

The cost of vigilance for intake rate in the mallard (*Anas platyrhynchos*): an approach through foraging experiments

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Vigilance while foraging incurs costs such as a reduction of the time available for feeding or a reduction in instantaneous intake rate. Vigilance has two major components: scan rate and scan duration. We investigated the cost of these components for the instantaneous intake rate in Mallard. We first modelled the relationship between food availability and instantaneous intake rate (i.e. the functional response), and looked at the relationship between the residuals of this relationship and scan rate and scan duration. Both scan rate and scan duration were negatively correlated with the residuals, but the cost associated with an increase in each component of vigilance differed. The average time spent in vigilance by ducks was 5 sec per minute: 5 scans of 1 sec decreased the maximum instantaneous intake rate by 2.4% whereas one scan of 5 sec decreased the maximum intake rate by 6%. This shows that an increase in the duration of scans has a greater effect than an increase in their frequency and confirms that vigilance not only affects the time spent feeding but also feeding efficiency through instantaneous intake rate. We explored the potential consequences of such costs in the time spent foraging on a daily basis.

KEY WORDS: *Anas platyrhynchos*, foraging, intake rate, mallard, scan rate, scan duration, vigilance cost.

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INTRODUCTION

Trade-offs between energy gains and vigilance suggest that vigilance while foraging is costly (e.g. BARNARD 1980, LENDREM 1983, PÖYSÄ 1987a, ILLIUS & FITZGIBBON 1994). An increase in vigilance can have a direct negative effect on the food intake rate of individuals either through a reduction in the time available for feeding, or through a decrease in foraging efficiency (LIMA & DILL 1990). For instance, it has been suggested that Great Tits (*Parus major*) can modify their vigilance while foraging to trade off feeding efficiency, and ultimately intake rate, against predation risk or territorial defence (KREBS 1980).

The time spent in vigilance per time unit is the product of the number of scans and the duration of these scans, and both parameters can vary (ROBERTS 1995). Crested terns, *Sterna bergii*, appeared to change their vigilance mainly through variations in scan rates while scan duration remained fairly stable (ROBERTS 1995). Teal (*Anas crecca*), on the other hand, modified their vigilance through scan length (PÖYSÄ 1987a). The time between two scans must be short enough to detect a predator's approach early enough to escape, hence scan rate must remain above a threshold value for vigilant behaviour to be efficient (HART & LENDREM 1984). An increase in scan length allows a more reliable assessment of the environment and may therefore be useful in situations when predators are known to be present (GLÜCK 1987) or when information has to be gathered from the behaviour of conspecifics such as the location of food patches (VALONE 1989). However, although the link between these two components was suggested in early studies on vigilance (MCVEAN & HADDLESEY 1980), their costs in terms of intake rate have not yet been explored. In the context of optimal foraging theory, the measure of these costs is crucial to make predictions on how individuals should allocate their time to feeding and vigilance while foraging (STEPHENS & KREBS 1986).

The intake rate can be defined as the 'absolute' intake rate (the number of grams of food ingested per unit of time spent foraging, i.e. including feeding interruptions), or the 'instantaneous' intake rate (the number of g of food ingested per sec spent feeding) (LENDREM 1984). The instantaneous intake rate is very sensitive to food availability, and vigilance patterns can also change with food supply (LIMA 1987, MCNAMARA & HOUSTON 1994). In this study we analysed the consequences of vigilance behaviour on the instantaneous intake rate with changes in food abundance. We used Mallards (*Anas platyrhynchos*), which, as most Anatidae, have to forage for a long time during winter to meet their daily energy requirements (BRUINZEEL et al. 1997). We used an experimental approach to assess the way in which different patterns of scan rate and scan length affected the instantaneous intake rate and to explore the consequences this may have for the daily foraging time of Mallards.

METHODS

We used 12 captive birds (7 females and 5 males) for the experiments at the Centre d'Etudes Biologiques de Chizé, all of them were reared in captivity and were third generation descendants of birds caught in the marshes of western France.

The experiments were carried out in the first 2 weeks of September 1997 using birds that had been at the laboratory for at least 6 months before the start of the experiments, and

were accustomed to the environment. The enclosure in which they were kept comprised 100 m² of grass, a 25 m² pond and 100 m² of concrete in which the experiments were carried out to prevent the animals from using other sources of food during the experiments.

We estimated the functional response with poultry pellets as food. We presented 0.5 m² patches with varying food abundance: 10, 20, 30, 40, 50, 75, 100, 150, 200 and 300 g of pellets spread evenly in the patch. Individual ducks were offered one patch at a time for 10 min, after one night of food deprivation. Those individuals which started to feed did so within 2 min. After 3 min without feeding behaviour, the trial was stopped. This seldom occurred, but was often related to human disturbance around the experimental area. We recorded the time spent feeding in the patch and the number and the duration of scanning bouts while feeding. We weighed the patch before and after each trial to estimate the amount of grain eaten and calculated instantaneous intake rate (in g per sec feeding). Trials were performed with single individuals to minimise the effects of social interference, but visual contact was still possible with the group to minimise the stress due to isolation: the tested bird was ca 5 m away from the group, separated by a net-like wired fence. All birds ate at patches with at least six different food densities.

Because of the non-linear shape of the relationship between instantaneous intake rate (IIR) and food availability (FA), we log-transformed our data to be able to use a multiple linear regression and covariance analyses (SAS GLM procedure, SAS INSTITUTE 1990). In order to account for individual variations we included individuals as a factor in the covariance analysis between IIR and FA. We tested for an effect of sex on the relationship between IIR and FA by controlling for the effect of the repeated measures done on individuals (repeated measurement option in SAS GLM procedure, SAS INSTITUTE 1990: 952). To study the costs of vigilance we used the approach of SAINO (1994) and calculated the residuals of the relation between IIR and FA, including the effect of individuals. We then used the residuals of this relationship and performed regression analyses with scan duration and scan rate as explanatory variables. The slopes of these relationship are a measure of the reduction in intake rate caused by these variables when controlling for food availability, hence provide estimates of the cost of these two components of vigilance, scan rate and scan duration, on instantaneous intake rate.

RESULTS

The covariance analysis on the log-transformed data with food availability as a covariate and individuals as a factor showed that the individuals did not differ significantly in the slope of the relationship between IIR and FA ($F_{11,69} = 1.72$, $P = 0.086$). Food availability strongly affected intake rate (83% of the explained variance) and the individuals showed significant differences in y-intercepts (Table 1), although this difference between individuals did not explain much of the variance in instantaneous intake rate (17%). Sex had no influence on the relationship once we controlled for the effect of individuals ($F_{1,79} = 1.18$, $P = 0.301$).

Table 1.
Analysis of covariance of Instantaneous Intake Rate (IIR, Log_e-transformed) with food availability (Food, Log_e-transformed) as a covariate and individuals as a factor (Model $F_{12,80} = 10.55$, $P = 0.0001$, $R^2 = 0.61$).

Source	df	SS	MS	F	P
Food	1	0.1771	0.1771	104.67	0.0001
Ind	11	0.0371	0.0034	1.99	0.039

The residuals of the relationship between instantaneous intake rate and food availability were significantly and negatively related to scan rate and scan duration (Table 2). We calculated the cost of each of the components of vigilance using the slope of the log-log relationship, which we back-transformed to give values in g/sec: an increase of vigilance by one look per minute reduced instantaneous intake rate

Table 2.

Multiple regression analysis on the residuals of the relationship between Log_eIRR and Log_eFood (cf. Table 1) with Scan Rate (Log_e -transformed) and Scan Duration (Log_e -transformed) as explanatory variables (Model $F_{2,86} = 7.85$, $P = 0.0007$, $R^2 = 0.16$).

Source	df	MS	F	P
Scan Duration	1	0.0032	5.60	0.0202
Scan Rate	1	0.0035	6.08	0.0157

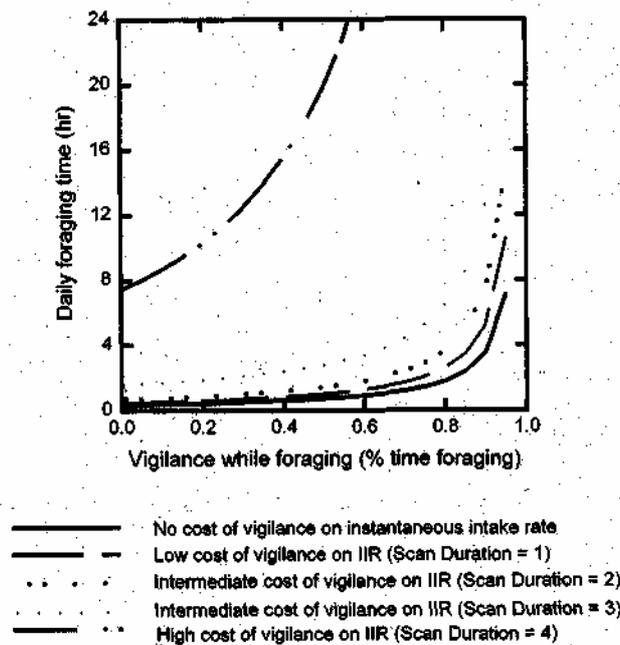


Fig. 1. — The relationship between daily foraging time and the proportion of time spent being vigilant while foraging under different scenarios of vigilance. The bottom line (continuous) represents the cost of vigilance for daily foraging time if vigilance behaviour had no additional effect on instantaneous intake rate. The broken lines incorporate the additional cost of vigilance on instantaneous intake rate with scan duration varying from 1 to 4. The impact of the different patterns of vigilance on instantaneous intake rate translates into an increase in the time needed for foraging to meet the daily requirements.

by 0.006 g/sec, and an increase of scan duration by 1 sec decreased instantaneous intake rate by 0.015 g/sec. This difference between these two components of vigilance can be exemplified further by calculating the maximum instantaneous intake rate (e.g. for 200 g of food) with the minimum vigilance level we recorded (1 look per minute lasting 1 sec), which amounted to 1.24 g/sec. If we take the average time spent in vigilance per minute, 5 sec, the cost of such an effort is different whether vigilance is done through 5 looks of 1 sec or 1 look of 5 sec. In the first case the instantaneous intake rate is decreased by 2.4%, i.e. 1.21 g/sec, in the second option the intake rate is decreased by 6%, i.e. 1.16 g/sec.

We did not find any significant relationship between scan duration and scan rate ($F_{1,76} = 3.12, P > 0.05$), and there was no difference between individuals ($F_{11,76} = 0.55, P > 0.05$). An increase in vigilance was therefore not necessarily due to an increase in both components.

Scan rate was negatively related to food availability with an average slope value of -0.26 SE 0.06 ($F_{1,76} = 24.07, P = 0.0001$), and the slopes of the of individuals did not differ ($F_{11,76} = 1.89, P > 0.05$). There was no significant relationship between scan duration and food availability ($F_{1,76} = 2.27, P > 0.05$), and no effect of 'individual' on the relationship ($F_{11,76} = 0.99, P > 0.05$).

We then modelled the consequences of such differences in cost between vigilance parameters for the daily foraging time of Mallards. We compared the relationship between the percentage of time spent vigilant while foraging and the daily foraging time of the Mallard under the different scenarios of vigilance with a food availability set at 10 g/m^2 , an average biomass density found in the wintering quarters around Rochefort (M. GUILLEMAIN unpublished data). We found, as expected, that the maintenance of a high level of vigilance increased the time spent foraging, and that this was particularly true when incorporating the cost of vigilance for instantaneous intake rate, in addition to the reduction in feeding time (Fig. 1).

DISCUSSION

Our experiments showed, as expected, that individual Mallards increased their instantaneous intake rate when food density increased. We found that vigilance affected instantaneous intake rate negatively, and that the cost of an increase in scan duration was greater than the cost of an increase in scan rate.

LENDREM (1984) suggested that the cost of vigilance for the instantaneous intake rate was related to the head lifting component in each peck (from the contact of a grain to the initiation of the next peck). This could explain the cost due to an increase in scan rate. The cost of an increase in scan duration could be due to a decrease in searching efficiency, or encounter rate in its broadest sense, which would lead to a decrease in intake rate. In our experiment, however, pellets were visible hence easy to find but the length of the feeding interruption appeared to amplify the cost of vigilance. This calls for further investigations of the mechanisms involved in the reduction of instantaneous intake by vigilance.

Our experiments showed that increasing scan rate is less costly, and is therefore likely to be the first parameter to vary adaptively with changes in feeding conditions (e.g. food abundance). Accordingly, scan rate was related to food availability whereas scan duration was not, hence the changes in vigilance of Mallards seemed to occur primarily through variations in the scan rate. However, since the level of

risk was not manipulated, the direct link between changes of vigilance and changes of risk intensity is difficult to define clearly. The fact that scan rate decreased with increasing food availability is consistent with the pattern of starvation risk showed by the curves of daily foraging time in relation to vigilance: because changes in food abundance alter the probability of starving at any level of vigilance, and since the value of daily foraging time (i.e. starvation risk) converges with increasing vigilance, the relationship between vigilance and food abundance is expected to be negative (see MCNAMARA & HOUSTON 1987, REPASKY 1996 for a theoretical discussion).

Since the cost of scan duration is greater than that of scan rate, individuals should minimise scan duration and therefore the frequency distribution of scan duration should be strongly skewed towards 1 sec, and the intensity of vigilance should be adapted mainly through scan rate. However, scan duration cannot be maintained at its minimum permanently because some disturbances may require an increase in the length of the scan in order to inspect the environment more closely. It is also possible that despite their high cost, long scans may be beneficial if they allow the location of better food patches, i.e. with higher intake rates, through the use of information from conspecifics (VALONE 1989). This is a possible explanation for the long scan duration found in Teal (PÖYSÄ 1987b).

An additional and striking result of our experiments was the strength of the differences in intake rate between individuals. This calls for more investigation through similar experiments, since these would allow measures of individual variations in foraging efficiency in an interference-free situation. This would be of major interest since foraging efficiency could be a major determinant of competitive ability in waterbirds (CALDOW et al. 1999).

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