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由人類受試者採集實驗探究視覺選擇對豆類馴化的影響

Deciphering the Role of Visual Selection in the Domestication of Beans: Evidences from Human Collecting Experiments

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本論文係 Muhammad Waseem（學號 R12B42025）在國立臺灣大學植物科學研究所完成之碩士學位論文，於民國 114 年 7 月 16 日承下列考試委員審查通過及口試及格，特此證明。

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Chinese Abstract

农业的发展可能是人类历史上最具革命性的转变。豆类的驯化涉及关键的形态和生理变化，特别是在种子传播、休眠和色素沉着方面。豆类驯化过程中最常见的变化是种子传播能力和色素沉着的降低。野生豆类的深色种皮在自然环境中起到天然伪装的作用，保护种子免受捕食者侵害。然而，人类对豆类的驯化选择不仅基于农业因素（如种子传播和休眠），也受到文化偏好（如视觉和感官特征）的影响。这种适应性特征可能影响了早期人类的选择行为，因为对较浅种皮颜色种子的视觉偏好可能促进了豆类最终的驯化。本研究探讨了视觉选择作为一种进化力量，是豆类驯化初期种皮颜色变化的重要原因。通过一系列的人类采集实验，参与者反复表现出对浅色种子的偏好，这意味着这些种子更易被察觉。然而，这种偏好并非刻意为之，而是视觉选择所产生的自然效果。统计分析（方差分析ANOVA）支持了参与者对浅色种子的选择，推测其原因是这些种子的可见性。本研究通过揭示豆类视觉选择在作物驯化中所起的作用，将人类感知与进化过程联系起来。

关键词：驯化，视觉选择，驯化综合征，人类采集行为，感知偏差

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Abstract

The development of agriculture is perhaps the most revolutionary transformation in human history. The domestication of beans involved key morphological and physiological changes, particularly in seed dispersal, dormancy, and pigmentation. The most frequent changes that happened during bean domestication are declines in seed dispersal and pigmentation. The dark seed coat color in wild beans serves as natural camouflage, protecting seeds from predators in the natural environment. However, Human selection for domestication is not solely based on agronomic factors (dispersal of seeds, seed dormancy), but also by cultural preferences, such as visual and sensory traits. This adaptive trait likely influenced early human selection practices, as visual preference for seeds with lighter seed coat colors may have contributed to the eventual domestication of beans. This research investigates visual selection acts as an evolutionary force that became the cause of the changes in seed coat coloration early in the process of domestication. Through a series of human collecting experiments, participants repeatedly preferred light-colored seeds, which implied that these seeds were more visible. This preference was not, however, deliberate, but an emergent effect of visual selection. The statistical analysis (ANOVA) supported that participant selected light-colored seeds, presumably because of their visibility. The study relates human perception to evolutionary evolution through the demonstration of how the visual selection of beans played a role in crop domestication.

Keywords:

Domestication, visual selection, domestication syndrome, human collecting behavior, perceptual bias

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Introduction

The transition from hunting and gathering to agriculture was a pivotal development in human history, fundamentally changing societies, diets, and environments (Gowdy, 2020). In early Mesoamerican and Andean agricultural systems, cereal-based diets, such as maize, were often supplemented with common bean (*Phaseolus vulgaris*), one of the first domesticated legumes in the Americas, which provided a stable protein source (Smýkal et al., 2015). More broadly, the domestication of legumes across multiple regions of the world has led to a suite of parallel morphological and physiological changes, commonly referred to as the "domestication syndrome." This syndrome typically includes reduced seed dispersal through the loss of pod shattering, increased seed size, loss of physical dormancy, and alterations in seed coat color and chemistry (Smýkal et al., 2018).

In wild legume populations, hard, dark-colored seed coats rich in tannins and flavonoids serve several adaptive functions: they deter herbivory, enhance seed dormancy, and offer protection against ultraviolet (UV) radiation and pathogens (Abbo & Gopher, 2022). However, these protective traits became less advantageous under cultivation, where human selection favored phenotypes that were easier to harvest, store, and cook. Consequently, domesticated legumes frequently exhibit lighter-colored seed coats, thinner seed walls, and greater uniformity in seed size and shape, whether through deliberate or unconscious human selection (Fuller et al., 2010). This pattern is evident across several major domesticated legumes. In lentils (*Lens culinaris*), chickpeas (*Cicer arietinum*), and peas (*Pisum sativum*), for instance, domestication has been associated with reduced dormancy and pigmentation, frequently linked to genetic changes affecting seed coat development and hardness (Weeden, 2007).

These shifts are best understood within the broader framework of human–plant co-evolution. Angourakis et al. (2022) described domestication as a strongly ecologically and behaviorally driven activity rather than a purely technological advancement, and raised curiosity about the idea of plant co-evolution with humans. This perspective believes that even unintentionally choices, such as choosing the most aesthetically pleasing seeds, can significantly influence the evolutionary trajectory of plant species (Altman et al., 2022). Plant domestication is frequently framed as a co-evolutionary process in which both humans and plants go through alterations (Bogaard et al., 2021).

In this broader context, the common bean, *Phaseolus vulgaris*, is a typical example of essential components of legume domestication. According to Marchese (2018), visual selection suggests that characteristics that are more aesthetically pleasing or noticeable are valued over those that are functionally beneficial. In pre-agricultural contexts, the prominence of seeds, particularly their contrast with leaves or soil, may have influenced the selection of individuals gathered and subsequently cultivated (Trognitz et al., 2013).

This theory serves as the basis for the visibility hypothesis, which postulates that because light-colored seeds were easier to see, prehistoric farmers were more likely to harvest and plant them (Dohle et al., 2019). While domesticated seeds in *P. vulgaris* have lighter or brighter seed coats, wild seeds have dark pigmented mottles that help them blend in with their surroundings and hide from predators (Aviezer & Lev-Yadun, 2015). Lighter

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phenotypes in domesticated populations may have resulted from unintentional shifts in allele frequencies related to seed coat pigmentation. (Plestenjak et al., 2024).

In wild environments, visual selection by animals, especially birds, plays a key role in shaping seed traits. Birds often target more visible seeds, such as lighter-colored ones, making seeds more likely to be eaten and less likely to survive. This creates a natural selection pressure that favors darker, camouflaged seeds in the wild (Zizumbo-Villarreal et al., 2005). In contrast, in agricultural context, humans often prefer and retain light-colored seeds, leading to a different direction of selection (Meghwal & Meena, 2024). This contrast highlights how seed color can be advantageous in one context (farming) and disadvantageous in another (wild predation).

Although both humans and birds rely on visual cues, birds have tetrachromatic vision and can perceive ultraviolet (UV) light, adding complexity to their selection behavior (Tedore & Nilsson, 2019). A seed that appears inconspicuous to humans may be highly visible to birds, leading to divergent selective pressures. These differences emphasize that domestication is not solely driven by human choices but also shaped by natural ecological interactions, with visual selection playing a central role in both contexts (Nawroth et al., 2023).

The hypothesis that visual salience may act as a selection-influencing factor has also been supported by findings in other crop species (Li & Camerer, 2022). For example, visual selection has been shown to be effective in breeding programs for soybean (dos Santos Silva et al., 2023), cotton (Bowman et al., 2004), and potato (Brown et al., 1984), where traits such as color, vigor, and architecture were used to guide early-stage selections based

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on visual cues. Similarly, a light-colored bean seed on a dark earth background would be easier to see (Dimitrova & Merilaita, 2010). As a result, in addition to deliberate selection for agronomic traits, unconscious perceptual bias may have played an underappreciated role in determining the path of early domestication (Leach, 2020). Although human psychology and sensory cues have historically been utilized for breeding purposes with less investigation, more recent summaries highlight how these biases most likely influenced crop evolution and validate their significance in domestication studies (Van Tassel et al., 2020).

Archaeological and genetic evidences also support this hypothesis. Ancient DNA analyses of early bean cultivars have revealed increasing frequencies of alleles associated with light-colored seed coats in post-domestication samples (Rocchetti et al., 2024). Similarly, multiple loss-of-function mutations in the *P* gene and other loci have been identified across geographically diverse landraces, indicating intense and repeated selection pressure for reduced pigmentation (Davies et al., 2022).

Beyond the *P* gene, numerous other loci influence seed coat color and pattern in beans. Some genes control the spatial patterning of color (for example, producing speckles or stripes), and others modify the biochemical composition of pigments, resulting in different hues (Mishra et al., 2022). Humans tend to prefer solid colors and easily recognizable patterns, a tendency supported by research in visual perception and aesthetic preferences (Palmer & Schloss, 2010). Domestication-induced mutations often disrupt pigment pathways biochemically (Jensen & Wright, 2022). Domesticated adzuki beans (*Vigna angularis*) exhibit red seed coats due to loss-of-function mutations in the MYB

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regulator and anthocyanidin reductase genes (*VaPAP1* and *VaANR1*), similar to mutations in common bean pigmentation genes. Such parallels in Common bean and related legumes suggest that early farmers repeatedly chose visually distinctive seeds in multiple crop domestications (Chien et al., 2025).

While these findings illustrate the molecular basis of pigmentation changes, they also suggest that broader evolutionary forces are at play. Bitocchi et al. (2017) documented the genetic changes in beans associated with domestication but noted the need to study selection pressures beyond genetic mutation, including human-mediated selection. Rani et al. (2022) highlighted those traits such as pod dehiscence, seed coat pattern, and seed size show high visual variability, making them likely targets of visual preference.

The influence of human cognition in domestication has been historically underappreciated. Studies in cognitive psychology show that human attention is naturally drawn to high-contrast, visually salient objects in complex environments (Wolfe & Horowitz, 2017). A light-color bean on dark soil creates a strong visual contrast that makes it stand out in natural foraging scenarios. Wolfe and Horowitz (2017) explain how bottom-up salience, such as bright or contrasting colors, directs our attention without requiring conscious effort. This cognitive bias made it more likely that early farmers selected lighter-colored bean seeds, since these visually stood out and attracted more attention than darker, camouflaged seeds. This attentional bias, a form of unconscious selection, could significantly skew the composition of seeds saved for planting, increasing the frequency of light-colored phenotypes in each generation (Fernandez et al., 2021).

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These perceptual tendencies are not limited to color alone. Hůla and Flegr (2021) found that humans have a preference for symmetrical and bright stimuli, rooted in evolutionary psychology. This finding has been extrapolated to plant selection: larger, more symmetrical seeds may be automatically perceived as more "valuable" or "desirable," thereby affecting which seeds are collected and replanted. Similarly, Ayzenberg and Behrmann (2024) demonstrated in behavioral experiments that humans are drawn to visual regularity and contrast during object recognition, supporting the idea that visual traits can unconsciously drive selection.

In addition to perceptual biases, cultural and symbolic factors may have also influenced seed choices. Traditional knowledge, aesthetic preferences, and symbolic meanings of plant traits influence human seed selection (Altman et al., 2022). Seed color is culturally significant in many farming societies, as evidenced by ethnographic records. Some cultures associate white or light-colored seeds with purity, fertility, or quality (Busatta, 2014). Due to their positive connotations, early farmers may have selected seeds that aligned with cultural ideals or rituals. According to Andean agricultural histories, white beans were sometimes symbolically linked to good things (e.g., offerings to rain or prosperity deities), which may have reinforced their preferential planting. Darker seeds were sometimes suspected of being bitter, impure, or unsuitable for consumption, leading to their deliberate exclusion from the seed stock (Leceta et al., 2024).

One of the best ways of testing the influence of visibility on selection is through experimentation on simulated ancient seed gathering under controlled conditions. Human collecting experiments have been used in ethnobotany and archaeology as a way of

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simulating prehistoric plant foraging. Visual salience inevitably influences what gets selected (Kuhn et al., 2023). When searching for food in a complex environment, Lancelotti et al. (2016) found that people tend to pick up the most obvious items. This experiment supports the idea that lighter beans would be picked more easily in an ancient bean field because they are more noticeable.

Although visual traits have been hypothesized to influence crop domestication, most studies have focused on modern varieties or inferred preferences from genetic data. What remains unclear is whether visual preference alone could have contributed to early selection during domestication. This study directly addresses this gap by using human collecting experiments to test whether visual salience affects seed selection between wild and domesticated beans. In these experiments, participants act out the process of collecting beans by placing dark-colored wild beans and light-colored domesticated beans on dark soil backgrounds from mixed seed pools. Keeping all other variables constant, one would expect participants to consistently pick up more light seeds than dark seeds if visual selection were a genuine factor in domestication. This would give numerical support for the visibility hypothesis and reflect what may have occurred in prehistory.

This study is motivated by a central inquiry based on the previously discussed background. Did visual selection influence the domestication of beans? To address this overarching question, several specific objectives are outlined: we examined whether human foragers show preferences for specific bean phenotypes (especially seed coat colors) in a way that could mimic ancient unconscious selection. This involves analyzing human collecting behavior in controlled experiments and comparing it to patterns expected under

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the visibility hypothesis. By measuring collection rates of light vs. dark seeds in simulated foraging tasks, we aim to discern whether visibility alone can bias harvest outcomes.

From these objectives, two primary hypotheses are formulated:

- Participants will collect light-colored bean seeds at a significantly higher rate than dark-colored seeds, reflecting a perceptual bias toward visual salience.
- Seed selection patterns will correlate with seed-soil visual contrast rather than intentional preference, demonstrating unconscious selection mechanisms.

To investigate the above hypotheses, the research combines experimental and analytical methods. In these experiments, groups of volunteers (entitled as participants) perform timed seed, collecting tasks in a laboratory condition, analogous to gathering wild beans. Different buckets were prepared with varying numbers of wild-type dark bean seeds and domesticated-type light-colored bean seeds. Participants were asked to collect as many seeds as possible within a fixed time. Their collections were then analyzed to determine the proportions of light versus dark seeds gathered in each scenario. By manipulating the repeating trials with 30 participants, the experiment dealt with the effect of visual contrast on selection. Statistical analyses (ANOVAs) were used to assess whether the differences in collection rates are significant and consistent with the visibility hypothesis (e.g., whether light seeds are picked up disproportionately on dark backgrounds).

By quantifying visual biases in real-time experiments, this research offers a novel contribution to domestication studies. It highlights the underappreciated role of human cognition alongside cultural values and agronomic factors in shaping crop evolution. The findings may extend beyond beans to offer broader insights into how sensory perception influenced early agricultural practices.

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Materials and Methods

Seed Preparation

Commercially available mung bean seeds were purchased from the market. Mung bean was used due to its relatively smaller seed size compared to current adzuki bean cultivars, which makes it a more appropriate model for mimicking the early stages of domestication. Seeds' length and width were measured using the vernier caliper. To mimic the seed color of the dark wild bean, the seeds were painted using a mixture of Mona acrylic polymer emulsion colors: Lamp Black (S-801) and Burnt Sienna (S-704) in a ratio of 4:1. To replicate the typical color of azuki bean (red bean) seeds, we mixed Scarlet (S-203), Middle Green (S-403), and Sky Blue (SG-501) in a ratio of 20:3:3. To create the ivory seed color, we combined titanium white (S-901) and middle yellow (S-209) in a ratio of 4:1. All paints were applied in a thin, even layer using a fine brush and allowed to air-dry for 24 hours before use in the experiment.

Soil Substrate

The soil used was a commercial mix of peat soil, vermiculite, and perlite (4:3:1, v/v/v), purchased by the Lee Laboratory (Institute of Plant Biology (IPB), National Taiwan University) from Dayi Agritech Co., Ltd., Pingtung, Taiwan. The soil exhibited a light brownish-black coloration, indicative of moderate organic matter content typically found in organically enriched surface soils. To replicate the natural crop field conditions at the harvesting stage, we added plant debris to the soil surface, consisting of dead leaves and broken twigs collected from the field. Approximately 20 grams of debris collected from the fields of the experimental station at IPB, National Taiwan University, were evenly distributed by hand over each experimental bucket to simulate the natural state. The same type of soil was used in all the experiments.

Buckets

We used three types of buckets for the experiment, all the same size, 45 cm long and 30 cm wide. Inside the bucket surface, we spread a thin layer of 1 cm of soil. Each bucket contained 60 g of wet soil, as measured by a digital weighing balance. Seeds were scattered randomly in such a way that both types of seeds could be equally distributed. We categorized the buckets as Light20, Light50, and Light80. The names were given according to the number of light-colored seeds they contain. Each bucket contains 100 seeds with varying numbers of seed colors. The visual representation of these buckets is illustrated in **Figure 1**.

- Light20 contains 20 light-colored and 80 dark-colored seeds.
- Light50 contains 50 light-colored and 50 dark-colored seeds.
- Light80 contains 80 light-colored and 20 dark-colored seeds.

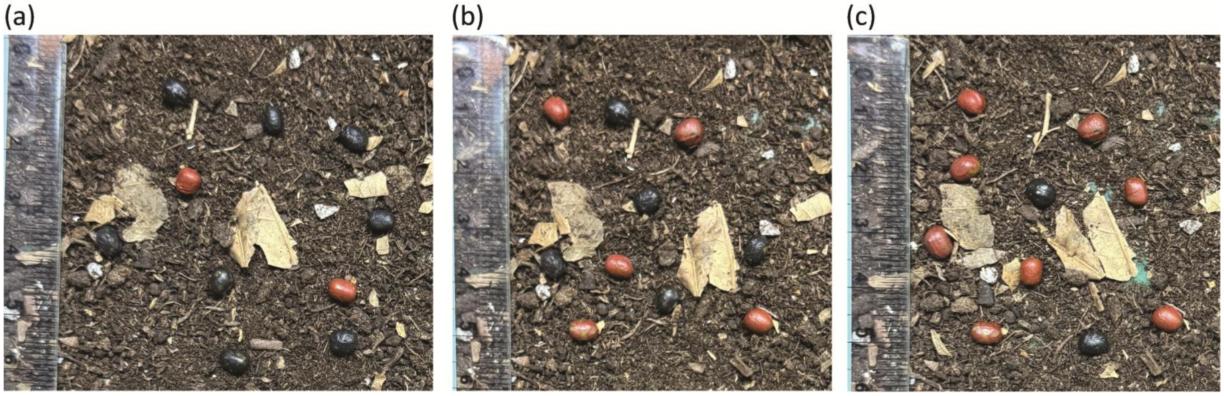

Figure 1 Visual representation of buckets (red vs black): (a) Light20 contains 20 light-colored and 80 dark-colored seeds. **(b) Light50 contains** 50 light-colored and 50 dark-colored seeds. **(c) Light80** contains 80 light-colored and 20 dark-colored seeds.

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Participants

The study engaged 30 participants. Participants were chosen from different countries (mainly from Taiwan) and other study backgrounds. All 30 participants were asked to participate in all experiments, allowing the repeated measures analysis of variance (ANOVA) with participant as the random effect. Participants were not informed of the study's expected outcomes to minimize bias and ensure objective responses. All participants were in the same lab condition and equally distant from the bucket.

Experimental Setup

To investigate visual discrimination in seed color, a series of single-bucket and competition experiments were conducted using specific color contrasts. The red vs. black was included in all experiments, allowing consistent assessment of participant preference across buckets. In contrast, the ivory vs. black was introduced in selective trials: it was absent in the single-bucket experiment (three-buckets) and in Competition-3, but present in the single-bucket experiments (two-buckets) and in Competition-2. This design enabled both single-bucket and competition experiments of color contrasts to evaluate how red and ivory seeds differed in detectability relative to black seeds, providing insights into human collecting behavior and visual selection strategies.

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Table 1 Layout of all the experiments

Experiment Type	Red vs Black	Ivory vs Black	Responses	Predictors
Single-Bucket experiment (three buckets)	Yes	No	- Red & Black seeds collected - Proportions of Red & Black seeds - Total seeds collected	Bucket, Time Participant (Random), Bucket * Time
Single-Bucket experiment (two buckets)	Yes	Yes	- Red & Black seeds collected - Proportions of Red & Black seeds - Total seeds collected	Bucket, Time, Participant (Random), Bucket * Time
Single-Bucket experiment (Comparison)	Yes	Yes	- Dark & Light seeds collected - Proportions of Dark & Light seeds - Total seeds collected	Bucket, Time, Participant (Random), Bucket * Time
Competition-3	Yes	No	- Total time spent - Total seeds - Time spent per seed - Seeds collected per second	Bucket, Participant (Random)
Competition-2	Yes	Yes	- Total time spent - Total seeds - Time spent per seed - Seeds collected per second	Bucket, Participant (Random)

Single-Bucket Experiment

In this experiment, foraging efficiency under time constraints was evaluated using three buckets separately: Light20, Light50, and Light80. For each bucket, participants completed a 120-second trial divided into six consecutive 20-second intervals. During each interval, they continuously collected seeds. At the end of each 20-second interval, seeds were counted and recorded separately by color, and the next interval resumed using the same bucket with the remaining seeds. They could choose which seed type (by color) to collect, allowing individuals to develop their foraging strategies.

Initially three separate buckets were used with red-colored seeds to represent the light seed category. In the subsequent single-bucket experiments, ivory-colored seeds were used instead to represent the light color. For the subsequent single-bucket experiments, we used ivory-colored seeds and selected only the Light20 and Light50 conditions to mimic the early stage of domestication, and the recording interval was set to 60 seconds instead of 20 seconds. In Competition-3 experiment, Light50 and Light80 did not differ significantly. Based on this result, we decided to exclude the Light80 from the subsequent single-bucket experiments as well. In addition to analyzing the red-black and ivory-black conditions separately, we also developed a combined model to compare participant responses across both light seed color types. This allowed us to assess behavioral differences between red and ivory seed conditions within a unified experimental framework. To analyze the red and ivory experiments together, in some statistical analyses we compiled the data into 60-second intervals for the red experiment.

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In the single-bucket experiment with red as the light color, we used JMP's Fit Model to run a repeated-measures ANOVA to examine the effects of bucket, time, and their interaction on foraging outcomes. At each 20-second interval point (20, 40, 60, 80, 100, 120 s), we recorded the number of black and red seeds collected. From those, we derived “black proportion" (number of black seeds collected / total black seeds present in that bucket), "red proportion" (number of red seeds collected / total red seeds present in that bucket). These proportional values allowed us to assess collection efficiency relevant to each seed color’s availability. Participant was included as a random effect. Bucket**,** time (a categorical fixed effect with six levels corresponding to each 20-second interval), and their interaction were treated as fixed effects. Tukey's HSD post-hoc tests were then applied to identify significant differences between buckets, across time points, and among the interaction of bucket and time. This approach allowed us to assess how foraging behavior in each color changed both across bucket conditions and over time while accounting for individual variability.

For the single-bucket experiments using ivory as the light color, we used a 60-second interval and analyzed the data at 60 seconds and 120 seconds. Here, Light20 and Light50 were used. A repeated-measures ANOVA was again performed in JMP, with bucket (Light20 or Light50), time (60 or 120 seconds), and their interaction treated as fixed effects, and participants included as a random effect. Tukey’s HSD test was applied to assess significant pairwise differences between conditions. For the statistical analyses compiling both the red and ivory experiments, the datasets were merged into a single JMP data table by stacking all rows. A new categorical variable, light color type (red or ivory), was added to distinguish the two conditions. Light color type (red or ivory), bucket (Light20 or Light50), time (60 or 120

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seconds), and their two-way and three-way interaction terms were treated as fixed effects, while participant remained a random effect.

Competition-3 Experiment

In this experiment, each participant foraged freely from all three buckets (Light20, Light50, Light80) at the same time for three minutes (180 seconds) in total. In this experiment, only red-colored seeds were used to represent the light color. The number of seeds collected from each bucket was recorded after the 180-second foraging period ended. We also measured the time each participant spent on each bucket and the final number of seeds collected from each bucket. Participants could transition freely between buckets within the 3-minute period. This competition-3 experiment was not conducted for ivory seeds. The goal of the competition experiments was to simulate a foraging context in which participants encountered multiple seed patches simultaneously and had to make active decisions about where to forage.

While both the Single-Bucket and Competition-3 experiments involved controlled seed ratios, participant choice, and time-limited foraging, Competition-3 uniquely introduced simultaneous access to multiple seed patches with longer time span (180 seconds) as compared to single-bucket experiments. This design allowed for the assessment of not only seed-level discrimination based on visual contrast, but also patch-level selection behavior. Specifically, it provided insights into whether participants preferentially chose patches with a higher proportion of visually salient (i.e., light-colored) seeds, thereby linking seed coat visibility to broader foraging decisions and spatial prioritization.

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For the competition-3 experiment, we measured four responses: total time spent in each bucket, total number of seeds collected per bucket, time spent per seed in each bucket (calculated as total time divided by the number of seeds collected), and seed collection rate (number of seeds picked per second). All analyses were conducted in JMP using the "Fit Model" feature. For each response variable, we used a repeated-measures analysis of variance (ANOVA). We treated bucket as a fixed effect and participant as a random effect. Post-hoc pairwise comparisons were performed using Tukey's HSD to evaluate the least-squares mean differences among buckets. Statistical significance was assessed at an α level of 0.05.

Competition-2 Experiment

In this experiment, each participant was asked to pick seeds from two buckets simultaneously over a fixed period of 2 minutes (120 seconds). This two-bucket setup was designed to further investigate foraging preferences, as the previous three-bucket experiment revealed no significant differences in participant responses between the Light50 and Light80 conditions. Participants were not restricted in the order in which they approached the buckets, and they were free to switch between buckets during the 2-minute foraging period. The number of seeds collected from each bucket was recorded after the 120-second foraging period ended.

Two independent competition-2 experiments were performed, one using red-colored seeds as the light-color and the other using ivory-colored seeds as the light-color seeds. The same experimental protocol used for both. The visual representation of ivory vs black experiment is provided in **Figure 2.**

For the competition-2 experiment, we measured four behavioral responses: total time spent in each bucket, total number of seeds collected per bucket, time spent per seed in each

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bucket (calculated as total time divided by the number of seeds collected), and seed collection rate (number of seeds picked per second). These responses were calculated for each experiment we did in competition-2 (using red as the light-color and the other using ivory as the light-color seeds) including the combined analysis of red and ivory against black as well.

For the statistical analyses compiling both the red and ivory experiments, the datasets were merged into a single JMP data table by stacking all rows. A new categorical variable, Bucket color type (red or ivory), was added to distinguish the two conditions. Light color type (red or ivory), and bucket (Light20 or Light50), were treated as fixed effects, while participants remained a random effect. All analyses were conducted in JMP using the "Fit Model" feature. For each response variable, we used a repeated-measures analysis of variance (ANOVA). Post-hoc pairwise comparisons were performed using Tukey's HSD to evaluate the least-squares mean differences among buckets. Statistical significance was assessed at an α level of 0.05.

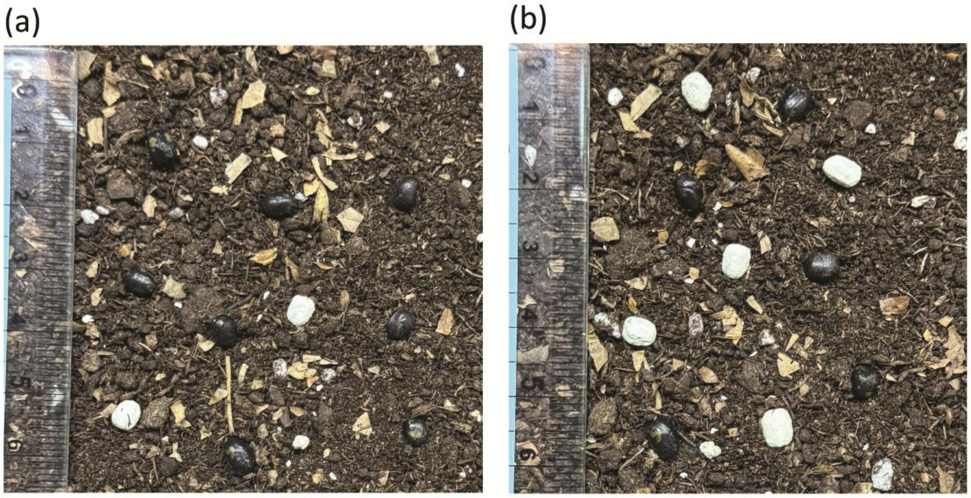

Figure 2 Visual representation of buckets (ivory vs black): (a) Light20 contains 20 light-colored (Ivory) and 80 dark-colored seeds. **(b) Light50** contains 50 light-colored (Ivory) and 50 dark-colored seeds.

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Results

Seed size of Beans

A total of 370 seeds were measured to assess average size, comprising 150 red, 150 black, and 70 ivory seeds. The lower number of ivory seeds reflects their limited use, as they were excluded from experiments involving the Light80 bucket. The average seed length was approximately 5.267 mm, and the average width was approximately 3.756 mm. The maximum and minimum seed lengths were also calculated, and they were as follows: 6.5347 mm and 4.067 mm. Meanwhile, the maximum and minimum seed length was observed at 4.4764 mm and 3.0145 mm, respectively. These findings are visually summarized in **Figure 3**, which shows the distribution and comparison of seed size dimensions.

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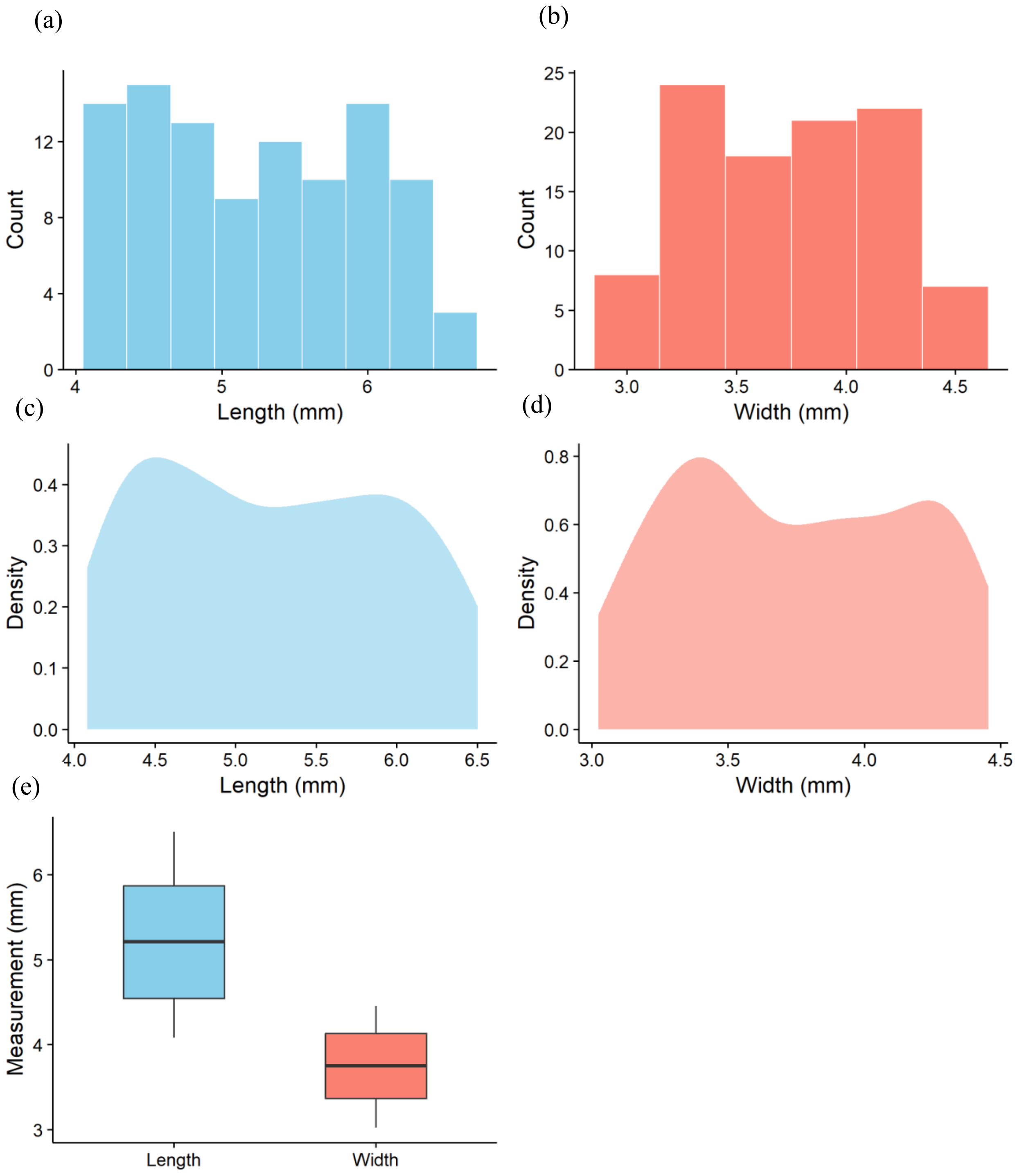

Figure 3 Distribution and comparison of seed size dimensions: Panels (a) and (b) show histograms of seed length and seed width (in mm), respectively, indicating frequency distributions. **Panels (c) and (d)** present kernel density plots for seed length and width, revealing the shape and spread of the data. **Panel (e)** displays a boxplot comparison between seed length and width, highlighting median values, interquartile ranges, and potential outliers. Measurements were taken using a vernier caliper.

Single-Bucket Experiment

A mixed-effects model was used to examine seed collection, with time, bucket, and their interaction as fixed effects and participant as a random effect.

According to the statistical results summarized in **Supplementary Table 1**, seed counts for both black and red seeds increased sharply across the 120-second trial (Time: $p < 0.0001$ for both). Bucket composition had a marginal effect on black-seed counts ($p = 0.058$) but a significant effect on red-seed collected ($p = 0.012$). Notably, the bucket × time interaction was highly significant for both colors ($p < 0.0001$), indicating that buckets richer in a given color yielded more accumulation of that seed over time (e.g., more black seeds in Light20; more red seeds in Light80). Bucket & time interaction for black and red seeds responses are visualized in **Figure 4 (a, b).**

The proportion of black seeds collected increased steadily (Time: $p < 0.0001$) with only a subtle Bucket × Time interaction ($p = 0.010$), whereas red-seed proportions were strongly shaped by both bucket and its interaction with time (both $p < 0.0001$). **Figure 4 (c, d)** illustrates the bucket & time interaction for the proportion of black and red seed responses. The mixed-effects model revealed a significant bucket × time interaction ($p < 0.0001$), indicating that the differences in seed collection across buckets changed over time.

The total number of seeds collected (red + black) increased sharply over time, with no significant differences among buckets (Light50 & Light80) by the end. Although estimated means suggested slightly higher yields in Light50, these were not statistically significant. The interaction between bucket and time for total seeds response is visualized in **Figure 4e.**

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Regardless of the bucket, the light-colored seeds appear to have higher selective advantage: In Light20, over 90%, (19/20) red seeds were collected, but only about 50% (44/80) of black seeds were collected. In Light80, the proportions of seeds collected were about 75% and 40%, respectively (60/80, 8/20). Therefore, despite the three buckets not differing significantly in the total number of seeds collected (i.e., higher light-colored seed proportion does not increase overall yield), the light seeds were always picked in higher proportions, and the advantage appears greater when light seeds were rare (negative frequency-dependent selection).

Overall, time had a robust effect on all measures, with counts and proportions increasing through the trial. Bucket composition had a significant impact on red-seed measures (both count and proportion) but only a marginal or no effect on black-seed measures and total seed collection. Interactions of bucket with time were significant for cumulative and proportional measures, indicating that bucket composition influenced not only the overall totals but also the rate at which seeds were collected over time. These findings suggest that participants' foraging behavior varied with the red/black mix. For example, buckets with more red seeds resulted in higher red collection (in count and proportion), whereas buckets richer in black seeds led to greater black seed collections. Overall, total seed collection (all seeds combined) was similar across buckets.

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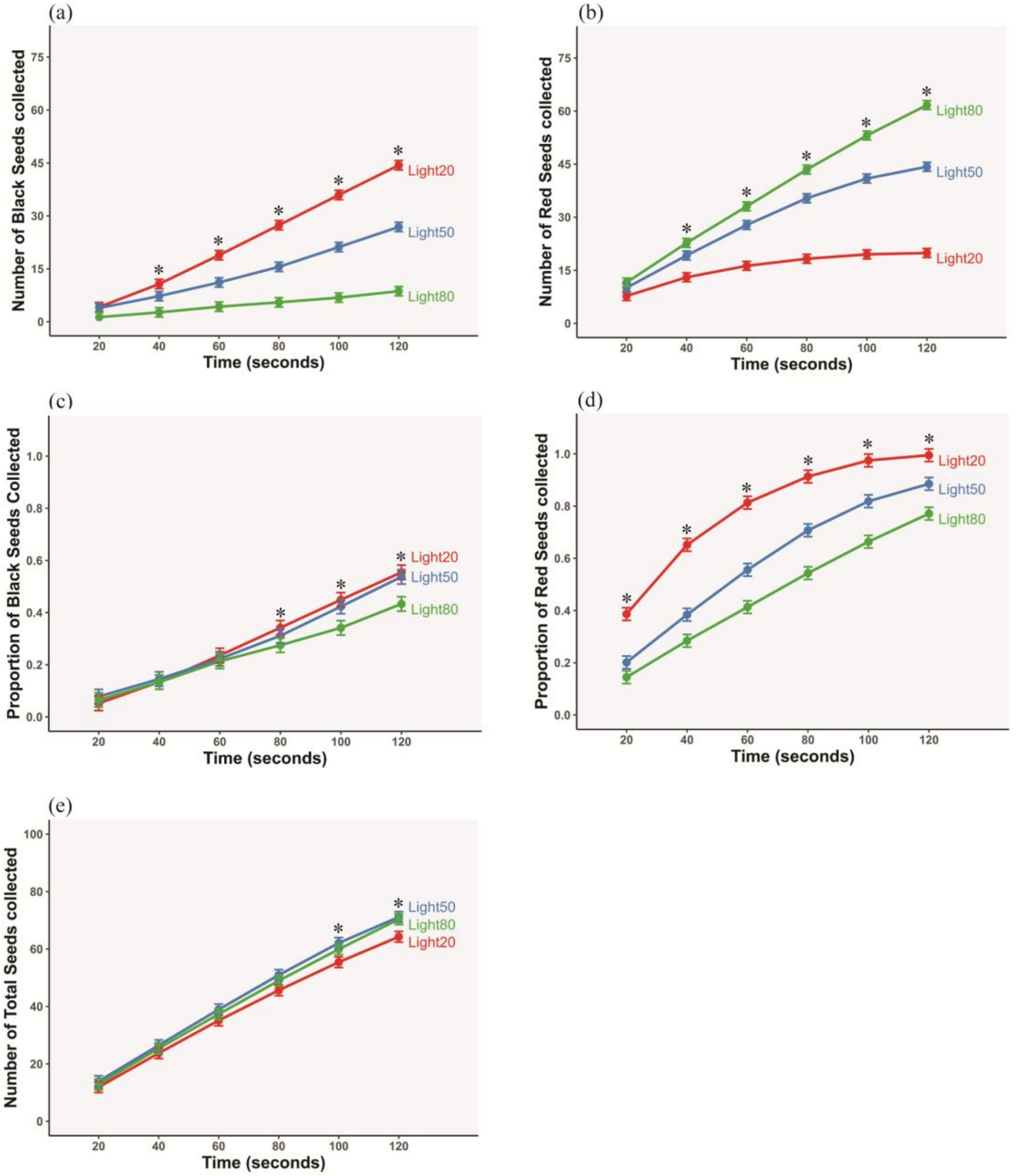

Figure 4 Foraging behavior responses from the single-bucket experiment using red and black-colored seeds: The figure illustrates the interaction between bucket type (Light20, Light50, and Light80) and time across multiple response variables. **Panel (a)** shows the number of black seeds collected, while **panel (b)** presents the number of red seeds collected. **Panels (c)** and **(d)** depict the proportion of black and red seeds collected over time, respectively. **Panel (e)** shows the total number of seeds collected. All measurements are based on least square means ± standard error, recorded at 20-second intervals over a 120-second trial. Asterisks indicate statistically significant differences ($p < 0.05$) between buckets based on Tukey's HSD test. The Light20 condition led to the highest collection of black seeds, whereas Light80 resulted in greater red seed collection.

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In addition to using red as the light color, we performed similar experiments using ivory as the light color. To simplify the experiment, we only used Light20 and Light50 setup to mimic the earlier stages of domestication syndrome evolution and only recorded seed collection every 60 sections. We first re-analyze the red seed experiment (above) in a 60-second interval here. Repeated measures ANOVA of seed collection data from the single-bucket experiment (Light20 and Light50) demonstrated the effects of time, bucket, and their interaction. Seed collection increased significantly over time across both bucket types (main effect of time: $p < 0.0001$). A significant bucket × time interaction ($p < 0.0001$) indicated that the pattern of seed collection differed between buckets over time. The complete statistics are provided in **Supplementary Table 2**.

For the black seed proportion, only time showed a significant effect ($p < 0.0001$), while the bucket ($p = 0.9463$) and the bucket × time interaction ($p = 0.4562$) were not significant, suggesting slight variation in black seed proportion across buckets or over time. In contrast, the proportion of red seeds showed significant effects of both bucket and time ($p < 0.0001$ for both), as well as a weaker but still significant bucket × time interaction ($p = 0.0194$), indicating a more stable and consistently higher preference for red seeds across trials and bucket types.

Total seed collection (red + black) also increased sharply over time ($p < 0.0001$) and was slightly higher in Light50 ($p = 0.0127$); however, the absence of a significant interaction ($p = 0.9611$) suggests that overall collection trajectories were parallel across bucket types. The bucket and time interaction for different responses are visualized in **Fig. 5 (a-e)**.

Together, these findings support the hypothesis that visual characteristics, particularly seed coat color, influence foraging decisions. Absolute counts of both seed types

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increased with time, reflecting cumulative collection. Proportional analyses showed that red seeds were collected at a significantly higher rate in the Light20 bucket compared to Light50, and this pattern remained consistent across both time points. In contrast, the proportion of black seeds collected increased over time and became similar across both buckets by the end of the trial. The persistent advantage in red seed collection under low-red conditions (Light20) suggests a visual bias favoring red seeds, likely due to their greater salience when less abundant and more visually distinctive.

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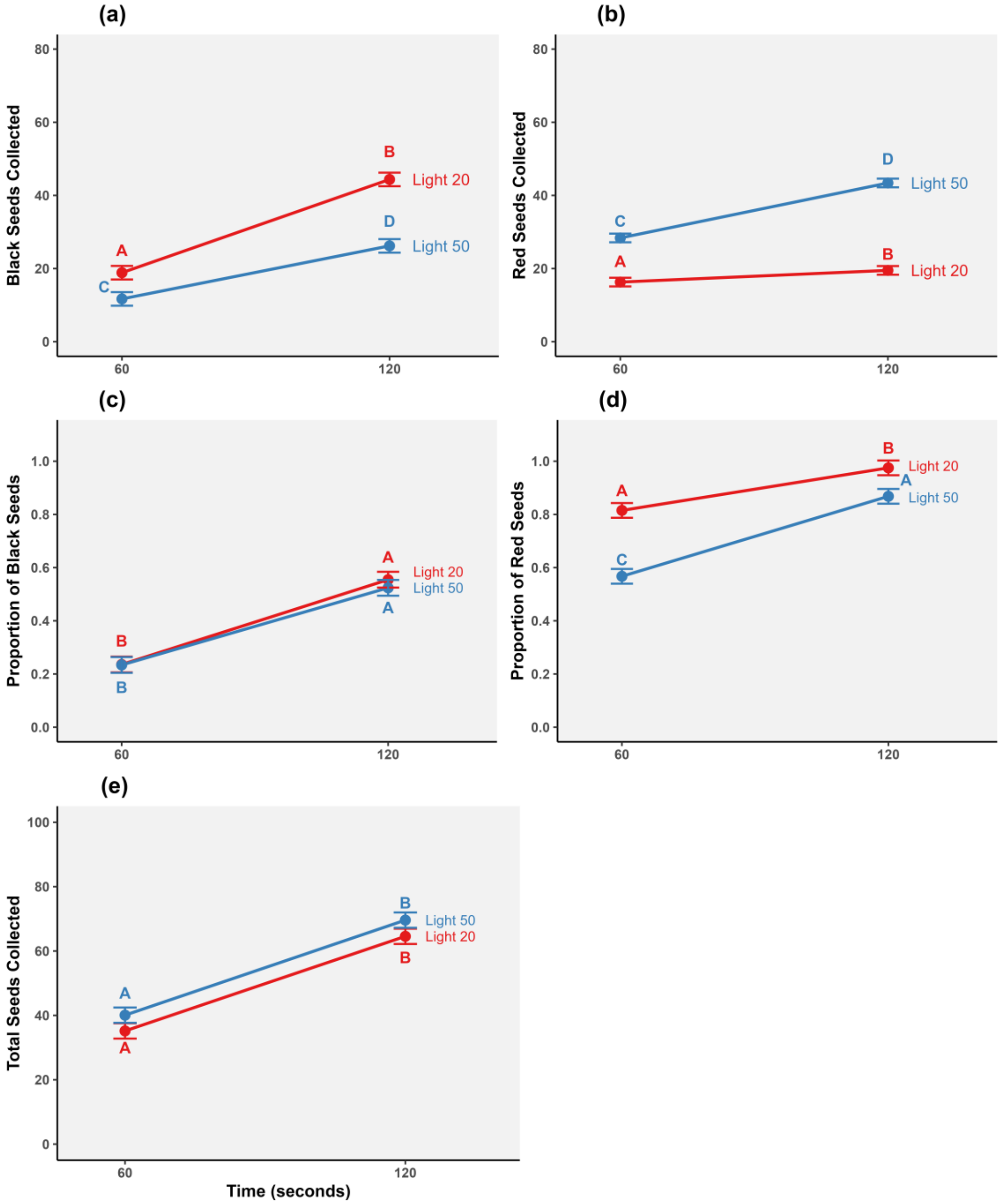

Figure 5 Foraging responses in the single-bucket experiment using red and black-colored seeds (Light20 and Light50 buckets only): This figure presents the interaction between bucket type and time across six response variables. **Figure (a)** shows the number of black seeds collected, and **figure (b)** displays the number of red seeds collected. **Figures (c)** and **(d)** represent the cumulative proportion of black and red seeds collected, respectively. **Figure (e)** shows the total number of seeds collected. Each data point represents the least square mean ± standard error, based on observations taken at 60-second intervals over a 120-second trial. The Light20 bucket consistently resulted in greater black seed collection, whereas Light50 led to higher red seed collection.

In the case of a single-bucket experiment comparing ivory and black, repeated-measures ANOVA revealed significant effects of both time and bucket composition on seed collection ($p < 0.0001$ for both), while the bucket × time interaction was not significant ($p = 0.0838$). Complete ANOVA statistics are presented in **Supplementary Table 3**. Participants consistently collected more seeds over time and collected more black seeds when black seeds were more abundant.

For the black seed proportion, neither the bucket ($p = 0.4698$) nor the interaction ($p = 0.0628$) was significant. At the same time, time remained highly significant ($p < 0.0001$), indicating that black seed proportions increased uniformly over time regardless of the bucket. In contrast, the proportion of ivory seeds collected showed significant effects of both bucket and time ($\mathrm{p} < 0.0001$ for both), as well as a significant bucket × time interaction ($\mathrm{p} = 0.0011$). These results indicate that ivory seed collection increased over time and differed significantly between bucket conditions. Notably, participants consistently collected a higher proportion of ivory seeds across both buckets and time points, suggesting a stronger visual salience and a more robust preference for ivory seeds throughout the experiment.

For total seed counts, both bucket and time effects were significant ($p = 0.0043$ and $p < 0.0001$, respectively). At the same time, the interaction was not significant ($p = 0.1362$), indicating that the total seed accumulation over time followed a broadly similar pattern across the different bucket types. The overall collection patterns are visually summarized in **Figure 6 (a–e).**

Overall, time exerted a substantial effect on all collection measures, with seed counts increasing steadily throughout the trial. Bucket composition had a strong influence on ivory seed accumulation, while black seed proportions were less affected by bucket type. The non-significant interactions for total seed count suggest that overall foraging rates remained broadly consistent across bucket conditions despite differences in seed composition.

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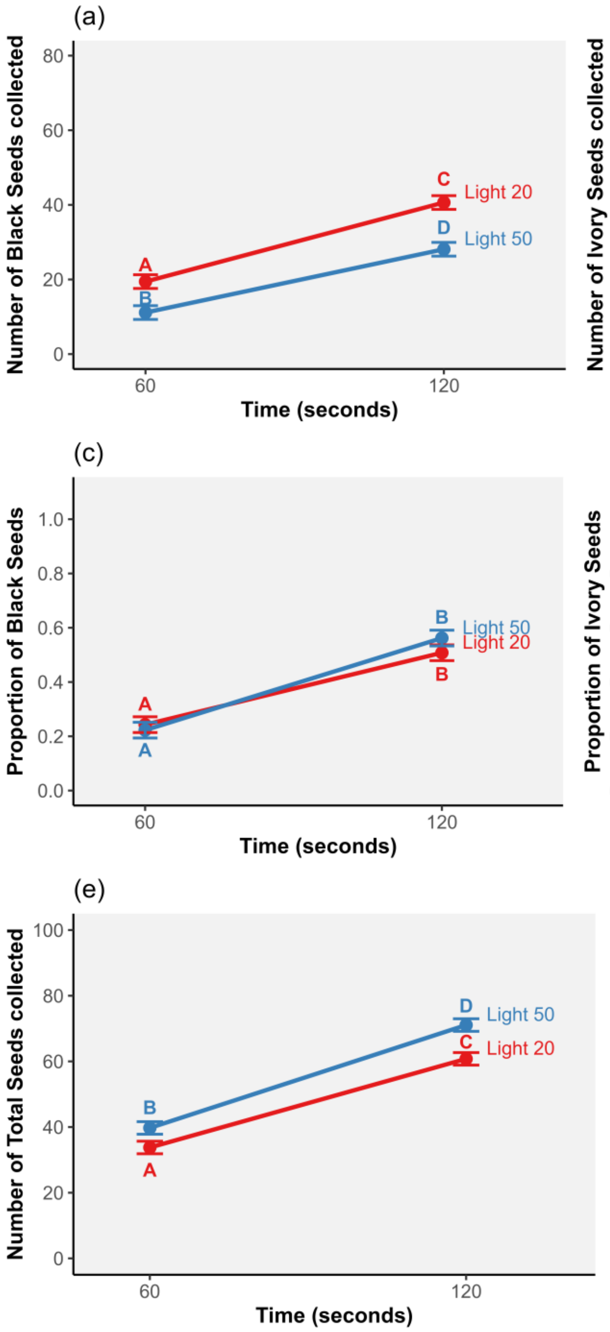

Figure 6 Foraging responses in the single-bucket experiment using black and ivory-colored seeds (Light20 and Light50 buckets): This figure presents least-squares mean responses of seed collection measured at two time points (60 and 120 seconds). **Panel (a)** shows the number of black seeds collected, while **panel (b)** displays the number of ivory seeds collected. **Panels (c)** and **(d)** represent the proportion of black and ivory seeds collected, respectively. **Panel (e)** shows the total number of seeds collected. Light20 consistently resulted in higher black seed collection, whereas Light50 led to greater ivory seed accumulation. Error bars represent the standard error (± S.E.) of the least-squares means across trials.

For comparison of the red & ivory vs black, repeated measures ANOVA revealed that there was a significant main effect of time ($p < 0.0001$), indicating that seed collection increased over time. Complete ANOVA statistics for both contrasts are presented in **Supplementary Table 4**. A significant main effect of bucket was also observed ($p < 0.0001$), showing overall differences in collection between seed colors. Additionally, a significant time × bucket interaction was found in each case, indicating that the difference in seed collection between colors changed across the trial.

When focusing on dark seeds (black seeds in both experiments), participants collected more black seeds in the high-density condition (Light20) than in Light50, with counts increased from 60 s to 120 s. The interaction was significant in the red vs. black comparison ($p = 0.0003$), indicating that the rate of seed collection increased more noticeably in the second half of the trial (from 60 to 120 seconds) when black seeds were more abundant. In contrast, in the ivory vs. black comparison, the bucket × time interaction for dark seeds was not significant ($p = 0.3028$), suggesting more parallel growth across bucket conditions. Proportion analyses for dark seeds revealed strong time effects ($p < 0.0001$). In contrast, the bucket ($p = 0.4577$) and bucket × time interaction ($p = 0.0063$) effects were limited or weaker, indicating largely stable collection efficiencies across seed mix for dark seeds.

For light seeds (red or ivory), participants collected more light seeds when they were denser (Light50 > Light20), with significant effects of the bucket ($p = 0.0043$), time ($p < 0.0001$), and bucket × time interaction ($p = 0.1147$), reflecting increasing selective efficiency as trials progressed under high-density conditions. Proportion analyses for light seeds showed significant effects of bucket, time, and interaction: bucket ($p = 0.0043$), time ($p < 0.0001$), and bucket × time interaction ($p = 0.0063$), indicating that both the quantity and the efficiency

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of light seed collection increased when light seeds were more abundant and as time progressed.

Total seed counts increased sharply over time (*p* < 0.0001) and were modestly higher in Light50 bucket (*p* < 0.05; specifically, *p* = 0.0043), while the bucket × time interaction was not significant (*p* = 0.1362), indicating parallel growth across conditions. The overall collection patterns are visually summarized in **Figure 7 (a-e).**

In summary, time uniformly enhanced foraging output and efficiency, while bucket composition selectively boosted harvests of the more abundant seed color. Significant bucket × time effects for light (and, in one case, dark) seeds demonstrate that participants' responsiveness to resource density increased as trials progressed. At the same time, overall yields remained comparable across treatments.

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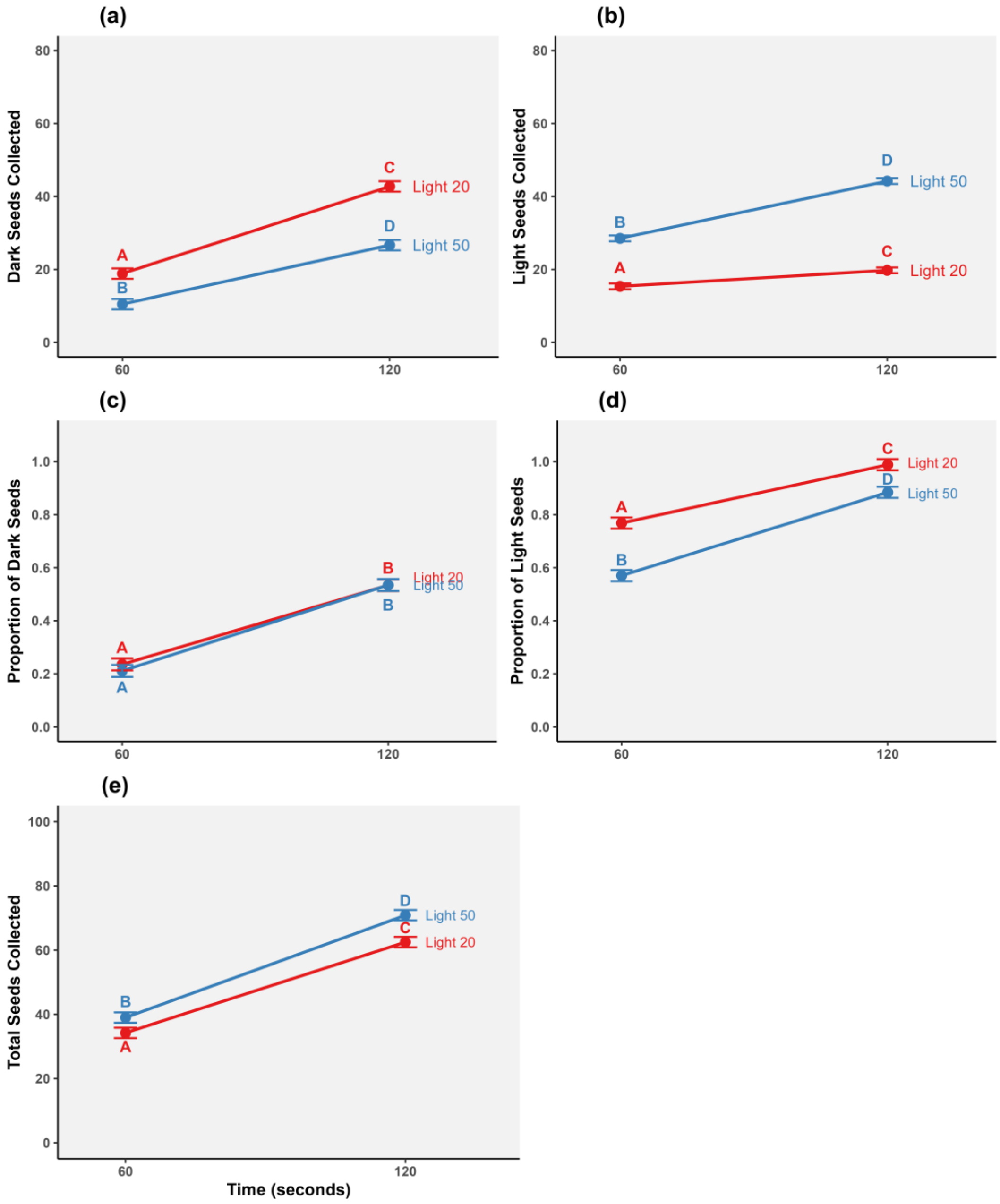

Figure 7 Foraging responses in the Single-bucket experiment of comparison between red & ivory (light) against black (dark) colored seeds for two buckets (Light20 and Light50): Panels (a-e) present least-squares mean responses measured at 60 and 120 seconds. Specifically, **panel (a)** shows the number of dark seeds collected; **panel (b)** shows the proportion of dark seeds; **panel (c)** displays the number of light seeds collected; **panel (d)** presents the proportion of light seeds; **panel (e)** shows the total number of seeds collected. Light20 consistently resulted in greater black seed accumulation, while Light50 yielded higher lighter seed collection. Error bars represent the standard error (± S.E.) of the least-squares means.

Competition-3

For the competition-3 experiment where participants have limited time to pick seeds from any of the buckets, we limit the time to three minutes for the 3 buckets together. Participants collected more seeds from buckets with more light-colored seed numbers. On average**,** Light80 bucket yielded the most seeds (LSM = 36.57, SE = 2.09), followed by Light50 (LSM = 35.73, SE = 1.65) and Light20 (LSM = 24.90, SE = 1.65). The time spent in each bucket followed this ordering: roughly 68.08 seconds (s) (SE = 1.68) in Light50, 62.8 s (SE = 2.38) in Light80, and 51.05 s (SE = 1.68) in Light20 (out of a 180-s trial). Overall, Light80 yielded the most seeds, consistent with participants' preference for the highest-light-colored seeds bucket. This pattern is consistent with the general principle of optimal foraging, which proposes that foragers tend to prioritize patches offering the highest returns. The tendency to focus on seed-rich buckets suggests a preference for more rewarding options (Reynolds, 2012). These descriptive trends are illustrated in **Figure 8a (time spent per bucket)** and **Figure 8b (total seeds collected).**

A one-way repeated-measures ANOVA revealed a significant effect of bucket type on the total number of seeds collected. These statistics are summarized in **(Supplementary Table 5)**. Tukey post-hoc comparisons showed that participants collected significantly more seeds in the Light80 bucket than in Light50 and Light20 ($p < 0.05$), and significantly more in Light50 than in Light20, establishing a statistically supported ordering: Light80 > Light50 > Light20 for seed collection. For the time spent, participants spent significantly more time in the Light50 bucket compared to both the Light80 and Light20 buckets ($p < 0.05$). However, there was no significant difference in time spent between Light80 and Light50 ($p > 0.05$). Participants predominantly initiated seed collection from the Light50 bucket, which was

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centrally positioned among the three buckets (Light20, Light50, and Light80) and directly aligned with their initial standing position. While this behavior might suggest a preference for intermediate visual salience or search challenge, it is equally plausible that the central positioning of the Light50 bucket introduced a spatial bias, making it the most immediately accessible option.

Time spent per seed was shortest in the Light80 bucket (LSM = 1.92 s/seed, SE = 0.11) and longest in the Light20 bucket (LSM = 2.22 s/seed, SE = 0.10), with Light50 intermediate (LSM = 2.02 s/seed, SE = 0.10). A one-way repeated-measures ANOVA revealed a significant effect of the bucket on time per seed. Post-hoc Tukey comparisons showed that Light20 differed significantly from both Light50 and Light80 ($p < 0.05$), but no significant difference was found between Light50 and Light80.

These results indicate that participants foraged more efficiently in buckets containing more light-colored seeds; however, the efficiency differences between the Light50 and Light80 buckets were not statistically distinguishable. Thus, while the trend suggests a general improvement in foraging efficiency with increasing light-seed ratio, only the Light20 was less efficient. Likewise, when considering seed color across all buckets, light-colored seeds were collected significantly faster than dark-colored seeds, with participants spending roughly half as long per light-colored seed. This likely reflects greater perceptual visibility of light seeds, supporting the idea that visual salience influences foraging efficiency. These patterns are illustrated in **Figure 8c.**

Across all bucket conditions, the rate of seed collection varied per second. **Figure 8d** illustrates the temporal dynamics of foraging behavior, highlighting how collection activity evolved throughout the observation period. A one-way repeated-measures ANOVA was conducted to examine the effect of bucket level (Light20, Light50, Light80) on the number of seeds picked per second. The results indicated a statistically significant effect of buckets. The least squares mean revealed that the number of seeds picked was lowest in the Light20 condition (LSM = 0.495, SE = 0.025), followed by Light50 (LSM = 0.536, SE = 0.025), and highest in the Light80 condition (LSM = 0.562, SE = 0.028). Post-hoc comparisons using Tukey's HSD test indicated that both Light50 and Light80 conditions resulted in significantly more seeds being picked compared to the Light20 condition. However, the difference between Light50 and Light80 was not statistically significant. These findings suggest that buckets with a more light-seed color were associated with greater seed-picking activity.

In summary, participants showed a clear preference for higher light-colored seed buckets in both time allocation and seed collection. They collected light-colored seeds faster than dark seeds and exhibited decelerating collection rates over time. Statistical tests confirmed that all reported differences were robust ($p < 0.05$). These results collectively indicate that foragers efficiently exploited the richest patch and adapted their behavior as returns diminished.

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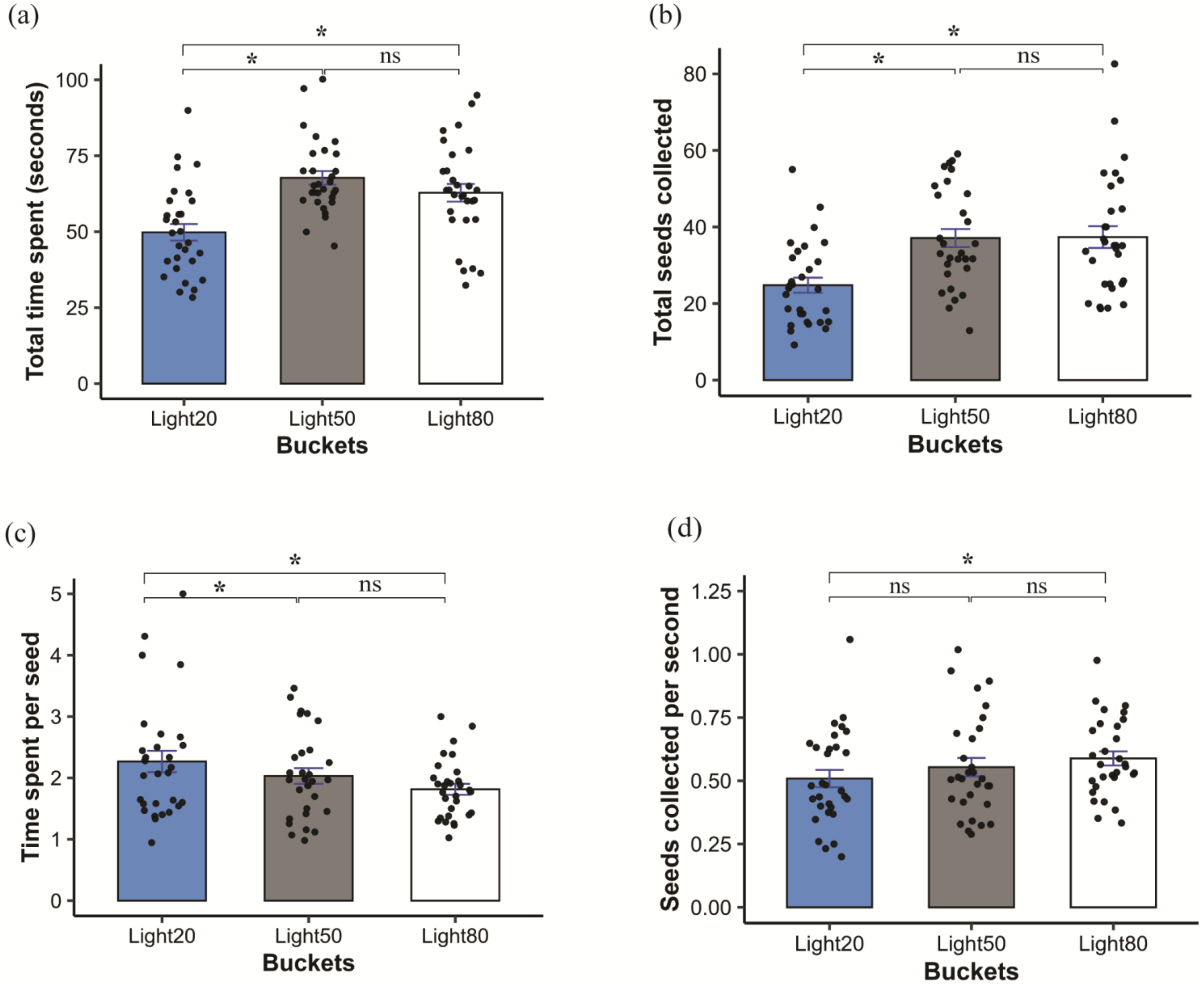

Figure 8 Effects of different buckets (Light20, Light50, and Light80) in the Competition-3 experiment (red and black seeds) on foraging behavior: in terms of **(a) Total time spent, (b) Total seeds collected, (c) Time spent per seed, and (d) Seeds picked per second.** Bars represent the least square mean values for each response. Each dot represents an individual participant. Vertical lines on top of the bars indicate the standard error of the mean. Significant differences between groups are indicated by asterisks (*p < 0.05), while 'ns' denotes non-significant differences based on Tukey's HSD test. Buckets are color-coded as follows: muted blue (Light20), grey (Light50), and white (Light80).

Competition-2

In competition-3, no significant differences were observed between the Light50 and Light80 bucket conditions across any of the measured response variables (e.g., total seeds collected, time spent, or seeds picked over time). These findings suggest that the differences between these two bucket types did not substantially influence foraging behavior. As a result, the Light80 bucket was excluded from subsequent experiments to simplify the design and focus on more influential variables.

Participants collected substantially more seeds from buckets with more light-colored seed numbers. These results are provided in **Supplementary Table 6**. The most seeds were collected from Light50 (LSM = 36.7, SE = 1.44) than Light20 (LSM = 24.96, SE = 1.44). The time spent in each bucket was roughly 52.7 seconds (s) (SE = 1.88) and 68.3 seconds (SE = 1.88) in Light20 and Light50, respectively (out of the 120-s trial). Consistent with participants' apparent preference for light-colored seeds, the majority of seeds were collected from the Light50 bucket. These descriptive patterns are illustrated in **Figure 9**, where **panel (a)** represents the time spent per bucket and **panel (b)** represents the total seeds collected.

The category of bucket had a significant impact on the total number of seeds collected, as indicated by a one-way repeated-measures ANOVA. Tukey's HSD test revealed that participants collected significantly more seeds from the Light50 bucket than from the Light20 bucket, and they spent more time in the Light50 bucket compared to the Light20 bucket ($p < 0.05$). Participants spent significantly more time in Light50 than in Light20, and the time spent varied by bucket as well. In conclusion, the most seeds were collected from Light50, while the fewest were collected from Light20. Participants spent the most time in the Light50 bucket, whereas in Light20, they spent the least. As would be predicted if

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participants distributed their effort to optimize gain in the richest patch, these results indicate a distinct bucket preference gradient (Light50> Light20).

Variations in bucket type resulted in significant differences in the time participants spent collecting each seed, thereby affecting foraging efficiency. Light50 had the shortest time per seed (LSM = 1.92 s/seed, SE = 0.068), while Light20 had the longest (LSM = 2.154 s/seed, SE = 0.068). Participants collected seeds more rapidly in the Light50 condition (LSM = 0.53 seeds/s, SE = 0.016) than in the Light20 condition (LSM = 0.48 seeds/s, SE = 0.016). **Figures 9c and 9d** depict these descriptive trends by representing the time spent per seed and the number of seeds picked per second, respectively.

A one-way repeated-measures ANOVA on time-per-seed (factor: bucket [Light20, Light50] revealed significant main effects of the bucket (F (1, 29) = 36.6910, p < 0.0001). This suggests that (a) foraging was more efficient (shorter time per seed) in buckets containing more light-colored seeds, and (b) light seeds were discovered faster than dark seeds overall. Tukey's HSD test revealed a significant difference in time spent per seed between bucket pairs (Light50 < Light20; all p < 0.01).

Tukey's HSD test revealed that participants spent significantly less time per seed in the Light50 bucket compared to the Light20 bucket ($p < 0.05$) and collected seeds at a significantly faster rate (seeds per second) in the Light50 bucket compared to the Light20 bucket ($p < 0.05$) indicating more efficient foraging in the light-colored condition. Similarly, light-colored seeds were gathered considerably more quickly than dark-colored seeds across all buckets.

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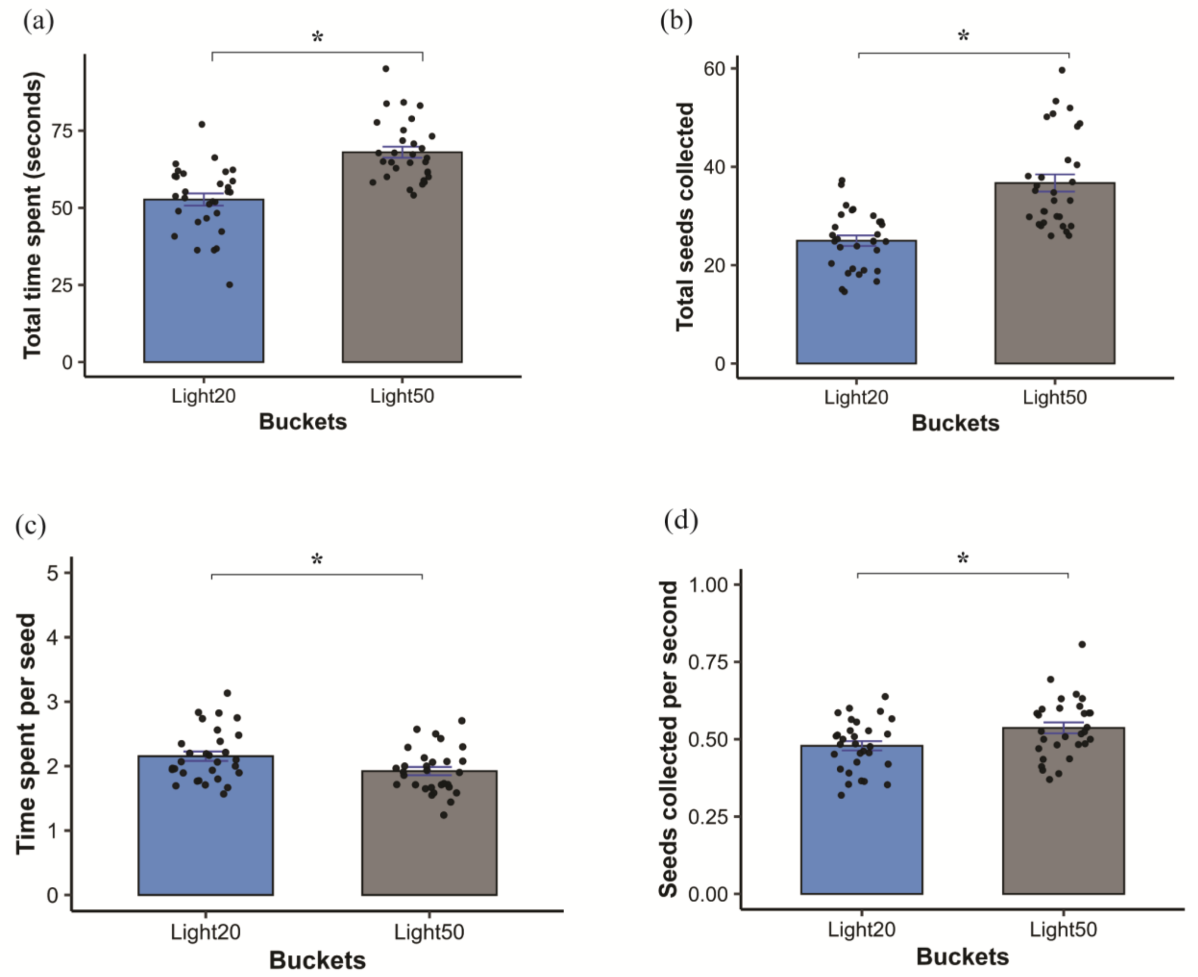

Figure 9 Effects of buckets (Light20 and Light50) on seed collection behavior for Competition-2 (red vs black): Bar plots compare the Least Square Means for two bucket types: Light20 (muted blue) and Light50 (gray). Each dot represents an individual participant. Significant differences between groups are marked with asterisks (*$p < 0.05$). Blue-colored error bars denotes standard error. **(a) Total seeds collected**: Participants collected significantly more seeds from Light50 than from Light20. **(b) Total time spent**: Participants spent more time overall with the Light50 buckets compared to Light20. **(c) Time spent per seed**: Time taken per seed was significantly lower in the Light50 condition, suggesting increased efficiency. **(d) Seeds picked per second**: Seed picking rate was higher in Light50 buckets, indicating faster foraging performance.

The ivory vs black seed color experiment was included to evaluate the potential role of visual contrast in influencing human-mediated selection during bean domestication. This pairing represents a maximal difference in seed coat brightness, allowing assessment of whether early cultivators exhibited unintentional selection biases based on visual salience rather than chromatic hue. The results offer insights into how perceptual factors may have influenced the fixation of specific seed phenotypes in domesticated gene pools.

As shown in **Supplementary Table 7**, buckets with higher proportions of light-colored seeds resulted in significantly greater time allocation by participants. Specifically, participants spent more time in the Light50 condition (Least Squares Mean = 67.50 seconds, SE = 3.15) compared to the Light20 condition (Least Squares Mean = 52.87 seconds, SE = 3.15), with this difference reaching statistical significance (F (1,58) = 10.82, p = 0.001). These results suggest a behavioral preference for buckets containing a higher ratio of light-colored seeds, potentially reflecting the influence of visual salience on attention and foraging behavior. A conceptual illustration of these time allocation patterns is presented in **Figure 10 (a).**

Buckets with higher densities of light-colored seeds also yielded significantly greater total seed collection by participants. The Light50 condition produced a higher mean number of seeds collected (Least Squares Mean = 42.57, SE = 1.92) compared to the Light20 condition (LSM = 28.83, SE = 1.92), with the difference being statistically significant (F (1,58) = 25.69, p < 0.0001). This finding reinforces the observed preference for high-density light-colored seed environments and suggests that seed visibility or perceptual contrast may have enhanced foraging efficiency. These results support the hypothesis that unconscious visual selection could have influenced early human behaviors related to seed gathering,

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contributing to the domestication process. Descriptive trends corresponding to these data are depicted in **Figure 10 (b).**

Foraging efficiency was significantly affected by the type of bucket, with the number of light-colored seeds influencing the time spent collecting each seed. Participants spent less time collecting seeds from Light50 compared to Light20. The average time per seed was 1.5729 seconds (SE = 0.0807) in the Light50 bucket and 1.8039 seconds (SE = 0.0807) in the Light20 bucket. Descriptive trends corresponding to these data are depicted in **Figure 10c.** A one-way repeated-measures ANOVA revealed a significant main effect of bucket type on time per seed (F (1, 29) = 36.6910, $p < 0.0001$), indicating that foraging was more efficient in the Light50 bucket.

Tukey’s HSD test confirmed that participants spent significantly less time per seed in the Light50 bucket than in the Light20 bucket, with all comparisons being statistically significant ($p < 0.01$). These results suggest that the higher number of light-colored seeds in the Light50 bucket contributed to faster seed collection times.

The rate of seed collection per second varied across both bucket conditions. To determine the effect of bucket condition on seed collection rate, a one-way ANOVA was performed with bucket type (Light20 vs. Light50) as the independent variable. The findings revealed a significant main effect of bucket type on the number of seeds collected per second (F (1, 29) = 13.2205, $p = 0.001$), indicating that participants collected seeds at varying rates depending on the bucket condition.

As illustrated in **Figure 10d**, least squares mean comparisons showed that participants collected fewer seeds per time unit in the Light20 (LSM = 0.5296, SE = 0.0273) than in the Light50 (LSM = 0.6169, SE = 0.0273). This indicates that seed collection was more efficient in the Light50 bucket, which contained a higher number of light-colored seeds. These findings further support the conclusion that bucket composition significantly influenced foraging performance, with higher proportions of light-colored seeds facilitating more rapid collection.

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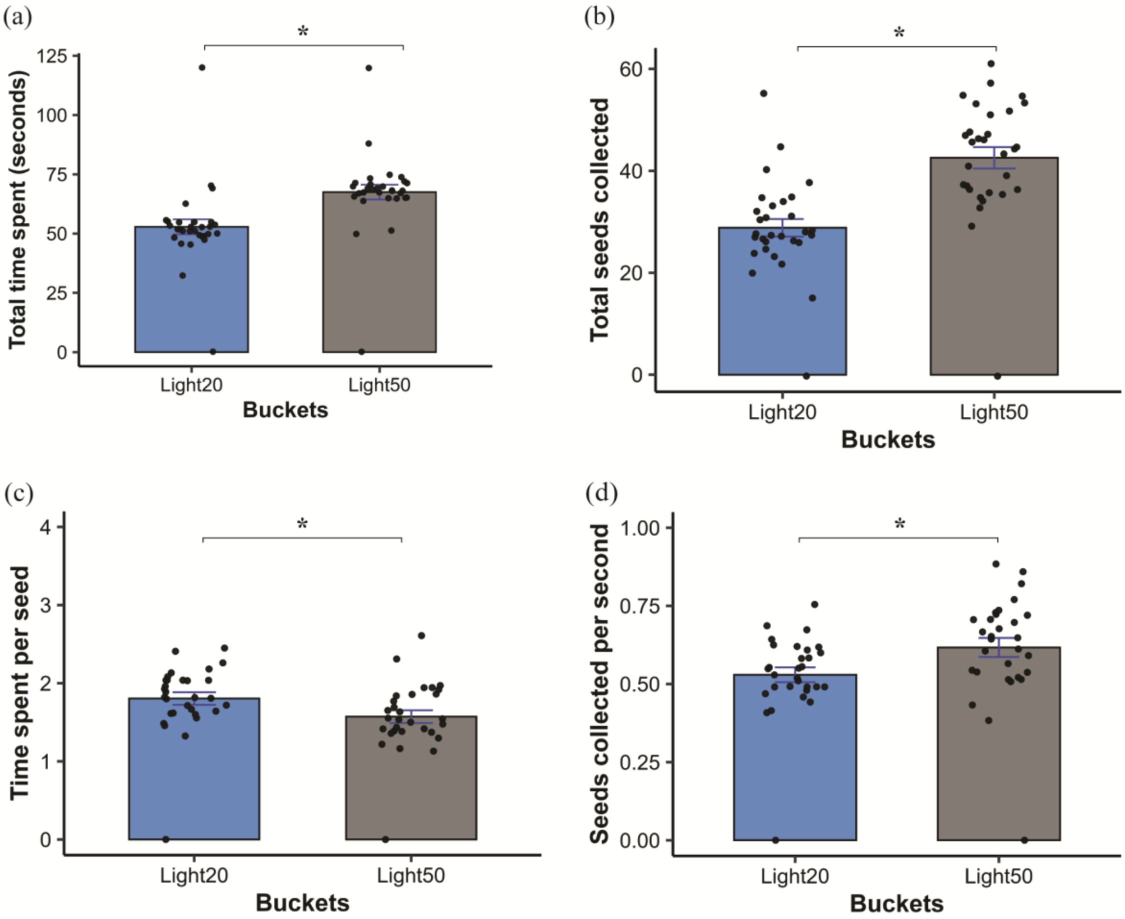

Figure 10 Effects of buckets (Light20 and Light50) on seed collection behavior for Competition-2 (ivory vs black): Bar plots compare the least square means for two bucket types: Light20 (muted blue) and Light50 (gray). Each dot represents an individual participant. Blue-colored error bars denotes standard error. **(a) Total time spent**: Participants spent more time overall with the Light50 buckets compared to Light20. **(b) Total seeds collected**: Participants collected significantly more seeds from Light50 than from Light20. **(c) Time spent per seed**: Time taken per seed was significantly lower in the Light50 condition, suggesting increased efficiency. **(d) Seeds picked per seed**: Seed picking rate was higher in Light50 buckets, indicating faster foraging performance. Asterisks indicate statistically significant differences between buckets based on Tukey's HSD test ($p < 0.05$).

For comparison of the red & ivory vs black, one-way repeated measures-ANOVA revealed that participants spent significantly more time on buckets containing a greater proportion of light-colored seeds. The complete statistics are detailed in **Supplementary Table 8**, participants spent an average of 67.50 seconds (SE = 3.15) in the Light50 bucket, while in the Light20 bucket spent only 52.87 seconds (SE = 3.15). A conceptual illustration of these time allocation patterns is presented in **Figure 11 (a).**

The difference was statistically significant (F (1, 58) = 10.82, p = 0.001). These findings indicate that buckets with more visible seeds likely grasped participants' attention for longer periods, increasing the possibility of collecting seeds. Over time, such unconscious visual preferences may have contributed to a gradual shift in seed coat coloration from darker to lighter hues in cultivated bean populations.

As shown in **Figure 11 (b),** participants collected significantly more seeds in the Light50 condition (LSM = 42.57, SE = 1.92) compared to the Light20 condition (LSM = 28.83, SE = 1.92), with a high level of significance (F (1, 58) = 25.69, p < 0.0001). This suggests that having more visually prominent seeds not only kept people's attention, but also made for more productive foraging. This unintentional selection may have increased the prevalence of light-colored seeds in early crop populations. It is important to note that such shifts do not necessarily reflect deliberate breeding decisions. Rather, simple perceptual biases during gathering could have gradually altered the genetic structure of cultivated bean varieties.

The efficiency of seed collection, measured as time spent per seed, was also affected by the seed color ratio. Participants took less time to collect individual seed in the Light50 condition (LSM= 1.5729 seconds, SE = 0.0807) than in the Light20 condition (LSM= 1.8039 seconds, SE = 0.0807). Descriptive trends corresponding to these data are visualized in **Figure 11c.** A one-way repeated measures-ANOVA confirmed this difference as statistically significant (F (1,29) = 36.69, $p < 0.0001$), and all pairwise comparisons were also significant (Tukey's HSD test, $p < 0.01$). The enhanced efficiency associated with higher light-seed density indicates that seed color affects both the frequency of selection and the speed at which foraging takes place.

Differences in seed collection rates per unit of time were similarly influenced by bucket composition. As illustrated in **Figure 11d**, participants collected seeds more rapidly in the Light50 condition (LSM = 0.6169 seeds/sec, SE = 0.0273) compared to the Light20 condition (LSM = 0.5296 seeds/sec, SE = 0.0273). This difference was statistically significant (F (1,29) = 13.22, $p = 0.001$), indicating that higher densities of light-colored seeds facilitated faster foraging overall.

The findings provide compelling evidence that light-colored seeds within a foraging environment significantly influence participant behavior. In comparison to buckets where light-colored seeds were fewer in numbers (Light20), Light50 consistently resulted in higher time searching, higher total seed collection, faster collection rate, and elevated collection rates. Together, these findings highlight the importance of visual selection as a key driver in seed selection behavior. Perceptual biases may have had evolutionary consequences during early plant domestication.

Additionally, the repeated collection of more visible, light-colored seeds, regardless of conscious intent, may have contributed to a gradual shift in seed phenotype frequencies over time. This behavioral tendency, observed under controlled experimental conditions,

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provides empirical support for the hypothesis that visual selection played an unintentional but influential role in the domestication trajectory of beans, favoring the transition from dark to light seed coat colors.

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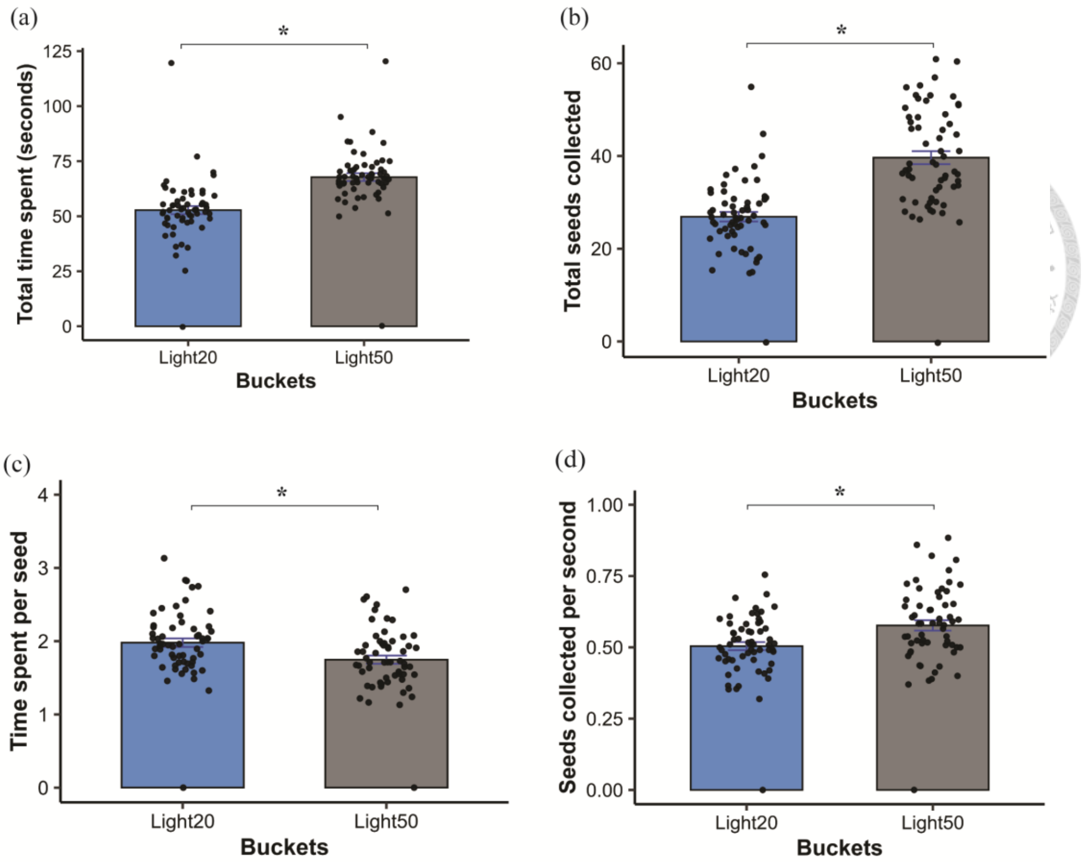

Figure 11 Effects of buckets (Light20 and Light50) on seed collection behavior for combined analysis of Competition-2 (ivory & red vs black): Bar plots compare the Least Square Means for two bucket types: Light20 (muted blue) and Light50 (gray). Blue-colored error bars denotes standard error. **(a) Total time spent**: Participants spent significantly more time interacting with Light50 bucket than Light20. **(b) Total seeds collected**: A significantly greater number of seeds were collected from Light50 bucket. **(c) Time spent per seed**: Participants spent less time per seed in the Light50 condition, indicating improved efficiency. **(d) Seeds picked per second**: Seeds were collected at a higher rate (seeds/second) in Light50 buckets, suggesting enhanced foraging speed. Each dot represents data from an individual participant. Statistically significant differences between conditions are indicated by asterisks (*$p < 0.05$), based on post hoc comparisons.

Discussion

In wild bean populations, dark, mottled seed coats served as camouflage, blending with soil and leaf litter to evade predators and pathogens, making seeds difficult for visual predators to detect and consume (Von Wettberg et al., 2018). Human visual preferences shifted the balance during domestication, favoring lighter, more uniform seed coats for cleanliness, ease of sorting, and market appeal (Plestenjak et al., 2024). Genetic studies correlate this phenotypic shift to mutations in MYB-like transcription factors and reductions in proanthocyanidin accumulation, resulting in light-colored seed phenotypes (Flores et al., 2022). Early cultivators introduced a novel, visual selection, pressure by selecting for conspicuous seeds, which surpassed natural camouflage strategies. This human-plant co-evolutionary process, driven by early agricultural selection for visually distinct seeds, altered the genetic architecture of pigmentation in beans and reduced diversity in seed coat traits (Bohra et al., 2022). While beneficial for human use, the loss of protective pigmentation indicates potential trade-offs in stress resilience and emphasizes the importance of conserving broader genetic diversity in modern breeding (Climent et al., 2024).

This same principle of visual selection preference emerges in our Single-Bucket experiment, in which participants adapted their visually driven foraging strategies to seed-color distributions, much like early farmers who likely favored light-colored seeds for easier harvesting and better market appeal. Participants collected light-colored seed types more often. This means they were attracted to seeds that were easier to forage against the dark background. The comparison between the ivory vs black and red vs black experiments exhibited consistent visual biases in human collecting behavior, particularly choosing lighter seed coat colors. In both conditions, participants collected more light-colored seeds (ivory or

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red) when these were more abundant. These findings strengthen the idea that human perceptual and behavioral responses to visual traits played a quiet but influential role in shaping the path from wild, dark-seeded beans to the light-colored varieties that dominate domesticated agriculture today.

In Competition 3 experiment, participants continued to prefer buckets having more light-colored seeds, collecting light-colored seeds more effectively and in higher amounts. This indicates that perceptual selection played a role in the selection of resources, and early humans would also have inclined towards seed types that were more visible during harvesting. The unexpected preference for Light50 bucket, even though the Light80 bucket had the greatest number of light-colored seeds than all, suggests that factors beyond simple visual salience influenced foraging behavior. In particular, participants may have been responding to a balance between the ease of detecting seeds and the perceived challenge or reward of the task, with Light50 offering an intermediate level of contrast that was visually engaging but not overly simple.

From the findings of the Competition-2 experiment, we also observed that in regards to time spent and foraging efficiency, participants consistently preferred buckets with brighter (contrasting) seeds. It is interesting that brighter seed color traits (ivory and red) were collected more quickly and this is interpreted as adaptive, suggesting that it would be easier to both detect and gather seeds with brighter seed coats. These unconscious visual biases explain why wild dark-mottled beans have been domesticated into light-colored forms. These foraging behaviors suggest that lighter seed coats may have been unconsciously

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favored during early domestication, as their greater visual salience made them more likely to be collected and dispersed, even without conscious selection for color.

Beyond perceptual biases, several cultural factors likely reinforced the selection of light-colored seeds during bean domestication. Ethnographic and historical evidence suggests that humans have preferences for homogeneity and aesthetic appeal in crop products (Sibbesson, 2022). Uniformly light-colored beans may have been valued for their visual attractiveness and consistency, especially when compared to the mottled or dark appearance of wild beans (Uebersax et al., 2022). Early farmers could more easily recognize and sort a homogeneous batch of light-colored seeds, improving efficiency in post-harvest processing. Indeed, light-colored seeds would be easier to spot among pods and debris during threshing and winnowing, reducing the labor needed to separate edible seeds from chaff. This aligns with Zhou et al. (2022)’s suggestion that traits facilitating simpler harvesting and sorting were favored by early cultivators. Additionally, light-colored seed coats often correlate with thinner seed coats, which can have practical benefits: such seeds cook faster and taste less bitter, and their lack of dark pigments can be associated with better culinary quality and marketability. The homogeneity of domesticated bean varieties, many of which produce uniformly light or solid-colored seeds, stands as testament to these combined practical and cultural selection pressures during domestication.

Domesticated beans (including species like adzuki and common bean) often carry loss-of-function mutations in key genes of the flavonoid/anthocyanin pathway that controls seed coat pigmentation (Le Signor et al., 2018) . For example, in adzuki bean two genes have been identified as major determinants of seed coat color: *VaPAP1* and *VaANR1*. *VaPAP1*

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encodes a MYB transcription factor regulating proanthocyanidin biosynthesis; a deletion of this gene abolishes the production of black pigments, yielding seeds with a pale background instead of the wild-type black mottling. Meanwhile, *VaANR1* encodes anthocyanidin reductase, an enzyme in the proanthocyanidin (tannin) pathway; a point mutation in *VaANR1* leads to accumulation of red anthocyanin pigments in the seed coat rather than brown or black tannins (Freixas Coutin et al., 2017). The result of these mutations in domesticated adzuki is a distinctive red or white seed coat in place of the dark, camouflaged seed coat of wild ancestors (Cortinovis et al., 2020). Thus, the genetic evidence reinforces the role of human visual selection, unconscious but persistent in driving mutations like *VaPAP1* and *VaANR1* to become fixed in domesticated bean gene pools (Cortinovis, 2022). Over time, what began as slight genetic variants became the dominant alleles in crops, demonstrating how human preferences shaped the bean genome (Lye & Purugganan, 2019).

The domestication histories of numerous other crops are consistent with the pattern observed in beans, where humans selected for seed traits that improved visibility and ease of use. In many domesticated plants, wild ancestors have darker, more camouflaged, or hard-to-discern seeds, while the domesticated forms evolved conspicuous, paler, or more exposed grains that facilitated human harvesting (Stetter et al., 2020). For instance, in cereal crops like rice and wheat, early farmers favored genetic variants that produced light-colored grains. Wild rice typically has a red pigmented seed pericarp (rich in tannins), whereas most cultivated rice carries a mutation in the *Rc* gene resulting in a white (non-pigmented) pericarp (Brooks et al., 2008). The ubiquity of white rice grains in domesticated varieties suggests ancient selection for grains that were visually distinguishable and more palatable (lacking the bitter tannins of red grains). A similar trend is seen in wheat and barley: ancestral forms often

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had red or dark seed coats and husks, but domestication led to “white” wheat and barley varieties with fewer polyphenolic pigments (Brooks et al., 2008). These lighter grains not only look uniform but also tend to have milder flavor and improved baking qualities, which likely increased their desirability (Hu et al., 2024).

In beans, the evolution of seed coat color reflects broader trends observed across legumes, suggesting a shared trajectory shaped by similar ecological and selective pressures. Domesticated lentils (*Lens culinaris*), for example, show a marked shift from the small, black or mottled seeds of wild relatives to larger seeds with light tan, yellow, or pale green coats (Liber et al., 2021). Wild lentils commonly exhibit a dark, hard seed coat, an adaptation to avoid predation and delay germination, whereas domesticated lentil landraces are often light-colored or translucent seeded, a trait that emerged under cultivation. The loss of dark pigmentation in lentils would have made them stand out against soil and gravel, aiding early gatherers in collecting spilled seeds, much as with beans (Guerra-García et al., 2025).

Other pulses like peas and chickpeas underwent analogous changes: wild chickpea seeds are tiny and nearly black, while domesticated chickpeas are typically larger and cream-colored; wild peas often have mottled brown seed coats and strong dormancy, whereas domesticated peas evolved uniform light-colored seeds with reduced dormancy (Von Wettberg et al., 2018). Even in maize (*Zea mays*), although color variation was not eliminated (modern maize can have kernels of many colors), a critical domestication changes improved seed visibility and accessibility, the loss of the hard fruitcase that encases teosinte seeds (Stitzer & Ross-Ibarra, 2018). Wild teosinte’s kernels are hidden inside tough glumes (making them inconspicuous and inedible without shattering), but domesticated maize has naked kernels exposed on the cob, effectively displaying the seeds openly for easy harvesting (Flint-Garcia, 2017).

This reflects an unconscious selection for plants that present their seeds in a more visible and accessible manner to human foragers. It is clear from these instances that human gathering and farming have continuously directed evolution toward making seeds more visible and usable, regardless of whether the trait in consideration is seed color or seed exposure. Similarities in domestication syndromes across diverse crops (e.g., beans, lentils, cereals) suggest that early selection may have favored phenotypes that enhanced the detectability, collectability, or usability of seeds and grains. While the underlying motivations, whether conscious or unconscious, cannot be directly inferred, traits such as lighter color may have been consistently favored due to multiple perceived advantages, including greater visibility, apparent size, or cleanliness.

One of the limitations of this study was that all the experiments were conducted under controlled laboratory conditions that lack the ecological complexity of natural environments. Factors such as variable lighting, and heterogeneous soil backgrounds, were not involved. These environmental variables could impact seed visibility and selection pressures in real-world contexts. Moreover, the study focused on only two seed color categories, dark and light seeds. However, in the case of wild bean populations, the range of seed coat patterns and intermediary colors, for instance, the mottled or speckled ones, are often involved. These intricate colors might affect visual selection in ways different from uniform colors. By overcoming these limitations, further study will be able to put together a more complete picture of how visual and ecological considerations, through human collecting experiments, to contribute to the domestication of beans.

There are several directions in which future investigations might profitably proceed. Replication of agronomic conditions in field experiments with multiple kinds of soil and natural light condition would determine whether the impact of visibility observed in the lab persist in more complex ecological scenarios. The addition of mottled, spotted, and intermediate seed colors present in wild beans would show whether selection is acting primarily on contrast color, pattern elaboration, or absolute color. Examining additional domestication traits alongside seed color would offer a broader view of the selective pressures shaping bean domestication. Exploring correlations or trade-offs among these traits could reveal more complex patterns of selection.

These findings refigure plant domestication history by establishing perceptual prejudice as unconscious forces of evolutionary change. Since pollinators function to modify floral traits through preference for hue, humans might have been "unintentional agents" of selection, indirectly choosing phenotypes coinciding with sensory competence (Ruiz-Hernández et al., 2021). This has two important implications: Breeding programs may employ visual characteristics to enhance harvesting efficiency, reduce yield loss, and sorting ease, emulating traditional methods. As an example, visually high-contrast seeds could reduce labor cost under mechanized agriculture. Secondly, restoring crop wild relatives may entail recreating ancestral levels of visibility to enable seed dispersal by native foragers.

Furthermore, the results challenge anthropogenic explanations of domestication as a deliberate process. Instead, they support a model whereby perceptual constraints drove crop

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evolution indirectly, a paradigm shift with parallels in animal domestication. In summary, this research combines behavioral, ecological, and evolutionary evidences to portray visual selection as a cornerstone of crop domestication. By bridging experimental psychology and agricultural history, the research demonstrates the vast yet unintended consequences of human-environmental relationships.

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Supplementary Data

Supplementary Table 1 Fixed effect tests for different responses of Single-Bucket Experiment for red vs black (three buckets)

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Response of Black Seeds	Bucket	2	2	493	2.8683	0.0577
	Time	5	5	493	269.6415	< 0.0001*
	Bucket*Time	10	10	493	45.2950	< 0.0001*
Response of Red Seeds	Bucket	2	2	493	4.5000	0.0116*
	Time	5	5	493	535.8894	< 0.0001*
	Bucket*Time	10	10	493	64.1872	< 0.0001*
Response of Black Proportion	Bucket	2	2	493	0.4446	0.6413
	Time	5	5	493	219.3991	< 0.0001*
	Bucket*Time	10	10	493	2.3457	0.0104*
Response of Red Proportion	Bucket	2	2	493	58.6254	< 0.0001*
	Time	5	5	493	644.7676	< 0.0001*
	Bucket*Time	10	10	493	6.4349	< 0.0001*
Response of Total Seeds	Bucket	2	2	493	0.8382	0.4331
	Time	5	5	493	1032.750	< 0.0001*
	Bucket*Time	10	10	493	1.0557	0.3953

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Supplementary Table 2 Fixed effect tests for different responses of Single-Bucket Experiment (red vs black (two-buckets))

Responses	Source	Nparm	DF	DFDen	F Ratio	Prob > F
Response of Black Seeds	Bucket	1	1	87	19.4976	< 0.0001*
	Time	1	1	87	303.6944	< 0.0001*
	Bucket*Time	1	1	87	22.9669	< 0.0001*
Response of Red Seeds	Bucket	1	1	87	71.0917	< 0.0001*
	Time	1	1	87	87.5121	< 0.0001*
	Bucket*Time	1	1	87	30.2597	< 0.0001*
Response of Black Proportion	Bucket	1	1	87	0.0046	0.9463
	Time	1	1	87	251.1576	< 0.0001*
	Bucket*Time	1	1	87	0.5602	0.4562
Response of Red Proportion	Bucket	1	1	87	62.3885	< 0.0001*
	Time	1	1	87	124.9450	< 0.0001*
	Bucket*Time	1	1	87	5.6783	0.0194*
Response of Total Seeds	Bucket	1	1	87	6.4774	0.0127*
	Time	1	1	87	468.4891	< 0.0001*
	Bucket*Time	1	1	87	0.0024	0.9611

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Supplementary Table 3 Fixed effect tests for different responses of Single-Bucket Experiment (ivory vs black)

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Response of Black Seeds	Bucket	1	1	87	23.5226	< 0.0001*
	Time	1	1	87	248.6949	< 0.0001*
	Bucket*Time	1	1	87	3.0596	0.0838
Response of Ivory Seeds	Bucket	1	1	87	109.2148	< 0.0001*
	Time	1	1	87	109.1126	< 0.0001*
	Bucket*Time	1	1	87	19.6893	< 0.0001*
Response of Black Proportion	Bucket	1	1	87	0.5271	0.4698
	Time	1	1	87	234.7448	< 0.0001*
	Bucket*Time	1	1	87	3.5515	0.0628
Response of Ivory Proportion	Bucket	1	1	87	11.4040	0.0011*
	Time	1	1	87	90.8122	< 0.0001*
	Bucket*Time	1	1	87	0.0019	0.9650
Response of Total Seeds	Bucket	1	1	87	8.5761	0.0043*
	Time	1	1	87	409.8559	< 0.0001*
	Bucket*Time	1	1	87	2.2617	0.1362

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Supplementary Table 4 Fixed effect tests for different responses of Single-Bucket Experiment for comparison of ivory & red vs black

Responses	Source	Nparm	DF	DFDen	F Ratio	Prob > F
Response of Dark Seeds	Bucket	1	1	203	32.6705	< 0.0001*
	Time	1	1	203	373.1286	< 0.0001*
	Bucket*Time	1	1	203	13.7808	0.0003*
Response of Light Seeds	Bucket	1	1	200.8	200.9365	< 0.0001*
	Time	1	1	200.8	234.7305	< 0.0001*
	Bucket*Time	1	1	200.8	74.1881	< 0.0001*
Response of Dark Seeds Proportion	Bucket	1	1	203.3	1.0673	0.3028
	Time	1	1	203.3	339.5516	< 0.0001*
	Bucket*Time	1	1	203.3	0.5537	0.4577
Response of Light Seeds Proportion	Bucket	1	1	201.6	67.5869	< 0.0001*
	Time	1	1	201.6	245.8014	< 0.0001*
	Bucket*Time	1	1	201.6	7.6165	0.0063*
Response of Total Seeds	Bucket	1	1	201.9	8.8028	0.0043*
	Time	1	1	201.9	701.2523	< 0.0001*
	Bucket*Time	1	1	201.9	2.5105	0.1147

Supplementary Table 5 Fixed effect tests for different responses of Competition-3

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Total Time Spent	Bucket	2	2	147	26.4266	< 0.0001*
Total Seeds	Bucket	2	2	117	24.2829	< 0.0001*
Time spent per Seed	Bucket	2	2	115.9	7.5658	0.0008*
Seeds picked per second	Bucket	2	2	116.5	5.0340	0.0080*

Supplementary Table 6 Fixed effect tests for different responses for Competition-2 (red vs black)

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Total Time Spent	Bucket	1	1	58	33.1235	< 0.0001*
Total Seeds	Bucket	1	1	58	32.8754	< 0.0001*
Time spent per Seed	Bucket	1	1	29	36.6910	< 0.0001*
Seeds picked per second	Bucket	1	1	29	32.6798	< 0.0001*

Supplementary Table 7 Fixed effect tests for different responses of Competition-2 (ivory vs black)

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Total Time Spent	Bucket	1	1	58	10.8180	0.0017*
Total Seeds	Bucket	1	1	58	25.6885	< 0.0001*
Time spent per Seed	Bucket	1	1	58	4.1008	0.0475*
Seeds picked per seed	Bucket	1	1	29	13.2205	0.0011*

Supplementary Table 8 Fixed effect tests for different responses of Competition-2 Experiment for comparison of ivory & red vs black

Responses	**Source**	**Nparm**	**DF**	**DFDen**	**F Ratio**	**Prob > F**
Total Time Spent	Bucket	1	1	117	33.6752	< 0.0001*
	Bucket color type	1	1	117	0.0050	0.9435
Total Seeds	Bucket	1	1	117	56.5664	< 0.0001*
	Bucket color type	1	1	117	8.2630	0.0048*
Time spent per Seed	Bucket	1	1	69.8	12.2792	0.0008*
	Bucket color type	1	1	116.9	21.2493	< 0.0001*
Seeds picked per second	Bucket	1	1	69.05	24.1291	< 0.0001*
	Bucket color type	1	1	105.9	16.4972	< 0.0001*

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