Intake rates and the functional response in shorebirds (*Charadriiformes*) eating macro-invertebrates

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ABSTRACT

As field determinations take much effort, it would be useful to be able to predict easily the coefficients describing the functional response of free-living predators, the function relating food intake rate to the abundance of food organisms in the environment. As a means easily to parameterise an individual-based model of shorebird Charadriiformes populations, we attempted this for shorebirds eating macro-invertebrates. Intake rate is measured as the ash-free dry mass (AFDM) per second of active foraging; i.e. excluding time spent on digestive pauses and other activities, such as preening. The present and previous studies show that the general shape of the functional response in shorebirds eating approximately the same size of prey across the full range of prey density is a decelerating rise to a plateau, thus approximating the Holling type II ('disc equation') formulation. But field studies confirmed that the asymptote was not set by handling time, as assumed by the disc equation, because only about half the foraging time was spent in successfully or unsuccessfully attacking and handling prey, the rest being devoted to searching.

A review of 30 functional responses showed that intake rate in free-living shorebirds varied independently of prey density over a wide range, with the asymptote being reached at very low prey densities (<150/m^{-2}). Accordingly, most of the many studies of shorebird intake rate have probably been conducted at or near the asymptote of the functional response, suggesting that equations that predict intake rate should also predict the asymptote.

A multivariate analysis of 468 'spot' estimates of intake rates from 26 shorebirds identified ten variables, representing prey and shorebird characteristics, that accounted for 81% of the variance in logarithm-transformed intake rate. But four-variables accounted for almost as much (77.3%), these being bird size, prey size, whether the bird was an oystercatcher *Haematopus ostralegus* eating mussels *Mytilus edulis*, or breeding. The four variable equation under-predicted, on average, the observed 30 estimates of the asymptote by 11.6%, but this discrepancy was reduced to 0.2% when two suspect estimates from one early study in the 1960s were removed. The equation therefore predicted the observed asymptote very successfully in 93% of cases.

We conclude that the asymptote can be reliably predicted from just four easily measured variables. Indeed, if the birds are not breeding and are not oystercatchers eating mussels, reliable predictions can be obtained using just two variables, bird and prey sizes. A multivariate analysis of 23 estimates of the half-asymptote constant suggested they were smaller when prey

were small but greater when the birds were large, especially in oystercatchers. The resulting equation could be used to predict the half-asymptote constant, but its predictive power has yet to be tested.

As well as predicting the asymptote of the functional response, the equations will enable research workers engaged in many areas of shorebird ecology and behaviour to estimate intake rate without the need for conventional time-consuming field studies, including species for which it has not yet proved possible to measure intake rate in the field.