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## Temporally fluctuating prey and coexistence among unequal conspecific interferers

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Coexistence among unequal conspecific interferers should be unlikely to persist if stronger interferers always experience a relative fitness increment from their higher foraging rates. In this study, we suggest that decreased relative costs to weaker interferers with increasing temporal fluctuations in prey availability may be a mechanism enhancing coexistence of unequal conspecific interferers. Previous work on fluctuation and coexistence has dealt with oscillations over a time-scale measured in generations of competitor species and their resources, while our work shows that fluctuations in prey availability facilitate coexistence of different phenotypic strategies within species and generations, and over short time-scales. With increasing amplitude of temporal fluctuation about an average prey density, cumulative intakes for differently strong interferers are affected differently. Because of the prey-dependent effect of interference, high amplitudes of fluctuation allow for relatively lower foraging-rate costs in weaker interferers, which decreases the difference in foraging success between strong and weaker interferers. This decreased difference in foraging success could thus significantly relax the conditions allowing for unequal interferer coexistence.

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Intraspecific competition may occur over resources such as space, food, shelter or mates, and dominant individuals may adopt behavioural tactics that suppress resource utilisation in subordinate individuals. When competition is over food resources, individual foraging rates could thus be interference-dependent, and interference strength may be unequal among individuals (Ruxton 1999, Giraldeau and Caraco 2000, Stillman et al. 2000). In such a situation, a subordinate may not be allowed to forage in a patch inhabited by a dominant, but be chased away or interrupted in its foraging (Nakano 1995). Interference over food resources could thereby be a significant cost to subordinates in terms of decreased foraging opportunities. If subordinates always experience this loss and dominants enjoy a benefit

of higher foraging rates, or if subordinates are forced to migrate to avoid competition, persistence of subordinates in the foraging group, and therefore coexistence of unequal interferers, should be unlikely. Yet, unequal interferers, i.e. individuals that have differing negative effects on conspecific competitors, do coexist in nature. For instance, juvenile salmonids (e.g. brown trout, *Salmo trutta*) and oystercatchers (*Haematopus ostralegus*) may forage in social groups where interference over foraging stations and/or food items is unequal among individuals, and several levels of interference strength persist in the populations (Elliot 1994, Goss-Custard 1996).

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coexistence. In previous work, evaluations of fluctuations have aimed at effects of dynamics (Huisman and Weissing 1999) and internally generated cyclicality (Armstrong and McGehee 1980) of consumer populations, or pulsed resource availability (Sommer 1985) or longer-term environmental variation (Chesson 1985) on coexistence among several competing species. These theoretical and empirical results all suggest mechanisms of enhanced competitor species coexistence, and operate over several generations involving changes in both consumer and resource densities. In this work, we suggest and evaluate a factor that decreases the cost of interference to weaker interferers within one species, over short time-scales, within generations and without changes in predator density, and thereby should be an important mechanism behind how unequal conspecific interferers may coexist; the effects of temporally fluctuating prey availability on individual foraging among interfering predators.

## The model and evaluation

Without interference, or in the absence of competitors, an individual predator's intake rate ( $I$ ) often follows a type II functional response (Holling 1959):

$$I = \frac{aN}{1 + ahN} \quad (1)$$

( $a$  = attack rate,  $N$  = prey density and  $h$  = handling time), and the shape of the functional response should be determined by attack rate and handling time (Fig. 1a). For interfering predators, individual functional responses ( $I_m$ ) could follow a type II functional response, but now including both predator density ( $P$ ) and an interference parameter ( $m_s$ ) (Beddington 1975):

$$I_m = \frac{aN P^{-m_s}}{1 + ahN} \quad (2)$$

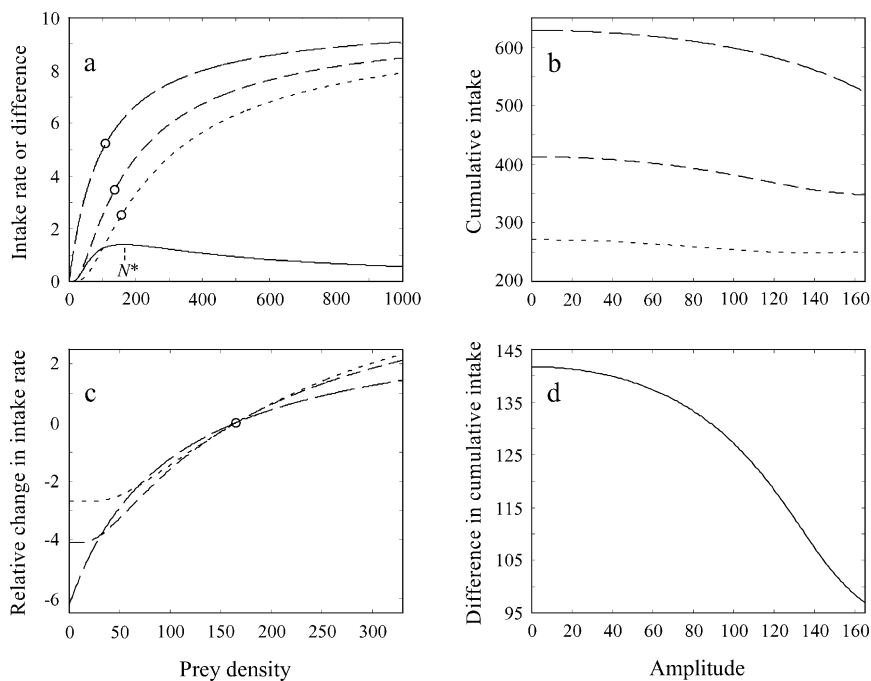


Fig. 1. Evaluations of effects of different levels of interference and fluctuating prey availability on foraging among predators. Interference levels are the functional responses of a forager not experiencing interference (long-dashed lines), a strong interferer (intermediately-dashed lines), and that of a weak interferer (short-dashed lines). a) The functional responses of the interference levels. The difference in intake rates between the strong and the weak interferer (solid line) is a function of prey density, and is maximised at  $N^*$ . Circles denote intake rates corresponding to the average intake rates at the highest amplitude in Fig. 1b. b) Cumulative intakes for predators experiencing different levels of interference are affected by amplitude of temporal prey fluctuation. c) The relative change in intake rate with increased or decreased prey density compared with intake at  $N^*$  for the different degrees of interference. The circle denotes the standardised intake rates, where intake rates for  $N^*$  from Fig. 1 are set to zero for each forager type. d) The difference in cumulative intake between the stronger and the weaker interferer is a function of prey fluctuation amplitude. In Fig. 1b and d, the cumulative intakes are obtained from 100 time-step simulations of foraging in each amplitude of sinusoidal prey fluctuation about an average of  $N^* = 165$ . For all models, where appropriate,  $a = h = 0.1$ ,  $P = 2$ ,  $F_s = 2$ ,  $F_w = 1$ ,  $\alpha = 100$ ,  $t = 0, 1, 2, \dots, 100$ , and  $A = 0, 1, 2, \dots, N^*$ .

such that interfering competitors decrease individual functional responses for all  $m_s > 0$ . The effect of interference on an individual's functional response should increase with increasing competitor interference strength ( $F$ ) and decrease with increasing density of available prey ( $N$ ) (Moody and Ruxton 1996, Triplett et al. 1999):

$$m_F = F\alpha N^{-1} \quad (3)$$

where  $\alpha$  is a constant, scaling the effect of prey density on interference.

In a situation with two predators competing and interfering over food, where the two predators differ in interference strength, both predators' functional responses should be affected by interference (i.e.  $F > 0$  in both cases). Thus, the stronger ( $s$ ) interferer should also suffer a decrease in its functional response, e.g. through time spent involved in interactions, but this decrease should always be smaller than the effect on the weaker ( $w$ ) interferer's (Fig. 1a). Since the effect of interference is prey-density dependent, the difference ( $I_{mdif}$ ) in intake rates between the two predators:

$$I_{mdif} = I_{ms} - I_{mw} \quad (4)$$

will be a function of prey density. When prey densities approach zero, the difference between the two unequal interferers will be low, since intake rates for both predators would also approach zero. The difference in food intake will then increase with increasing prey densities, reach a maximum, and then decrease monotonically with increasing prey density (Fig. 1a).

The difference between the functional responses reaches its maximum at prey density  $N^*$  (Fig. 1a). If prey is always available in this density, the stronger interferer should presumably enjoy a greater differential food intake, which would imply a fitness increment. Weaker interferers could then choose to migrate to avoid competition or stay and face the high competitive pressure and lower fitness potential. In any case, this provides no mechanism explaining how unequal interferers coexist. This is however under the premise that prey temporal availability pattern is stable; the objective of this work is to evaluate the effects of temporally fluctuating prey on unequal interferers staying and foraging in the same patch. We here use a sinusoidal pattern of temporally fluctuating prey to evaluate these effects. A sinusoidal fluctuation pattern could plausibly arise from, for example, prey behaviour and/or diurnal cyclicality, and also provides reliable and convenient opportunities for mathematical evaluations of effects on functional responses. For the chosen examples of juvenile salmonids and oystercatchers, the sinusoidal prey fluctuation resembles the diurnal changes in stream prey drift activity, and the tidal variation in

available prey on mudflats or mussel banks, for the two predators, respectively.

Prey density is set to fluctuate around the average of  $N^*$  over time ( $t$ ). The amount of prey present at each time-step ( $N_t$ ) is set to follow

$$N_t = N^* + A \sin(t) \quad A = 0, 1, 2, \dots, N^* \quad (5)$$

where  $A$  denotes the amplitude of the sinusoidal fluctuation.  $A_{max}$  is set to  $N^*$ , in order to make total prey numbers available to the predators remain the same between amplitudes. We then analyse how cumulative intakes ( $I_C$ ) over a 100 time-step period change with amplitude of fluctuation:

$$I_C = \sum_{t=0}^{100} I_X \quad \Delta t = 1 \quad (6)$$

where  $I_X$  is either intake without interference ( $I$ ), intake for the stronger interferer ( $I_{ms}$ ), or intake for the weaker interferer ( $I_{mw}$ ). Cumulative intake without interference is always highest, that of the stronger interferer intermediate, and cumulative intake for the weaker interferer always lowest, and as the amplitude increases, all cumulative intakes are affected, but in different ways (Fig. 1b). Cumulative intake for the functional response without interference decreases with increasing amplitude, and the rate of decrease increases with increasing amplitudes of fluctuation. Cumulative intake for the stronger interferer also decreases with increasing amplitude, but here the rate of decrease decreases at higher amplitudes of prey fluctuation. Finally, for the cumulative intake of the weaker interferer, rate of decrease starts decreasing at lower amplitudes than that for the stronger interferer, and cumulative intake actually starts increasing at the highest amplitudes.

These differences originate in the effects of prey density on intake capacity and interference. As the amplitude of fluctuation increases, the deviations from the average of  $N^*$  increase. This means that at higher amplitudes, prey are sometimes very scarce, and sometimes very abundant. This has different implications for the different functional responses (Fig. 1c). As prey density decreases from  $N^*$ , all functional responses decrease compared with their respective intakes at  $N = N^*$ . However, they do so in different ways, in that the functional response without interference continues decreasing as  $N$  approaches zero, while functional responses with interference level out at small but positive intake rates for low prey densities before reaching zero at  $N = 0$  (Fig. 1c). These differences are explained by the different effects of prey density and interference between functional responses. At very low prey densities, both the stronger and the weaker interferer would suffer greatly from interference, and their intake rates would be low. Intake rates would however not reach

zero until  $N=0$ , which is why they level out towards  $N=0$ . There are also differences in the relative decrease in intake rate at which the functional responses of the two interfering predators level out (Fig. 1c). The weaker interferer has a lower intake rate than the other functional responses at  $N^*$ , and could thus not decrease as much with decreasing prey density. The relative cost with decreasing prey densities would therefore be smaller for the weaker interferer, and it thereby levels out at a smaller relative decrease than for the stronger interferer.

As prey density increases above  $N^*$ , the effect of interference decreases for interfering foragers (eq. 3). Since the interference strength acting on the weaker interferer is greater, an increased prey density would release the weaker interferer from this interference to a relatively greater extent. This is because when prey density starts to decrease substantially the effect of interference, the weaker interferer's intake will be lower than that of the stronger interferer, and therefore also less constrained by handling time ( $h$ : eq. 2). Thus, as prey density increases from  $N^*$ , the weaker interferer enjoys the greatest relative increase in intake rate, the stronger interferer an intermediate, and the functional response without interference the smallest relative increase (Fig. 1c). Thus, as amplitude of fluctuation increases, creating alternating periods with either high, intermediate or low prey densities, the weaker interferer should benefit relatively most from high prey densities and lose the least at low prey densities, explaining the different shapes of cumulative intake in Fig. 1b.

As a means of further visualising the different effects of temporally fluctuating prey among types of functional responses, we translate the cumulative intakes at the highest amplitude of fluctuation to the corresponding intake rates at stable prey availability. The cumulative intakes at the highest amplitude of prey fluctuation in Fig. 1b are  $I_C(I) = 523.08$ ,  $I_C(I_{ms}) = 347.77$ , and  $I_C(I_{mw}) = 250.84$ . Since  $t = 0, 1, 2 \dots 100$  in the cumulative intake models, the cumulative intakes translate to average intake rates of  $I = 5.231$ ,  $I_{ms} = 3.478$  and  $I_{mw} = 2.508$ . These intake rates correspond to different prey densities in the functional responses (Fig. 1a,  $N = 109.69$ ,  $N = 136.69$  and  $N = 156.11$ , respectively). Thus, at high amplitudes of prey fluctuation, the weaker interferer enjoys an indirect effect acting as if it had access to more prey than both the stronger interferer and the functional response without interference.

The effects of temporally fluctuating prey availability would affect the relative benefit of being the stronger interferer, since increasing amplitude of prey fluctuation acts differently on the unequal interferers (Fig. 1b). When we let the difference in cumulative intake ( $I_{Cdif}$ ) between the stronger and weaker interferer follow:

$$I_{Cdif} = \sum_{t=0}^{100} I_{ms} - \sum_{t=0}^{100} I_{mw} \quad \Delta t = 1 \quad (7)$$

and evaluate the effects of fluctuating prey density for the different amplitudes (eq. 5), the relative benefit of being the stronger interferer decreases with increasing amplitude of fluctuation (Fig. 1d). This decrease may act as a stabiliser in the competition between unequal interferers, and short-term temporal fluctuations in prey availability may therefore be an important mechanism allowing for among-individual intraspecific phenotypic diversity in predators that interfere over foraging opportunities.

The mechanism behind the decreased difference in cumulative intake between interferers with increased amplitude of fluctuation could be associated with resource defence. Resource defensibility changes with prey density; at low prey density resource defence is possible and pays off, while at high prey density resource defence should be neither as possible nor as beneficial (Monaghan and Metcalfe 1985, Grant and Kramer 1992). Therefore, as high amplitudes of fluctuation produce alternating high and low prey densities, resource defence decreases at high prey density, where subordinates may forage successfully from temporally super-abundant food (Martin-Smith and Armstrong 2002). Resource-defence efficiency in dominants has previously been demonstrated to decrease with addition of subordinate individuals, allowing for increased foraging in subordinates (Ruxton 1999). Our results suggest that such addition of individuals is not necessary to obtain decreased resource-defence efficiency, but that high-amplitude temporal fluctuations may cause similar effects.

Unequal interferers may have different life-history strategies, and different phenotypic characteristics have previously been suggested to promote unequal interferer coexistence through various costs to dominants. For instance, being a stronger interferer could be associated with increased levels of activity and aggression (Hogstad 1986), which may lead to increases in both time occupied fighting and risk of predation or energy expenditure (Ens and Goss-Custard 1986, Jakobsson et al. 1995). Also, a high metabolic activity could, via stress, increase risk of infections (Pedersen and Hoffman-Goetz 2000). However, these costs to dominants have to be relatively large to enhance unequal interferer coexistence on their own. As suggested in this work, short-term temporal fluctuations in prey density may decrease the relative benefit to stronger interferers by around a third. Thus, short-term temporal fluctuations in prey availability would allow unequal interferer coexistence under much smaller phenotypic differences between interferers, and thereby extensively relax the conditions under which coexistence may appear and persist. The effects of temporally fluctuating prey on functional responses among interfering predators

should therefore be an important mechanism behind how they may coexist. We thus recommend that short-term temporal distribution of prey availability should be taken into consideration in theoretical and empirical investigations of effects of prey density on food intake and coexistence among unequal interferers.

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