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Title: Interaction between seed crypsis and habitat structure influences patch choice in a granivorous bird.

JONES, K.A.[1*] & WHITTINGHAM, M.J.[2]

[1]Edward Grey Institute of Field Ornithology, Zoology Department, University of Oxford, South Parks Road, Oxford

[2]School of Biology, Ridley Building, University of Newcastle, Newcastle-Upon-Tyne, NE1 7RU

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*Author and address for correspondence:

Edward Grey Institute of Field Ornithology, Zoology Department, University of Oxford, South Parks Road, Oxford OX1 3PS

Tel: (01865) 271244

Fax: (01865) 271221

e-mail: katherine.jones@zoo.ox.ac.uk

Abstract

Food abundance is an important determinant in habitat and patch selection but food accessibility and detectability is less often considered. Foraging on more cryptic seeds may increase predation risk by increasing the length of head down periods. Habitat structure may interact with this as birds are less able to detect predators with their head lowered in riskier obstructed habitats. We investigated patch choice in chaffinches foraging in obstructed and open habitats and artificially manipulated the search times of seeds by colouring them either yellow or black. One trial consisted of a choice between the conspicuous seed in the open patch, and the cryptic seed in the obstructed patch; in the second trial the treatments were reversed. Individuals were more willing to forage in the obstructed habitat when the yellow seeds were present (43% of pecks made in the obstructed patch) than when the black seeds were present (18% of pecks in the obstructed patch). Differences in search time are likely to explain this result: yellow seeds were located almost twice as fast (1.26 ± 0.60 seconds) as black ones (2.36 ± 0.88 seconds). This experiment shows that individual foraging decisions may be influenced not only by food abundance but by the properties of individual food items (in this case seed crypsis) and the structure of the habitat they are present in.

Keywords:-diet, vigilance, foraging, predation risk.

Introduction

Animals face a multitude of interacting factors when choosing suitable foraging patches. Factors that have been identified as having an influence on habitat suitability include: food abundance (Butler *et al.*, 2005b; Robinson, 1997; Sutherland, 1996); physical obstruction (Butler *et al.*, 2005b; Devereux *et al.*, 2004); visually obstructive habitat structure which reduces predator detection (Devereux *et al.*, 2006; Whittingham *et al.*, 2004); presence of refuges (Robinson & Sutherland, 1999; Whittingham & Evans, 2004) and the complexity of substrates on which animals forage (Moorcroft *et al.*, 2002; Whittingham & Markland, 2002). One area that has received little attention is how the physical properties of dietary items may themselves influence habitat choice by altering the detectability of food, and how this might interact with differences in habitat structure, such as stubble height (Butler *et al.*, 2005b). Obstructed habitats may increase the risk of predation and also reduce accessibility of food items.

Theoretical studies make explicit assumptions that prey with their head lowered are at greater risk from predation than those with their heads raised (e.g. (Lima, 1987; McNamara & Houston, 1992; Pulliam, Pyke & Caraco, 1982)) and recent empirical work has supported this view (Lima & Bednekoff, 1999). A recent companion study showed that chaffinches *Fringilla coelebs* L. foraging in an obstructed habitat are 17% slower to detect a model hawk with their head lowered versus raised, whereas in open habitat there is only a 2% difference in detection time between the head positions (Whittingham et al. 2004). This suggests that prey foraging in obstructed patches are at more risk from predators when their head is lowered than those in open patches, thus foraging on cryptic foods which require more time with the head down searching might be riskier than foraging on conspicuous food items or more open environments.

Few empirical studies have looked at the interaction between predation risk and properties of food items. Some empirical work has shown that birds select items with different handling times under different predation risk. For example, (Lima, 1988a) found Dark-eyed Juncos *(Junco hyemalis* L.*)* ate more whole seeds, rather than 'bits' of seeds, when flock size was smaller (i.e. greater predation risk) despite 'bits' being more profitable (as they had virtually no handling time), because feeding on whole seeds allowed more time with the head-up being vigilant due to the longer handling time. However, we are aware of only one study that investigated the interaction between diet and patch choice. (Metcalfe, 1984) showed one species of wading bird switched to feed on smaller prey that was easier to find in areas where visibility of the surroundings was reduced. However, Metcalfe did not control for prey abundance as his study was conducted under natural conditions.

In this study we test under controlled conditions whether a granivorous bird is more willing to forage in high risk patches (in which visibility of the surroundings is reduced), when the patches contain more conspicuous prey items which are faster to locate. Our study follows on directly from an earlier companion study by Butler et al. (2005) which showed that using an identical experimental set-up chaffinches needed 2.5 times higher seed densities in order to make equal use of short and long stubble (using an identical stubble board to that shown in Figure 1). We also test for possible factors that might explain why some individuals take more risks than others. We predicted that faster foragers might be more willing to forage in high risk patches as previous experiments with this model system have shown that faster foragers are better at detecting aerial predators (Cresswell *et al.*, 2003).

Methods

Study species

Thirty eight chaffinches were trapped under English Nature license at Wytham field station and Wytham woods in January and February 2004. Three birds died in captivity due to unknown causes. At capture, birds were aged and sexed according to (Svensson, 1992. Body condition was measured by dividing wing length by mass at time of experiment. After experiments birds were released on fair weather days near point of capture (with food supply). Chaffinches were housed indoors in a single room in individual standard small-bird keeping cages (75 x 45 x 45 cm) for a maximum of one week at the Wytham Field Laboratory, University of Oxford. The room temperature was maintained between 10 and 15 ^{o}C and the light cycle reflected natural daylight hours. Birds were provided with wild bird seed mixture including both types of dyed millet used in the experiment and water ad libitum.

Experimental trials

The two experimental trials were conducted on consecutive days the day after capture or later (mean 2.99 days after capture, s.d.=1.09, range=1-5 days) in a whitewashed greenhouse containing the experimental cage set-up. Before each experiment birds were food deprived for two hours and then transferred by hand between the husbandry cage and experimental cage.

The experimental set-up (see figure 1.) consisted of an artificial yellow-drinking straw stubble board covered in peat located on the floor of the greenhouse. A wire cage (which enclosed the bird) measuring 0.5x0.5x0.5m was placed over the stubble thus the foraging area exposed to the bird was $0.25m^2$. Half of the stubble board was open (3cm high straws) and half was obstructed (13cm long straws). The orientation of the stubble board was altered randomly between birds by rotating 180° and controlled for in analysis.

A previous experiment with this model system (Butler *et al.*, 2005b) used exactly the same stubble board and manipulated seed densities in the two patches and found chaffinches preferred to forage in the open habitat when seed densities were equal. In this experiment we present birds with equal densities of food in the short and long stubble, but the food items differ in their conspicuousness.

To manipulate seed conspicuousness we used white millet seed (C J Wildbird foods, UK) that was de-husked to reduce handling time. The seed was dyed either black (cryptic) or yellow (conspicuous) using food colouring (Supercook, UK) following established methods (Whittingham *et al.*, 2002).

In the Yellow Short Black Long (YSBL) trial 25 yellow seeds were placed on the short stubble, and 25 black seeds on the long stubble. In the Black Short Yellow Long (BSYL) trial treatment was reversed. These seed densities were equivalent to 200 seeds per m^2, which lies in the typical range of densities found in natural stubble fields (Moorcroft *et al.*, 2002). The time of day the trial was conducted for each individual was kept the same in both trials.

To remove the possibility that patch choice was influenced by white noise played during trials to minimise external disturbances we changed the direction of noise between trials. The position of the white noise was not near significance ($p>0.5$) in any subsequent statistical models so was assumed not to affect patch choice.

Trials were terminated ten minutes after the first peck or if the bird did not make any pecks for ten minutes after the beginning of the trial (this was scored as a non-foraging trial).

Video Analysis

Experiments were recorded onto a digital video camera. The videos were initially scored in real time to determine patch choice (proportion of time and proportion of pecks on open versus obstructed patch, excluding time spent flying). We recorded latency to forage (latency from trial start to first peck) as a possible indicator of individual motivation. More detailed measures of foraging and vigilance within foraging bouts were made by coding tapes at ¼ speed playback using Jwatcher event recording software (Blumstein, Evans & Daniel, 2000). Foraging bouts were defined as at least four consecutive pecks on the same stubble and seed type each separated by no more than 20 seconds, with the bird remaining on the ground for the entire duration of the bout. If the bird moved between the two patches bouts were recorded on each patch. Behaviours recorded during bouts were peck rate, peck success rate, mean number and duration of head up periods, and mean number and duration of head down periods. The average of each behaviour across bouts but within patch type was recorded for each bird on each trial. Head down periods in the first bout on the short stubble of each trial were used to determine differences in search time between the seed types.

We used a five-minute period from the first peck to measure time in a patch or time spent foraging. Replacing this with shorter time periods gave similar results. Increasing the time (e.g. to 10 minutes) altered the results as birds would forage in their less preferred patch once they had depleted their first choice, as the relative seed densities in each patch would approach the 2.5x switching point found in Butler *et al.* (2005).

Data analysis

We employed the General Linear Model (GLM) procedure using Minitab version 14.0 (Grafen & Hails, 2002). Individual was entered into the model as a random effect to control for repeated measurements (one replicate of each of two treatments). All models included time in captivity, body condition, stubble board orientation and log10 transformed latency to forage as potentially confounding variables.

THIS IS TOO VAGUE AS YOU have n=30 later on. REWORD CAREFULLY. We put 35 birds through our experimental procedure. Twenty-six birds fed in both trials. The remaining nine birds did not forage for long enough in either trial to enable enough data to be collected for analysis. We tested the following specific hypotheses:

1. *Does seed type alter patch choice within and between trials?*

We predicted that birds would be more willing to forage in the long stubble in the BSYL trial than in the YSBL trial. The proportion of pecks in the open patch was specified as the response variable with trial as the predictor of interest, controlling for trial order. The analysis was also repeated with proportion of time in the open patch as response variable.

2. *How do individuals differ in use of risky patches?*

We predicted that individuals might differ in their willingness to use the obstructed habitat in the BSYL trial. The number of pecks in the long stubble in the BSYL trial was specified as the response variable with age, sex, body condition and log10 transformed latency to forage as predictors of interest.

Results

Yellow-dyed seeds were found almost twice as fast (mean search time for first foraging bout 1.26 ± 0.60 seconds) as black-dyed seeds (mean search time for first bout 2.36 ± 0.88 seconds) SHORT TEST HERE.

Peck rate did not represent absolute intake rate as there appeared to be a large number of 'false' pecks. However, the mean proportion of successful pecks (on short stubble, yellow=0.22+/-0.11, black=0.24+/-0.16) did not differ significantly between black and yellow seeds (paired t-test, n=16, p=0.363), thus this should not influence our results.

<u>1.*Does seed type alter patch choice within and between trials?*</u>

Chaffinches preferred to forage in the open patch in both trials (27 out of 30 in the YSBL trial and 17 out of 26 in the BSYL trial had greater than 50% of pecks in open patch). However, there was a significantly higher proportion of pecks in the short stubble in the YSBL trial (mean 0.82 ± 0.04, i.e. 82% of pecks made in short stubble, see figure 3) than in the short stubble in the BSYL trial (mean 0.57 ± 0.06, see figure 2) ($F_{1,19}$= 44.08, P<0.001, see 'Trial' in Table 2). Thus, there appeared to be a greater willingness for the birds to forage in the obstructed environment when the yellow seeds were present.

We also found that birds were more likely to forage in the long stubble in the BSYL trial when they had been in captivity for longer and when they experienced the YSBL trial first (Table 2).

2. *How do individuals differ in use of risky patches?*

We found that latency to forage was significantly related to the number of pecks in the long stubble in the BSYL trial ($p<0.001$, $F_{1,25}=21.58$, all other factors $p>0.1$, R-sq(adj) for model=37.7%): individuals that began foraging sooner preferred foraging in the long stubble (see figure 4).

Discussion

These results suggest that the properties of food items may affect their detectability, and that measuring food abundance alone may not always provide an accurate estimate of individual foraging choice. Most chaffinches in our experiments preferred to forage (>50% of pecks) in the open patch rather than the obstructed patch (27 out of 30 in the YSBL trial and 17 out of 26 in the BSYL trial) regardless of the location of the two coloured seeds. This supports previous findings where 2.5 times more food (using identical seeds in both patches) was needed before equal use was made of open and obstructed patches (Butler *et al.*, 2005b). Chaffinches adjusted their willingness to forage in the risky obstructed patch depending upon the arrangement of seed types. Birds made an average of 82% of pecks in the open habitat when conspicuous seeds were present compared with 57% when cryptic seeds were present (and conspicuous seeds were in the obstructed habitat).

Some confounding factors such as trial order, time in captivity and orientation of the patch had a significant effect on patch choice. All of these affects are controlled for in full models and so our key results are robust to them and our key result (effect of switching different coloured seeds in the two trials) explained over three times as much variance as the most significant of these effects (Table 2).

Chaffinches had longer interscan intervals (head down search times) when foraging on black (2.36 ± 0.88 seconds) versus yellow seeds (1.26 ± 0.60 seconds) (P = 0.011, see methods for further details). Theoretical studies (Bednekoff & Lima, 1998; Bednekoff & Lima, 2002; Hart & Lendrem, 1984; Pulliam, 1973) suggest that longer interscan intervals may increase predation risk. A companion study (Whittingham *et al.*, 2004) showed a greater difference between vigilant (scanning) and non-vigilant (interscan intervals) reaction times of individuals to a model predator in an obstructed long stubble habitat. Therefore cryptic seeds are likely to be much riskier to forage on in obstructed patches. There may also be an additional ‘attention’ cost to searching for cryptic seeds that may mean less attention can be devoted to observing predators (Dukas & Kamil, 2000).

In addition to the within individual difference in patch choice between trials, there were some more subtle differences in the willingness of individuals to use the obstructed patch when conspicuous seeds were present. Those individuals that were quicker to begin foraging in the trial made more pecks in the obstructed habitat than individuals that took longer to forage. Risk taking behaviour has been shown to be correlated with early exploratory behaviour in Great Tits, (van Oers *et al.*, 2004); it is possible that latency to begin to forage in this trial was correlated with a behavioural syndrome such as exploratory behaviour, thus explaining differences in risk taking behaviour. Further work investigating use of risky environments and behavioural syndromes is needed to investigate this.

This study suggests that properties of individual food items may influence patch choice. Although there is much theory on optimal diets (Pulliam, 1974; Stephens & Krebs, 1986), the influence of habitat structure and predation risk are seldom considered (but see, Godin, 1990; Lima, 1988b). Dietary data is rarely examined in conjunction with food availability and habitat choice in the field (Wilson, Arroyo & Clark, 1996). We suggest studies should focus more on the properties of individual food items rather than overall food abundance.

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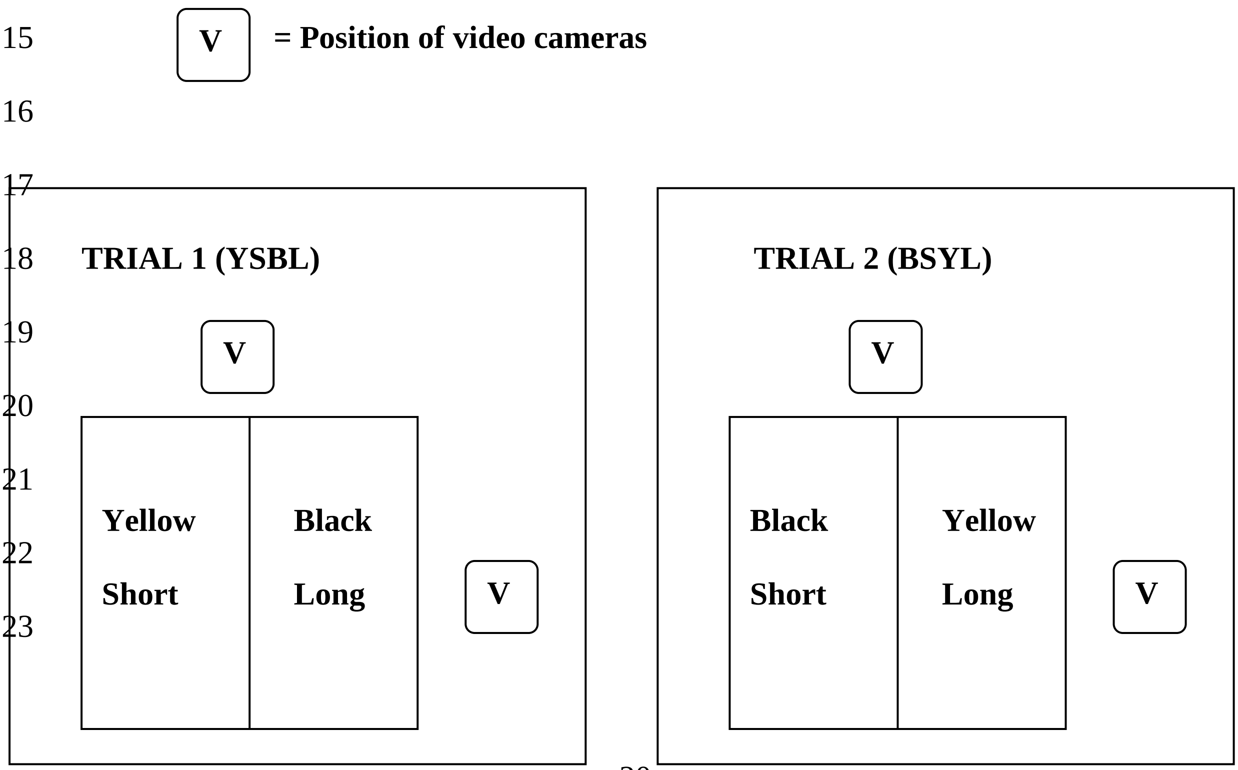
Table 2. Model of the proportion of pecks made in the open patch by twenty-six chaffinches that fed in two trials (with yellow seeds in the open patch and black seeds in the obstructed patch – YSBL; and with black seeds in the open patch and yellow seeds in the obstructed patch - BSYL). Chaffinches spent more time foraging in the open patch in the YSBL trial than in the BSYL trial (indicated by predictor 'trial' in BOLD). R-sq(adj) = 63.38%.

Predictor	**DF**	**Adj SS**	**F**	**P**
Trial order	1	0.4332	13.40	0.002
Stubble board orientation	1	0.2560	7.92	0.012
Time in captivity	4	0.7484	5.79	0.004
Condition (Mass/Wing length)	1	0.02244	0.69	0.416
Individual	25	2.2192	2.74	0.018
(Log)Latency to forage	1	0.08373	2.59	0.126

Trial	**1**	**1.42558**	**44.08**	**<0.001**
Error	19	0.5498		

Figure 1. Diagram showing the artificial patches used in the two trials. Yellow or black indicates the colour of the dyed seeds used in the area indicated on the patch. Short or long indicates the stubble length on the half of the patch (either 3cm or 13cm lengths of yellow drinking straws attached to the plywood board). Birds could move freely between the two halves of the patch in each trial.



Bird released into cage here **Bird released into cage here**

Figure 3. The mean proportion of pecks (+/- one standard error of the mean) on the short stubble in the two experimental trials. (YSBL=Yellow seeds on short, Black on long, BSYL=vice versa). Birds preferred the short stubble more in the YSBL trial than the BSYL trial.

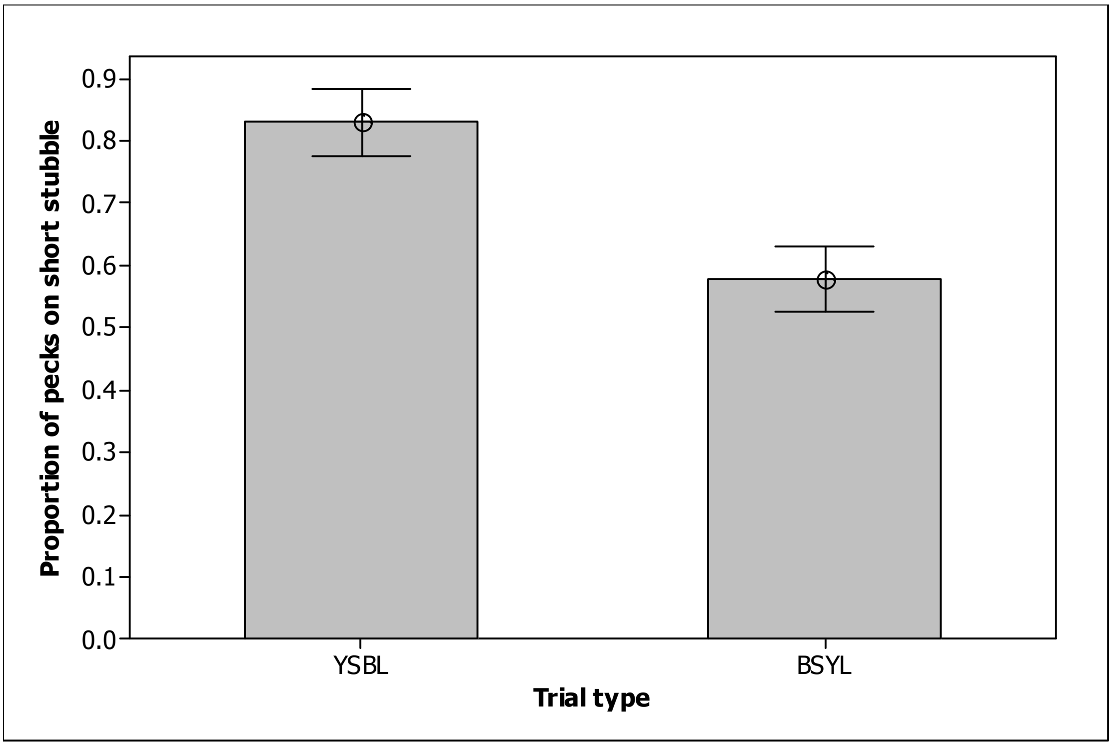
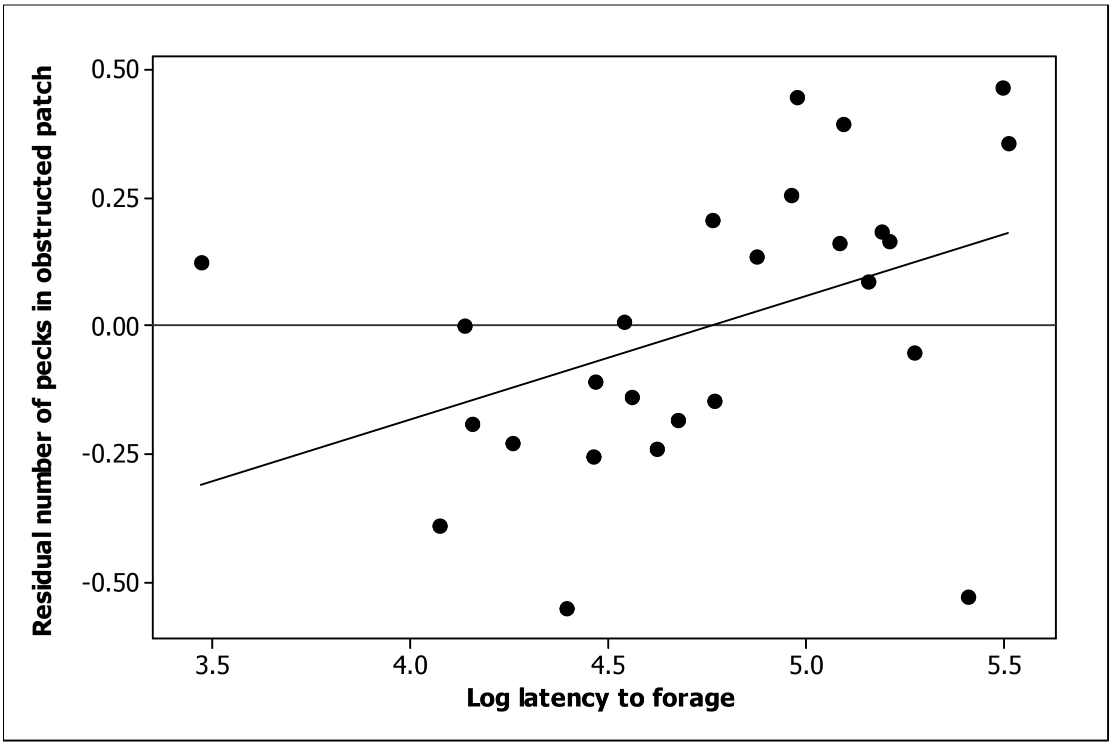


Figure 4. The relationship between latency to forage and number of pecks in the obstructed habitat in the BSYL trial. Birds that were quicker to start foraging preferred to forage in the longer stubble, than birds that initiated foraging later in the trial.


Residual number of pecks in obstructed patch
0.50
0.25
0.00
-0.25
-0.50
3.5
4.0
4.5
5.0
5.5
Log latency to forage