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More opportunities to peck for identical food availability increases foraging efficiency in pigeons

Neslihan Wittek, **Fatma Oeksuez**, **Onur Güntürkün and Patrick Anselme** *
Department of Biopsychology, Faculty of Psychology, Ruhr-University Bochum,
Universitätsstraße 150, D-44801 Bochum, Germany
*Corresponding author's e-mail address: Patrick.Anselme@rub.de
ORCID iD: Anselme: 0000-0001-6650-0962

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Abstract
The opportunity and the information available to secure food resources drives foraging behaviour. We tested how inconsistent hole-food pairings and coverings could alter foraging performance, even when food availability is held constant. In our first experiment, we exposed pigeons (*Columba livia*) to a board in which each of the 60 covered holes contained one food item and to another board in which only one third of the 180 covered holes randomly contained one food item. In a second experiment, only the 60-hole board was used and the holes were not covered. The pigeons increased their body weight, gave fewer pecks per hole, revisited holes less often, and inspected fewer adjacent holes with 180 rather than 60 covered holes while eating similar amounts. However, their pecks were disproportionately higher near the edges of the board with 60 covered holes. This behaviour was not evident in the second experiment, when the food items were visible and individuals could know where food was available. Thus, the information about food location may drive foraging behaviour more directly than the information about food availability.

Keywords
foraging, exploration, semi-natural environment, unpredictability, information availability.

1. Introduction

Animals in their environment spend a significant part of their activity period trying to find food (e.g., McNamara et al., 1994; Lovette & Holmes, 1995; Olsson et al., 2000; Daunt et al., 2006). However, foraging is sensitive to multiple factors that limit access to food, such as predation risk, unfavourable weather conditions, and the risk of injury (e.g., Lima, 1986; McNamara

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& Houston, 1990; Witter & Cuthill, 1993; Gosler et al., 1995; Cresswell, 1998; Krams, 2000; Ratikainen & Wright, 2013). The need to manage these constraints reduces the time and energy that animals can allocate to foraging and may cause missed opportunity costs in case of suboptimal situations or bad decisions (Lima & Dill, 1990). Environmental conditions associated with a need for risk avoidance behaviour and unpredictable access to food resources should lead to greater search effort that may incur survival costs. For example, snow cover in winter may interrupt foraging and postpone resource acquisition for a long duration that imperils survival (e.g., Brodin, 2007).

Unpredictable food resources — here, defined as an uncertainty-related reduction in food access (e.g., Nettle & Bateson, 2019) — is common in the wild and it can easily be simulated in the laboratory. One method typically used in behavioural ecology, mainly in birds, consists of providing limited access to food following an unpredictable delay. As a result, organisms often increase their body weight owing to an accumulation of fat deposits (e.g., Ekman & Hake, 1990; Wiersma & Verhulst, 2005; Ratikainen & Wright, 2013). In this respect, there is some evidence that food uncertainty selects for individuals to maximize foraging efficiency when food is available, which could increase consumption rates and hence fattening (Pravosudov & Grubb, 1997; Laran & Salerno, 2013; Swaffield & Roberts, 2015; Cheon & Hong, 2017; Anselme & Güntürkün, 2019). But other studies suggest that fattening is independent of consumption rate (Wiersma & Verhulst, 2005; Cornelius et al., 2017; Nettle & Bateson, 2019). Recently, Bateson et al. (2021) conducted a meta-analysis based on a heterogeneous set of experiments with starlings (*Sturnus vulgaris*) in a controlled apparatus. The birds could peck at an illuminated response key for food delivery and their body weight was measured while perching in front of the key. In the experimental designs to which they refer, the starlings ate less under food uncertainty but showed a higher body weight in comparison with starlings exposed to predictable food delivery. This phenomenon can be interpreted in terms of a bet-hedging strategy — where biological traits, here responsible for fattening, evolved as adaptations to unpredictability itself (Simons, 2011).

Another method used to induce unpredictable food resources, consists of repeatedly exposing an animal to a cue whose brief presentation is randomly followed or not followed by a food reward during a training session. Almost no attention has been paid to changes in body weight in the studies based on this procedure. But higher response rates to the cue typically occur following inconsistent rather than consistent cue-food pairings in a variety of animal species (Perkins et al., 1975; Crawford et al., 1985; Pearce et al., 1985; Ishida et al., 1992; Gottlieb, 2004; Anselme et al., 2013; Glueck et al., 2018; Bateson et al., 2021; but see Rescorla, 1999; Wittek et al., 2021). Overall, inconsistent cue-food pairings are more stimulating than consistent ones and could therefore possibly lead to distinct foraging patterns. But studying the behaviour of animals in front of a cue or a food cup in a confined environment in which only one relevant response is possible may limit the panel of expression of foraging behaviours. As Timberlake (1994) pointed out, “laboratory research is most useful when researchers tune their procedures and apparatus to create ties to natural appetitive behavior and report the topography of the resultant behavior” (p. 407).

The present study assesses several foraging variables such as pecks and their spatial distribution, in addition to food consumption and body weight, in freely moving pigeons (see also Feenders & Smulders, 2011; Heppner, 1965; Howery et al., 2000). Pigeons (*Columba livia*) were exposed to two semi-natural environments — i.e., ‘foraging boards’ perforated with holes, in which food items could potentially be found. The boards differed in search-reward ratio, that is, in food accessibility but not in food availability. In Experiment 1, each hole was covered with a thin plastic layer with a cross cut above each hole to create an opening, which allowed a hole to be explored while preventing the pigeon from detecting the presence of food from a distance. In Experiment 2, only one board was used and the holes were no longer covered; the pigeons could directly see whether a hole was baited or empty. Indeed, animals tend to adjust their behaviour to the fact that food is hidden or visible (e.g., Forkman, 1996; Bean et al., 1999). In our study, differences in foraging and body weight could not be attributed to the opportunity to eat more in one condition/experiment than in the other, because the number of food items was equivalent and the duration of a session was sufficient to explore all the holes available. Given the physiological and behavioural effects of reward uncertainty traditionally reported, we expected that more opportunities to peck for identical food availability would increase the body weight and the propensity of pigeons to explore in case of a higher search-reward ratio (Experiment 1). Also, we expected an increase in both speed and efficiency of foraging when the food items are visible, because handling time and effort are necessarily reduced (Experiment 2).

2. Experiment 1

2.1. Methods

2.1.1. Animals and housing conditions

Sixteen adult homing pigeons (5 males, 11 females; age 6.75 ± 0.68 years) obtained from local breeders and already used in unrelated experiments were maintained at 85–90% of their free-feeding body weight for the duration of the experiment. Water was accessible ad libitum in their home cage. Eight pigeons were individually housed, while the other eight individuals were housed in an aviary under a 12 h light/dark cycle (lights on at 7:30 am). All procedures followed the German guidelines for the care and use of animals in science, and were in accordance with the European Communities Council Directive 86/609/EEC concerning the care and use of animals for experimentation. They were also approved by our university.

2.1.2. Apparatus

The experiment was conducted in a rectangular wooden box with a net on top to prevent the pigeons from flying away. The floor consisted of a horizontally removable brown wooden board (120 cm long × 70 cm width × 40 cm height) perforated with holes (1.5 cm diameter and 2 cm depth) in which a grain (corn, green pea, yellow pea, or sunflower) could be placed (Figure 1A). One foraging board, referred to as Board 60 hereafter, contained 60 holes organized as 6 rows of 10 holes regularly spaced in a lengthwise direction. Another, referred to as Board 180 hereafter, contained 180 holes (3 times more) organized as 9 rows of 20 holes regularly spaced. The holes were closer to the edges of Board 180 (5.7 cm and 7 cm) than of Board 60 (15 cm and 10 cm). Both boards were covered with opaque black plastic tape and two slits were cut through it where the tape covered a hole, to form a cross-shaped opening. This allowed the pigeons to get the food items without being able to visually detect their presence from a distance. As the boards were heavy and difficult to manipulate, each was cut in two equal parts in a widthwise direction, and these two parts were placed next to each other during a session to form a complete board. There was a small entrance compartment (28.7 cm long × 20.4 cm width × 36 cm height) with two vertical doors, one allowing the experimenter to introduce the pigeon in the compartment and another giving the pigeon access to the board. The entrance compartment was located in the middle of one long side of the box. Each session was recorded with an external camera (Hero4 Session, GoPro), placed

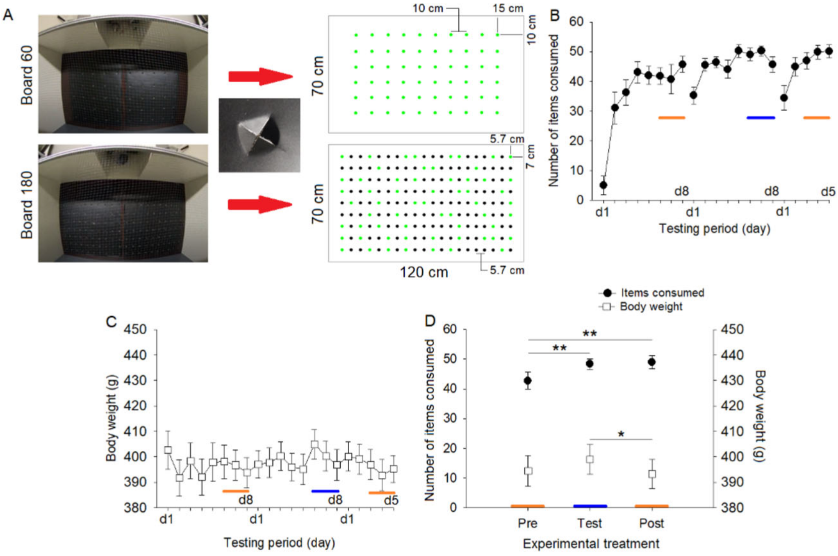

Figure 1. Experiment 1: Changes in food consumption and body weight in the different treatments. (A) Apparatus: Board 60 (top) and Board 180 (bottom) with the detail of a covered hole. On the right, annotated schemas representing both boards (green dot = baited hole; black dot = empty hole). (B) Food consumption across days (or sessions) for each treatment. (C) Body weight across days (or sessions) for each treatment. (D) Blocks of the last three sessions for each treatment with respect to food consumption and body weight. The colours used in graphs B and C indicate the data averaged from the last three sessions in each treatment to form graph D. The data points represent means and standard errors.

above the apparatus. These recordings were used for a manual extraction of the relevant data and offline deep learning analysis.

2.1.3. *Procedure*

After being weighed, one pigeon was placed in the entrance compartment via the external vertical door, which remained closed during a session. A second vertical door giving the pigeon access to the board was then immediately removed and remained open during the session. The pigeon could then freely move and consume grains on the board or spend time in the entrance compartment for a total of 10 min.

At training, the pigeons were habituated to Board 60, where each hole contained one food item and was not covered to facilitate the learning of the hole-food association. This training phase lasted for 5 consecutive days (or sessions), although a few more days (sessions) were necessary for four individuals (5.75 ± 0.36 days). At least 50% of the food items available had to be consumed to start the first experimental treatment. Then, the pigeons were exposed to three successive experimental treatments with covered holes. At pre-test, Board 60 was used, and each hole contained one food item. The pigeons were pre-tested for 8 days (or sessions). At test, Board 180 was used, and 60 random holes were baited with one food item. Given that the remaining 120 random holes were empty (but covered as well), the number of food items available on Board 180 was identical to that on Board 60, but their accessibility was reduced owing to their random distribution and the larger number of holes to be inspected. Test also lasted 8 days (or sessions). Finally, at post-test, Board 60 was used again in the same conditions as at pre-test and lasted 5 days (or sessions) — because the pigeons had already experienced Board 60.

After a session, the pigeon was picked up from top and the number of food items consumed was manually counted. The board was cleaned and prepared for the next pigeon. The placement of the new food items in Board 180's holes followed a randomly generated pre-established plan that changed every day and guaranteed the randomness (uncertainty) of their location relative to the empty holes. Each quarter of Board 180 (45 holes) contained 15 food items to avoid side preference. After placing the new food items, the corners of the crosscut tape above the holes were realigned using a manual tweezer. Each new experimental phase started on a Monday, and the animals were not tested during the weekends. At the end of the procedure, the sex of the pigeons was determined by means of a PCR test for each individual.

2.1.4. Data extraction and statistical analyses

The data were manually counted or extracted from the videos. We collected information from the last three days (or sessions) only. The last three sessions of each treatment were averaged to avoid random daily variations in performance and obtain more stable, robust effects in case they occur. No data selection was carried out. The data collected every day (body weight and the number of food items consumed), were both processed on a daily basis and as averaged blocks of the last three sessions. Reporting daily measurement/counting was useful to determine how stable these variables were over time, as they could have direct impact on the foraging behaviours we aimed to assess.

Besides body weight and food consumption, we assessed the number of pecks per hole, the number of revisits per hole, the density distribution of pecks on a board, the missed pecks, the time latency before the first peck at a hole, the duration between the first and the last peck at a hole, and the distance travelled. A missed peck meant that the pigeon tried to extract a piece of grain from a hole but dropped it onto the board. Occasional pecks out of a hole, even when given at a grain that had rolled on the board (missed pecks), were counted independently. Determining whether a peck at a hole was successful (food item grasped) or not was mostly impossible from videos, so that peck is not a synonym of consumed item. A peck simply meant a vertical movement of the pigeon's head above a hole. The time latency before the first peck was the time between complete opening of the vertical door giving access to the board and the first peck at a hole.

The distance travelled by the pigeons on the boards was assessed using the machine-learning-based tracking software DeepLabCut (Nath et al., 2019). To extract multivariate time-series data, we tracked different points on the pigeons (beak, head, shoulders, back, different parts of wings and tail — see video samples in the Appendix at 10.6084/m9.figshare.19939724). The time-series data consisted of coordinate information of these tracked points in each frame, whether they were related to foraging or not. For further analysis, we used the middle of the spine point (body) in all videos because this point allowed stable tracking. We calculated the Euclidean distance of the tracked body between two frames (as if this distance was a straight line) and calculated the sum of all frames within a session, which added up as the total distance travelled per video, expressed as a number of pixels. The Ramer–Douglas–Peucker algorithm was used as a noise reduction filter. A second method consisted of not measuring a physical distance but rather an abstract value whose unit corresponded to the separation between two adjacent holes. Pecking at one hole and then at the next one represented a distance of 1; pecking at one hole and then 3 holes further on the same row or column represented a distance of 3; and so forth. If the pigeon pecked at one hole and then at a hole on a different row/column, the distance corresponded to the hypotenuse of a triangle whose other two sides were the number of horizontal (row) and vertical (column) holes necessary to travel from the first to the second hole. The distance was calculated using the Pythagorean Theorem: $\text{Travel event} = \sqrt{n_{\text{row}}^2 + n_{\text{col}}^2}$, where n_{row} and n_{col} denote the number of holes in the row and in the column, respectively. The distances were calculated between two pecks, from the first to the last peck over a session. Finally, foraging bouts were sometimes interrupted by foraging-unrelated behaviours, and we counted those bouts within a session. A foraging bout started when a pigeon came to look for food (screening around with its head up or inspecting the holes while walking or standing) and ended when a food-unrelated behaviour took place (preening, body shaking, tail shaking, rest, or unfocused walking).

In short, automated tracking was used when measurements via manual counting were impossible. Conversely, DeepLabCut did not allow us to measure pecking reliably on the board. First, the vertical movements of a pigeon's head were difficult to detect from marks on its body, which was filmed by a single camera placed above the apparatus (see video samples in the Appendix at 10.6084/m9.figshare.19939724). Second, because the tracking method used with regards to identifying if there was a peck was unreliable, distinguishing a peck at a hole (counted) and a peck outside of a hole (not counted) or a missed peck (counted separately) was not possible.

As we used a within-subject design, most statistical analyses were carried out by means of two-tailed repeated measures ANOVAs (Statistica 13). All the p-values were corrected for multiple comparisons using the Tukey post-hoc test, and statistical significance was accepted at $p < 0.05$ (corrected value only). Effects sizes were reported as partial eta-squared values. Means and standard errors were used for all calculations.

2.2. Results

2.2.1. Initial learning of the task

At training, the pigeons learned to find the food item contained in each non-covered hole of Board 60 ($F_{4,60} = 11.995$, $p < 0.001$, $\eta_p^2 = 0.44$). The number of food items consumed was manually counted and significantly increased from the first (14.1 ± 4.0) to the last day of exposure (42.6 ± 5.2; $p = 0.0001$). The pigeons ate less food on day 1 than on any of the next four days (d1 vs. d2 to d5: p values $\leqslant 0.002$), which only showed non-significant changes over time. Thus, foraging performance stabilized quickly. In parallel, their body weight significantly decreased across the 5 training days ($F_{4,60} = 6.760$, $p = 0.0001$, $\eta_p^2 = 0.31$). It was 435.8 ± 8.7 g on day 1 and 407.6 ± 7.6 g on day 5 ($p = 0.001$). Like with the items consumed, body weight differed between day 1 and any of the next four days (d1 vs. d2 to d5: p values $\leqslant 0.007$), which were statistically similar relative to each other. Body weight was also quickly stabilized. On this basis, the experiment — consisting of a pre-test, test, and post-test with covered holes — could take place.

2.2.2. Body weight and the number of food items consumed

Changing the board from a hole non-covered (training) to a hole covered situation (pre-test) had a detrimental effect on the number of food items consumed on pre-test day 1, which dropped to 5.0 ± 3.2 ($F_{1,15} = 32.254$, $p < 0.001$, $\eta_p^2 = 0.68$). With respect to the mean number of food items consumed on each day of each treatment, there were strong overall significant effects at pre-test (Figure 1B; $F_{7,105} = 19.429$, $p < 0.001$, $\eta_p^2 = 0.56$), test ($F_{7,105} = 9.418$, $p < 0.001$, $\eta_p^2 = 0.38$), and post-test ($F_{4,60} = 13.162$, $p < 0.001$, $\eta_p^2 = 0.47$). Like with training, one noticeable phenomenon is the lower consumption rate on the first day of each treatment relative to the second day (pre-test: $p = 0.0002$; test: $p = 0.0004$; post-test: $p = 0.0009$) and all other days (d1 vs. d3 to last day: p's $\leqslant 0.004$). Performance stabilized from the second to the last day within each treatment, as no significant effects were found — but one at pre-test between days 2 and 8 ($p = 0.018$).

The variations in body weight on each day of each treatment (Figure 1C) showed significant overall effects at pre-test ($F_{7,105} = 4.063$, $p < 0.001$, $\eta_p^2 = 0.21$), test ($F_{7,105} = 6.162$, $p < 0.001$, $\eta_p^2 = 0.29$), and post-test ($F_{4,60} = 7.420$, $p < 0.001$, $\eta_p^2 = 0.33$). More specifically, at pre-test, day 1 differed from days 2, 4, and 8 (p values $\leqslant 0.018$). At test, day 6 differed from days 1, 2, 4, 5, 8 (p values $\leqslant 0.003$). Finally, at post-test, day 1 differed from days 4 and 5 and day 2 from day 4 (p values $\leqslant 0.019$).

In this study, we were not interested in the daily variations in food consumption and body weight but rather in how reduced access to food for identical availability could influence these two dependent variables in animals familiar with the experimental conditions. To generate robust comparisons, we averaged the last three sessions at pre-test (Board 60), test (Board 180), and post-test (Board 60), and these blocks of sessions were compared. Figure 1D represents together the number of food items consumed ($F_{2,30} = 8.207$, $p = 0.001$, $\eta_p^2 = 0.36$) and the body weight of pigeons ($F_{2,30} = 4.915$, $p = 0.014$, $\eta_p^2 = 0.25$) in each block. The pigeons ate more food items at test than at pre-test ($p = 0.007$). On average, this represented 5.56 additional items ingested on Board 180 despite the presence of three times more holes to check than on Board 60 and an equivalent amount of food available on both boards. At post-test, the pigeons ate a similar number of food items than at test ($F_{1,15} = 0.180$, $p = 0.677$) and consumption remained significantly higher than at pre-test ($F_{1,15} = 10.630$, $p = 0.003$). With respect to body weight, we found a non-significant increase from pre-test to test

($F_{1,15} = 3.824$, $p = 0.064$) but a significant decrease from test to post-test ($F_{1,15} = 43.997$, $p = 0.016$). The body weight values at pre- and post-tests were similar ($F_{1,15} = 0.283$, $p = 0.811$).

2.2.3. Density distribution of hole-directed pecks

The number of pecks in each hole of Boards 60 and 180 was manually counted, so that foraging distribution could be represented in a 3D format (x-axis = holes per column; y-axis = holes per row; z-axis = pecks per hole). For each hole, we used the sum of the number of pecks per pigeon, averaged across the sixteen individuals. This information was collected for the last three sessions of each treatment and averaged within each treatment. We see that the density of pecks was qualitatively similar at pre- and post-test on Board 60, where each hole contained one food item, and different at test on Board 180, where only 1/3 of the holes contained one food item (Figure 2A). At pre- and post-test, the pigeons concentrated a large number of pecks in several areas, especially close to the edges of the board. The centre of the board remained poorly explored in comparison. By contrast, at test, the areas of intense pecking were almost absent, the pigeons having pecked in a more uniform, less frantic manner everywhere. In the Appendix at 10.6084/m9.figshare.19939724, we provide a 3D distribution of the averaged pecks per pigeon at post-test (days 8, 9 and 10), where the edge effect was mostly visible (Figure A1 in the Appendix at 10.6084/m9.figshare.19939724). Pecks

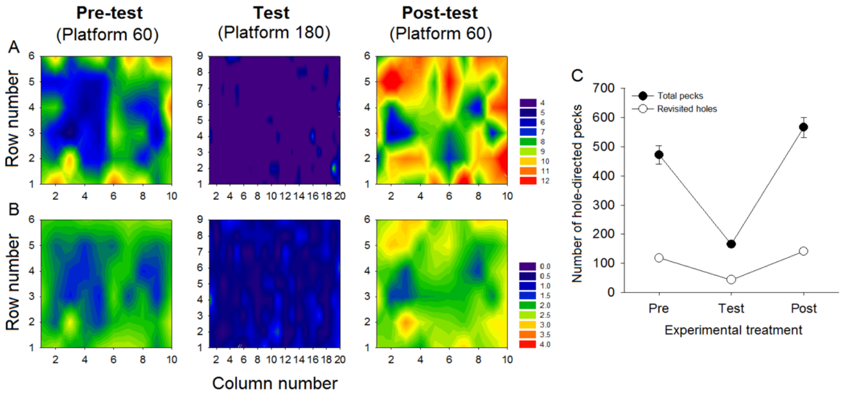

Figure 2. Experiment 1: Hole-directed pecks (blocks of last three sessions). (A) Density distribution of pecks on a board across treatments. (B) Density distribution of revisited holes on a board across treatments. (C) Total number of pecks and revisited holes (performance reported for 60 holes) on a board across treatments (means and standard errors).

were assumed to be near an edge when they occurred in rows 1–2 or 5–6 and/or in columns 1–2 or 9–10. On this basis, we identified 9 (out of 16) pigeons as preferring to peck close to the board's edges: 229, 252, 395, 543, 598, 633, 758, 802 and 868. Four pigeons were hard to classify, as they often pecked near the edges but also gave a noticeably high number of pecks in more central areas: 90, 104, 257 and 554. Finally, three pigeons were indifferent between the edges and the central areas: 115, 757 and 857. These results suggest that a majority of pigeons preferentially pecked nearer the edges of Board 60, even if this preference was less pronounced when analysed individually rather than across individuals (see Figure 2A). The same analysis was conducted with respect to the number of revisited holes, and depicts similar patterns (Figure 2B). This indicates that the pigeons were not just exploring some areas more than others, especially on Board 60, but gave multiple pecks at the same holes in those areas.

The absolute number of pecks — counted independently of the number of holes — did not differ between pre-test and test ($p = 0.365$) and it was significantly lower in these two treatments than at post-test (p values $\leqslant 0.041$), for an overall significant effect ($F_{2,92} = 7.513$, $p = 0.001$, $\eta_p^2 = 0.14$). (These absolute values are reported in Figure 2C for the 60 holes at pre- and post-test, and the absolute value for the 180 holes at test was divided by three to make comparisons possible — see below.) Changing the treatment did not have any noticeable effect on the pecking rates — beyond learning effects. However, when the pecks were measured relative to the same number of holes, the quantitative analysis of the total number of pecks corroborated the 3D imaging: Pecking activity appeared lower at test than in the other two treatments. On average, the pigeons pecked 7.86 and 9.44 times per hole at pre- and post-test, respectively, and only 2.76 times per hole at test. Using 60 holes as a baseline for comparisons, a disproportionate number of pecks occurred on Board 60 before and after an exposure to Board 180 (Figure 2C; $F_{2,92} = 121.802$, $p < 0.001$, $\eta_p^2 = 0.72$). The pigeons pecked significantly less at test than at pre- and post-test (p values $= 0.0001$), and they also pecked less at pre- than at post-test ($p = 0.001$). Accordingly, we see that the number of revisited holes followed a similar pattern (Figure 2C; $F_{2,92} = 92.845$, $p < 0.001$, $\eta_p^2 = 0.67$), in which less holes were revisited at test than at pre- and post-test (p values < 0.001) and less at pre- than at post-test ($p = 0.008$).

Table 1.
Experiment 1: Different behaviours manually collected from videos of pigeons on a board.

Behaviour	Pre-test	Test	Post-test
Number of missed pecks	7.396 (1.090)	5.333 (0.805)	7.2 (1.315)
Time latency (s)	12.083 (2.834)	7.667 (1.856)	8.596 (2.524)
Foraging duration (s)	475.5 (23.143)	474.042 (21.777)	493.596 (19.356)
Number of bouts	9.771* (0.852)	4.833 (0.407)	4.191 (0.467)

The upper number is the mean and the other (in parentheses) is the standard error. Statistical significance is noted with an asterisk (*). More details in the text.

The pigeons sometimes failed to properly catch a food item, which rolled on the board. Those missed pecks were manually counted because they might reflect a higher stress level in one type of treatment relative to another. However, the number of missed pecks was similar across treatments for the blocks of last three sessions ($F_{2,88} = 0.884$, $p = 0.417$, $\eta_p^2 = 0.02$). Also, the time latency before the first peck on a board and the total duration between the first and the last peck did not differ across treatments (latency: $F_{2,92} = 1.726$, $p = 0.184$, $\eta_p^2 = 0.04$; duration: $F_{2,92} = 0.513$, $p = 0.600$, $\eta_p^2 = 0.01$). However, the number of foraging bouts over a session did not remain stable ($F_{2,92} = 38.342$, $p < 0.001$, $\eta_p^2 = 0.45$). It was higher at pre-test than at test and post-test (p's $= 0.0001$). These latter two treatments did not differ significantly ($p = 0.656$). The values for these dependent variables were calculated from manually collected data (Table 1).

2.2.4. *Distance travelled*

The distance travelled, as a measure of pixel change from the first to the last peck by means of the DeepLabCut software, was averaged for the last three sessions. There was no overall significant difference across treatments ($F_{2,30} = 0.133$, $p = 0.876$, $\eta_p^2 = 0.01$; Pre-test: 51 809.8 ± 4 917.8 pixels; Test: 51 214.6 ± 6 790.6 pixels; Post-test: 55 381.7 ± 5 803.4 pixels). But this measurement only reflected the overall distanced travelled, independent of pecking. Examining the ‘abstract’ distance between two successive pecks by means of the Pythagorean theorem was possibly more informative. For each treatment, the averaged sum of the number of pecks across pigeons for

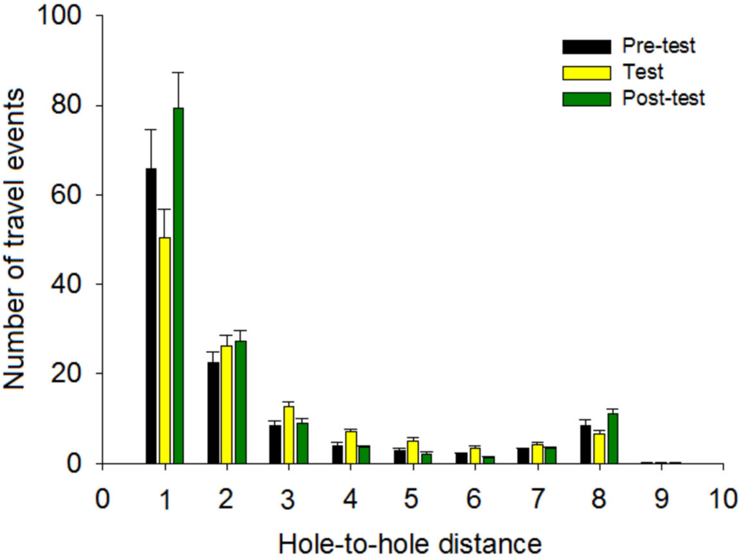

Figure 3. Experiment 1: Number of pecks at a given hole-to-hole distance. Intermediate distance values were rounded to the nearest integer. Of note, the absence of pecks in several treatments at a hole-to-hole distance of 10 and even 11 (maximal distance travelled without peck, not depicted) made statistical analyses impossible for those distances. The data points represent means and standard errors.

different hole-to-hole distances (Figure 3). This information was collected for and averaged between the last three sessions of each treatment. We found overall significant effects across treatments ($F_{26,390} = 64.436$, $p < 0.001$, $\eta_p^2 = 0.81$). Post-hoc comparisons showed that, in all treatments, the pigeons had a higher propensity to give the next peck to a hole directly adjacent — a hole-to-hole distance of 1 — to the previously visited one than to a hole further away (p's = 0.000021). Nevertheless, the pigeons visited less often an adjacent hole at test than at pre- and post-test ($p = 0.005$ and $p = 0.000021$, respectively). The pigeons also visited the adjacent holes more at post-test than at pre-test ($p = 0.039$). All other inter-treatment comparisons were non-significant (p values = 1.0).

3. Experiment 2

The results of Experiment 1 showed that pigeons were sensitive to a reduction in food accessibility (more opportunities to peck for identical food availability), as some reversible effects were obtained on Board 60 after an exposure to Board 180 — both with covered holes. On Board 60, the pigeons gave a disproportionately higher number of pecks near the edges of the board. This effect was unrelated to the inconsistency of the hole-food associations since it was only shown on Board 60, where each hole contained one food item at start. Also, this effect could not be the consequence of a learning deficit since it was more visible at post- than at pre-test. How would information availability alter the speed and the efficiency of foraging? In Experiment 2, we examined the behavioural effects of the absence of a hole cover on foraging, a situation allowing the pigeons to immediately locate the available food items. Both speed and efficiency should increase when the food items are visible because the handling time and effort are necessarily reduced. Consumption should occur within a shorter period and require fewer pecks. In this respect, if the edge effect found in Experiment 1 was, for any reason, related to handling costs, it should disappear. As no edge effect was obtained with covered holes on Board 180, despite having its holes slightly closer to the edges, testing this phenomenon with Board 180 was unnecessary and would provide no more information with respect to the role of handling costs in this phenomenon.

3.1. Methods

Ten new pigeons (5 males, 5 females; age 5.9 ± 0.99 years) were housed in the same conditions (individual cages) and tested in the same apparatus as in Experiment 1. They had a 10-min exposure per day (or session) to Board 60 without cover for a total of 8 days. Even from a distance, they could directly see whether a hole was baited or empty. These pigeons had already experienced both boards (60 and 180) for an experiment not reported here, so they were not naïve. Doing so, the effects or lack of effects could not be attributed to neophobia or any learning deficit. Mixed ANOVAs were used to compare these individuals with those of Experiment 1.

3.2. Results

A comparison of consumption rate and body weight between the present pigeons (Figure 4A and 4B, respectively) and those of Experiment 1 (Figure 1B and 1C, respectively) indicates that, at least on average, the former ate more food items per day (51.2 ± 3.9) and were heavier (424.2 ± 6.2 g) than the latter on Board 60. Consumption was stable over the 8-day period ($F_{7,63} = 1.779$, $p = 0.107$, $\eta_p^2 = 0.16$). Body weight remained relatively

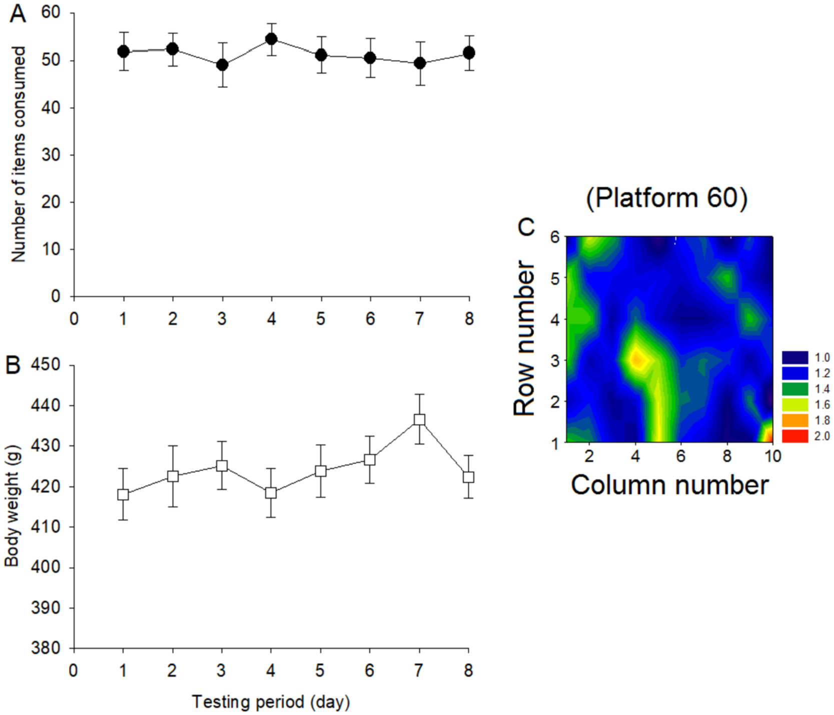

Figure 4. Experiment 2: Exposure of pigeons to Board 60 without hole cover. (A) Food consumption. (B) Body weight. (C) Density distribution of pecks. The data points represent means and standard errors.

stable as well, despite an overall significant effect of day ($F_{7,63} = 17.159$, $p < 0.001$, $\eta_p^2 = 0.65$) mainly due to day 7 — which differed from any other day (p values $= 0.0001$) — for unknown reason. But no significant difference was shown between days 1 and 8 ($p = 0.390$).

An influence of the hole cover on the foraging strategy was revealed in several ways. First, a qualitative visualization of the density distribution of pecks on the board demonstrated that the pigeons stopped giving a disproportionally higher number of pecks on Board 60 compared to Experiment 1 (Figure 4C). Across the last three sessions, the number of pecks was on average 74.5 ± 4.3 — i.e., an increase of only 24.2% relative to the number of food items available. This value radically differs from the 471.5 ± 31.7 pecks at pre-test and the 566.3 ± 34.1 pecks at post-test in Experiment 1, representing increases of 785.8 and 943.8%, respectively, relative to the number of food items available. During the block of the last three sessions, the pigeons in Experiment 2 gave a significantly lower number of pecks than at pre-test, post-test, and test in Experiment 1 ($Fs_{1,76} \geqslant 34.740$, p values $<$ 0.001, $\eta\text{'s}_p^2 \geqslant 0.31$). Figure 4C also shows that the pecks did not specifically occur near the edges of the board. The regions of higher peck densities can be found in various places, and probably reflect repeated attempts to get the food item from this or that non-specific hole.

Second, additional statistical analyses related to time latency and foraging duration confirm that the absence of a hole cover changed the foraging strategy of pigeons. The averaged time latency before giving the first peck on the board was 33.5 ± 1.1 s, whereas it was much shorter in Experiment 1 at pre-test (12.1 ± 2.8 s), test (7.7 ± 1.8 s), and post-test (8.6 ± 2.5 s). The increase in time latency by pigeons in Experiment 2 was significant in each case ($Fs_{1,76} \geqslant 33.685$, p values < 0.001, $\eta\text{'s}_p^2 \geqslant 0.31$). Third, the averaged foraging duration (the time elapsed between the first and the last peck) over the 600 s available was 249.8 ± 28.2 s, whereas it was much longer in Experiment 1 at pre-test (475.5 ± 23.1 s), test (474 ± 21.8 s), and post-test (493.6 ± 19.3 s). The effect was significant in each case ($Fs_{1,76} \geqslant 37.579$, p values < 0.001, $\eta\text{'s}_p^2 \geqslant 0.33$).

4. General discussion

These two experiments examined how inconsistent hole-food pairings for identical food availability could alter foraging performance and efficiency. Beyond learning effects denoting greater expertise in the task, the presence of reversible effects across treatments — which could only be shown using a within-subject design — revealed that hole-food inconsistency influenced foraging patterns in several ways, independent of the food amount available. In Experiment 1, more opportunities to peck for identical food availability (Board 180 vs. 60) tended to increase body weight and decreased the values of foraging variables such as the total number of pecks per hole, the propensity to revisit a hole, and the inspection of adjacent holes. The density distribution of pecks was also more homogeneous, less focused on the edges of the board. But we also discovered that the hole cover itself induced a form of uncertainty, independent of the hole-food inconsistency, with non-negligible effects on foraging. In Experiment 2, the absence of a hole cover considerably reduced the total number of pecks, and the pecks occurred less often near the edges of Board 60. Also, the pigeons started to forage after a longer delay and spent less time on the board than in Experiment 1. Together, these results indicate that the foraging context influences the dynamics of foraging behaviours more than the objective amount of food per se.

At first glance, the increase in body weight between pre-test and test seems to result from a larger number of food items ingested. However, between test and post-test, food consumption did not change, whereas body weight decreased. The intuitive hypothesis that a lower body weight on Board 60 resulted from a higher activity is unlikely because the distance travelled and the absolute number of pecks given were similar on both boards. Such a dissociation is consistent with a number of studies indicating that fattening and food consumption are not causally related (Cuthill et al., 2000; Wiersma & Verhulst, 2005; Cornelius et al., 2017; Bateson et al., 2021). The sensitivity of fattening to inconsistent hole-food pairings on Board 180 might suggest that this configuration was perceived as unpredictable by pigeons. At this stage, however, it was not possible to determine whether the decrease in body weight at post-test was due to a return to food predictability (Board 60 again) or to re-stabilization after a short period of adjustment to uncertainty (Board 180). If the re-stabilization hypothesis is correct, a decrease in body weight should occur at test following a longer exposure to uncertainty conditions. Nevertheless, some findings suggest that re-stabilization is not shown after several weeks under unpredictable food resources (Cornelius et al., 2017; Bateson et al., 2021). Even though food uncertainty was likely to become globally predictable over days on Board 180, it remained locally unpredictable per hole and might continue to generate a feeling of insecurity. More research is needed to clarify this question with the present experimental setup.

Food consumption did not follow the same trend, and therefore appears independent of food uncertainty — although we cannot rule out the possibility that the sudden reduction in food accessibility boosted the willingness of pigeons to respond to hole-food pairings, as noted in other experimental designs and various animal species, including pigeons (e.g., Perkins et al., 1975; Pearce et al., 1985; Gottlieb, 2004; Anselme et al., 2013; Cheon & Hong, 2017; Bateson et al., 2021).

Of note, food consumption performance decreased at the beginning of each new treatment, which resembles the transient avoidance behaviour of rats exposed to a 4%-sucrose solution after having repeatedly experienced a 32%-sucrose solution (e.g., Flaherty, 1996; Pellegrini et al., 2004). In rats, this avoidance behaviour is interpreted in terms of frustration or anxiety, a negative emotion also shown with similar procedures in dogs and starlings (Freidin et al., 2009; Bremhorst et al., 2019). However, despite repeated attempts, pigeons have never demonstrated any consistent evidence of frustration following an unexpected reduction in food delivery or an unexpected extension of food timing (Papini et al., 2019; Wittek et al., 2021). Also, in rats, a drop in performance is observed after a change from 32 to 4% sucrose but not in the reverse situation, whereas our pigeons showed this effect regardless of whether the access to food in the next treatment was harder (Board 180) or easier (Board 60). Although the interruption during the weekends had no effect within a treatment, the abrupt change in the experimental conditions disturbed the pigeons at the beginning of any new treatment, which may cause them to require 1–2 sessions to readjust their consumption rate.

The pigeons experienced each experimental treatment for several (5 to 8) days, so they were reasonably able to estimate the amounts of food available as well as their distribution near the end of each treatment. In this context, the marginal value theorem could potentially explain the lower number of pecks and revisits per hole, in addition to the greater avoidance of adjacent holes, on Board 180 as opposed to Board 60. Indeed, this theoretical framework predicts that when a next expected reward in a patch is below the average reward, the depleting resource will be abandoned (Charnov, 1976). Each hole of a board may be treated as a patch with a lower expected reward value on Board 180 than on Board 60, at least initially. Accordingly, the pigeons invested less time and energy in the former than in the latter situation. Searching and handling time is perhaps a more appropriate currency than energy expenditure (difficult to measure) for costing prey handling (Rovero et al., 2000; Okuyama, 2010), and more time spent searching and handling prey in a patch increases the total energy that can be extracted from that patch. Similarly, repeating attempts to obtain a hard-to-access (covered) food item increases the chance of consuming it, especially where food density is higher — i.e., on Board 60 vs. 180. As this was expected, handling time drastically decreased on Board 60 with uncovered holes (Experiment 2). In this case, the content of each hole was visible and could be extracted more easily; there was no need to spend as much time as with its covered counterpart.

The fact that our pigeons foraged faster and longer on Board 60 with covered (vs. uncovered) holes is likely to be a consequence of the greater search effort required to find enough food items over a 10-min period. With the covered boards, however, the search for food was more efficient when the pigeons had more opportunities to peck for identical food availability — i.e., when access to food was reduced. Indeed, energy expenditure was much higher on Board 60 than on Board 180, given the high number of pecks provided relative to the number of food items ingested. Also, the distribution of pecks was less homogenous on Board 60 than on Board 180, the pigeons being more prone to visit the edges of their environment. One explanation might be that Board 180 generated a dilution effect: More opportunities to peck decreased the probability of revisiting the same holes — especially because 10 min were possibly not long enough to allow the pigeons to revisit the holes many times. In addition, the pigeons were perhaps unable to remember which holes were inspected or not, re-visiting many times the same holes on Board 60. In support of this second point, Roberts (1988) tested pigeons exposed to several patches of eight feeders, and the probability that a feeder was baited differed among those patches. He found no evidence that his pigeons used memory of feeders entered and not entered to guide their choice of a feeder when revisiting a patch. However, although these hypotheses might mostly account for the observed pattern, it does not tell us why the pigeons gave more pecks close to the edges on covered Board 60 in comparison with uncovered Board 60 (fully available information where to find food) and covered Board 180. After all, the holes went closer to the edges of Board 180 than of Board 60, so the reverse pattern should have occurred in case the edges per se were of any significance to the pigeons. In addition, our results showed that the pigeons were similarly incited to peck on both boards, as the distance travelled remained unchanged and the absolute number of pecks was quite similar as well. Since each item consumed was not replaced, the pigeons should have left any preferred location and search elsewhere. Finally, there was no evidence that the pigeons started to peck close to the edges and then had no time to visit more the central areas. Given that the edge effect was obtained with covered holes on Board 60 only, we suspect that its emergence resulted from costs — other than handling costs — associated with the limited opportunities to seek hidden food items. Here, the effect to be explained is mainly a question of distribution rather than intensity of pecking (for another critical perspective, see also Forkman, 1991).

We propose that the high number of pecks near the edges on Board 60, as opposed to Board 180, might reflect an anti-competitor strategy. When the opportunities to peck were moderate (Board 60) and the holes covered, the pigeons stayed near the edges because they were partly hidden and also because this reduced the portion of space to monitor (180 instead of 360°) in case a competitor arises. In other words, the pigeons maximally attempted to protect their limited resources. This strategy resembles the thigmotactic response — i.e., the motion of an organism in response to a touch stimulus such as a wall in an open field — encountered in several animal species to avoid aversive events such as predators (e.g., Simon et al., 1994; Lamprea et al., 2008; Walz et al., 2016; Laurent Salazar et al., 2018). In the present situation, the propensity to peck near the edges on Board 60 is perhaps less likely to be an anti-predator behaviour; otherwise, this strategy should have been observed on Board 180 as well. The anti-competitor hypothesis can explain the response asymmetries between the two boards because more opportunities to peck reduce the risk of competition. There is also no reason to stay and peck near the edges on Board 60 when its holes are not covered since the pigeons can directly see whether they contain food items. In this case, they try to find food elsewhere and come to explore central areas more often. In other words, Board 60 with cover might induce strong competitive behaviours because (a) the opportunities to peck are limited and, (b) the pigeons are not sure which holes have been visited or not. This leads them to remain near the edges and to revisit the same holes many times. By contrast, on Board 180, the pigeons do not feel under competitive pressures because the number of holes is much larger, so the risk of competition-induced food shortage is reduced. Also, when the holes of Board 60 are not covered, the uncertainty associated with the presence or the absence of food disappears, and the pigeons simply move to locations where food items can be found — there is no need to protect and revisit empty holes. If correct, this means that the pigeons have determined the risk of competition based on the total number of holes to be inspected instead of the amount of food available, which was the same on both boards. More research involving real competitors is needed to clarify this question.

5. Conclusion

This project aimed to determine how inconsistent hole-food pairings for identical food availability could alter foraging performance and efficiency.

The variations in body weight across treatments indicate that the pigeons detected food uncertainty on Board 180. The other reversible effects also found attest that hole-food inconsistency influenced foraging patterns in several ways. But we also showed that the hole cover itself, independent of the hole-food inconsistency, generated a form of uncertainty (Is there a food item here? Was this hole already checked?) that impacted foraging as well: Pigeons pecked at higher rates and nearer the edges when Board 60 was covered rather than not covered. Thus, the hole cover seems to be a significant source of uncertainty for the pigeons when the opportunities to peck are limited.

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