 total time cubed root, mean bout length square root; Experiment 2 total time fine gravel vs pebbles square root, total time pebbles vs cobbles cubed root, mean bout length fine gravel vs pebbles square root; Experiment 2 total time square root. In all models, as each fish was used in each condition, fish identity was used as a random effect.

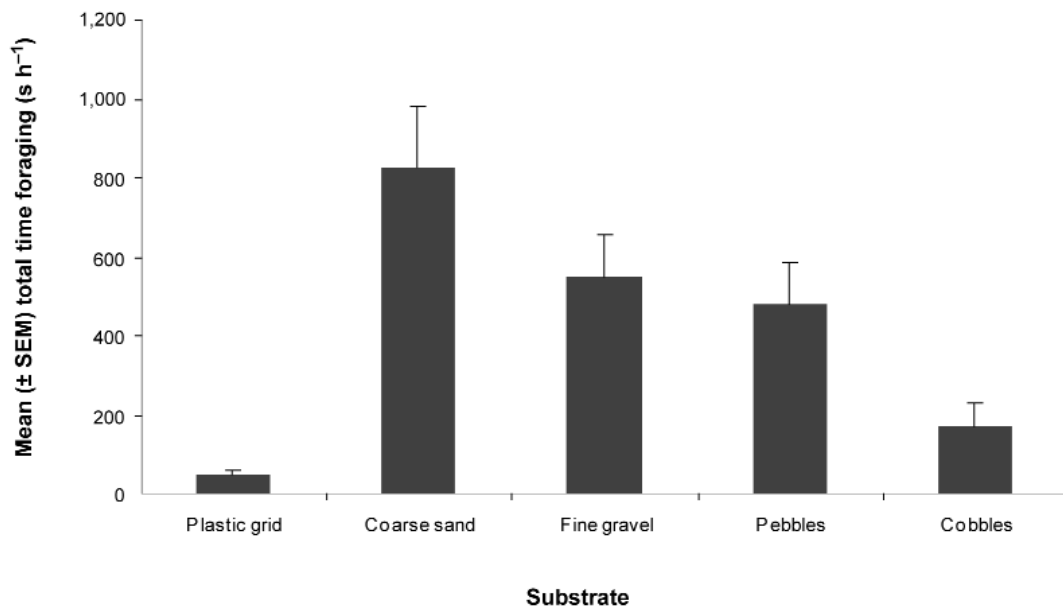
For Experiments 2 and 3, where there were two or more explanatory variables, initial models containing all variables were used to test for significant interaction terms. Step-wise simplification of the model was then performed by removing non-significant terms (Crawley 2007). Tests of deletion, using the ANOVA function with an *F*-test were used to compare sequential models to determine whether removal of terms was justified for Gaussian models and with a Chi-squared test for Poisson models.

## Results

### Experiment 1

When kept in tanks with a uniform substrate, the three response variables of the goldfish, the total time foraging (Figure 1), mean bout length and number of bouts, were influenced by the substrate over which the fish were housed

Figure 1



Mean ( $\pm$  SEM) total time goldfish spent foraging when housed over five different substrates (all comparisons  $P < 0.05$  except coarse sand vs fine gravel, fine gravel vs pebbles and cobbles vs plastic grid).

**Table 1** Summary of statistics from generalised linear mixed model comparisons of the total time spent foraging, number of bouts and mean bout length for goldfish housed over different substrates (between-tank comparisons).

| Substrates | Response variable                                              |        |         |         |                                                                    |         |         |         |                                                                      |        |         |         |
|------------|----------------------------------------------------------------|--------|---------|---------|--------------------------------------------------------------------|---------|---------|---------|----------------------------------------------------------------------|--------|---------|---------|
|            | Time spent foraging (n = 10 fish)<br>Gaussian distribution (t) |        |         |         | Number of foraging bouts (n = 10 fish)<br>Poisson distribution (Z) |         |         |         | Mean foraging bout length (n = 10 fish)<br>Gaussian distribution (t) |        |         |         |
|            | Sand                                                           | Gravel | Pebbles | Cobbles | Sand                                                               | Gravel  | Pebbles | Cobbles | Sand                                                                 | Gravel | Pebbles | Cobbles |
| Gravel     | -1.57                                                          |        |         |         | -5.55*                                                             |         |         |         | -1.29                                                                |        |         |         |
| Pebbles    | -2.44*                                                         | -0.87  |         |         | -7.59*                                                             | -2.09*  |         |         | -1.89                                                                | -0.60  |         |         |
| Cobbles    | -5.66*                                                         | 4.09*  | 3.23*   |         | -16.20*                                                            | -11.32* | -9.40*  |         | -5.04*                                                               | 3.75*  | 3.15*   |         |
| None       | -7.01*                                                         | -5.43* | -4.57*  | -1.34   | -18.93*                                                            | -14.52* | -12.75* | -383*   | -6.89*                                                               | -5.60* | -5.00*  | -1.85   |

\*  $P < 0.05$ .

(Table 1). Typically, they foraged for longer, in longer bouts and a greater number of bouts over smaller particle substrates.

### Experiment 2

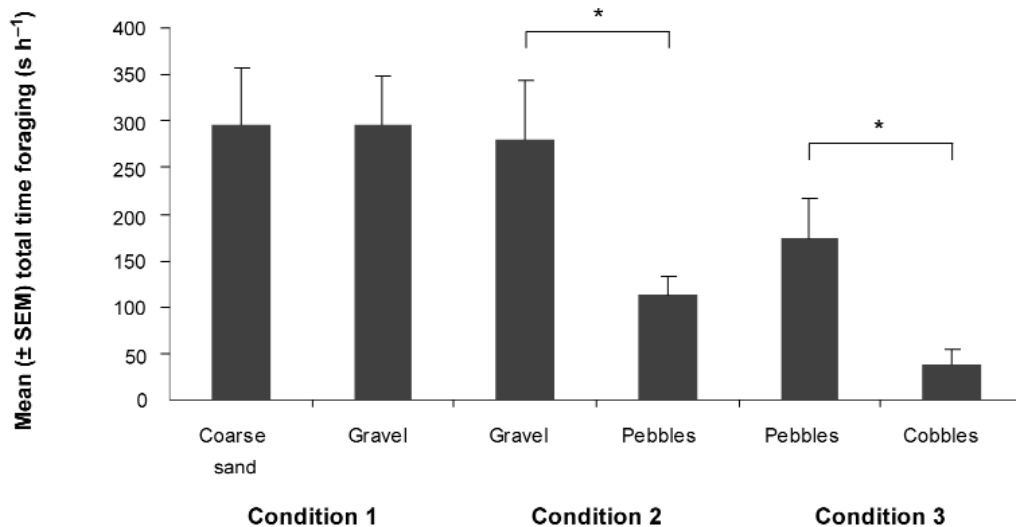
When kept in preference test tanks with half the floor covered with one substrate and half by the next particle size, goldfish foraged significantly longer (Figure 2) and with a significantly greater number of bouts over the smaller particle substrate when given a choice between fine gravel and pebbles and between pebbles and cobbles (Table 2). Mean bout length did not differ between conditions, nor were there significant differences between the fishes' response variables when kept over the two smallest particle substrates, sand and fine gravel. Fish size did not significantly affect any of the response variables in any of the

conditions. The interaction between fish size and particle size was only significant for total time foraging over fine gravel and pebbles; it was removed from the model for all other conditions.

### Experiment 3

When kept in preference tanks with half the floor covered with sand and half in cobbles, where one side was seeded with a high food density and the other a low food density, the time goldfish spent foraging (Figure 3) and the number of foraging bouts they engaged in were significantly greater over the smaller substrate (Table 3). Food and its interaction with substrate particle size were only significant for the number of bouts. The mean bout length was not significantly affected by substrate particle size, food density or their interaction.

Figure 2



Mean (± SEM) total time goldfish spent foraging when housed over three pairs of substrates. \*  $P < 0.05$ .

**Table 2** Summary of statistics from generalised linear mixed model comparisons of the total time spent foraging, number of bouts and mean bout length for goldfish housed in preference test tanks over two different substrates (within-tank comparisons). Non-significant interactions were removed from the model and the test rerun without them.

|                                      | Response variable                                              |                    |                     |                                                                    |                    |                     |                                                                      |                    |                     |
|--------------------------------------|----------------------------------------------------------------|--------------------|---------------------|--------------------------------------------------------------------|--------------------|---------------------|----------------------------------------------------------------------|--------------------|---------------------|
|                                      | Time spent foraging (n = 12 fish)<br>Gaussian distribution (t) |                    |                     | Number of foraging bouts (n = 12 fish)<br>Poisson distribution (Z) |                    |                     | Mean foraging bout length (n = 12 fish)<br>Gaussian distribution (t) |                    |                     |
|                                      | Sand/<br>Gravel                                                | Gravel/<br>Pebbles | Pebbles/<br>Cobbles | Sand/<br>Gravel                                                    | Gravel/<br>Pebbles | Pebbles/<br>Cobbles | Sand/<br>Gravel                                                      | Gravel/<br>Pebbles | Pebbles/<br>Cobbles |
| Substrate                            | -0.006                                                         | -4.108*            | 3.584*              | 1.878                                                              | -9.467*            | 13.778*             | -1.053                                                               | -2.054             | -1.856              |
| Size                                 | -0.178                                                         | -1.774             | -0.952              | -0.890                                                             | -0.853             | 0.818               | -1.604                                                               | -0.054             | 0.688               |
| Interaction<br>(substrate ×<br>size) |                                                                | 2.608*             |                     |                                                                    |                    |                     |                                                                      |                    |                     |

\*  $P < 0.05$ .

## Discussion

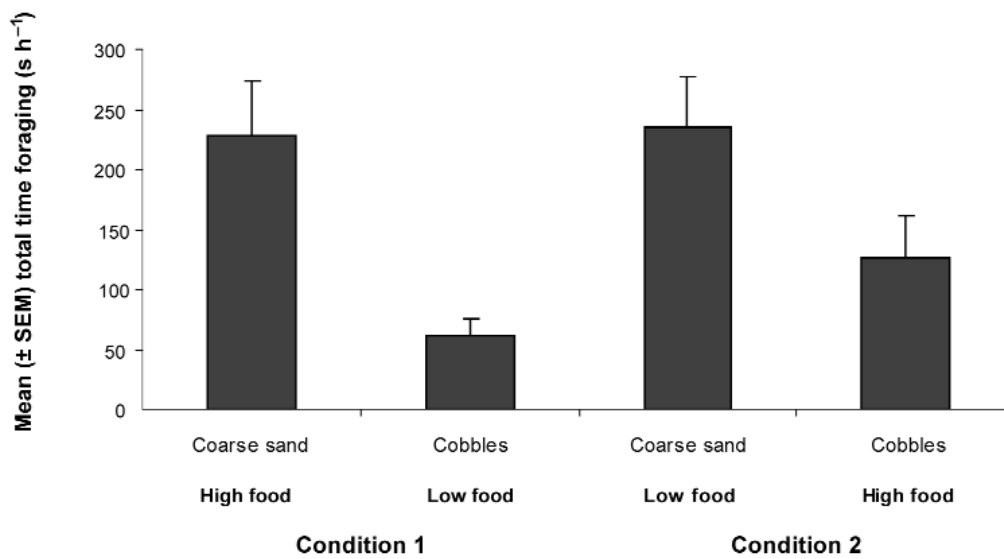
Foraging was observed in all three experiments and over all substrate types. The behaviour in fish has been described as sifting, whereby they bite the substrate and suck in food particles (Lester 1984) yet only in Experiment 3 was food provided on the substrate. The foraging observed in Experiments 1 and 2 suggests that the goldfish may have been fulfilling a behavioural need as only minimal amounts of leftover food was present in the substrates. Moreover, in Experiment 1 with no substrate over the plastic grid of the filter system, the fish would have been unable to reach any motes of food that had fallen to the tank floor, yet they continued to orientate to and mouth the grid. Since all fish were well fed prior to being observed, it is unlikely they had a nutritional need to search for food. In this situation, de Leeuw and Ekkel (2004) question whether the manipulation

of substrate should be termed foraging. Further, because at best only minimal amounts of food were able to be found, it is debatable as to whether the observed behaviour can be viewed as contra-free-loading since the fish were not being rewarded nutritionally for their efforts.

### Manipulation of substrate and behavioural needs

The ability of a substrate, or other objects, that can be manipulated to reduce stereotypies and increase species-typical behaviours is well documented in mammals and birds (eg Chamove *et al* 1982; Blokhuis & Arkes 1984; Kastelein & Wiepkema 1989; Fraser *et al* 1991; Baker 1997; Swaisgood *et al* 2001; de Leeuw & Ekkel 2004) however it is only now being explored in fish. That the goldfish in Experiment 1 foraged more when provided with suitable substrates is in line with Galhardo *et al*'s (2008)

Figure 3



Mean (± SEM) total time goldfish spent foraging when housed over two pairs of substrates containing differing densities of food.

**Table 3 Summary of statistics from generalised linear mixed model comparisons of the total time spent foraging, number of bouts and mean bout length for goldfish over two pairs of substrates containing differing densities of food (between-tank comparisons). Non-significant interactions were removed from the model and the test rerun without them.**

|                                   | Response variable                                              |                                                                    |                                                                      |
|-----------------------------------|----------------------------------------------------------------|--------------------------------------------------------------------|----------------------------------------------------------------------|
|                                   | Time spent foraging (n = 12 fish)<br>Gaussian distribution (t) | Number of foraging bouts (n = 12 fish)<br>Poisson distribution (Z) | Mean foraging bout length (n = 12 fish)<br>Gaussian distribution (t) |
| Substrate                         | -2.450*                                                        | -11.212*                                                           | 0.386                                                                |
| Food                              | 0.229                                                          | -2.618*                                                            | 1.576                                                                |
| Interaction<br>(substrate × food) | -1.385                                                         | -2.713*                                                            | -2.182                                                               |

\*  $P < 0.05$ .

finding that African cichlids expressed a fuller range of mainly reproductive behaviours and were more active when provided with a substrate they could manipulate for nest building. In the case of goldfish, the behaviours expressed are linked to foraging, presumably in much the same way as a pig's need to root is (Breland & Breland 1961; Nicol 1995; Beattie & O'Connell 2002). Key here is that the behaviours are expressed in the absence of nutritional reward, it is the act of rooting that seems to be rewarding for these species. This may not be true for all species. For example, although Pacific walrus (*Odobenus rosmarus divergens*) are benthic feeders like goldfish, they do not seem to have a behavioural need to root, and will only do so in the presence of food (Kastelein & Wiepkema 1989).

The behavioural and welfare implications of facilitating or thwarting a pig's need to root are well known (eg de Jong *et al* 1998; de Leeuw & Ekkel 2004). However, there is little consistency in the regard we show for the

animals affected by our actions (Iwama 2007); with current welfare legislation based more on the values we place on the species concerned than their capacities to suffer (Broom 2007). For example, as Webster (2001) notes, what may be accepted practice on an intensive pig farm, may be deemed as failure to provide adequate care in a boarding kennel. This gap is widened when species perceived as more dissimilar to us, such as fish and invertebrates, are considered. Whilst some argue against the capacity of fish to experience boredom and to suffer (Rose 2007), it may be prudent to adopt a precautionary ethical position in the absence of conclusive proof to the contrary that assumes they are sentient and thus might be able to suffer (Volpato *et al* 2007). Keeping benthic foraging fish, such as goldfish and other cyprinids, without a suitable substrate may cause psychological distress, not least because the motivation to perform such behaviours may increase when deprived of the opportunity to do so (eg Dellmeier *et al* 1985; Jensen 1993).

### Particle size

The results of all three experiments show that the highest levels of foraging were over the substrates with the smallest particles. This suggests that particle size is a critical releaser for rooting behaviour in goldfish as it is in pigs (Stolba & Wood-Gush 1984; Beattie *et al* 1998). Differences in foraging were achieved through altering the number of foraging bouts rather than their length. In contrast, one of the few comparable studies found no effect of substrate particle size on the time either rock crabs (*Cancer irroratus*) or sea stars (*Asterias vulgaris*) spent searching for sea scallop (*Placopecten magellanicus*) prey (Wong & Barbeau 2003). The difference between that and the present study may be due to the foraging methods used by the predators. Since goldfish feed by taking substrate particles into their buccal cavity and filtering out their prey (Hinkle-Conn *et al* 1998), particle size may be expected to play an important role in facilitating this behaviour. There is a maximum size that a goldfish can fit into its mouth or pick up. Cobbles were too large to be either moved or drawn into the mouth, but in comparison to a barren tank provided a more complex environment with clefts and spaces between adjacent cobbles where fish could try to forage for food. Pebbles, while again too large to be drawn into the fish's mouth, were small enough to be moved by the animal. These stimulated more foraging presumably because they could be manipulated to some degree. Fine gravel and coarse sand were both small enough to be drawn into the mouth. This characteristic may have made them more rewarding in terms of the appetitive phase of a behavioural-needs model, and thus most likely to elicit the behaviour. The preference for such substrates may also be linked to an innate preference since grain dimension affects the burrowing ability and distribution of many benthic invertebrates (Ferber & Lawrence 1976; Nel *et al* 1999, 2001). In their native rivers and lakes of East and Central Asia (Chen & Fang 1999), wild goldfish probably evolved to forage over silt, since typically only fast-flowing mountain streams have larger particle substrates. Thus, whilst a preference was shown for finer substrates, it may be that fine sand, a choice not offered, would provide the most naturalistic foraging substrate.

### Food density and other factors

Experiment 3 showed food density had little effect on the foraging when compared to substrate particle size. Since goldfish are capable of complex patterns of behaviour when selecting between food sources (Sánchez-Vásquez *et al* 1998), and are known to respond to patch profitability (eg Pitcher & Magurran 1983; Lester 1984; Warburton 1990; Stenberg & Persson 2005), this result illustrates the strength of the substrate effect on foraging. The failure of a higher food density to stimulate a greater level of foraging over a larger particle substrate refutes the potential for the findings of Experiments 1 and 2 to have been due simply to more food particles remaining in smaller grained substrates.

In the wild, goldfish are group foragers (Magurran 1984; Stenberg & Persson 2005), demonstrating a positive rela-

tionship between shoal size and the amount of time devoted to foraging (Pitcher & Magurran 1983). Further, social enhancement and inhibition have both been demonstrated in fish (Brown & Laland 2002). In light of this, future work should examine the role of substrate on foraging, and other behaviours, of socially housed goldfish. The relative effects of substrates finer than those used in the current study may be a useful area for exploration since they may be more akin to those that goldfish forage through in the wild. It is also possible that different substrates may be used for different behaviours, as has been reported for laboratory rats (*Rattus norvegicus*) (van de Weerd *et al* 1996). Ideally, captive husbandry should be informed by the behaviour of animals in their natural habitats, but obtaining such data for goldfish and others may prove somewhat challenging.

### Animal welfare implications

In summary, the foraging of aquarium-housed goldfish is strongly influenced by the particle size of the substrate within their tank. The occurrence of foraging-like behaviour in the absence of food suggests a behavioural need to express this appetitive-phase behaviour. As such, welfare may be lower in goldfish not provided with suitable substrates to facilitate this behaviour. Further work is needed to examine the effects of alternative husbandry practises on the behaviour and welfare of the many species of fish kept for aquaculture, research and as pets.

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