Using the functional response to determine the nature of unequal interference among foragers

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The functional response as a tool for characterizing interference

We use a type III functional response with an interference component to illustrate interference types,

\[ I = \frac{aN^mP^{-w}}{1 + ahN^{-\omega}} \]  

(2.1)

where \( I \) is the intake rate, \( a \) is the attack rate, \( N \) is the prey density, \( P \) is the number of predators, \( m \) is an interference parameter, and \( h \) indicates that food handling restricts the rate of food intake. When \( P = 1 \), the equation reduces to a functional response without interference, and when \( P > 1 \) it implies interference for all \( m > 0 \). The different types of interference correspond to different interference parameters for stronger (s) and weaker (w) interferers. For \( m_s > 0 \) and \( m_w = 0 \) the equation describes constant intimidation interference (figure 1a). For direct aggression and filtering interference, we should expect prey-dependent effects on functional responses (Wilson 1974; Moody & Ruxton 1996).

\[ m_s = c_s N^{-\omega} \]  

(2.2)

where all constant \( c > 0 \) imply interference. If interference is mediated by direct aggression, using \( m_s \) in equation (2.1) should produce \( 0 < c_t < c_s \) (figure 1b). To describe filtering, it should produce \( c_w > 0 \) and \( c_t = 0 \) (figure 1c). If filtering is the only effective type of interference, stronger and weaker interferer functional responses (equation (2.1); \( P = 1 \)) should not differ when analysed for the different amounts of prey available to the different interference strengths, i.e. total prey density \( (N) \) for strong, and filtered \( (f) \) prey density \( (N_f = N - I_f) \) for weak (figure 1d).

By using regression to analyse functional responses it is thus possible to identify types of interference among unequal competitors by stepwise elimination of alternatives. We performed these analyses on functional responses from an experiment on juvenile salmon.

(b) Experimental methods

We monitored individual intake rates of eight hatchery-reared salmon \((85.1 \pm 2.0 \text{ mm fork length})\) foraging alone (no interference) and in pairs (interference) in compartments of a laboratory stream (see Valdimarsson et al. (1997) for stream details). Intake rates were monitored across seven prey densities (blood worm; 10, 20, 30, 40, 60, 80 and 100 individuals per trial). Prey was gravity-fed from water containers to each compartment as a replenishing food supply unpredictably distributed over trial time. Since fishes grew over the experiment and trial times varied within and among compartments \((10.7 \pm 1.04 \text{ min})\), intake rates (observed number of consumed prey) were recalculated as the number of individual prey consumed per gram of individual fish body mass and minute of trial time. Prey densities (observed number of prey entering each compartment) were recalculated as the number of individual prey arriving per minute of
3. RESULTS

The intake rates for individuals foraging alone followed the type III functional response \((a = 0.060 \pm 0.017, h = 2.640 \pm 0.349, R^2 = 0.916 \pm 0.049, \text{mean} \pm \text{s.d.}; \text{figure } 2a; \text{equation } (2.1); P = 1)\). There was no difference in functional responses among individuals (ANOVA on individual residuals from curve produced by average parameters, \(F_{7,44} = 0.569, p = 0.777\)).

When analysing individual functional responses in the pairs for constant intimidation (i.e. \(m\) as a constant; equation \((2.1); P = 2\)), the average \(m\) for strong interferers was negative \((m_s = -0.088 \pm 0.069, R^2 = 0.863 \pm 0.074)\), but not significantly different from 0 (one-sample \(t\)-test. \(t_s = -2.550, p > 0.1; \text{figure } 2b\)). There was no difference in intake rates among stronger interferers \(F_{5,24} = 0.364, p = 0.779\), so interference over foraging opportunities does not affect the foraging rates of strong interferers. The average value of the constant \(m_w\) for weaker interferers was \(0.692 \pm 0.148\) with \(R^2 = 0.574 \pm 0.089\) (figure \(2b\)). There was no significant difference in intake rates among weaker individuals \(F_{5,24} = 1.242, p = 0.316\). This suggests that interference has a negative effect on the foraging of weaker individuals, but the \(R^2\)-value indicates low predictive power. Intimidation and direct aggression are thus unlikely to be mediating interference in the experiment since functional responses of weak interferers are not well predicted by a constant intimidation effect, and since strong interferer intake rates are not affected by interference.

The analysis of prey-dependent interference on functional responses, i.e. for direct aggression or filtering interference (equation \((2.2); P = 2\)), revealed positive interference constants and high \(R^2\) for weak interferers \((c_w = 19.100 \pm 3.684, R^2 = 0.846 \pm 0.071)\). There were no differences in individual functional responses among weaker interferers \(F_{5,24} = 0.596, p = 0.624\). Their functional responses are hence greatly reduced at low prey densities, but approach those of stronger interferers at high prey densities (figure \(2b\)). This rules out constant intimidation as the effective type of interference, since an intimidation effect should persist across prey densities (Griffiths & Armstrong 2002). Functional responses of stronger individuals were not affected by interference and hence not analysed according to equation \((2.2)\).

The analysis evaluating filtering as the only type of interference provided high \(R^2\)-values for both strong and weak interferers. Average parameters and \(R^2\)-values were \(\alpha_s = 0.082 \pm 0.032, \alpha_w = 0.115 \pm 0.033, h_s = 2.570 \pm 0.352, h_w = 2.620 \pm 0.938, R^2_s = 0.914 \pm 0.086, R^2_w = 0.863 \pm 0.074\).

Figure 1. Illustrations of different types of interference and their effects on functional responses in foragers of unequal interference strengths. Types of interference are: (a) constant intimidation, where the presence of a strong interferer (black line) decreases functional responses in a weaker (grey line) interferer across prey densities (grey dashed line: foraging alone); (b) direct aggression, where interferers compete by aggressive interactions but stronger interferers compete more efficiently; and (c) filtering interference, where stronger interferers get first access to food and weaker interferers may only forage on food missed or ignored by the stronger. (d) Shows the functional responses of a strong and a weak filtering-interferer when the \(x\)-axis is compensated for the prey densities actually available to the different individuals; total prey density for the stronger, and filtered prey density for the weaker interferer.
4. DISCUSSION

The behaviours that we observed could have been interpreted as evidence of direct aggression interference, because aggressive displays and food intake were asymmetric at the lower end of the range of prey densities. However, by applying the functional response, we revealed that filtering interference was the sole determinant of between-fish variation in food intake. Contrary to the findings of some previous studies, there was also no evidence of intimidation interference among the salmon parr. Variation among studies may be related to the complexity of the physical and social environment (Sloman & Armstrong 2002). We considered virtually the simplest arrangement, where food emanated from a point source and a single pair of fishes competed in a simple arena. Our findings provide a baseline for exploring how environmental variability, risk of predation, forager group size and social and habitat complexity (e.g. Reinhardt 1999; Giraldeau & Caraco 2000; Sloman et al. 2001; Elliott 2002; Højesjø 2002) could affect types of interference among foragers. Analysis of the functional response constitutes a powerful tool for such development, particularly because it has the capacity to reveal the form of variations in interference across relevant prey densities, an issue that hitherto has apparently received little attention.

Our method also links individual behaviours to foraging economies and population processes. For example, strong intimidation interference would result in large asymmetries in foraging economy among individuals because a differential in prey intake between unequal interferers would exist under all conditions of prey availability. By contrast, filtering interference, as detected in this study, would be likely to be more dependent on prey availability. Large foraging-economy asymmetries would be expected at low, constant prey availability, whereas large peaks in prey abundance would allow weak interferers to capitalize on resources when they are highly abundant or dominant individuals are satiated (Alanàr & et al. 2001). However, to produce a complete understanding of these economies and their effects on higher-level processes, different costs associated with upholding an interference strength should be incorporated (e.g. Ens & Goss-Custard 1986; Hogstad 1986; Jakobsson et al. 1995; Pedersen & Hoffman-Goetz 2000). Also, temporal clumping of food may affect resource defensibility (Grant 1997). Nevertheless, the interference-mediated asymmetric foraging economies should have implications for individual success, social foraging theory and population processes, which is why we suggest that the evaluation of interference types should be incorporated into investigations of these topics.

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Figure 2. Functional responses of juvenile Atlantic salmon foraging alone and in pairs evaluated for different types of interference. (a,b) When foraging alone (open circles and grey dashed curve), salmon intake rates follow a type III functional response. (b) When paired, salmon individuals establish themselves as strong (black circles and curve) or weak (grey circles and curves) interferers. Weak interferer functional responses are analysed for constant intimidation (dotted grey), and prey-dependent aggressive or filtering interference (solid grey). (c) Intake rates (I) of strong and weak interferers from the same data as in (b), but here the x-axis represents the amount of prey available to the different predators, i.e. total prey density (N) for strong (s) interferers, and filtered prey density \( N_f = N - I_f \) for weak interferers. Data points are individual data from eight individuals, but intake-rate curves represent among-individual average functional response parameters from individual analyses.

0.981 ± 0.014. The functional response parameters did not differ significantly between strong and weak interferers (paired t-test on individually estimated parameters from foragers in each pair; a: \( t_3 = -1.288, p = 0.288 \); b: \( t_3 = -0.155, p = 0.887 \); figure 2c). These results strongly corroborate the suggestion that interference acts only as a filtering effect in this system (see also Elliott 2002).


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