Time in captivity, individual differences and foraging behaviour in wild-caught chaffinches

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Summary

Wild-caught animals are often given a settling in period before experimental trials are initiated. We used wild-caught chaffinches (*Fringilla coelebs*) to investigate (a) the effect of settling in period duration on the likelihood that chaffinches foraged during experimental trials and (b) whether settling in period duration influenced measures of foraging and vigilance behaviour recorded from those experiments. The probability of collecting foraging data from an individual's first trial fell below 50% if it had been in captivity for more than 12 days prior to that trial, whereas the probability was >75% if trials were completed within two days of capture. The successful collection of foraging data from subsequent trials was also dependent on the number of days an individual spent in captivity prior to its first trial and on whether that individual foraged in its first trial, suggesting that some individuals were more inclined to forage in captivity. Individuals that foraged in their first trial had a 94% higher success rate in subsequent trials than those that did not. However, settling in period duration did not significantly influence the peck rate, mean search period or mean vigilance period of individuals that did forage. Our results show that allowing a settling in period actually reduced the likelihood of collecting foraging data from chaffinches and that commencing experiments shortly after capture increased data collection efficiency. We discuss the possibility that the inability to collect data from certain birds following a settling in period could lead to potentially important biases in results, particularly if propensity to forage is linked to an individual's coping strategy or personality. We conclude that it may not always be beneficial to allow wild-caught animals to habituate to captivity before commencing experiments. In some cases, testing animals soon after capture may increase the likelihood of data collection, reducing both the number of study animals required and the length of time they spend in captivity.

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Introduction

Wild animals taken into captivity are frequently given a considerable settling in period before starting experiments to allow them to habituate to captive conditions, such as the novel photoperiod and temperature regimes. Indeed, Day & O'Connor (2000) state that the successful habituation of their study species, brushtail possums (*Trichosurus vulpecula*), to captivity is essential if they are to be used for research purposes. Their study suggested that individuals adjusted to captivity within about four weeks of capture (Day & O'Connor, 2000). Ekman & Hake (1990) showed that the body mass of greenfinches (*Carduelis chloris*) took approximately one month to stabilize under aviary conditions. As a consequence, a similar time period between capture and experiment, to allow habituation to captivity, has been applied in a range of other studies using passerine birds (e.g. Lilliendahl, 1998, 2000; van der Veen & Sivars, 2000).

However, it remains unclear how the settling in period affects the likelihood of animals displaying the measurable behaviours necessary for experimental success or whether this is predetermined by some other individual difference, perhaps linked to competitive ability, coping strategy or personality (e.g. Benus et al., 1991; Verbeek et al., 1994; Slotow & Rothstein, 1995; Drent & Marchetti, 1999; Marchetti & Drent, 2000). Furthermore, it is important to know whether the data subsequently collected from an individual habituated to captive conditions can be taken as being broadly representative of the wider population or whether it is largely determined by the period of time an animal has been in captivity.

Understanding the potential for settling in period duration, and thus degree of habituation, to influence experimental outcome is potentially important for two reasons. First, ethical considerations highlight the importance of using the minimal number of individuals necessary to accomplish the research goals (McConway, 1992; ASAB, 2003). Second, any potential influence of an individual's degree of habituation to captivity on its behaviour should be of particular concern when the results of experiments on captive individuals are translated into predictions of the response of wild populations under comparable conditions (Lambrechts et al., 1999).

In this experiment we tested whether the time an individual spent in captivity prior to its first trial influenced the likelihood of collecting foraging data from that trial and whether the probability of an individual foraging in subsequent trials was dependent on whether it foraged in its first trial. We also tested whether measures of foraging and vigilance behaviour varied according to the time an individual spent in captivity prior to the trial from which the data were collected.

Methods

A total of 118 chaffinches were caught under license from English Nature between November 2001 and March 2002 (50 individuals), November 2002 and March 2003 (60 individuals) and March 2004 (8 individuals). These comprised 32 juvenile females, 32 juvenile males, 18 adult females and 36 adult males. On capture birds were aged, sexed and had their maximum wing chord measured (see Svensson, 1984). Chaffinches were housed individually in standard small-bird keeping cages (75 × 45 × 45 cm) in a single room at the Wytham Field Laboratory, University of Oxford. Birds were provided with food (wild birdseed mixture) and water *ad libitum*. Lighting followed the natural light : dark cycle and included 30 minutes of twilight in the mornings and evenings. Room temperature was maintained between 10 and 15°C throughout the course of the experiment. Once an individual had completed its trials it was released at its capture site. To control for any effect of catch date on the likelihood of collecting foraging data, 'season' was included in all models. Individuals caught before 14th January (the mid-point of catch dates) were scored as early-season (60 individuals) and those caught after the 14th January were scored as late-season (58 individuals).

Experimental set-up

The experimental arena consisted of a 0.5-m^3 wire cage placed over a substrate of artificial stubble designed to mimic natural wheat stubble. This artificial stubble was created by attaching vertical yellow drinking straws to a plywood board and spreading peat compost thinly between them. Prior to each experiment the peat was replaced and a number of canary grass seeds (*Phalaris canariensis* L.) were spread over the 0.5-m^2 basal area of the experimental cage. In conjunction with other experiments investigating the influence of stubble structure and food abundance on foraging and vigilance behaviour (Butler & Gillings, 2004; Whittingham et al., 2004; Butler et al., 2005) four artificial stubble types which varied in structural complexity and degree of visual obstruction were used and the number of canary grass seeds available varied between 400 and 800 seeds m^{-2}. These seed densities are within the range of natural densities found on stubble fields (Moorcroft et al., 2002). The order and type of stubble used for each individual's trials were randomised. To control for any effects of stubble type or food abundance on the likelihood of collecting foraging data from a trial, stubble type was included in all models.

Chaffinches were food deprived for two hours prior to their trial and transferred from their keeping cage to the experimental arena in a bird bag. To aid the capture of individuals from their keeping cages prior to experiments, the lights were switched off and a torch used to locate the bird before capture by hand and transfer to a bird bag. The removal of birds from their keeping cages took a matter of seconds and birds were released into the experimental arena within two minutes. A digital video camera was used to remotely view and record the behaviour of the bird once released into the experimental arena. Once the bird had foraged for approximately 30 seconds, or if the bird did not forage within ten minutes, the trial was terminated; the bird was caught, weighed and returned to its keeping cage with food and water again provided *ad libitum*. Any confounding effects of body condition on the likelihood of foraging were controlled for by including the mass of the bird divided by its wing length (i.e. mass controlling for size) in all models.

The number of days between capture and first trial allocated to each individual (i.e. settling in period duration) was varied to investigate the effect of time in captivity on foraging behaviour (mean $\pm$ 1 SE = 6.05 $\pm$ 0.72 days; range 1-39). The number of trials each individual completed varied according to the specific protocol of the other experiments being run concurrently with this study (see Butler & Gillings, 2004; Whittingham et al., 2004; Butler et al., 2005 and analysis section below for further details). The mean number of trials ($\pm$1 SE) undertaken by each individual was 4.5 ± 0.1 (range 2-5). Individuals were allowed to recover for at least 24 hours between experiments.

During the first year, all trials took place outside. In the second and third year, experiments took place within a whitewashed glasshouse. To control for these differences, and any other unmeasured variation between years, a year term was included in all models.

Analysis

Chaffinches fed by scanning the ground, pecking at a seed and then raising their head to handle the seed during which time the chaffinches were effectively vigilant (Whittingham et al., 2004). A vigilance period was defined as when the chaffinch had its head above the level of its back and a food search period was defined as when the chaffinch had its head below its body level.

Video footage from each trial was analysed using an event recording program (RECORDER). For each foraging bout, values for vigilance period, search period and peck rate were recorded; mean values were calculated for each foraging bout and then for the whole trial if more than one foraging bout occurred. A foraging bout is defined here as at least five pecks, each separated by less than ten seconds. A trial was scored as successful if at least one foraging bout occurred within ten minutes of the bird entering the experimental arena.

We tested the following models that correspond to the results sections:

(1) Does settling in period duration influence the likelihood of collecting data from an individual's first trial? — We tested this using a binary logistic regression (specifying a binomial error structure with a logit link function; Crawley, 1993). The response variable was specified as foraged (1) or not foraged (0) in the first trial that an individual underwent, with age, sex, stubble type, season and year as factors and body condition and days in captivity as covariates in the model. Only one datum was included from each of 118 individuals. The statistical significance of excluding each predictor, in turn, from the full model (i.e. all predictors fitted together) was assessed by the change in deviance (ΔD) (which approximates to the likelihood ratio test), the results of which are distributed asymptotically as χ^2.

(2) Does the proportion of successful trials subsequently completed by an individual depend on the outcome of its first trial? — We tested this using logistic regression (again specifying a binomial error structure with a logit link function; Crawley, 1993), with the number of trials in which an individual was recorded foraging after its first trial specified as the response variable and the total number of trials an individual completed after its first trial as the binomial denominator. Age, sex, season, year and success of first trial were factors in the model and number of days in captivity prior to first trial was a covariate. Again one datum was used from each of 118 individuals. The significance testing was carried out as described in section 1

above. The best way to assess the fit of binomial error models is to compare the ratio of residual deviance / residual degrees of freedom (Collett, 1991; Crawley, 1993). Although these ratios only indicate a rough guide to the fit of the model, Crawley (1993) suggests that ratios close to 1 indicate a reasonable fit to the data, whereas ratios greater than 2.5 indicate a poor fit. We found a ratio of 2.1 suggesting that the data were not overdispersed (note that the binary logistic regression models outlined in section 1 above cannot be overdispersed (Crawley, 1993) and so no such tests were needed).

(3) Does time in captivity alter foraging behaviour? — We used general linear modelling (GLM), specifying either peck rate, mean search period or mean vigilance period as the dependent variable with age, sex, season, year, stubble type and the number of previous trials undertaken as factors and body condition and days in captivity prior to the first successful trial as covariates in the model. One datum from each of 100 individuals (that foraged in one or more trials) was used. Data from the first trial in which an individual foraged were used. The effect of a predictor was tested using an F-ratio by excluding it from the full model.

Analyses for sections 1 and 2 were undertaken using GLIM 4 (NAG, 1993) and the SPSS statistical programs (Norusis, 1990) were used for the analyses detailed in section 3. All dependent variables were tested for normality and transformed where appropriate (only mean search period was non-normally distributed and was consequently arcsin square-root transformed). All probabilities quoted are two tailed. Means and standard errors are quoted in the form mean $\pm$ 1 standard error (SE).

Results

(1) Does settling in period duration alter the likelihood of collecting data from an individual's first trial? — Individuals kept in captivity for longer periods before their first trial were less likely to forage during that trial than individuals which underwent their first trial soon after capture ($\chi^2 = 9.81$, $p < 0.005$). There was no effect of year, season, sex, age, stubble type or body condition on the probability of collecting foraging data from an individual's first trial (Table 1). The model predicts that if an individual undergoes its first trial within two days of capture, there is a 75% probability that foraging data will be successfully collected. If an individual is kept in captivity for more than 12 days prior to its first trial, this probability

Table 1. Results of binary logistic regression analysis on the likelihood of collecting foraging data from an individual's first trial (note only one datum per individual used). Direction of any association (+ or −) between predictor variables and likelihood of foraging in first trial are given. The best-fit line from the effect of days in captivity on probability of collecting foraging data is illustrated in Figure 1.

	χ^2	df	p
Year	0.24	2	>0.50
Season	0.35	1	>0.50
Sex	0.48	1	>0.25
Age	0.08	1	>0.75
Stubble type	6.66	5	>0.25
Days in captivity prior to 1st trial	9.81	1	<0.005 (−)
Body condition	0.96	1	>0.25

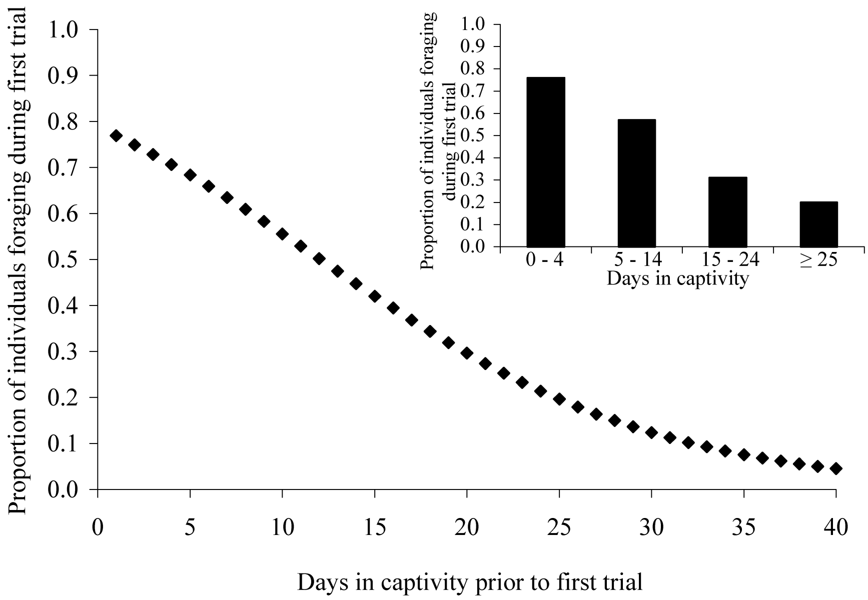

Figure 1. The likelihood of collecting foraging data from an individual's first trial declined with the number of days it spent in captivity prior to that trial ($\chi^2 = 9.81$, $p < 0.005$). Main graph shows predicted relationship from binary logistic regression model excluding non-significant predictors (year, season, sex, age, stubble type and body condition). The insert shows experimental data.

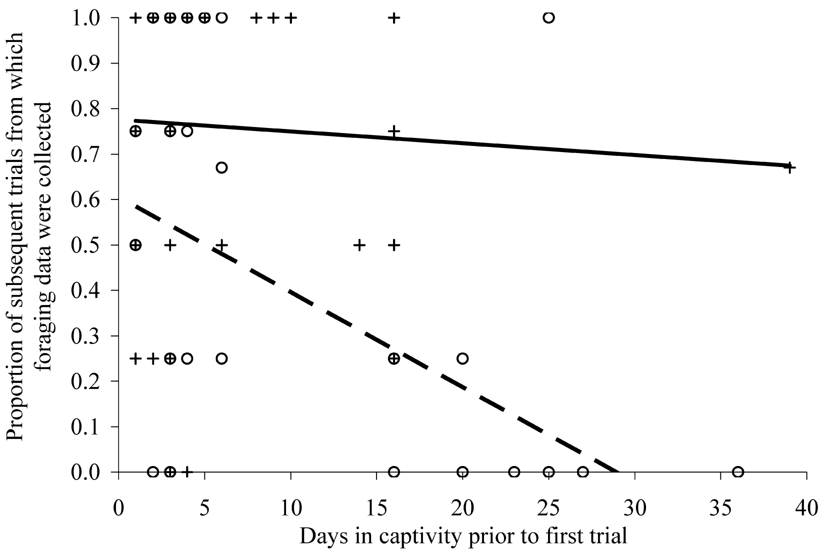

Figure 2. The proportion of an individual's trials, subsequent to its first trial, from which foraging data were collected depended both on the number of days the individual spent in captivity prior to its first trial and on whether it successfully completed its first trial (Table 2). Dotted line represents linear regression for individuals that did not forage in their first trial (○); Solid line represents linear regression for individuals that did forage in their first trial (+).

falls below 50% and after 21 days in captivity the probability of collecting foraging data falls below 25% (Figure 1).

(2) Does the proportion of an individual's subsequent trials from which foraging data are collected depend on the outcome of its first trial? — Individuals that foraged during their first trial foraged in a significantly higher proportion of subsequent trials than individual's that did not forage in their first trial (mean proportions 0.77 ± 0.03 and 0.39 ± 0.07 respectively; $\chi^2 = 5.8$, $p < 0.05$). The proportion of subsequent trials an individual successfully completed was also negatively related with how long it had spent in captivity prior to its first trial but the strength of this effect was significantly greater if the individual did not successfully complete its first trial (Figure 2; Table 2).

(3) Does time in captivity alter the foraging data collected? — There was no effect of the number of days an individual spent in captivity prior to a trial on its peck rate, mean vigilance period or mean search period during that trial ($p > 0.5$ in all cases).

Table 2. Results of logistic regression analysis on the proportion of an individual's trials, subsequent to its first trial, from which foraging data were collected (note only one datum per individual used). Directions of any associations between predictor variables and likelihood of foraging in first trial are given.

	χ^2	df	*p*
Year	2.78	2	>0.25
Season	8.16	1	<0.01 (early < late)
Sex	0.98	1	>0.5
Age	6.01	1	<0.05 (juv > ad)
Data collected from 1st trial	5.8	1	<0.05 (no < yes)
Days in captivity prior to 1st trial	0	1	1
Data * days[1]	6.73	1	<0.05

[1] Represents interaction between data collected from first trial and days in captivity prior to 1st trial.

Discussion

Increasing time in captivity prior to an individual's first trial reduced the likelihood that foraging data would be successfully collected, with the probability of collecting data falling below 50% if an individual had been in captivity for more than 12 days before undergoing its first trial. The likelihood of collecting foraging data from subsequent trials was also dependent on the number of days an individual spent in captivity prior to its first trial and on whether that individual foraged in its first trial. Those individuals that foraged in their first trial had a 94% higher success rate in subsequent trials than those that did not forage in their first trial. However, time in captivity did not significantly influence the peck rate, mean search period or mean vigilance period when individuals did forage.

Whether or not an individual foraged during its first trial is likely to have been dictated by a number of factors such as its perceptions of relative starvation risk and predation risk (Milinski & Heller, 1978) in the experimental arena compared to its keeping cage, the type and level of stress response induced by the experimental procedure or the individual's personality type, which could influence its response strategy for coping with that stress (Drent et al., 2003). The observed decrease in likelihood of foraging with increased settling in period duration therefore suggests that the perceptions of starvation or predation risk associated with a trial and/or the type and level of stress induced by the experimental procedure changed with time in captivity. The result could also be explained if there was a correlation between the settling in period duration allocated to an individual and its position along a personality axis, for example from 'bold' to 'shy' (Wilson et al., 1994; Greenberg, 1995). However, any such relationship is highly unlikely given that individuals were tested randomly with respect to time since capture.

Perceived predation risk and starvation risk are manifest in the trade-off between foraging and vigilance behaviour (Metcalfe, 1984; Lazarus & Symonds, 1992). One would therefore expect to see changes in the relative allocation of time to these behaviours according to settling in period duration if a relationship between the latter and perceived risk existed. Previous experiments have demonstrated that chaffinches can compensate for changes in perceived predation and starvation risk by altering foraging and vigilance behaviour (Whittingham et al., 2004; Butler et al., 2005) but there was no evidence of any such compensation in this experiment, with no relationships between settling in period duration and any of the measures of foraging and vigilance behaviour tested. This suggests that settling period duration affects response latency rather than foraging behaviour itself. However, it is possible that, rather than being a continuous function, our results demonstrate that the predation/starvation risk trade-off is a step function, with perception of risk dictating simply whether or not an individual chose to feed rather than the amount of time allocated to foraging and vigilance behaviours once feeding had commenced. Birds that had longer settling in periods, with *ad libitum* food available, were likely to have had lower perceptions of starvation risk than recently caught birds (Ekman & Hake, 1990). For these birds, the trade-off between predation and starvation risk in the experimental arena may therefore have been heavily influenced by the increased perceived predation risk of the novel surroundings, making them less likely to feed.

The observed decrease in the likelihood of foraging with settling in period duration could also be due to changes in the level of stress induced by the experimental procedure. Identifying an unambiguous stress indicator can prove problematic (Jensen & Toates, 1997) and, without a clearer understanding of stress responses to our experimental procedure, we cannot conclusively say whether 'foraging' or 'no foraging' was indicative of elevated stress levels. However, two factors suggest that individuals which had spent longer in captivity may have been more stressed by the experimental procedure and, therefore, that 'no foraging' during a trial is an appropriate indicator of stress in these circumstances. Firstly, a number of experiments using feeding tests to measure fear or stress levels in a range of mammals have concluded that hyponeophagia, the reluctance to forage in novel surroundings, is an indication of increased fearfulness or stress (e.g. Hall, 1934; Trullas & Skolnick, 1993; Rekilä et al., 1997). Secondly, individuals in our experiment tended to lose weight as time in captivity increased and Jones et al. (1997) demonstrated that underlying fearfulness was greater in Japanese quail (*Coturnix coturnix japonica*) with lower body weight.

Alternatively, the decline in likelihood of foraging may reflect a change in stress response type to the experimental procedure rather than a change in level of stress induced. There is increasing evidence from laboratory experiments of duration-dependent differences in types of behavioural responses to challenging events (Heller et al., 1999). Two types of stress response pattern have been characterised: the Cannonian fight-flight pattern (Cannon, 1929) is characterised by increased activity, approach and aggression and tends to be shown in short-term stress situations, whilst the Selyean conservation-withdrawal pattern (Selye, 1950) is characterised by avoidance, flight or immobility and tends to occur in longer-term stress situations. Thus, individuals with shorter settling in periods may have been displaying Cannonian response patterns whilst those with longer settling in periods may have been demonstrating Selyean response patterns.

It is clear from our results that if an individual foraged in its first trial it was also significantly more likely to forage in subsequent trials. Given that the collection of foraging data from an individual's first trial was principally dictated by time in captivity, this result is also likely to be largely driven by degree of habituation to captive conditions. The time an individual spent in captivity before it entered the first trial was highly correlated with time to trials subsequent to the first trial because, once an individual had started the experiment, all trials were completed within a short time period. However, there was a significant interaction between settling in period duration and whether or not foraging data were collected from the first trial (Figure 2; Table 2). The effect of settling in period duration on the likelihood of foraging in subsequent trials was greatly reduced for individuals that foraged in their first trial compared to the effect on individuals that had not foraged in their first trial. Our results suggest that some individuals were more inclined to forage during experimental trials whilst others were much less likely to forage, regardless of their time in captivity prior to commencing experiments.

This observed relationship can also be explained in terms of individual differences in risk perception. Individuals of poor competitive ability are likely to have very high perceptions of starvation risk and may therefore take longer to respond to any changes in perceived starvation risk arising from being brought into captivity. These individuals would be expected to forage in later trials. This explanation is supported by the fact that juveniles foraged in an increased proportion of trials subsequent to their first trial compared to adults (Table 2). This relationship could also have arisen through variation in personality traits, such as reaction to stress (Carere et al., 2001) or boldness (Drent & Marchetti, 1999), between individuals. Another experiment using the present chaffinch system suggested that hypoactive or 'slow' personality types were indeed better able to discriminate between high and low predation risk situations (Quinn & Cresswell, 2005). However, it is not possible from our results to determine the overriding factor that dictates the observed propensity to forage in this experiment.

Implications for experimental design

The results of this study suggest that it may not always be beneficial, in terms of data collection efficiency, to allow wild-caught individuals to habituate to captive conditions before commencing experiments (Ekman & Hake, 1990; Day & O'Connor, 2000). In this study, not only was the likelihood of collecting foraging data from an individual's first trial increased by undertaking experiments shortly after capture but the proportion of subsequent trials in which the individual foraged was also higher. It was evident that if a longer settling in period was allocated, data collection was largely limited to trials on individuals that were somehow predisposed to forage, potentially generating a bias in the results and the subsequent interpretation of foraging data. Adopting a methodological approach with reduced settling in period duration increased experimental efficiency and generated a more representative dataset by increasing the likelihood of collecting foraging data from all individuals. This approach also had ethical merits as it reduced the number of study animals required and the length of time they spent in captivity.

Here we provide a species- and behaviour-specific example of the effects of settling in period duration and readily accept that the observed results cannot be generalised across species or behavioural responses. However, whatever the mechanism driving the observed results in this experiment, we strongly believe that this finding merits further investigation and that the potential impact of settling in period duration on an individual's behaviour are given due consideration when designing future studies.

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