



RESEARCH PAPER

Experimental Predictions of The Functional Response of A Freshwater Fish

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Abstract

The functional response is the relationship between the feeding rate of an animal and its food density. It is reliant on two basic parameters; the volume searched for prey per unit time (searching rate) and the time taken to consume each prey item (handling time). As fish functional responses can be difficult to determine directly, it may be more feasible to measure their underlying behavioural parameters in controlled conditions and use these to predict the functional response. Here, we tested how accurately a Type II functional response model predicted the observed functional response of roach *Rutilus rutilus*, a visually foraging fish, and compared it with Type I functional response. Foraging experiments were performed by exposing fish in tank aquaria to a range of food densities, with their response captured using a two-camera videography system. This system was validated and was able to accurately measure fish behaviour in the aquaria, and enabled estimates of fish reaction distance, swimming speed (from which searching rate was calculated) and handling time to be measured. The parameterised Type II functional response model accurately predicted the observed functional response and was superior to the Type I model. These outputs suggest it will be possible to accurately measure behavioural parameters in other animal species and use these to predict the functional response in situations where it cannot be observed directly.

Introduction

Functional response models describe the relationship between the feeding rate of a forager and its prey density (Solomon 1949; Holling 1959) and are useful in describing the foraging performance of species (Baker et al. 2010). Functional responses are important ecologically as animals under resource restrictive conditions strive to maximise their energy intake, whilst minimising the costs associated with their searching and handling of prey (Stephens & Krebs 1986; Galarowicz & Wahl 2005; Oyugi et al. 2012a,b). Conversely, *ad libitum* resource conditions promote satisfying over optimal foraging behaviour (Myers 1983; Krebs & McCleery 1984; Stephens & Krebs 1986). Measuring the differential responses of animals to varying food availabilities also provides important

explanatory information underpinning the tendency and ability to optimise foraging behaviour, as well as their associated levels of condition, growth and, ultimately, fitness (Mittelbach 1981; Werner et al. 1983; Galarowicz & Wahl 2005). Functional responses also provide important insights into the dynamics of consumer–prey systems (Buckel & Stoner 2000; Nilsson & Ruxton 2004) and can have consequences for population stability as it impacts higher trophic levels through its relationship with prey availability, with cascading effects on lower trophic levels (Koski & Johnson 2002).

Foraging studies on fishes are often restricted to estimating their feeding rates, for example calculating the number of prey taken per unit time (e.g. Caiola & de Sostoa 2005; Oyugi et al. 2012a,b). In considering fish functional responses, the Type I, II and III

functional responses are often described (Holker & Breckling 2001; Galarowicz & Wahl 2005; Gustafsson et al. 2010). All are based on the foraging parameters of searching rate and handling time, but differ in how these parameters are treated. The Type I functional response assumes handling time is either negligible or that searching and handling can occur simultaneously (Jeschke et al. 2002). This results in a linear increase in feeding rate with prey density until it reaches a constant value at saturation and has only been reported in filter-feeding species (Jeschke et al. 2004). Conversely, Type II responses assume that handling time and searching time are mutually exclusive (Kaspari 1990; Baker et al. 2010), producing a feeding rate that increases at a decreasing rate with prey density as it approaches a maximum value. As such, it typically describes the foraging behaviour of a species capable of handling only one prey item at a time and in environments of reduced complexity, without the influence of factors including capture success, learned behaviour and prey clumping (Real 1977; Abrams 1990). Finally, a Type III response produces a characteristic sigmoidal response (Nachman 2006) through factors that alter the probability of detection or attack of prey items, such as learned behaviour, prey item switching, capture success or prey item clumping (Murdoch 1973; Morgan & Brown 1996).

There are functional response models available for some fish species that directly incorporate searching and handling times, such as for walleye *Stizostedion vitreum* (Galarowicz & Wahl 2005), brown trout *Salmo trutta* (Gustafsson et al. 2010) and lake trout *Salvelinus namaycush* (Barnhisel & Kerfoot 2004). The time spent searching for food may be further divided into discrete foraging parameters, such as reaction distance and swimming speed, enabling further separation of the time spent foraging at specific prey densities. For example, Aksnes & Giske (1993) and Aksnes & Utne (1997) described the importance of visual range in determining fish foraging rates and Baker et al. (2010, 2011) split searching time into several discrete behaviours in the determination of the functional response of granivorous birds. For many fish species, searching times have not been split further due to the difficulty of separating searching into its discrete behaviours at a sufficiently fine scale. This has now become much easier to achieve as videography techniques have improved, enabling efficient video capture and post-experiment analysis (Kane et al. 2004, 2005) that use reference markers to accurately estimate distances moved by the foraging fish through validation processes (Hughes et al. 2003).

Consequently, the aim of this study was to test how the Type II functional response model could predict the observed functional response of a model fish species, when parameterised using directly observed behavioural parameters and was completed through two research objectives. The first was to validate the accuracy of measurements of distances moved by the model fish within their experimental arena (tank aquaria), in response to food item exposure. The second was to parameterise a Type II functional response model using recorded behavioural parameters and then compare it with an experimentally obtained observed functional response to determine its accuracy. The output was then also compared with a Type I model; note a Type III response was not also tested as the experimental design precluded the development of more complex foraging behaviours that would typically lead to this response. The Type II functional response used in the study was based on the Holling's Disc Equation (Holling 1959), which has been used extensively to determine functional response curves in a wide range of animals (e.g. Goss-Custard et al. 2006).

Methods

Ethical Note

All animal work was conducted in accordance with national and international guidelines to minimise discomfort to animals. All regulated procedures completed under the Animals (Scientific Procedures) Act 1986 were licensed by the UK Home Office under project licence number PPL 30/2626. The Ethics Review Panel of the School of Applied Sciences of Bournemouth University approved this project licence.

Model Species

The model species was roach *Rutilus rutilus*, a visual foraging fish (Diehl 1988) of the cyprinidae family widely distributed throughout Eurasia. While components of roach foraging behaviour have been described previously, this was through estimation from a functional response, derived from field data on energetic costs and growth rate (Johansson & Persson 1986; Persson 1986, 1987; Holker & Breckling 2001), rather than through direct observation as per this study. Information on their functional response has also been determined from direct observation using live prey with individual fish (Winkler & Orellana 1992), where both Type II and Type III responses were described. Thus, their use here enables refine-

ment of their functional response parameters under controlled experimental conditions and a different prey item.

Experimental Species and Arena

The foraging experiments used 36 roach of age 1 + yrs (mean total body length + SE = 129 + 2.5 mm and mean body mass + SE = 20.5 + 1.3 g) of aquaculture origin that had been raised primarily on fishmeal pellets. Following transfer to aquaria (20 l tanks of 0.46 × 0.31 × 0.39 m; 18°C; 12:12-h light: dark cycle), the fish were acclimatised for 35 d before being paired for initial foraging trials. In these, their foraging behaviour appeared constrained and it was only when they were held in groups of three that their behaviour return to the normal state observed at higher densities during acclimatisation. Thus, for the actual foraging experiments, the fish were randomly divided into three and placed across 12 experimental tanks, each with a volume of 20 l.

To minimise external visual stimuli and disturbance to the fish to promote their natural behaviour, curtains were placed around the tanks and card was taped to the side and rear panels of the tanks. The card on the rear panel of the tank was also marked with a grid of 0.01 m² lines (Fig. 1) that assisted distance estimation during subsequent analyses. Identification of the individual fish was enhanced through a pelvic fin-clipping process that had been completed on the fish upon their arrival to the facility for the purposes of trophic analyses (G.P.D. Murray, R.A. Stillman, R.E. Gozlan & J.R. Britton, unpubl. data), with the three fish per tank comprising fish with a left-clip, right-clip and no-clip. Note fin-clipping in this manner does not adversely affect fish behaviour, survival or growth (Gjerde & Refstie 1988; Pratt & Fox 2002). To facilitate measurement of the distances moved by

fish during experiments and to record growth over the experimental period, weight and total body lengths were measured every two weeks throughout the study. To test the changes in length and weight of the fish over the study period, only their initial and final data were used, however, to prevent pseudoreplication (Hurlbert 1984).

Video Capture and Validation of Fish Movement Data

The foraging experiments were captured using a combination of two digital SD video cameras (Panasonic SDR-S26), with the video files subsequently transferred to a personal computer in .wmv format (640 × 480 pixels, variable bitrate at 25 frames per second). These cameras were attached to a movable frame that ensured their position, relative to one another, was consistent across all the experiments and tanks. One camera was positioned horizontally, facing the only uncovered side of the tank, with the second camera positioned vertically, above the surface of the water. Both cameras were positioned at a distance of approximately 16 cm in the front of the tank and from the surface of the water. The movable frame was positioned so as to ensure the cameras were parallel with the pane of the tank and surface of the water and that the entire tank was visible during each foraging experiment.

To subsequently analyse the video footage from both cameras, a purpose-built event-logger programme (Stillman 2012) was used that allowed frame-by-frame viewing and recording of the on-screen position from the horizontal and vertical pixel count. The video footage from both cameras was also edited to place the vertical footage above the horizontal and rendering them together into a single file. The pixel coordinate information then enabled the position and movement of the fish to be determined in the tank. As fish movement was not always parallel to the horizontal camera, the angle of movement was considered by reading the angle of movement from the footage recorded on the vertical camera. This was expressed in degrees away from a direct across screen movement, that is, 0° would be parallel to the front pane of the aquarium and directly across the screen when viewing footage from the horizontal camera (*cf.* Fig. 1). The actual position or distance travelled by the fish was then calculated using trigonometry from the apparent position or distance travelled (horizontal camera) and angle of movement relative to the front pane of the aquarium (vertical camera).

This system was used to determine fish positions and distance of movement from pixel coordinates

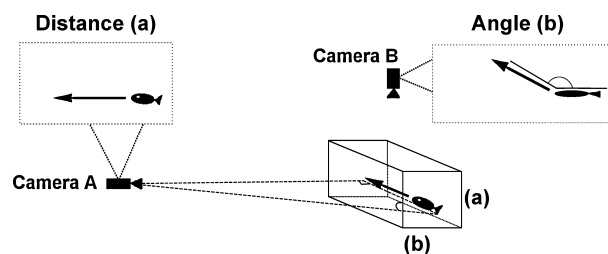


Fig. 1: The experimental set-up of cameras for estimating actual from apparent movement distance or position, where the horizontal camera (A) produces the apparent values (*a*) and the vertical camera (B) allows estimation of the actual values by providing information on angle of movement (*b*). The estimated distance (*c*) is calculated using the trigonometric formula $c = a/\cos b$.

using two methods. The first was to relate the number of pixels to the 0.01 m² grid pattern printed on the card on the rear of the tank that allowed the observed distance in pixels to be described in centimetres. The second was to compare the number of pixels from apparent distance to the number of pixels that make up the length of the fish. As the body length of the fish was known from their regular biometric measurements, this enabled conversion of pixel coordinates into cm. These methods were tested for accuracy by analysing video footage of the movements of an artificial 8 cm roach that was moved across 60 randomly assigned distances (5–45 cm) and angles (0–90°) by an independent operator. These were analysed in a blinded manner, and the two different methods for estimating distance were compared with the known distance using linear regression. The most accurate method was identified by its lower value of the Akaike Information Criterion (AIC).

Experimental Design and Data Analysis

The experiment required two aspects of data collection from the video footage; (1) feeding rates of the fish at different food densities (observed functional response); and (2) data on reaction distance, swimming speed and handling time of each fish in relation to food density, to enable parameterisation of the Type II functional response model (predicted functional response). Throughout the experiments, the food used was fish-meal-based pellets (1 mm diameter) as per their food source at the culture site. Moreover, cyprinid fish tend to respond well to fish-meal pellets in foraging experiments in tanks (Britton et al. 2012; Oyugi et al. 2012a,b). The foraging experiments were completed on alternate days, feeding on the day in between was on a daily maintenance ration of approximately 1.5% body weight (approximately 75 pellets) that was calculated in accordance with the fortnightly weighing of the fish, with maintenance used rather than *ad libitum* to ensure feeding motivation on the experimental days, given that functional responses relate to optimal foraging. Thus, feeding on experimental days occurred 24 h after the last exposure to the maintenance ration. It comprises exposing a tank of roach to one randomly selected food density from 10, 25, 50, 100 or 150 pellets per tank, equivalent to 75, 187, 375, 750 and 1125 items m⁻², respectively. Food items were introduced to the tank by being spread evenly over the surface of the water, after which they sank through the water column and settled on the bottom of the tank. On the release of the food, the filming of the foraging behaviour com-

menced for 5 min (Oyugi et al. 2012a,b). At the end of this period, all uneaten food was removed immediately using a siphon.

Each food density was used in every tank on two occasions, providing the potential for 72 individual data points per food density. In practice, the number of data points per food density was lower, as each experiment did not always produce three fish for each tank that displayed the foraging behaviours required to estimate reaction distance, swimming speed and handling time. In such cases, these fish were omitted from the analyses, reducing the available data. Furthermore, to reduce the effects of depletion at the lowest food density, only the first fish to feed was considered in the analysis. In the video analysis, feeding rate was recorded during the time between the fish taking its first and fifth food item and expressed as the number of items consumed per second.

To determine the observed functional response, the mean feeding rate was expressed as a function of food density. To predict the functional responses from foraging parameters, the video footage was analysed to estimate (1) swimming speed (*s*) whilst searching for food, characterised by relatively slow swimming, with frequent changes in body orientation and leading to food item capture; (2) reaction distance (*d*), determined as the distance a fish would travel in a straight line directly towards a food item, quickly followed by capture of the food item, often following a change in body orientation towards the food item; and (3) handling time (*h*), determined as the time taken to move towards and consume a food item, and then be ready to consume a further food item. Handling time was determined on occasions when food items were captured in rapid succession and when no other behaviour was observed between food item capture.

These parameters were used to parameterise the Type I and Type II functional response models:

The Type I model was:

$$F = \begin{cases} aD & \text{if } D \leq \frac{1}{ah} \\ \frac{1}{h} & \text{if } D > \frac{1}{ah} \end{cases} \quad (1)$$

The Type II model was Holling's Disc Equation (Holling 1959):

$$F = \frac{aD}{1 + aDh} \quad (2)$$

where *F* = feeding rate (items s⁻¹), *a* = searching rate (i.e. search area per unit time) (m² s⁻¹), *D* = food density (items m⁻²) and *h* = handling time (s) (Holling 1959).

In both cases, *a* was defined as follows:

$$a = 2ds \quad (3)$$

where s = swimming speed (ms^{-1}) and d = reaction distance (m). This equation assumes that fish consumed prey on the bottom of the tanks and detected prey at up to twice the observed reaction distance, that is, the fish can search over the same distance on either side around their search path, multiplied by the distance travelled. Thus, a was derived directly from the foraging behaviour parameters. This is an approach frequently used to describe searching rate in birds (Baker et al. 2009) but not before in fish. Note that 'searching rate' also includes the success rate of a predator capturing prey. Typically, Type I and Type II functional responses include probability of discovery (i.e. of detecting prey), but here, the probability of discovery was equal to 1 so was omitted. Equation 3 describes fish as searching for prey in two dimensions, although the recorded foraging behaviour enabled description of movement to be measured in three dimensions. A simplified approach was used as this reflected the foraging behaviour of the fish as they generally consumed food items only once they were on the tank bottom. Meanwhile, h was measured directly from video footage. As per Hjelm & Persson (2001), the data were combined from across all of the fish to parameterise the above equations, rather than predicting a functional response for each individual fish. The rationale for this was that at the individual level, there was often a low number of data points per fish resulting from, for example, only one fish being used per tank at the lowest food density.

To quantify the ability of these parameters to predict the functional response, they were used in Eqs 1, 2 and 3, with the predicted Type I and Type II functional responses compared with the observed functional response. The parameters were also directly compared with previously described behavioural parameters for roach (Persson 1987). All statistics and testing were completed in R (R version 2.12.2; R Development Core Team 2011).

Results

Validation of Data From Video Capture

Both of the methods for converting pixel coordinates into actual distances accurately estimated the distances moved by the artificial fish, independent of the angle and distance moved (Fig. 2). Significant relationships were obtained between known and estimated distances for both the grid (linear regression: adjusted $R^2 = 0.84$, $F_{1,56} = 315.1$, $p < 0.01$) and body length method (linear regression: adjusted $R^2 = 0.51$, $F_{1,56} = 62.2$, $p < 0.01$). Akaike's Information Criteria

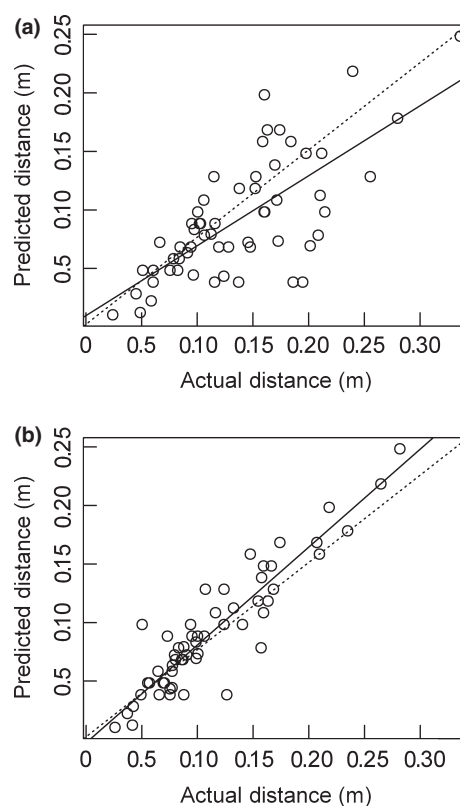


Fig. 2: Relationships between actual and estimated movements of an artificial roach comparing the output of (a) the number of pixels moved to number of pixels in body length; and (b) the number of pixels moved to number of pixels in 0.01m^2 grid. Solid Lines are fitted Linear Regression equations; Dotted lines are 1:1 relations between estimated and actual distances.

indicated that the grid method provided the most reliable estimates of distance moved (AIC: grid: 83.5; body length: 149.9) and so was used for all subsequent analyses.

Fish Length and Body Weight Over The Study Period

The two weekly measuring and weighing of the fish over the study period revealed minimal growth in the fish. Comparison of their initial and final lengths and weights also revealed that no significant increase in length or weight had occurred (paired t-tests: length $t_{1,35} = -1.269$, $p > 0.05$; weight: $t_{1,35} = 3.296$, $p > 0.05$).

Functional Response

Of the functional response parameter values, handling time (Fig. 3a) and swimming speed (Fig. 3b) showed no overall relationship with food item

density, and whilst reaction distance (Fig. 3c) showed some indication of a negative relationship with food density, this was not significant (handling time: adjusted $R^2 = -0.01$, $F_{1,161} = 0.78$, $p > 0.378$; swimming speed: adjusted $R^2 = -0.02$, $F_{1,37} = 0.01$, $p > 0.917$; reaction distance: adjusted $R^2 = 0.16$, $F_{1,14} = 3.91$, $p > 0.067$). As handling time and swimming speed did not change significantly with food item density, these parameter values were derived from data collected at all experimental densities.

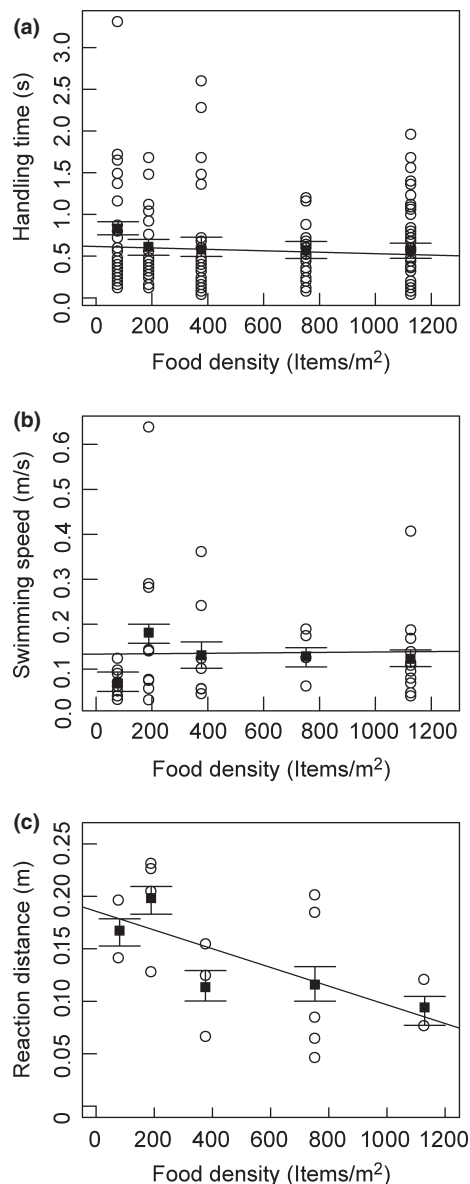


Fig. 3: Observed relationships between behavioural parameters and food density for (a) handling time; (b) swimming speed; and (c) reaction distance. Open circles are observed values, while filled squares are means for each food density with associated 95% confidence intervals.

Conversely, although reaction distance was not significantly related to food density, there is reason to expect that reaction distance will decrease with food density as more food items are likely to be closer to the fish, as per experiments in birds (e.g. Stillman & Simmons 2006; Smart et al. 2008; Baker et al. 2009, 2011). Thus, at higher densities, reaction distance is likely to be underestimated as fish forage optimally by moving to food items well within their maximum reaction distance. Therefore, the reaction distance parameter value was derived from data collected only during feeding experiments at the lower three of the six food item densities.

The observed functional response of the roach was best described by a Type II functional response. The feeding rate significantly increased at a decelerating rate with increasing food density (adjusted $R^2 = 0.94$, $F_{1,3} = 48.22$, $p < 0.01$; Fig. 4). The lowest feeding rate was measured at the lowest tested food density, with this then increasing almost fivefold at the highest food density (Fig. 4). The increase in foraging rate between the food densities of 75 and 750 m^{-2} food density was significant (linear regression adjusted $R^2 = 0.95$, $F_{1,3} = 13.39$, $p < 0.05$), with the rate then decelerating to 1125 m^{-2} (Fig. 4). The observed parameters of searching rate, reaction distance and handling time were then fitted to Eqs 1, 2 and 3 to obtain the predicted functional response. The predicted Type II functional response provided a strong fit with the observed across all food densities (RSS + SE = 0.0002 + 0.00781, $p < 0.05$; Fig. 4). A mean value for handling time (h) was observed at 0.605 seconds, compared with 0.75 (± 0.19) reported by Persson under similar artificial conditions and temperature (18°C). A one-way ANOVA showed no significant difference between the values of handling

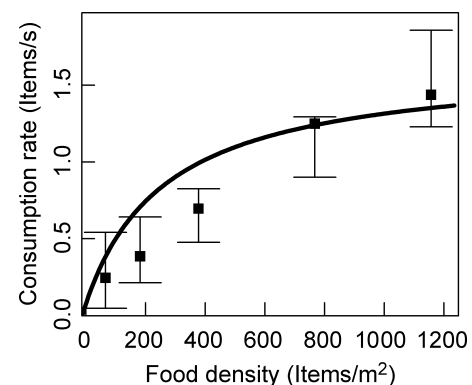


Fig. 4: Comparison of observed and predicted functional responses, showing mean observed feeding rates (filled squares; 95% confidence intervals) and the predicted functional response (solid line).

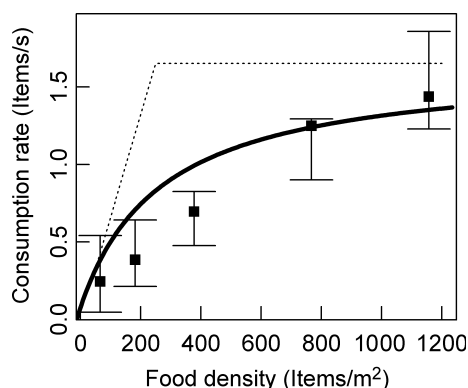


Fig. 5: Comparison of observed and predicted functional responses, showing mean observed feeding rates (filled squares; 95% confidence intervals) and the predicted functional responses (Type II solid line and Type I dashed line).

time ($F_{1,165} = 0.230$, $p = 0.632$). Similarly, the value of searching rate (a) (equal to instantaneous search rate or attack coefficient as reported in Persson 1987) was calculated at 4.45 in this study based on direct observation of swimming speed and reaction distance (Eqn 3), compared with a value of 5.10 (± 2.41) reported by Persson. This is again reflected in a one-way ANOVA showing a non-significant difference between the values ($F_{1,2} = 1.256$, $p = 0.379$).

Given the significant increase in foraging rate at the lower food densities (Fig. 4), the Type I and II functional responses were then compared (Fig. 5). This revealed that the predicted Type I functional response was a poor fit compared with the observed functional response (adjusted $R^2 = 0.12$, $F_{1,3} = 1.59$, $p > 0.05$) as it overestimated consumption rate over most food densities (Fig. 5). It was also a poor fit of the data when compared to the Type II predicted functional response, as reflected in the relative goodness of fit of the models versus the observed, where the lowest AIC was in the predicted Type II (AIC = -941.98) compared with the predicted Type I functional response (AIC = -560.79).

Discussion

The study demonstrated that the foraging behaviours of a visual foraging fish could be measured under controlled conditions, and, through analysis of their behaviour in three dimensions, their distance of movement and swimming speeds were accurately estimated. This enabled handling time, swimming speed and reaction distance of the fish to be estimated in relation to their exposure to different food item densities and enabled parameterisation of a Type II

functional response model (Holling's Disc Equation). This predicted functional response matched the directly observed functional response and was shown to be superior to the Type I functional response model.

Holling's disc equation assumes that at high food densities, the feeding rate is limited by the handling time of the individual rather than the time taken to locate food (Baker et al. 2010). Whilst this appeared true in the roach of this study, other studies have shown this is not always apparent. For example, Caldow & Furness (2001) described kleptoparasitic behaviour where handling time was seen to vary with host abundance. Moreover, as food density increases, an increase in food selectivity may also be observed. Individuals may selectively targeting only the most attractive food items, reducing the number food items consumed per unit time with a trade-off of an increase in food quality (Magnhagen & Wiederholm 1982). Another effect of increased food density is the confusion effect, whereby excessive numbers of evasive prey can reduce attack rates and/or capture efficiencies, especially in cases of visual predators with mobile prey (Ioannou et al. 2007; Tosh et al. 2009). Similarly, the rate at which the digestive system can process food may also be below that determined solely by the handling time (Jeschke et al. 2002). In the current study, however, handling time did appear to determine the asymptote of the functional response. This may be related to the food item being a pellet of consistent size and quality, and so selectivity with food item density was negligible. Similarly, there would be the absence of a confusion effect as the food items lacked evasive behaviour or mobility. Furthermore, as the foraging experiments ran for a maximum of five minutes, there was little opportunity for individual fish to be satiated. Indeed, some recordings showed some of the fish going on to consume over 10 food items within the 5 min. Thus, the short-term functional response of roach was described here, rather than the longer term, daily functional response when time is also allocated to non-feeding activities (Mills 1982; Henson & Hallam 1995). In addition, the non-significant increases in fish length and weight over the study period confirmed their feeding regime was a maintenance diet, and, thus, their behaviours would have been optimal foraging behaviours rather than feeding to satisfaction as per feeding *ad libitum* (Myers 1983; Krebs & McCleery 1984; Stephens & Krebs 1986).

Reaction distance (d) was defined here as the distance a fish would travel in a straight line directly towards a food item, immediately before its capture. It

was uncertain at the start of the study as to whether this type of behaviour could be measured with sufficient accuracy. However, during the video analysis, a clear change in behaviour was observable in each roach when moving towards a food item that aligned to the d definition. Applicability of this method to other fish species is dependent upon the foraging behaviours of the fish concerned. In the wild, roach tend to be zooplanktivorous and herbivorous (Garcia-Berthou 1999), and their feeding rate appears to be very low when compared to species such as common carp *Cyprinus carpio* (e.g. Oyugi et al. 2012a,b). Thus, roach behaviours tend to be relatively easy to observe and interpret as they are relatively slow and deliberate. For fish species such as walleye, for which functional response data are available (Galarowicz & Wahl 2005), their piscivorous feeding may mean their reaction distance is much more difficult to interpret, as their foraging strategy is likely to be quite different (e.g. ambush predation). Similar issues have been noted in determining the reaction distance of different bird species (Caldow & Furness 2001; Stillman et al. 2002). Alternatives exist, for example, estimating reaction distance can be completed by correlating reaction distance with time, the number of paces or by being estimated from their general behaviour (Stillman & Simmons 2006).

When fish forage optimally, their reaction distance may decrease with higher food densities. This was not, however, observed here although this may relate to low statistical power due to the sample sizes used. With increased power, this relationship may be significant, either as a linear or non-linear relationship. Thus, future work should consider greater replication, although this should be in the number of individual fish and tanks used rather than repeated measures of the same fish to avoid pseudoreplication (Hurlbert 1984). Increasing the number of individuals used in experiments may also be useful given that optimal foraging behaviour has been shown to have a significant heritability coefficient (Morris & Davison 2000; Gibbons et al. 2005). Consequently, this provides high potential for individual variation in foraging parameters that are ultimately linked to fitness. The constraints of sample size already outlined prevented the prediction of individual functional responses here that might have revealed this individual variability, and so increasing the sample size should be considered in future studies.

The functional response of other animals may display increased complexity including different foraging behaviours that were not considered in this study, such as the influence of interference competition

(Elliott 2003; Vahl et al. 2005) and the trade-off between vigilance and foraging (Baker et al. 2010; Bartosiewicz & Gliwicz 2011). Habitat structure may also impact foraging behaviour and thus the functional response. In both aquatic and terrestrial environments, vegetation cover may influence food item visibility and/or movement costs (Butler et al. 2005; Stillman & Simmons 2006). Consequently, considering the predicted functional response of roach in more complex experimental systems, or more natural systems, may require measuring and accounting for other factors that influence their foraging, such as water turbidity and temperature, prey types and predation pressures. This would enable the prediction of foraging outcomes in relation to environmental and biological changes, in situations where direct observation was not possible. The degree to which these influencing factors can be investigated depends upon how they may be replicated under laboratory conditions, although both water turbidity (Vollset & Bailey 2011) and temperature (Oyugi et al. 2012a,b) effects should be feasible in the current system.

The functional response of roach has also been previously described as a Type II functional response, based on an estimated functional response using data gathered on metabolic costs and food availability in a eutrophic lake system (Johansson & Persson 1986; Persson 1987). The functional response of roach from direct observation has also been previously described (Winkler & Orellana 1992), although this was based on zooplankton feeding experiments with individual fish, rather than groups of three as per this study. In that study, a Type III response was described (Winkler & Orellana 1992) a likely consequence of the evasive behaviour of the zooplankton prey and the developing of searching behaviours in the fish. Here, a Type II response was the best fit of the foraging data, suggesting that the functional response of roach is context dependent and reinforces the requirement to develop complexity into functional response experiments.

Recording and measuring behavioural movements on a small scale are often necessary but can be prohibitively expensive, requiring specialist hardware or software (Gingras et al. 1998; Delcourt et al. 2006). Furthermore, this type of videography often relies upon reference markers which may influence a subject's behaviour, limit the scope of the investigation or be avoided altogether (Hughes & Kelly 1996). Previous work on terrestrial organisms which rely upon recording pace length (Poole et al. 2006) for measuring d assume that this is constant or, as in the case of fish, cannot be measured at all (Stillman et al. 2002). The use of single camera systems also precludes

description of distances in all planes of movement (Laurel et al. 2005). The methods described in this article, however, overcame these issues. The software used is freely available and was user-friendly. When using the grid lines as reference markers, the system was unobtrusive and avoided having to use fish lengths as a way of measuring distances. Movement and position were also described in all planes using a simple two-camera videography system. Thus, using manual over automated analysis, the foraging behaviour of roach was able to be quantified using more rigorously defined behavioural parameters than previously.

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