

# Good foragers can also be good at detecting predators

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The degree to which foraging and vigilance are mutually exclusive is crucial to understanding the management of the predation and starvation risk trade-off in animals. We tested whether wild-caught captive chaffinches that feed at a higher rate do so at the expense of their speed in responding to a model sparrowhawk flying nearby, and whether consistently good foragers will therefore tend to respond more slowly on average. First, we confirmed that the time taken to respond to the approaching predator depended on the rate of scanning: as head-up rate increased so chaffinches responded more quickly. However, against predictions, as peck rate increased so head-up rate increased and mean length of head-up and head-down periods decreased. Head-up rate was probably dependent on peck rate because almost every time a seed was found, a bird raised its head to handle it. Therefore chaffinches with higher peck rates responded more quickly. Individual chaffinches showed consistent durations of both their head-down and head-up periods and, therefore, individuals that were good foragers were also good detectors of predators. In relation to the broad range of species that have a similar foraging mode to chaffinches, our results have two major implications for predation/starvation risk trade-offs: (i) feeding rate can determine vigilance scanning patterns; and (ii) the best foragers can also be the best at detecting predators. We discuss how our results can be explained in mechanistic terms relating to fundamental differences in how the probabilities of detecting food rather than a predator are affected by time. In addition, our results offer a plausible explanation for the widely observed effect that vigilance continues to decline with group size even when there is no further benefit to reducing vigilance.

**Keywords:** vigilance; predator detection; escape response; foraging rate

## 1. INTRODUCTION

The degree to which foraging and vigilance are mutually exclusive is crucial to understanding the management of the predation and starvation risk trade-off in animals (Bednekoff & Lima 1998). In many animals the conflict between scanning for predators and foraging appears clear because vigilance and foraging both require time and visual attention, which are both limited resources (Stephens & Krebs 1986; Dukas 1998; Dukas & Kamil 2000), and because animals frequently have to lower their head to forage in a visually obstructive environment (e.g. Bertram 1980). Indeed this conflict has been so self evident that the assumption of overtly non-vigilant (or feeding) individuals not being able to detect attacking predators has historically underpinned all of the most influential models of vigilance behaviour (e.g. Pulliam *et al.* 1982; Lima 1987; McNamara & Houston 1992).

It is clear, however, that in some animals predator detection may be possible while feeding (Lendrem 1984; Lima & Bednekoff 1999), particularly in visually unobstructed environments (Metcalf 1984; Cresswell 1994), and at least in some species of birds there may be considerable adaptation of the eye to facilitate this (Martin 1986; Martin & Katzir 1995). Also, many animals such as granivorous birds or ungulates handle food with their heads raised so that even time allocated to feeding may

not conflict greatly with time allocated to vigilance (Studd *et al.* 1983; Illius & Fitzgibbon 1994). There are, however, few empirical studies that have explicitly examined the relationship between feeding rate and predator detection rate and whether there is in fact a conflict (Lima & Bednekoff 1999).

The temporal pattern of feeding and vigilance bouts is one crucial factor that will determine the degree to which feeding and vigilance conflict. Feeding affects vigilance: the type of prey being eaten and its handling time have clear effects on vigilance behaviour (Metcalf 1984; Lawrence 1985; Popp 1988). Similarly, vigilance affects feeding: certain patterns of feeding may reflect the risk posed by different predators and the vigilance required to detect them (Lendrem 1983; Metcalf *et al.* 1987). Breaking off a feeding bout to scan may also interfere with optimal prey search behaviour, although this will probably depend on the type of prey being sought or the complexity of the environment in which the search is taking place (Dukas & Clark 1995a; Dukas & Kamil 2001). Theoretically, however, there are situations where feeding and vigilance bouts may be complementary. For example, if head-down feeding periods are interspersed with frequent short, but effective, head-up scanning periods then predator detection is unlikely to be affected (Pulliam 1973; Cresswell 1994), particularly if the head-up periods are combined with time spent moving between prey items. Therefore individual animals may choose to feed on a particular prey or in a particular environment because this minimizes the conflict between feeding and vigilance (e.g. Metcalf 1984; Guillemain *et al.* 2001). Similarly, some animals

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that feed more efficiently, in the sense that their feeding conflicts less with vigilance, may be able to use more dangerous feeding areas and prey types. At present, however, we know little about the consequences of individual variation in vigilance and feeding bouts and whether some individuals are more efficient at minimizing the conflict.

In this study, we explore the degree to which predator detection is possible while feeding and how individuals vary in their feeding and scanning behaviour. We used captive, wild-caught chaffinches (*Fringilla coelebs*) to investigate the relationship between foraging rate and the ability to detect a model predator. Chaffinches are granivorous birds that feed typically by lowering their heads to search the ground for seeds in a similar way to juncos, sparrows, buntings or other finches: while searching for seeds it seems much less likely that a predator will be detected compared with when a bird has its head up. First, we confirmed that the hypothesis that increased vigilance increases the speed of responding to a model predator applies to our system. Second, we tested the hypothesis that vigilance and foraging efficiency conflict so that those birds with higher intake rates have lower vigilance rates. We then tested the hypothesis that, as a consequence of the conflict between feeding efficiency and vigilance, birds with higher feeding rates would take longer to respond to the model and vice versa. Finally, we tested whether there were some individuals in the population that consistently allocated more time to searching for food than searching for predators and thus determined whether individuals that were good foragers were also consistently slower at responding to predators.

## 2. METHODS

Chaffinches were caught under licence from English Nature and kept in captivity from one to four months over the winter (2001–2002) at the Wytham Field Laboratory, Oxford. On capture birds were aged, sexed and had their maximum wing chord measured (see Svensson 1984). Chaffinches were housed in standard, small-bird aviary keeping cages on a 12 h daylight cycle and fed *ad libitum* wild bird seed mixture and water. Prior to experiments, birds were deprived of food for 2–3 h. Individuals were allowed at least 48 h to recover between experiments. Any chaffinch that did not feed repeatedly in the experimental set-up or that showed distress was released. Chaffinches were weighed after each experiment: any confounding effects of body condition on feeding and vigilance rates were controlled for by including the mass of the bird divided by its wing length (i.e. mass controlling for size) in all models.

### (a) *Experimental set-up*

The experimental set-up is illustrated in figure 1. Each chaffinch was transferred from its keeping cage in a roosting box or a bird bag to an outside experimental cage. The experimental cage was a 0.5 m<sup>3</sup> wire box placed over a substrate of artificial short stubble. The artificial stubble was created by attaching yellow drinking straws, 3 cm in length, to plywood board and spreading peat compost thinly between them. Straws were arranged in rows at a density of 60 straws m<sup>-1</sup>, with 12.5 cm between rows, equivalent to the stubble density of natural stubble fields, the primary feeding environment for chaffinches wintering on farmland (Wilson *et al.* 1996). Prior to each experiment, the peat was replaced and 200 canary grass (*Phalaris*

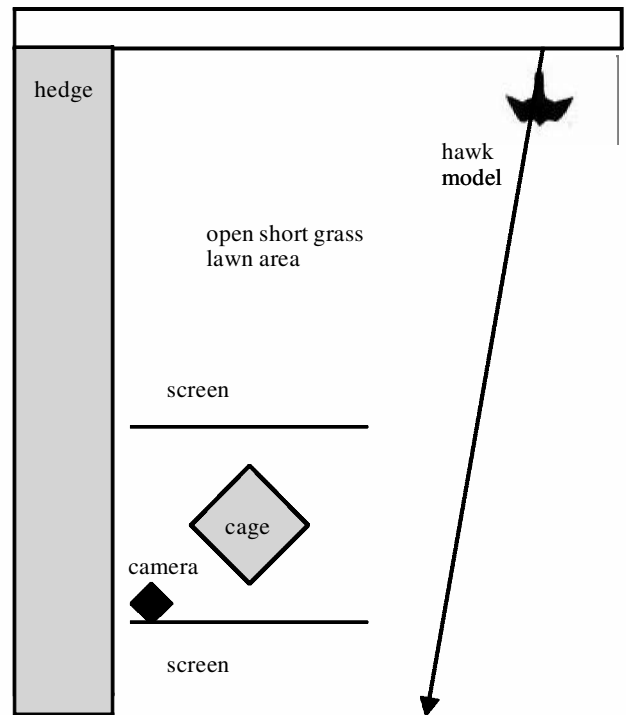


Figure 1. Experimental set-up. Diagram is not to scale.

*canariensis* L.) seeds were placed at random over the 0.5 m<sup>2</sup> basal area of the cage. Feeding trials before the start of the experiments to determine the functional response of the chaffinches found that at this seed density all birds were feeding at their maximal rate: this density is at the upper end of the natural densities found on stubble fields (Moorcroft *et al.* 2002).

The chaffinch was released into the experimental cage and was filmed by a video camera close to the cage. The camera was also positioned so that it captured the first potential appearance of the approaching sparrowhawk model to a chaffinch anywhere in the cage. The experimenter moved behind a screen and observed the bird covertly through a dark glass panel. The trial continued until the chaffinch had fed for more than 20 s and then the experimenter released the model sparrowhawk. The model sparrowhawk was a commercial taxidermic mount of a first winter female fixed in an attacking glide posture (which had become available for taxidermy because of a collision with a window). This slid down a line (see figure 1) and became visible to the chaffinch after a few seconds, emerging from behind the screen to fly past the experimental cage. The model made little noise when released or on descent; however, if the chaffinch changed its foraging behaviour before the sparrowhawk became potentially visible to it (possibly because of this potential noise) then the observation was excluded from the analysis. The model did not always travel down the wire at a uniform speed ( $2.8 \text{ m s}^{-1} \pm 0.1 \text{ s.e.}$ , range of 1.3–4.1) and we therefore controlled for any possible effects of this variation by including model speed when it was visible to the chaffinch in all analyses. The point of first visibility also depended on the position of the chaffinch in the experimental cage: a bird feeding at the front of the cage would be able to see the model earlier than one at the back of the cage. The position of the feeding chaffinch in the cage was therefore recorded to account for this variation: the cage was divided into eight equal areas and the area number in which the chaffinch was feeding was recorded. Once the sparrowhawk had passed the cage, the trial was terminated and the chaffinch was returned to its indoor cage.

Table 1. Variables recorded from each experiment. (Standard variables are in bold and were in all initial models.)

type of variable	variable
individual birds	individual <b>age</b> <b>sex</b> <b>body condition (mass/wing length)</b>
confounding variables	<b>trial number</b> <sup>a</sup> days in captivity <sup>a</sup> number of previous exposures to model <sup>a</sup> <b>model flight speed</b> <b>position of the chaffinch in the experimental cage</b>
vigilance variable	head-up rate <sup>b</sup> mean duration of head-up periods <sup>b</sup> proportion of time spent with head up <sup>b</sup>
foraging variable	mean duration of head-down (food searching) period <sup>b</sup> peck rate <sup>b</sup>
response variable	time from first possible appearance of the model to response (transformed by log) <b>response type (flight or freezing)</b>

<sup>a</sup> Trial number is correlated with days in captivity,  $r_s = 0.66$ ,  $p < 0.001$ , and number of previous exposures to the model,  $r_s = 0.98$ ,  $p < 0.001$ .

<sup>b</sup> Vigilance and feeding variables were correlated. For example, head-up rate was correlated with proportion of time spent with head up ( $r_s = -0.46$ ,  $p = 0.003$ ), mean duration of head-up period ( $r_s = -0.95$ ,  $p < 0.001$ ), mean duration of head-down period ( $r_s = -0.53$ ,  $p = 0.001$ ) and peck rate ( $r_s = 0.79$ ,  $p < 0.001$ ).

## (b) Analysis

There were two groups of experimental chaffinches. One group of 20 birds was kept throughout the winter and up to 10 trials were performed on each bird (mean of 7.8, range of 5–10). Some trials resulted in no data being collected because the chaffinch was flying around the cage and not on the ground when the sparrowhawk became visible to it. Therefore, more than two effective trials were available from only 13 birds (mean of 3.9 trials, range of 2–7). For these birds the trial order in a day was randomized. A second group of 30 birds were caught and kept in captivity for only one to two weeks until a single successful trial was carried out (where feeding and response data were collected). Some chaffinches did not give any usable simultaneous feeding and response data in the two-week period and so sample sizes in total were 24 single trial birds. Throughout the paper the unit of analysis is the individual. For most analyses ((i)–(iii) below), where an individual was sampled more than once, the first usable feeding and response trial data were used. For the test to determine whether individuals had consistently similar feeding rates, ‘individual’ was entered as a random factor in the model to control for individual variation in the number of trials.

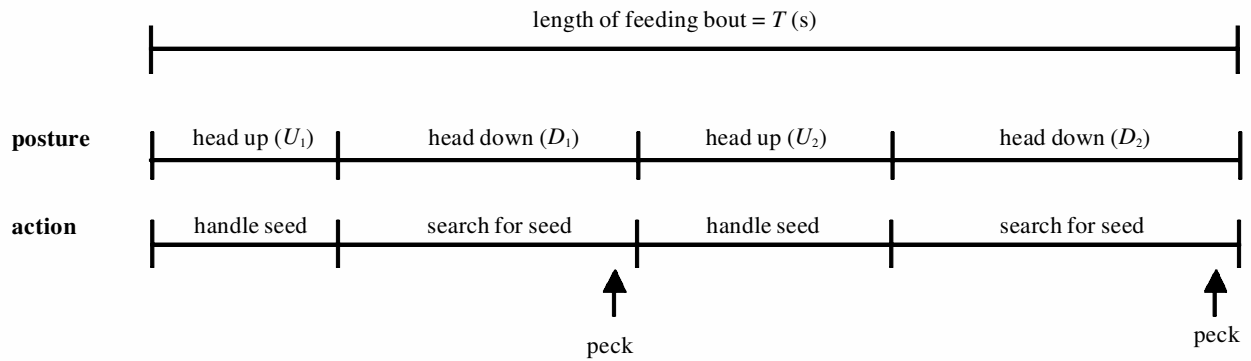
The video tape of each trial was analysed frame by frame and a number of variables were recorded (table 1). The chaffinches usually took a few minutes to settle down after being put into the cage during which they sometimes flew back and forth or perched on the sides of the cage. Eventually the bird would begin a feeding bout, defined here as at least five pecks, each separated by less than 10 s. We then collected data only from birds foraging in the absence of alarmed or disturbed vigilance periods associated with external disturbance. For each foraging bout values for vigilance, search time and peck rate were recorded (figure 2); means were then calculated per foraging bout and then for the trial if more than one foraging bout occurred. Chaffinches fed by pecking at the ground and then raising their head to handle the seed and/or to scan. A peck almost always resulted in a seed being handled and eaten: for

16 birds randomly sampled for a feeding bout of five pecks at the start of the bout and five pecks at the end of the bout, a mean of  $0.83 \pm 0.03$  s.e. seeds per peck were gained. Thus peck rate approximated intake rate. A vigilant period (or head-up period) was defined when the chaffinch had its head above the level of its back, and a food search period (or head-down period) was defined as when the chaffinch had its head below its body level. In practice, all of our measurements come from birds that were foraging constantly (with look ups) and not from birds that were interspersing foraging periods with non-foraging alarmed or alert periods.

Response time was defined as the period between when the model sparrowhawk first became potentially visible and the point at which the chaffinch reacted to the simulated attack (e.g. Lima & Bednekoff 1999). Chaffinches either froze or flew in response to the sparrowhawk: we included this information in all models to control for any confounding effects of overall response type on detection speed. The frame at which chaffinches responded was scored blind with respect to the foraging rate measures of the individual and the frame at which the sparrowhawk first appeared (i.e. before both of these data were determined).

The effects of variables were determined by generalized linear modelling: all relevant independent variables (table 1) were entered into the model and removed sequentially (i.e. backwards selection) until minimum adequate models were derived. Some groups of variables were highly correlated and so only one from each group was used in subsequent models (table 1): the number of previous trials (trial number) was used (rather than also the number of days in captivity or number of previous exposures to the hawk). Which variable was used made no difference to the overall results. All vigilance and feeding variables were highly correlated (table 1) and so these variables were tested in separate models.

The following models were constructed by using a single trial's data per bird to test what determined response time.



overall proportion of time vigilant =  $(U_1 + U_2)/T$   
 number of head-up periods per bout =  $N_U$  (equals 2 in this schematic example)  
 number of head-down periods per bout =  $N_D$  (equals 2 in this schematic example)  
 mean duration of head-up or handling period =  $(U_1 + U_2)/N_U$   
 mean duration of head-down or food search period =  $(D_1 + D_2)/N_D$   
 number of pecks =  $N_p$  (equals 2 in this schematic example)  
 peck rate =  $N_p/T$   
 head-up rate =  $N_U/T$

Figure 2. Calculation of food searching, intake rate and vigilance variables.

- (i) Response time was dependent on vigilance. The response time as the dependent variable and all standard variables as in table 1, with the three measures of vigilance (head-up rate, duration of head-up periods and proportion of time spent vigilant) tested separately as independent variables.
- (ii) Measures of vigilance or duration of head-down periods were dependent on feeding efficiency. Head-up rate, mean duration of head-up period, proportion of time spent vigilant and mean duration of head-down period were each tested as dependent variables in separate models, with peck rate and all standard variables as in table 1, as independent variables included in all models.
- (iii) Response time was dependent on feeding efficiency. The response time as the dependent variable and peck rate as the independent variable; all standard variables as in table 1 were also included as independent variables.

The following models were constructed by using multiple trial data per bird (with 'individual' as a random factor in the model) to test whether there were consistent differences between individuals in the amount of time that they allocated on average to a handling/scanning period and/or a food search period.

- (iv) The time allocated to vigilance and food searching was consistent between individuals, i.e. was a significant proportion of the variance in mean head-up or mean head-down period length accounted for by individual chaffinch identity? Mean head-up or head-down period length as the dependent variable and individual, trial number, position of the feeding chaffinch and response type as independent variables.

We analysed data by using the SPSS statistical programs (Norusis 1990), and according to Sokal & Rohlf (1981). All dependent variables were tested for normality and transformed where appropriate (only response time was non-normally distributed and so was log transformed). All probabilities quoted are two-tailed. Means and standard errors are quoted in the form mean  $\pm$  1 s.e.

### 3. RESULTS

#### (a) Does response time depend on vigilance?

Response time depended on head-up rate (table 2). As head-up rate increased, so response time decreased (figure 3). Other vigilance measures were poor predictors of response time: proportion of time spent with head up ( $F_{1,23} = 0.5$ ,  $p = 0.48$ ) and mean duration of head-up period ( $F_{1,23} = 1.9$ ,  $p = 0.17$ ); terms included in the latter two models were as in table 2 except for choice of vigilance variable used. Consistent effects of several other predictors were found in our models. Not surprisingly, chaffinches responded more quickly when the model hawk was travelling faster and when they were positioned at the front of the experimental cage. Finally, individuals carrying greater mass for their size also showed a tendency to respond more rapidly.

#### (b) Does vigilance depend on feeding efficiency?

As peck rate increased, so did head-up rate (figure 4). Both mean duration of head-up (figure 5) and of head-down periods decreased with peck rate (figure 6). There was a trend for the overall proportion of time spent being vigilant to increase with peck rate ( $F_{1,36} = 3.2$ ,  $p = 0.08$ , overall  $r^2 = 0.06$ : non-significant variables removed from the model were age, sex, response type, trial number and body condition; all had  $F_{1,31} < 1.0$ ,  $p > 0.34$ ).

#### (c) Does response time depend on feeding efficiency?

Response time was dependent on peck rate (table 3). Response time decreased as peck rate increased, i.e. faster feeders responded more quickly to the approaching model (figure 7).

#### (d) Individual variation in duration of head-up and head-down periods

Individual chaffinch identity accounted for a significant proportion of the variance in mean duration of a head-up

Table 2. The effect of head-up rate on response time to a model sparrowhawk controlling for the position of the chaffinch relative to the model, the speed of the approaching model, trial number and the body condition of the chaffinch.

(Non-significant variables removed from the model were age:  $F_{1,23} = 0.01$ ,  $p = 0.43$ ; sex:  $F_{1,23} = 0.0003$ ,  $p = 0.86$ ; and response type:  $F_{1,23} = 0.002$ ,  $p = 0.69$ .)

dependent variable: log (time to respond)					
source	type III sum of squares	d.f.	<i>F</i>	<i>p</i>	regression coefficient
corrected model	0.7	11	6.5	<0.001	
intercept	0.6	1	54.8	<0.001	1.5
head-up rate <sup>a</sup>	0.06	1	5.6	0.025	-1.5
position of chaffinch	0.3	7	4.1	0.004	
model speed	0.4	1	4.9	<0.001	-11.6
trial number	0.05	1	4.9	0.036	-0.03
body condition	0.04	1	4.3	0.048	1.8
error	0.3	26			
corrected total	1.0	37			
adjusted $r^2 = 0.62$					

<sup>a</sup> There was no significant effect of proportion of time spent vigilant ( $F_{1,25} = 0.09$ ,  $p = 0.77$ , overall  $r^2 = 0.61$ ) when this was added to the model above including head-up rate.

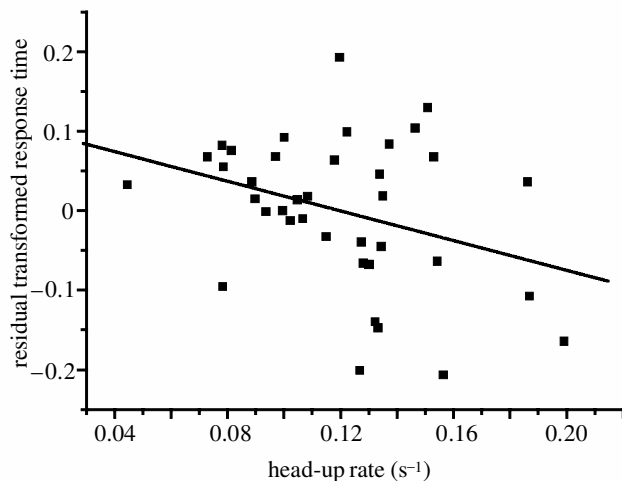


Figure 3. The speed of chaffinch response to an approaching model sparrowhawk was dependent on the head-up rate. The graph illustrates residual transformed response time (controlling for position of the chaffinch, model speed, trial number and body condition) with head-up rate ( $F_{1,36} = 4.5$ ,  $p = 0.04$ ,  $r^2 = 0.09$ ).

period (using data from the 13 long-term birds: individual,  $F_{12,36} = 2.1$ ,  $p = 0.04$ , partial  $r^2 = 0.41$ ; trial number,  $F_{1,36} = 4.8$ ,  $p = 0.035$ , partial  $r^2 = 0.12$ ; with both response type,  $F_{1,22} = 0.02$ ,  $p = 0.89$ , and position of the feeding chaffinch,  $F_{1,22} = 0.02$ ,  $p = 0.89$ , removed from the model). Individual chaffinch identity also accounted for a significant proportion of the variance in mean duration of a head-down period using the same dataset (individual,  $F_{12,37} = 2.1$ ,  $p = 0.046$ , partial  $r^2 = 0.40$ ; with trial number,  $F_{1,22} = 1.2$ ,  $p = 0.29$ , response type,  $F_{1,22} = 0.06$ ,  $p = 0.82$ , and position of the feeding chaffinch,  $F_{1,22} = 0.4$ ,  $p = 0.52$ , removed from the model).

#### 4. DISCUSSION

Response time in chaffinches depended on the head-up rate. This was unsurprising as head-up behaviour affects probability of detection of an approaching predator

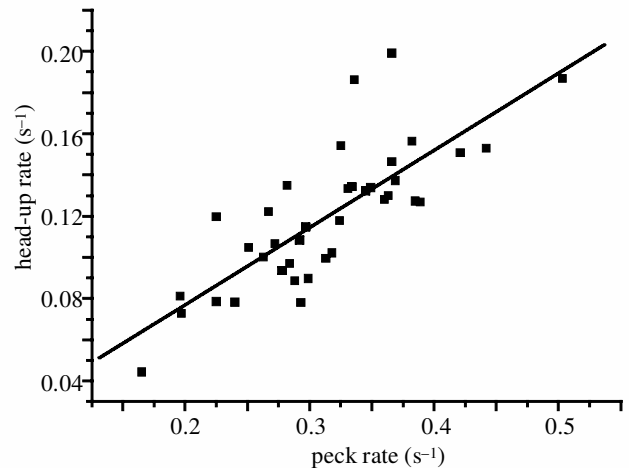


Figure 4. Head-up rate was dependent on the peck rate ( $F_{1,36} = 58.6$ ,  $p < 0.001$ , overall  $r^2 = 0.61$ ). Non-significant variables removed from the model were age, sex, response type, trial number and body condition; all had  $F_{1,31} < 0.7$ ,  $p > 0.4$ .

(Fitzgibbon 1989; Krause & Godin 1996). However, the result that high vigilance rates may have been a consequence of high intake rates was unexpected. Faster feeders had shorter search times (head-down periods) and so had greater head-up rates because after most pecks birds raised their head while handling the seed. Better feeders also had shorter head-up periods so that, for any given length of time, the number of head-up periods was further increased. The reason for this is unknown; perhaps birds that are better at finding seeds are also better at handling them. A few previous studies have also suggested that feeding demands may be important in determining the spatial pattern and duration of vigilance events (Metcalf 1984; Lawrence 1985; Popp 1988).

Clearly it was better for a chaffinch to look up little and often to have the highest probability of detecting the approaching sparrowhawk model (and so respond quickly), and this rate of look up seems likely to have been determined by peck rate. Vigilance rates might be deter-

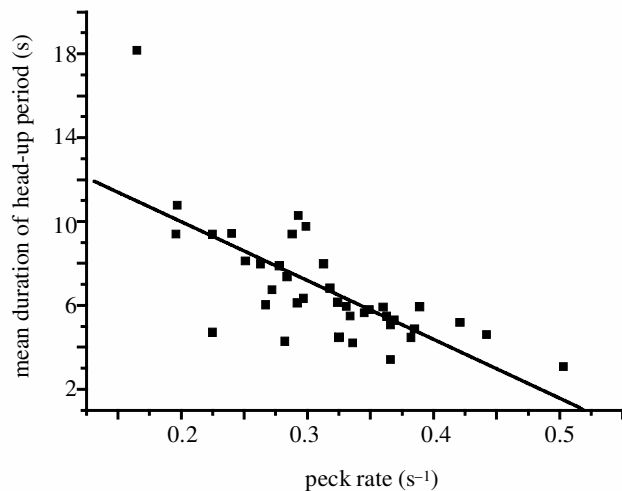


Figure 5. The mean duration of head-up periods was dependent on the peck rate ( $F_{1,36} = 38.3$ ,  $p < 0.001$ , overall  $r^2 = 0.50$ ). If the top left outlier is removed the relationship remains significant ( $F_{1,35} = 33.6$ ,  $p < 0.001$ ,  $r^2 = 0.48$ ). Non-significant variables removed from the models were age, sex, response type, trial number and body condition; all had  $F_{1,31} < 1.3$ ,  $p > 0.27$ .

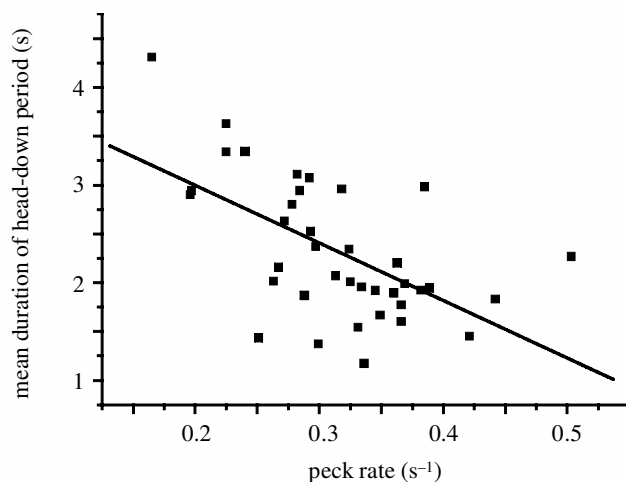


Figure 6. The duration of the head-down period was dependent on the peck rate ( $F_{1,36} = 18.8$ ,  $p < 0.001$ , overall  $r^2 = 0.33$ ). Non-significant variables removed from the model were age, sex, response type, trial number and body condition; all had  $F_{1,31} < 0.4$ ,  $p > 0.53$ .

ined by peck rate, rather than the reverse, because of the fundamental difference in how the probabilities of detecting a seed rather than a predator are affected by time. If animals searching for cryptic prey interrupt a search task then they suffer a temporary decline in the probability of success when resuming the search (see Dukas & Clark 1995a). However, the probability of detecting a moving object depends primarily on the speed and proximity of the object and, for neurological reasons, the efficiency of this actually declines with increasing scanning time (Dukas & Clark 1995b). There is some suggestion from our data that this may be true: there was a non-significant but positive correlation between the time taken to respond to the model sparrowhawk and the length of time that an individual had its head up prior to the model's appearance ( $F_{1,28} = 3.4$ ,  $p = 0.076$ ). Although

this efficiency decrement also applies to long-term scanning for seeds (Dukas & Clark 1995b), efficiency initially increases (Pietrewicz & Kamil 1979; Plaisted & Mackintosh 1995). Therefore it may be much more efficient to schedule brief look ups after finding a seed rather than interrupting searching for a seed to scan for predators.

The results of the study show that it is the pattern of vigilance, rather than simply the time allocated to vigilance that determines the probability of predator detection. For example, if two birds look up on average 50% of the time, but one bird looks up once every 10 s for 10 s, whereas the other looks up every 1 s for 1 s then the first bird would on average not detect a predator that approaches over 2 s at least some of the time, but the second bird would always do so. Our results cannot tell us, however, whether this pattern of vigilance is appropriate for all predator detection scenarios. As risk changes, so chaffinches may increase the duration of their scans, rather than their frequency. Scan durations may be longer in smaller and hence riskier groups (Studd *et al.* 1983), but this may be because of how predators change their attack behaviour or attack rate with respect to different group sizes. Similarly, scan durations may be longer when animals are foraging in areas of increased predation risk (Lima *et al.* 1999), but again this may be because of differences in predator suite, attack type and predator targeting behaviour.

The suggestion that intake rate may determine vigilance and detection rate in some cases may help our understanding of the problem with the widely reported group size effect on vigilance (see Elgar 1989), where vigilance continues to decline with group size even when there is no further benefit to reducing vigilance. Above small group sizes (less than 20) the probability of detecting a predator almost instantaneously approaches and remains very close to one (Pulliam 1973) even when individual rates of vigilance are very low (e.g. Cresswell 1994). Despite this, individuals may continue to steadily decrease their vigilance rates as group size increases (see studies cited in Elgar (1989)) even though the probability of detection will be effectively unchanged. Probability of detection cannot therefore be the primary reason for further major decreases in individual vigilance rate as groups become very large. If intake rates drive vigilance, however, then the explanation for the continued decline seems likely to be competition for food, with scramble and/or interference competition occurring (see Milinski & Parker 1991). For example, where resources are limited individuals may scramble for food and so faster intake rates result as group size increases, as well as lower scan rates as individuals devote more time to feeding (e.g. Beauchamp & Livoreil 1997). Alternatively, interference competition may continue to rise with group size (Goss-Custard 1980; Van Der Meer & Ens 1997) so that intake rate per unit time decreases because prey is made less available (Dolman 1995).

The results of this study therefore suggest a general testable hypothesis: if feeding competition increases with group size then both intake rate and vigilance will decline, but if vigilance does not conflict with feeding or competition is minimal then we would not expect a decline in vigilance with increasing group size above and beyond that associated with the probability of predator detection. A test of a similar hypothesis by Lima *et al.* (1999), however,

Table 3. The effect of peck rate on response time to a model sparrowhawk controlling for the position of the chaffinch relative to the model, the speed of the approaching model, trial number and body condition.

(Non-significant variables removed from the model were age:  $F_{1,23} = 0.5$ ,  $p = 0.47$ ; sex:  $F_{1,23} = 0.01$ ,  $p = 0.92$ ; and response type:  $F_{1,23} = 0.05$ ,  $p = 0.83$ .)

dependent variable: log (time to respond)						
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intercept	0.6	1	55.9	<0.001	1.5	
peck rate	0.06	1	6.1	0.021	-0.7	
position of chaffinch	0.3	7	4.8	0.001		
model speed	0.4	1	36.5	<0.001	-10.8	
trial number	0.06	1	5.5	0.026	-0.03	
body condition	0.04	1	4.0	0.05	1.7	
error	0.3	26				
corrected total	1.0	37				
adjusted $r^2 = 0.63$						

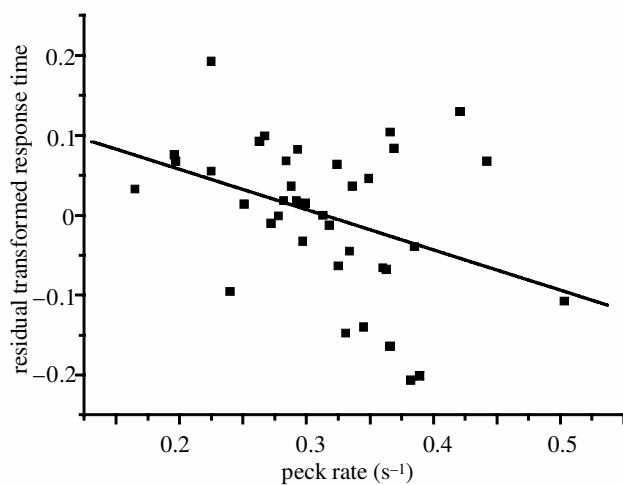


Figure 7. The speed of chaffinch response to an approaching model sparrowhawk was dependent on the peck rate. The graph illustrates residual transformed response time (controlling for position of the chaffinch, model speed, trial number and body condition) with peck rate ( $F_{1,36} = 6.1$ ,  $p = 0.018$ ,  $r^2 = 0.12$ ).

showed that the decline in scan rate with group size still occurred where food was unlimited and so in the absence of scramble competition. This, however, does not rule out the effect of interference competition that can occur even where food is apparently unlimited because individuals simply get in the way of each other or try to avoid each other (e.g. see Cresswell 1997). For example, as was noted in the Lima *et al.* (1999) study, some birds were forced to feed in unfavourable high predation risk patches because of crowded conditions, suggesting strong effects of interference competition and the potential for it to have accounted for at least some of the observed decline in vigilance rates in the study.

In general, it is unclear what determines the pattern of scanning in animals (Scannell *et al.* 2001; Bednekoff & Lima 2002). Look ups tend to occur according to a random Poisson distribution (Scannell *et al.* 2001), although sequences of interscan intervals may affect later interval duration (Roberts 1994). Intake rate has not previously been considered as a major causal factor for vigilance

(Bednekoff & Lima 2002) and may provide the missing mechanism to account for many species' vigilance patterns. What is clear now from previous work, however, is that it is no longer helpful to consider vigilant and non-vigilant states: searching for food in many cases is simply a less vigilant state and different types of searching for food may occur because of their vigilant properties as well as their effects on intake rate.

Another unexpected result was the relationship between foraging rate and ability to detect predators: we found that individuals that were efficient feeders were also good at detecting predators. Individual chaffinches had consistently high or low intake rates suggesting that it was absolute intake rate (see Milinski & Parker 1991) or competitive ability that was driving vigilance and detection rates. Those birds that found seeds quickly also had shorter head-up periods. This may be because those individuals that are better at finding prey are also better at handling prey and/or better at detecting predators per unit time of scanning, but these ideas remain to be tested. Differences in competitive ability (absolute intake rate and handling time) are likely to arise through differences in morphology and experience (Partridge 1976). If the differences recorded in this study do reflect fundamental differences between individuals in their foraging ability, as our results suggest, rather than shorter-term state-dependent solutions (see Houston *et al.* 1988), then our study may provide new evidence of the link between competitive ability and predation risk. Thus individuals of greater competitive ability not only need to feed for less time exposed to predators (Houston *et al.* 1993), but they may also have a lower probability of capture by a predator per unit time during the time they are foraging. Our study shows that good foragers may also be good predator detectors: there is therefore likely to be selection in the natural population for efficiency in reconciling the conflict between looking for food and for predators. This conflict can be resolved either by choice of easily found prey that requires handling that is compatible with scanning, or by increased efficiency in finding prey during head-down search periods.

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