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

P. Anders Nilsson[1*]**, Felicity A. Huntingford**[1]
and John D. Armstrong[2]

[1]*Division of Environmental and Evolutionary Biology,
University of Glasgow, Glasgow G12 8QQ, UK*
[2]*Fisheries Research Services Freshwater Laboratory, Faskally,
Pitlochry PH16 5LB, UK*
[*]*Author and address for correspondence: Lund University,
Ecology Building, SE-223 62 Lund, Sweden
(anders.nilsson@limnol.lu.se).*

The food intake rate of foragers may be reduced as a result of interference, which may be asymmetric among individuals and occur as a result of intimidation, direct aggression or filtering. It is important to distinguish among these types of interference, because each can have different consequences for individuals, foraging groups and populations. We demonstrate the application of the functional response as a tool for distinguishing between types of interference. We apply the approach to juvenile Atlantic salmon and show that stepwise elimination of interference types is possible from regression analyses of functional responses, identifying filtering as the only effective type of interference in the study environment.

Keywords: aggression; Atlantic salmon; filtering; functional response; interference; intimidation

1. INTRODUCTION

Predators competing for prey may interfere and hence mutually reduce individual rates of prey intake (Beddington 1975). Understanding interference is fundamental in the development of theory on social foraging (Giraldeau & Caraco 2000) and population dynamics (Fryxell & Lundberg 1998). Intraspecific interference may be asymmetric among individuals (Ruxton 1999) and may occur through several distinct mechanisms. Constant intimidation occurs when the simple presence, or even the possibility of a strong competitor appearing, causes weaker individuals to reduce foraging (Griffiths & Armstrong 2002). Direct aggressive interactions (Sirot 2000), where individuals fight over foraging items and strong interferers fight more successfully, can cause interference. Filtering interference (Wilson 1974) can occur, whereby a weaker interferer can access only those resources undetected or ignored by stronger individuals. It is important to distinguish between these different types of interference because they may have different consequences for energy allocation and behaviour of individual animals (e.g.

Hogstad 1986; Jakobsson *et al.* 1995; Ruxton 1999) that underpin population processes.

We propose and apply a novel approach for identifying types of interference by studying the functional responses of competing individuals. The functional response (Holling 1959) is of fundamental importance in population dynamics theory (Fryxell & Lundberg 1998), describing the relationship between prey density and predator intake rates. Functional responses may vary among types of foragers, and the function parameters can be used to categorize the type of interference occurring.

The first part of this paper explains how the form of the functional response differs between strong and weak interferers depending on the type of interference. The second part of the study uses the functional response to examine interference among juvenile (parr) Atlantic salmon (*Salmo salar*). Under various conditions, salmonid fishes are thought to exhibit aggressive (Sloman & Armstrong 2002), intimidatory (Griffiths & Armstrong 2002) and filtering (Elliott 2002) interference. The functional response was used to determine the type of interference in pairs of Atlantic salmon occupying a simple arena with a point source of food.

2. MATERIAL AND METHODS

(a) *The functional response as a tool for characterizing interference*

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

$$I = \frac{aN^2P^{-m}}{1 + ahN^2},\tag{2.1}$$

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 $m_w > 0$ and $m_s \approx 0$ the equation describes constant intimidation interference (figure 1*a*). For direct aggression and filtering interference, we should expect prey-dependent effects on functional responses (Wilson 1974; Moody & Ruxton 1996)

$$m_c = \frac{c}{N^2},\tag{2.2}$$

where all constant $c > 0$ imply interference. If interference is mediated by direct aggression, using m_c in equation (2.1) should produce $0 < c_s < c_w$ (figure 1*b*). To describe filtering, it should produce $c_w > 0$ and $c_s \approx 0$ (figure 1*c*). 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 ($N_f = N - I_s$) for weak (figure 1*d*).

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 ± 2.0 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 (10.77 ± 1.04 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
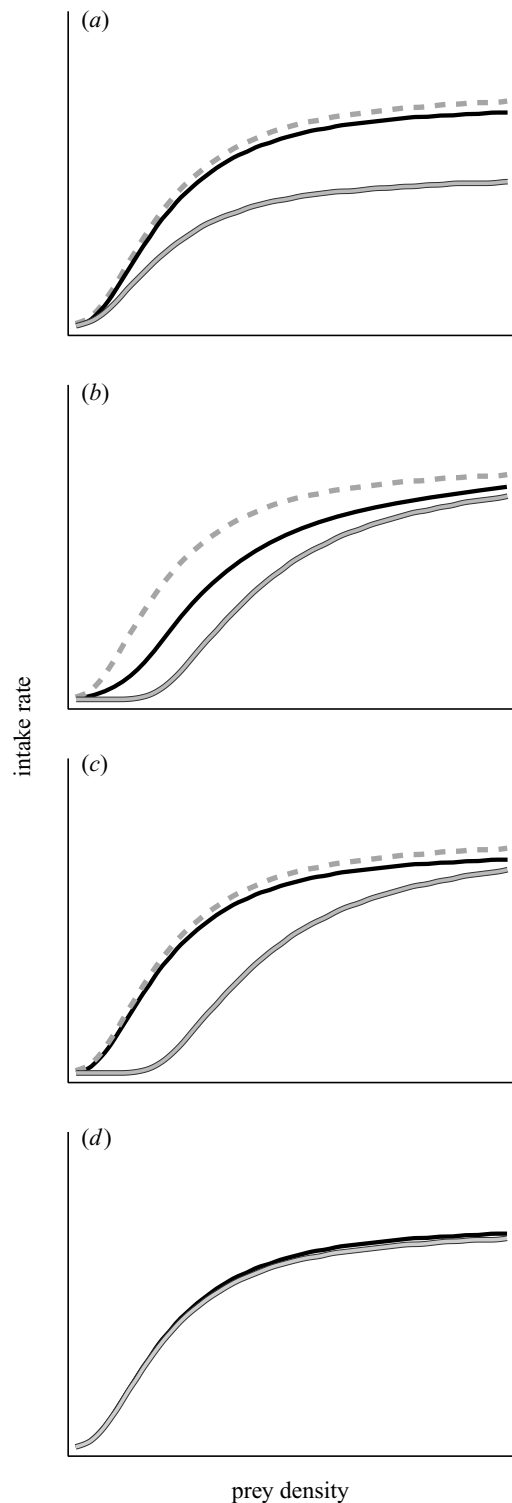
(a)

(b)

(c)

(d)

intake rate

prey density

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.

$h = 2.640 \pm 0.349$, $R^2 = 0.916 \pm 0.049$, mean ± s.d.; figure 2a; equation (2.1); $P = 1$). There was no difference in functional responses among individuals (ANOVA on individual residuals from curve produced by average parameters, $F_{7,48} = 0.569$, $p = 0.777$).

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. $t_3 = -2.550$, $p > 0.1$; figure 2b). There was no difference in intake rates among stronger interferers ($F_{3,24} = 0.364$, $p = 0.779$), 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 ± 0.148 with $R^2 = 0.574 \pm 0.089$ (figure 2b). There was no significant difference in intake rates among weaker individuals ($F_{3,24} = 1.242$, $p = 0.316$). 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 ($F_{3,24} = 0.596$, $p = 0.624$). 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 $a_s = 0.082 \pm 0.032$, $a_w = 0.115 \pm 0.033$, $h_s = 2.570 \pm 0.352$, $h_w = 2.620 \pm 0.938$, $R^2_s = 0.914 \pm 0.086$, $R^2_w = $

trial time. Interference–strength relationships are easily and reliably determined from behavioural observations of salmon (Sloman & Armstrong 2002), and individuals that controlled space, fed first and showed more aggressive displays in the trials (paired t-test: $t_3 = 3.893$, $p = 0.030$, number of aggressive displays: 10.3 ± 7.7 and 1.2 ± 3.7, respectively, mean ± s.d.) were designated the stronger interferer in each pair. Prior to the experiments, fishes were acclimatized to experimental conditions by running the full experimental procedure without data collection.

3. RESULTS

The intake rates for individuals foraging alone followed the type III functional response ($a = 0.060 \pm 0.017$,
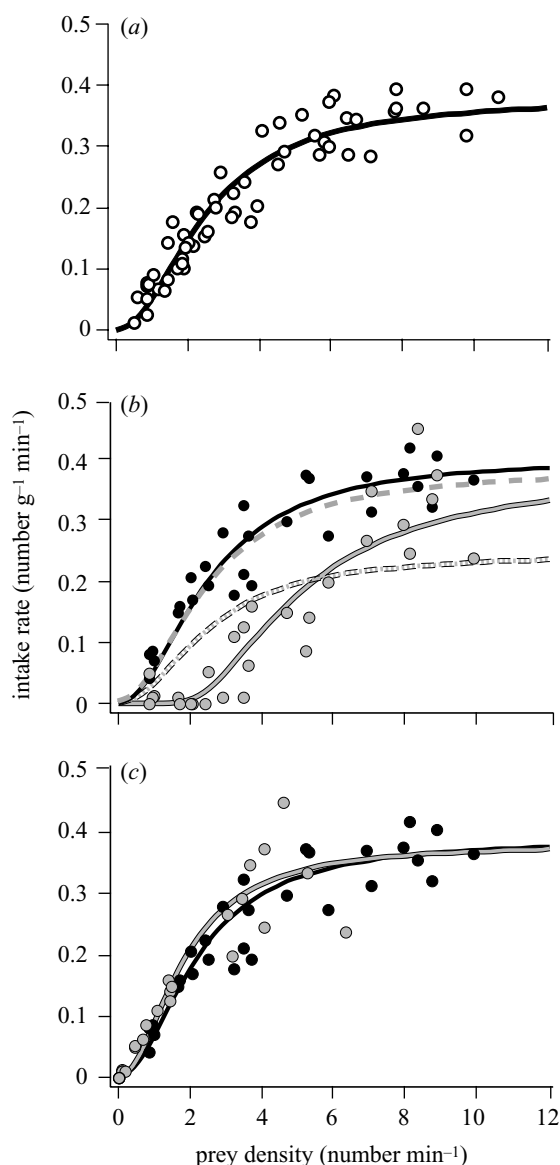
Figure 2. Functional responses of juvenile Atlantic salmon foraging alone and in pairs evaluated for different types of interference. (*a*,*b*) When foraging alone (open circles and grey dashed curve), salmon intake rates follow a type III functional response. (*b*) When paired, salmon individuals establish 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 ($N_f = N - I_s$) 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*: $t_3 = -1.288$, $p = 0.288$; *h*: $t_3 = -0.155$, $p = 0.887$; figure 2*c*). These results strongly corroborate the suggestion that interference acts only as a filtering effect in this system (see also Elliott 2002).

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; Höjesjö 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 likely 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 (Alanärä *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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