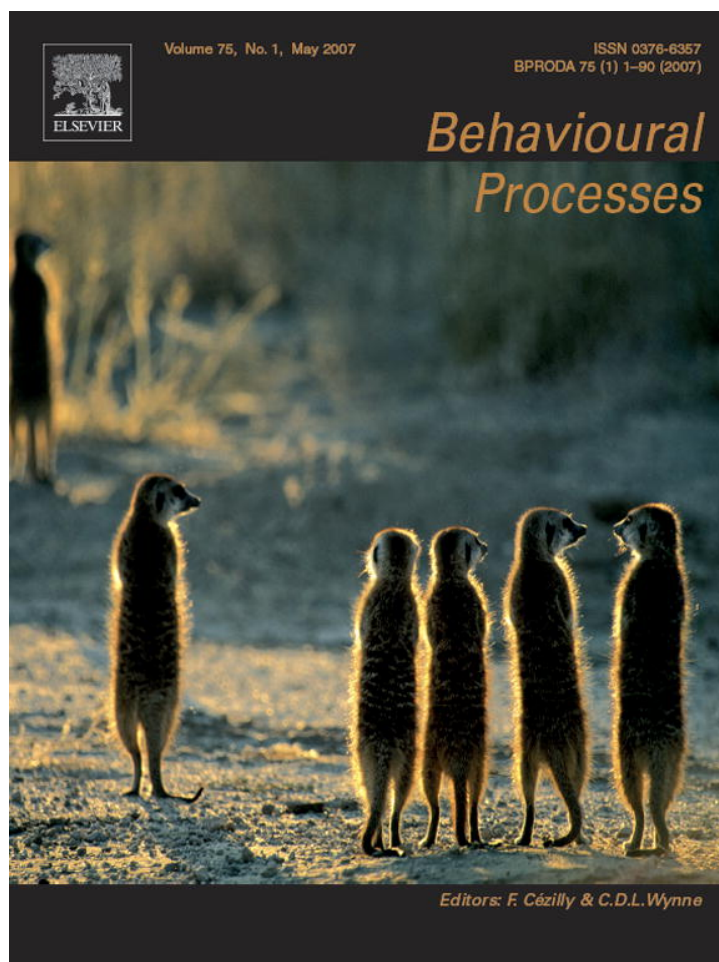


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## Experimental functional response and inter-individual variation in foraging rate of teal (*Anas crecca*)

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### Abstract

The functional response, i.e. the change in per capita food intake rate per time unit with changed food availability, is a widely used tool for understanding the ecology and behaviour of animals. However, waterfowl remain poorly explored in this context. In an aviary experiment we derived a functional response curve for teal (*Anas crecca*) foraging on rice (*Oryza sativa*) seeds. We found a linear relationship between intake rate and seed density, as expected for a filter-feeder. At high seed densities we found a threshold, above which intake rate still increased linearly but with a lower slope, possibly reflecting a switch from filter-feeding to a scooping foraging mode.

The present study shows that food intake rate in teal is linearly related to food availability within the range of naturally occurring seed densities, a finding with major implications for management and conservation of wetland habitats.

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**Keywords:** *Anas crecca*; Aviary experiment; Food intake rate; Functional response

### 1. Introduction

The functional response, defined as the change in a predator's instantaneous food intake rate with increasing density of food in the environment (Solomon, 1949), is a keystone concept in foraging theory (Stephens and Krebs, 1986). Because of their fundamental importance in predator–prey systems, functional responses are now centrepieces of theoretical modelling exercises dealing with foraging (e.g. Morgan et al., 1997; Hobbs et al., 2003; Joly and Patterson, 2003; Drossel et al., 2004) as well as, more recently, behaviour-based individual models of population dynamics (e.g. Pettifor et al., 2000; Stillman et al., 2000).

A major source of difficulty when describing a functional response is the foraging behaviour of the studied animals, and this is particularly true when observations are done in situ. Most functional response studies to date have been carried out on carnivorous mammals (e.g. O'Donoghue et al., 1998; Hayes and Harestad, 2000; Hoener et al., 2002) or birds of prey (e.g. Korpimäki and Norrdahl, 1989, 1991; Nielsen, 1999; Redpath and Thirgood, 1999), as well as invertebrate-eating waders (e.g. Goss-Custard and Durel, 1988; review in Goss-Custard et al. pers. comm.). The functional response of herbivores, mainly mammals but also to a lesser extent herbivorous waterfowl, has also been the subject of many studies (waterfowl: Rowcliffe et al., 1999; Lang and Black, 2001; Durant et al., 2003; mammals: e.g. Andersen and Saether, 1992; Spalinger and Hobbs, 1992; Bergman et al., 2000; Illius et al., 2002). In all these cases, the number of successful foraging attempts was quite easy to distinguish and quantify, e.g. all “bites” being considered as successful foraging attempts in herbivores. Conversely, functional responses of animals with less overt foraging behaviour have rarely been described, mainly because costly field equipment

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or laboratory experiments with captive individuals are required. For example, the use of very sophisticated electronic data loggers allowed the functional response of underwater-foraging pinnipeds to be described only recently (e.g. Mori and Boyd, 2004).

Functional responses for underwater-feeding wildfowl are poorly known (e.g. Wood and Hand, 1985; Nolet et al., 2002), because it is impossible to quantify in the wild whether a foraging event was successful or not, and how much food was ingested (but see Grémillet et al., 2004). This is unfortunate, because such information is essential to predict habitat selection from known food densities, a potentially valuable tool for the management and conservation of these species and their wetlands habitats, and also to better understand intra- and interspecific competition within foraging guilds (e.g. Sutherland and Allport, 1994).

The only published food intake rates for dabbling ducks (*Anas* sp.) concern either discrete data obtained at one or a few food densities (Van Eerden and Munsterman, 1997), or experimental measurements of functional response to poultry pellets (Fritz et al., 2001) or planktonic invertebrates (Tolkamp, 1993; Mott, 1994). However, many dabbling ducks feed largely on seeds for a large part of the year (fall, winter and, to some extent, spring, Del Hoyo et al., 1992). To our knowledge, only one functional response has been described for waterfowl consuming seeds (Van Eerden and Munsterman, 1997; teal *Anas crecca* foraging on Millet). Dabbling ducks are opportunistic feeders that use a variety of foraging behaviours from pecking to filter-feeding (Kooloos et al., 1989; Kooloos and Zweers, 1991; Gurd, 2005). Fritz et al. (2001) demonstrated that the pecking behaviour of mallard (*Anas platyrhynchos*) corresponded to a type II functional response, i.e. food intake rate increased in a decelerating, asymptotic fashion with food density. Filter-feeders, however, are generally thought to be more likely to have a type I functional response, described as a linear increase in intake rate with increasing food density up to a threshold, above which intake rate remains constant (Begon et al., 1990). Indeed, Van Eerden and Munsterman (1997) showed that the food intake rate of teal foraging on Millet increased linearly with seed density, thus suggesting a type I functional response, although the range of seed densities offered may not have included values at which intake rate would reach a plateau.

Van Eerden and Munsterman (1997) as well as Fritz et al. (2001) found major inter-individual differences in feeding efficiency in ducks. This puts the determinants of individual behavioural traits in focus, as the latter may explain subsequent inter-individual differences in survival, body condition, and even reproductive success (e.g. Caldow et al., 1999). In grazing waterfowl, bill size and body size have been shown to influence individual maximum intake rate (Durant et al., 2003), and this may also be the case in filter-feeding teal, as bill dimensions may affect how much water can be filtered (Kooloos et al., 1989).

The objective of the present paper was to test whether teal feeding on rice seeds, a common food in this species and other dabbling ducks in winter (Tamisier, 1971a), exhibit a type I or a type II functional response and to quantify individual variation in foraging rate.

## 2. Methods

### 2.1. Birds and experiments

This study was carried out in the Camargue, southern France, from October 2004 to March 2005. Six captive-bred teal (two males and four females) were kept in a 111 m<sup>2</sup> aviary, starting 1 year before the experimental trials in order for the birds to become accustomed to the environment, the feeding conditions and human presence. All procedures in this study adhered to the ethical standards for use of animals as approved by the French Ministry for Environment and Sustainable Development, and further satisfied the requirements of the Animal Welfare Regulations from the French Ministry of Research. H. Fritz has been granted a certificate for the ethics in animal experiments by the CNRS and the French Ministry of Research in June 2000, and a capture/handling permit for anatids (no. 2102933791). The ground in the aviary was covered by natural vegetation dominated by grass, and it was sheltered from direct sunlight by tall trees. Foraging trials were done in a 24 m<sup>2</sup> pond in the middle of the aviary, also used for swimming and foraging before the experimental period started.

The night before each experiment birds were deprived of food. One trial was performed per day, usually taking place in the morning. Teal could access poultry pellets, wheat and rice ad libitum between trials, and they could always access water in the pond. In each experimental trial, seeds were offered on a tray divided into eight square compartments (10.5 cm × 10.5 cm) and submersed 2 cm into the water. Rice seeds averaged 0.5950 cm in length ( $\pm 0.0045$  SE;  $n = 50$ ). In order to prevent visual detection of food items and thus to mimic natural conditions (Guillemain et al., 2000), the seeds in each compartment were covered by 4 g of sand grains, whose diameter was 0.1–1 mm. Using the same density in each of the eight compartments per trial, we offered 10, 20, 30, 50, 100, 200, 300, 400, or 500 seeds per patch (i.e. tray compartment), representing a range from 18 to 913 g m<sup>-2</sup>. Before each trial, we counted the seeds instead of weighing them, because the latter would have required oven-drying the rice before and after each experiment, as well as sieving the sand, a treatment that caused the seeds to crumble into pieces in pre-experiment trials. The order in which the different seed densities were offered was randomized, and 9–13 trials were performed for each density, resulting in 94 separate trials over a period of more than four months.

Nasal saddles permitted individual recognition of the birds. These markers do not affect duck behaviour, as previously tested under a wide range of situations (Guillemain et al., 2007). Bird behaviour was video-recorded from a hide 10 m from the tray. A trial started when the first teal put its bill in the tray, and was generally stopped before another individual started feeding from the same compartment of the tray. In this way individual intake rate could be calculated by counting the number of seeds remaining and by relating this value to the foraging time as determined from the video footage. Occasionally, when two or more birds foraged in the same compartment, the food intake rate of each individual was assumed to be the same as the intake rate the individual had in other compartments during the same trial.

This provided us with an estimate of the potential intake rate of the bird per compartment considering that potential biases linked to food depletion, saturation of the bill and digestive apparatus might be reached at the same scale than for a bird foraging at the same patch for the whole trial. Moreover, to avoid the potential bias of inter-individual differences, we calculated the food intake rate separately per individual. If such a reference was not available, then the data from compartments used by several individuals were not considered. Moreover, to avoid the confusing effect of food depletion on measures of intake rate (Royama, 1971, see also Fritz et al., 2001), trials never lasted more than a few minutes (the maximum feeding time in one tray compartment was 41 s). Because teal foraged largely by filter-feeding, it was not possible to estimate peck rate and bite size, both of which are generally measured in functional response studies. Rather, we directly measured the number of seeds taken per second of filtering, similar to the dry mass of *Zostera* spp. taken per second head down by Brent Geese (*Branta bernicla bernicla*) measured by Pettifor et al. (2000).

## 2.2. Statistical analyses

To avoid pseudoreplication, the average food intake rate per second was calculated for each bird for each seed density over all trials. The data set thus consisted of 54 measures of food intake rate (6 individuals  $\times$  9 food densities). To test which type of functional response fit our data best, we first explored the classical type II response derived from Holling's (1959) disc equation. As a second option we fit a model that consisted of two linear segments that join at a 'break-point'. If ducks exhibit a type I relationship, we expected a relationship with a linear increase at low rice densities, then a linear relationship with slope = 0 after a threshold density (i.e. the 'break-point'). Type II functional responses were fitted to our data using Statistica (Statsoft, 2002). SAS (SAS Institute, 1997) was used to fit the type I response.

## 3. Results

The overall fit of the type II functional response to our data was significant:  $F_{2,53} = 305.55$ ,  $r^2 = 0.56$ ,  $p < 0.0001$ . The estimated values of the two parameters in Holling's disc equation were  $0.20 \pm 0.04$  SE and  $0.17 \pm 0.01$  SE, so that the fitted model was  $IR = (0.20 \times FD) / (1 + 0.20 \times FD \times 0.17)$ , where IR = seed intake rate (seeds  $s^{-1}$ ) and FD = offered seed density (seeds patch $^{-1}$ ). Teal, therefore, showed a clear type II functional response with an asymptotic intake rate of  $1/0.17$  seeds  $s^{-1}$  (Fig. 1a).

However, the fit of the break-point model indicated that there was a threshold in foraging rate when seed density was between 100 and 200 per patch. We assumed this threshold was at 101 seeds per patch (corresponding to a weight of 2.03 g per patch, or 0.02 g  $cm^{-2}$ ), though it could be anywhere between 101 and 199 without affecting the statistical fit of the model. The break-point model fit the data even better than the type II functional response ( $F_{4,50} = 197.18$ ,  $r^2 = 0.94$ ,  $p < 0.0001$ ; Fig. 1b). However, the break-point model did not correspond to a classical type I func-

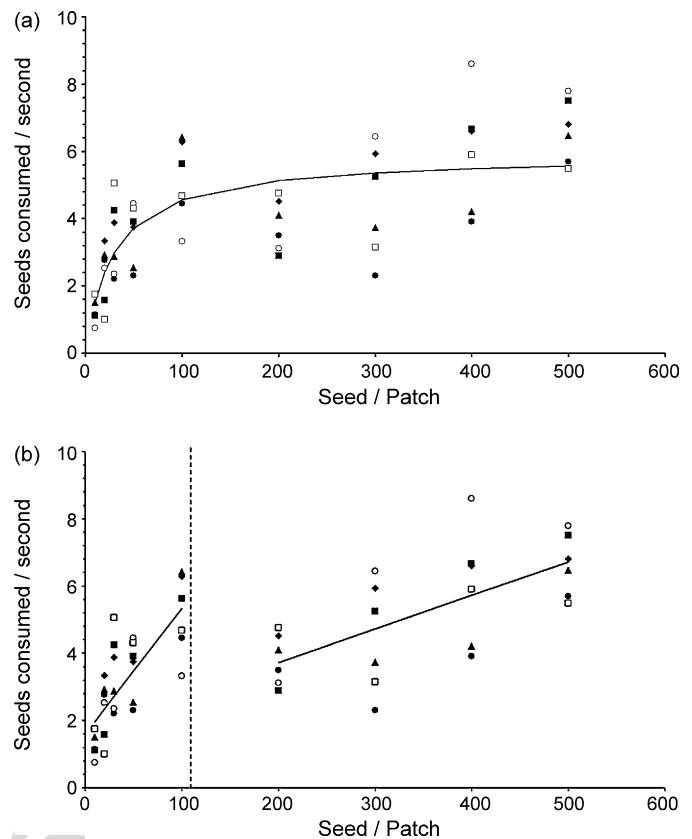


Fig. 1. Food intake rate (seeds  $s^{-1}$ ) of teal as a function of food density (seeds per patch in an experimental tray). Symbols denote values for each of the six individuals. (a) Top: the curve is the fitted type II functional response (see text); (b) bottom: the lines show the two successive linear functional responses. The dotted, vertical line indicates the estimated break point at 101 seeds per patch.

tional response (i.e. a linear increase followed by a plateau). Rather, it described a set of two successive linear increases: the intercept and slope of the first linear increase (i.e. below 101 seeds) were  $1.59 \pm 0.34$  and  $0.037 \pm 0.01$  (mean  $\pm$  SE), respectively. At densities of 101 seeds per compartment and higher, the slope was  $0.01 \pm 0.002$ . The difference in intake rate between the two linear relationships when seed density was equal to 101, the break-point in this analysis, was computed to be  $-2.62 \pm 0.72$ . The intercept of the second linear increase (when seed density was above 199) was therefore 1.74. Note that the intercepts of the two successive linear increases were not significantly different, which is what would be expected if they represent two separate linear functional responses.

Note also that according to this model the intake rate was different from zero when seed density was equal to zero for both linear relations obtained. Consequently, we fitted linear relationships with a first intake rate value of zero at a seed density of nil. We then obtained slopes that differed slightly from the previous: the slope of the functional response when seed density was below 101 seeds was  $0.06 \pm 0.01$  ( $t_5 = 6.86$ ,  $r^2 = 0.81$ ,  $p < 0.001$ ) and  $0.01 \pm 0.00$  ( $t_4 = 18.87$ ,  $r^2 = 0.98$ ,  $p < 0.0001$ ) when it was above 199 seeds. Note that the slope of the first functional response was in the same range of values as that estimated by Van Eerden and Munsterman (1997) for teal consuming Millet, i.e. 0.04. The difference between the linear relationships estimated by the model

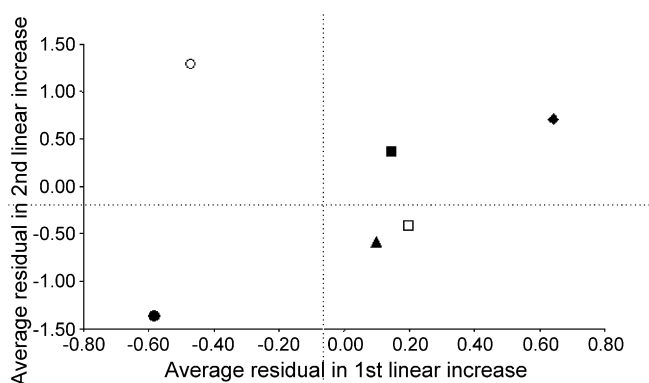


Fig. 2. The relationship between individual average residuals for the 1st and the 2nd linear patterns of food intake rate. Symbols denote individuals as in Fig. 1. Value for male “A” is indicated by a circle.

and the linear relationship forced to pass zero might thus only be an artefact of the fit.

We used the Akaike Information Criterion with the adjustment for small sample size ( $AIC_C$ ; Burnham and Anderson, 2002) to further test which model fit the data best. Even by this criteria, the break point model was retained as the best model because its  $AIC_C$  value was much lower ( $AIC_C = 19.9$ ;  $k = 6$ ) than that of the type II functional response ( $AIC_C = 185.4$ ,  $k = 5$ ).

Considering inter-individual variation in foraging rate, the birds that fed the fastest at low seed densities also seemed to feed the fastest at high seed densities (Fig. 2). This is especially the case if we exclude one obvious outlier individual (male “A” in Fig. 2).

#### 4. Discussion

Understanding functional responses is vital for predicting how individuals value habitats that differ in food density, how intra- or interspecific competition may develop in such a habitat, and how birds respond to changes in food availability. In this last case, managers will benefit greatly from knowing the shape of the functional response, as an increase in food abundance will not have the same effect on intake rate if it is linear (i.e. type I) as when it is non-linear (i.e. type II).

Animals eating immobile prey or food items that are easy to detect visually usually have non-linear type II functional responses (Begon et al., 1990; Sutherland, 1996) simply because at high prey densities there is virtually no searching time. On the other hand, Holling (1959) predicted that filter-feeders should show a type I functional response because they have negligible handling time, allowing them to ingest many items simultaneously. At very high prey densities, animals would then be limited by the volume of fluid they can filter per unit of time, which determines the number of food items they can process with their feeding apparatus, limiting their maximum intake rate. Mott (1994) and Tolkamp (1993) studied the functional response in dabbling ducks eating swimming *Cladocera*, but there are only two studies concerning non-moving, non-floating prey. In the first, Fritz et al. (2001) observed a type II functional response for mallard eating poultry pellets. The feeding mechanism involved

in this experiment was, however, similar to a pecking behaviour. To date, the only published functional response we know about for a granivorous duck filter-feeding seeds is for teal foraging on Millet in an experimental set-up (Van Eerden and Munsterman, 1997). These authors found a linear relationship (i.e. the first part of a type I functional response) between seed density and intake rate for densities ranging from 0 to 430  $\text{g m}^{-2}$ .

We also found that variation in seed intake rate was well explained by changes in seed density. A succession of two linear increases, rather than a type II functional response, fit our data the best. Below 101 seeds per patch, the linear relationship that we observed had the same slope as the relationship Van Eerden and Munsterman (1997) found for teal filter-feeding Millet seeds, which weigh roughly 1/8 of the rice seeds we used. This is consistent with a filtering behaviour, where intake rate always increases at the same rate with increasing food density, but where instantaneous intake rate expressed in mass per unit of time for a given density of food particles is determined by the individual mass of the latter. The second linear relationship that we observed, at densities above 199 seeds per patch, had a slope almost four times lower, but which was nonetheless significantly different from zero. This indicates that the observed pattern does not actually describe a classical type I functional response, but rather, a more complicated pattern of two successive linear increases for the range of seed densities considered. The break point in our study occurred between 101 and 199 seeds per patch, i.e. between 184.39 and 363.31  $\text{g m}^{-2}$  (average seed mass was  $0.02 \text{ g} \pm 0.01 \text{ SE}$ ,  $n = 50$ ). It is striking that Van Eerden and Munsterman, who presented teal with millet densities ranging from 0 to 431  $\text{g m}^{-2}$ , did not observe such a break. However, it cannot be excluded that the difference in seed size between the two studies affected the break point, especially if the latter is linked to a saturation of the feeding apparatus. It is also noteworthy that the computed intake rate for 200 seeds per patch ( $3.73 \text{ seeds s}^{-1}$ ) was lower (paired  $t$ -test, mean difference  $1.32 \text{ seeds s}^{-1}$ ,  $t_5 = 2.83$ ,  $p = 0.037$ ) than that for 100 seeds per patch ( $5.33 \text{ seeds s}^{-1}$ ), and then subsequently increased gradually with increasing seed density. We hypothesize that the break point and the decrease in food intake rate were due to a switch in foraging methods at, and above, 200 seeds per patch. Although we video-taped the birds from a hide 10 m from the tray it was not possible to check whether this behavioural switch really occurred. Nevertheless, we have already shown that below this density teal were most likely filter-feeding (see above). Above the threshold, if birds remained filter-feeders and if 101 seeds per patch was the saturation point, then their food intake rate would remain constant as in type I functional responses. What we observed, however, was a drop in food intake rate between 101 and 199 seeds per patch. It may be that, above 199 seeds per patch, teal switched to scooping (i.e. the birds filling their bill by pushing it into a thick layer of food items) as observed for mallard by Fritz et al. (2001). Because it is such a different method compared to filter-feeding, it is quite natural that individual food intake rate does not increase at the same rate with increasing seed density. The reason why intake rate dropped at the moment of this supposed switch in methods calls for further examination.

Whatever the reason, it has to be kept in mind that seed densities leading to the observed switch in foraging methods probably only rarely occur in the wild: seed density in duck foraging habitats in the Camargue do not exceed  $50 \text{ g m}^{-2}$  (Tamisier, 1971b), while Baldassare and Bolen (1984) consider  $70 \text{ g m}^{-2}$  as an upper limit for natural conditions. However, seed densities up to  $140\text{--}330 \text{ g m}^{-2}$  have been recorded in crop fields (Clark et al., 1986). Two hundred seeds per patch in our experimental set-up correspond to more than  $360 \text{ g m}^{-2}$ . The main result of this study, therefore, is that for the range of seed densities corresponding to those occurring in the wild, teal show a linear increase in food intake rate with increased food density, i.e. the initial increasing part of a type I functional response.

Foraging efficiency differed quite markedly between individuals, in the first as well as in the second linear increase of food intake rate. When the outlying individual had been removed we observed that the same individuals always seemed to have the highest intake rates regardless of the offered seed densities. Bill volume has been found to be positively related to foraging rate in filter-feeding ducks (Kooloos et al., 1989; Gurd, 2007). In addition, food intake rate may be related to individual body mass, as it has been found in the Wigeon (*Anas penelope*) by Durant et al. (2003). Unfortunately, because the number of sampled individuals did not provide enough statistical power, we were unable to test whether differences in intake rate are associated with differences in body mass, bill volume or other bill characteristics.

From the wetland manager's point of view, our results suggest that any change in the density of available food will dramatically alter the expected benefit for foraging teal in the field. Still it has to be kept in mind that this was an experiment with captive birds. A study based on wild individuals under natural conditions would be highly valuable, but we think it is impossible to carry out with the present predatory–prey system. Still our results are crucial information, implying that the suitability of foraging habitats can almost always be improved by appropriate management actions. The reference curve provided by this study will allow people in charge of management and conservation of granivorous waterfowl habitats to predict teal choice and foraging behaviour, a major step forward for decision-making in this area. Even if food is not the sole driving factor affecting individual abundance, distribution and behaviour (Crome, 1985), functional responses remain a key parameter in this domain.

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### References

- Andersen, R., Saether, B.E., 1992. Functional response during winter of a herbivore, the Moose, in relation to age and size. *Ecology* 73, 542–550.
- Baldassare, G.A., Bolen, E.G., 1984. Field-feeding ecology of waterfowl wintering on the Southern high plains of Texas. *J. Wildl. Manage.* 48, 63–71.
- Begon, M., Harper, J.L., Townsend, C.R., 1990. *Ecology—Individuals, Populations and Communities*, second ed. Blackwell Scientific Publications, Oxford, 945 pp.
- Bergman, C.M., Fryxell, J.M., Gates, C.C., 2000. The effect of tissue complexity and sward height on the functional response of wood bison. *Funct. Ecol.* 14, 61–69.
- Burnham, K.P., Anderson, D.A., 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, second ed. Springer, New York, USA, 102 pp.
- Caldow, R.W.G., Goss-Custard, J.D., Stillman, R.A., Durell, S.E.A., Dit, L.V., Swinfen, R., Bregnballe, T., 1999. Individual variation in the competitive ability of interference prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *J. Anim. Ecol.* 68, 869–878.
- Clark, R.G., Greenwood, H., Sudgen, L.G., 1986. Estimation of grain wasted by field-feeding ducks in Saskatchewan. *J. Wildl. Manage.* 50, 184–189.
- Crome, F.H.J., 1985. An experimental investigation of filter-feeding on zooplankton by some specialized waterfowl. *Aust. J. Zool.* 33, 849–862.
- Del Hoyo, J., Elliott, A., Sargatal, J., 1992. *Handbook of the Birds of the World*, vol. 1. Lynx Edicions, Barcelona, Spain, 696 pp.
- Drossel, B., McKane, A.J., Quince, C., 2004. The impact of nonlinear functional responses on the long-term evolution of food web structure. *J. Theor. Biol.* 229, 539–548.
- Durant, D., Fritz, H., Blais, S., Duncan, P., 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *J. Anim. Ecol.* 72, 220–231.
- Fritz, H., Durant, D., Guillemain, M., 2001. Shape and sources of variations of the functional response of wildfowl: an experiment with mallards, *Anas platyrhynchos*. *Oikos* 93, 488–496.
- Goss-Custard, J.D., Durell, S.E.A., LeV. Dit, 1988. The effect of dominance and feeding method on the intake rates of Oystercatchers, *Haematopus ostralegus*, feeding on Mussels. *J. Anim. Ecol.* 57, 827–844.
- Grémillet, D., Kuntz, G., Delbart, F., Mellet, M., Kato, A., Robin, J.-P., Chailion, P.-E., Gendner, J.-P., Lorensen, S.-H., Le Maho, Y., 2004. Linking the foraging performance of a marine predator to local prey abundance. *Funct. Ecol.* 18, 793–801.
- Guillemain, M., Fritz, H., Blais, S., 2000. Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*). *Behav. Proc.* 50, 123–129.
- Guillemain, M., Poisbleau, M., Denonfoux, L., Lepley, M., Moreau, C., Massez, G., Leray, G., Caizergues, A., Arzel, C., Rodrigues, D., Fritz, H., 2007. Multiple tests of the effect of nasal saddles on dabbling ducks: combining field and aviary approaches. *Bird Study* 54, 35–45.
- Gurd, D.B., 2005. The ecology of adaptive radiation of dabbling ducks (*Anas* spp.). Ph.D. Thesis, Simon Fraser University, Canada, 135 pp.
- Gurd, D.B., 2007. Predicting resource partitioning and community organization of filter-feeding dabbling ducks from functional morphology. *Am. Nat.* 169, 334–343.
- Hayes, R.D., Harestad, A.S., 2000. Wolf functional response and regulation of moose in the Yukon. *Can. J. Zool.* 78, 60–66.
- Hobbs, N.T., Gross, J.E., Shipley, L.A., Spalinger, D.E., Wunder, B.A., 2003. Herbivore functional response in heterogeneous environments: a contest among models. *Ecology* 84, 666–681.
- Hoener, O.P., Wachter, B., East, M.L., Hofer, H., 2002. The response of spotted hyenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *J. Anim. Ecol.* 71, 236–246.
- Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Ent.* 91, 385–398.

- Illiis, A.W., Duncan, P., Richard, C., Mesochina, P., 2002. Mechanisms of functional response and resource exploitation in browsing roe deer. *J. Anim. Ecol.* 71, 723–734.
- Joly, D.O., Patterson, B.R., 2003. Use of selection indices to model the functional response of predators. *Ecology* 84, 1635–1639.
- Kooloos, J.G.M., Kraaijeveld, A.R., Langenbach, G.E.J., Zweers, G.A., 1989. Comparative mechanics of filter-feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes). *Zoomorphology* 108, 269–290.
- Kooloos, J.G.M., Zweers, G.A., 1991. Integration of pecking, filter feeding and drinking mechanisms in waterfowl. *Acta Biotheor.* 39, 107–140.
- Korpimäki, E., Norrdahl, K., 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. *Oikos* 54, 154–164.
- Korpimäki, E., Norrdahl, K., 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* 72, 814–826.
- Lang, A., Black, J.M., 2001. Foraging efficiency in barnacle geese *Branta leucopsis*: a functional response to sward height and an analysis of sources of individual variation. *Wildfowl* 52, 7–20.
- Morgan, R.A., Brown, J.S., Thorson, J.M., 1997. The effect of spatial scale on the functional response of fox squirrels. *Ecology* 78, 1087–1097.
- Mori, Y., Boyd, I.L., 2004. The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. *Ecology* 85, 398–410.
- Mott, K.M., 1994. A functional morphological approach to the study of filter-feeding in dabbling ducks (*Anas* spp.). M.S. thesis, University of Guelph, Canada, 27 pp.
- Nielsen, O.K., 1999. Gyrfalcon predation on ptarmigan: numerical and functional responses. *J. Anim. Ecol.* 68, 1034–1050.
- Nolet, B.A., Bevan, R.M., Klaassen, M., Langevoord, O., Van Der Heijden, Y.G.J.T., 2002. Habitat switching by Bewick's swans: maximization of average long-term energy gain? *J. Anim. Ecol.* 71, 979–993.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., Hofer, E.J., 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79, 1193–1208.
- Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.H., Houston, A.I., Lang, A., Webb, J., 2000. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J. Appl. Ecol.* 37, 103–135.
- Redpath, S.M., Thirgood, S.J., 1999. Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *J. Anim. Ecol.* 68, 879–892.
- Rowcliffe, J.M., Sutherland, W.J., Watkinson, A.R., 1999. The functional and aggregative responses of a herbivore: underlying mechanisms and the spatial implications for plant depletion. *J. Anim. Ecol.* 68, 853–868.
- Royama, T., 1971. A comparative study of models of predation and parasitism. *Res. Popul. Ecol.* 1 (Suppl.), 1–91.
- Solomon, M.E., 1949. The natural control of animal populations. *J. Anim. Ecol.* 18, 1–35.
- Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *Am. Nat.* 140, 325–348.
- Statsoft Inc., 2002. Statistica–Prise en main. Statsoft Inc., Tulsa, USA, 140pp.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, USA, 247 pp.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., Le, V., Dit Durell, S.E.A., Caldow, R.W.G., McGrorty, S., Clarke, R.T., 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *J. Appl. Ecol.* 37, 564–588.
- Sutherland, W.J., Allport, G.A., 1994. A spatial depletion model of the interaction between bean geese and wigeon with the consequences for habitat management. *J. Anim. Ecol.* 63, 51–59.
- Sutherland, W.J., 1996. *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford, 213 pp.
- Tamisier, A., 1971a. Régime alimentaire des sarcelles d'hiver *Anas crecca* L. en Camargue. *Alauda* 39, 261–311.
- Tamisier, A., 1971b. Les biomasses de nourriture disponibles pour les sarcelles d'hiver *Anas c. crecca* en Camargue. *Rev. Ecol. (Terre Vie)* 25, 344–377.
- Tolkamp, C.R., 1993. Filter-feeding efficiencies of dabbling ducks (*Anas* spp.) in relation to microhabitat use and lamellar spacing. M.S. thesis, University of Guelph, Canada, 40 pp.+appendices.
- Van Eerden, M., Munsterman, M.J., 1997. Patch use upon touch: filter-feeding European Teal *Anas crecca* have environmentally and socially determined foraging goals. In: Van Eerden, M.R. (Ed.), *Patchwork. Patch Use, Habitat Exploitation and Carrying Capacity for Water Birds in Dutch Freshwater Wetlands*. Rijksuniversiteit Groningen, The Netherlands, pp. 165–185.
- Wood, C.C., Hand, C.M., 1985. Food-searching behavior of the common merganser (*Mergus merganser*). I. Functional responses to prey and predator density. *Can. J. Zool.* 63, 1260–1270.