Sex differences in patch-leaving foraging decisions in rats

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Summary

The ubiquity, importance, and sophistication of foraging behavior makes it an ideal platform for studying naturalistic decision making in animals. We developed a spatial patch-foraging task for rats, in which subjects chose how long to remain in one foraging patch as the rate of food earnings steadily decreased. The cost of seeking out a new location was varied across sessions. The behavioral task was designed to mimic the structure of natural foraging problems, where distinct spatial locations are associated with different reward statistics, and decisions require navigation and movement through space. Male and female rats generally followed the predictions of theoretical models of foraging, albeit with a consistent tendency to persist with patches for too long compared with behavioral strategies that maximize food intake rate. The tendency to choose overly-long patch residence times was stronger in male rats. We also observed sex differences in locomotion as rats performed the task, but these differences in movement only partially accounted for the differences in patch residence durations observed between male and female rats. Together, these results suggest a nuanced relationship between movement, sex, and foraging decisions.

Introduction

Foraging is a naturally motivated form of decision making that is essential for survival in most animal species. Efficient foraging requires principled evaluation of the costs and benefits associated with different courses of actions (Calhoun & Hayden, 2015; Hayden, 2018; Stephens & Krebs, 1986; Stephens, 2008). Understanding the neural basis of foraging decisions holds great potential for understanding decision making generally, as mechanisms that evolved to support food-related decisions may also contribute to other forms of decision making and cognition. Further, in recent years there has been growing recognition that studying natural behaviors like foraging may be an especially productive way to understand brain function (Cisek & Hayden, 2021; Gomez-Marin & Ghazanfar, 2019; Hein et al., 2020; Krakauer et al., 2017; Miller et al., 2022; Yoo et al., 2021).

The patch-leaving problem is one foraging decision that has inspired much theoretical analysis and empirical work in the past decades (Kolling & Akam, 2017; MacArthur & Pianka, 1966; Stephens & Krebs, 1986; Stephens et al., 2007; Stephens, 2008). In this scenario, a forager searches for food in an environment containing spatially-constrained, resource-rich densities referred to as patches. As a forager occupies a patch and harvests food, subsequent bits of food take increasingly long to collect—that is, patches deplete and the forager's rate of food intake decreases over time. At some point, the forager will be better off abandoning its current location and seeking out a replete patch elsewhere. However, because food is not available in the locations between patches, seeking out a new patch entails a cost whose magnitude depends on how long the forager must travel to find the next patch. Sophisticated foragers must therefore balance diminishing returns from their current patch against the expected cost of travelling to a new location. To optimize food intake rate, foragers must select patch residence time between the extremes of remaining in patches for too long (thereby enduring low rates of reward when replete patches exist elsewhere) and leaving patches too quickly (thereby spending most available foraging time travelling between patches).

Patch foraging decisions have been studied in the laboratory in species including humans (Constantino & Daw, 2015; Hall-McMaster et al., 2021, 2021; Heron et al., 2020; Kolling et al., 2012), non-human primates (Barack et al., 2017, 2022; Blanchard & Hayden, 2015; Cash-Padgett & Hayden, 2020; Eisenreich et al., 2019; Hayden et al., 2011; Turrin et al., 2017), and rodents (Cazettes et al., 2022; Kane et al., 2017, 2019, 2022; Lottem et al., 2018; Vertechi et al., 2020). Frequently, such studies simulate foraging decisions in ways that require relatively little movement from subjects. However, when foraging depends on locomotion and navigation—as it frequently does in natural settings—the neural circuits that subserve such processes effectively become a part of the foraging system (Gordon et al., 2021, 2022). This means that while the computational goal of efficient foraging may be the same across topologically-equivalent behavioral tasks, its neural implementation may well be different. To complement existing laboratory studies of foraging, it would therefore be desirable to have a foraging task that involves locomotion between distinct spatial contexts as a way of approximating naturalistic foraging conditions.

Here, we examined patch-leaving decisions in male and female rats on a spatial foraging task. Rats' behavior largely matched the predictions of theoretical models of foraging, though rats systematically remained in patches for longer than the rate-maximizing strategy, a behavioral pattern previously described as over-harvesting patches. The tendency to over-harvest patches was significantly stronger in male rats. We also observed sex differences in movement speed,

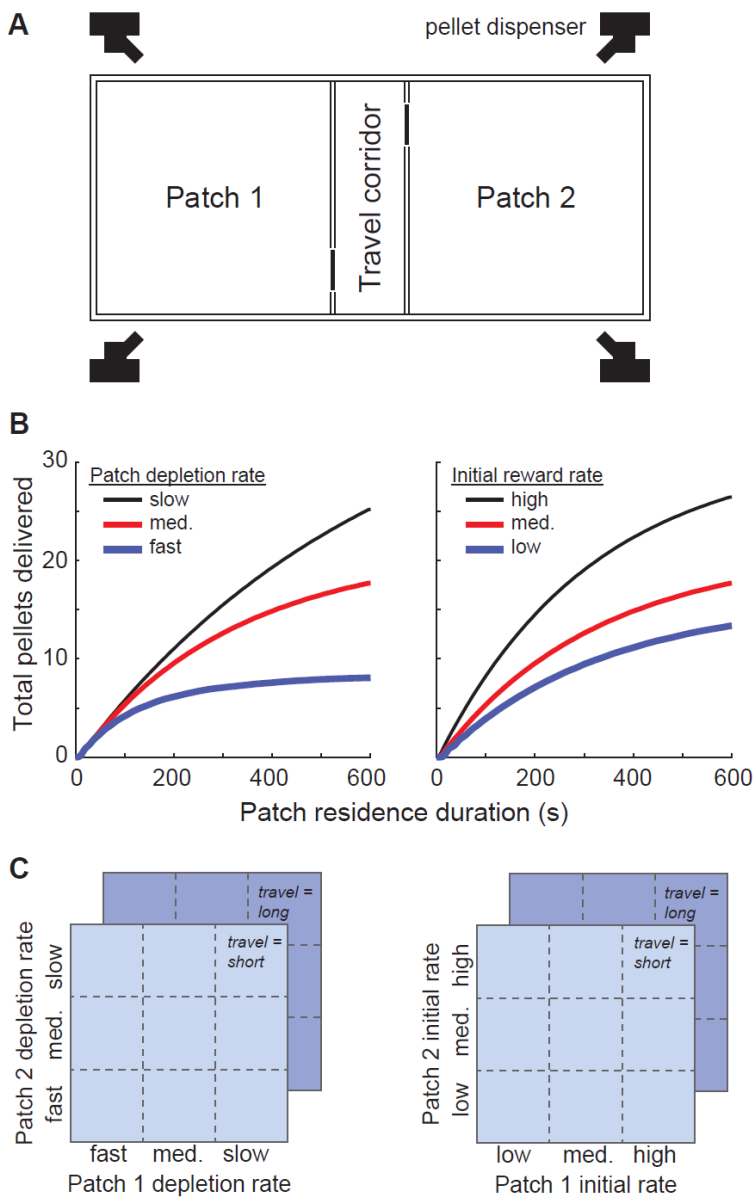

Figure 1. A spatial patch foraging task for rats. (A) The behavioral apparatus consisted of two open field foraging patches connected by a rectangular corridor. Doors at each end of the corridor controlled access to different parts of the apparatus. Food pellet dispensers mounted above each patch distributed food evenly across both foraging patches. (B) Reward schedules determined how many food pellets were delivered on average while rats remained within a patch. Three schedules were created by varying the rate at which patches depleted (left). Three additional reward schedules were created by holding patch depletion rate constant but varying the initial rate of food delivery (right). (C) Rats experienced combinations of the reward schedules depicted in (B) along with two different travel times in pseudorandom order.

distance travelled, and occupancy of different parts of the apparatus, but these differences in locomotion only partially explained differences in patch-leaving decisions. Together, these results suggest a nuanced relationship between movement, sex, and foraging decisions and highlight the promise of spatial tasks as a means of studying foraging decisions.

Results

A laboratory test of patch-leaving decisions.

We tested rats (n = 10; 5 female) on a foraging task designed to mimic the structure of natural patch-leaving decisions. The test apparatus (fig. 1a) consisted of two open-field foraging patches connected by a corridor. Computer-controlled doors at each end of the corridor controlled access to the patches and dispensers mounted above each patch allowed food pellets to be delivered. Rats began each session in the travel corridor, with the door to one randomly-selected patch open and the door to the opposite patch closed. On entering the accessible patch food pellet delivery began and rats were free to forage for as long as they cared to. To switch between patches, rats entered the travel corridor and approached the closed door to the opposite patch. This caused the door to the

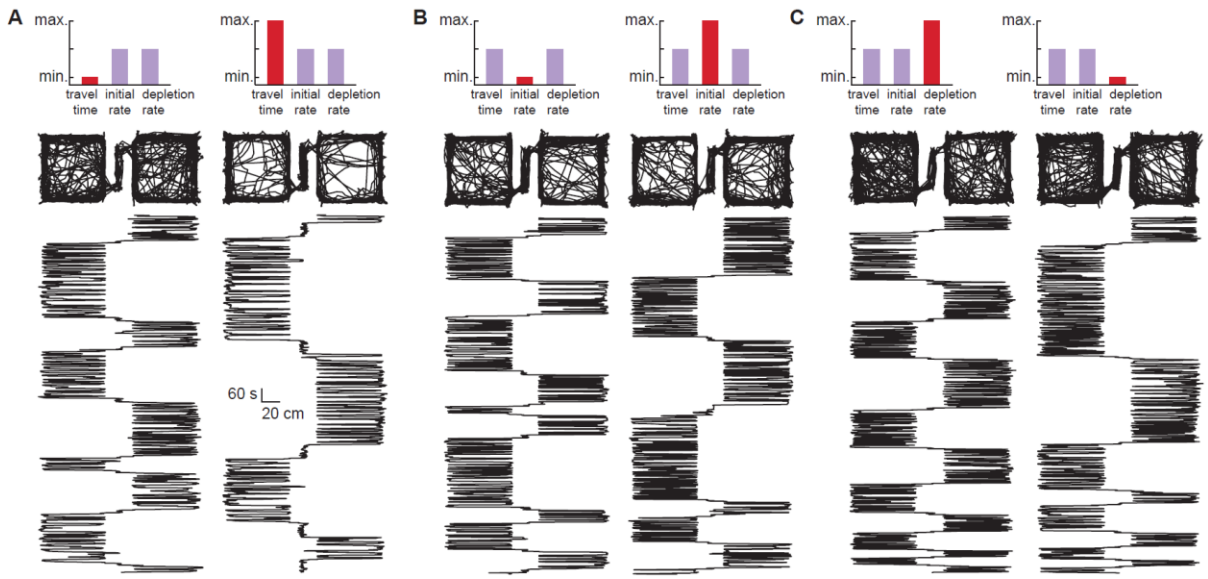

Figure 2. Example behavioral sessions. Each panel displays position-tracking data for an example session, in a top-down view (top row) and with x-coordinate position plotted with time increasing along the y-axis (bottom row), such that session start is at the bottom of the figure. Pairs of sessions that differed in a single task parameter were selected to show how patch residence time was affected by differences in travel time (A), initial reward rate (B), and patch depletion rate (C).

recently-exited patch to close, and the rat was then confined to the travel corridor for either a long (60 s) or short (0 s) travel time delay to simulate time spent moving between patches. No food was available in the travel corridor, so switching between patches was costly in terms of lost opportunity to collect food pellets. When the travel time elapsed, the door to the unvisited patch opened, and the rat was free to enter and begin foraging.

Food pellets were delivered at unpredictable intervals according to a time-dependent schedule (fig. 1b). In all cases, patches depleted as rats remained in them, with the rate at which food pellets were delivered decreasing over time. For some schedules the rate of reward began at the same initial value and patch depletion occurred more or less quickly (fig. 1b, left); in other cases, the rate at which reward decreased was held constant but the initial reward rates differed (fig. 1b, right). Each time that rats re-entered a patch the reward schedule reset to its maximum rate. For each behavioral session, one gain function was assigned to each patch and one travel time was selected. The combinations of task parameters we tested comprised 36 unique session types that each rat experienced once in pseudo-random order (fig. 1c).

Sex differences in patch-leaving decisions.

Figure two shows position-tracking data for example sessions, with the rat's x-coordinate position plotted over time (start of session at the bottom of plot), a view that makes it easy to visualize how much time rats spent in the left and right patches. The pairs of example sessions differed in travel time (fig. 2a), initial reward rate (fig. 2b), or reward depletion rate (fig. 2c), with otherwise identical task parameters. When travel time was short, the rat switched between patches frequently (fig. 2a, left); however, when travel time was long, the rat remained in patches longer on each visit (fig. 2a, right), consistent with the predictions of foraging models. Rats similarly spent longer in

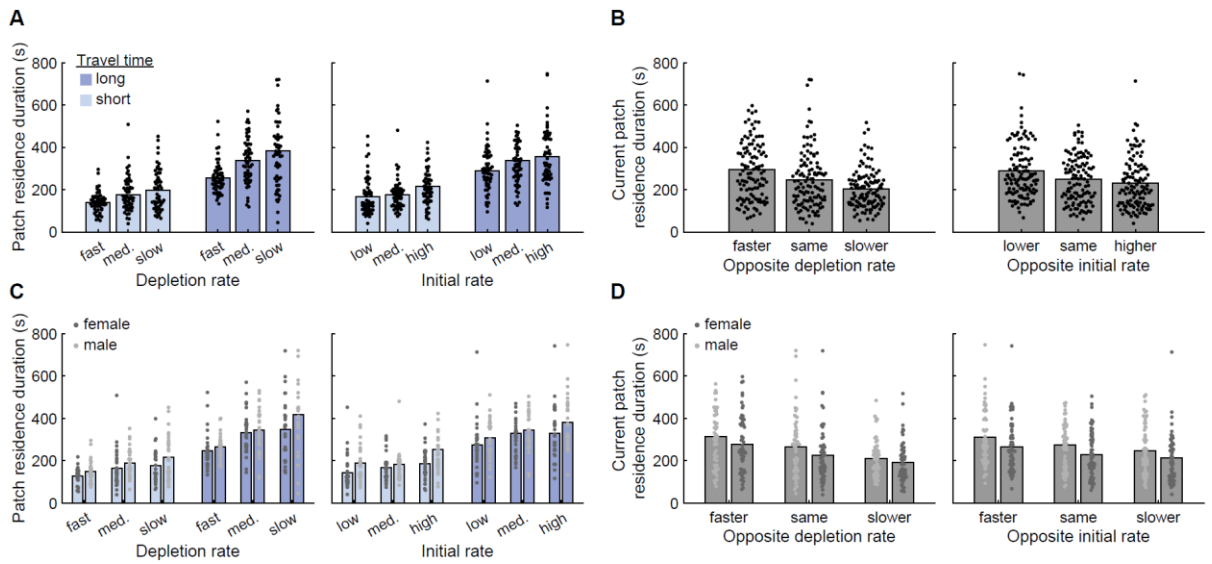

Figure 3. Sex differences in foraging. (A) Patch residence duration is aggregated by patch depletion rate (left), initial rate (right), and travel time (both plots). Each point depicts patch residence duration for one patch in one behavioral session; bars indicate group means. (B) Patch residence time is aggregated based on whether the other patch in the session had more favorable reward statistics (i.e. slower patch depletion rate or higher initial rate), less favorable reward statistics (i.e. faster patch depletion rate or lower initial reward rate), or identical reward statistics. Each point depicts patch residence duration for one patch in one behavioral session; bars indicate group means. (C) Same data presentation as in (A), except that data are separated by sex. (D) Same data presentation as in (B), except that data are separated by sex.

patches with higher initial reward rates (fig. 2b, right) and slower reward depletion rates (fig. 2c, right).

We computed patch residence duration as the median duration of all visits to a patch within a behavioral session. Patch residence duration increased with decreasing reward depletion rates and with increasing initial reward rates (fig. 3a). Rats were also sensitive to travel time, with longer travel times resulting in increased residence durations for all reward schedules (fig. 3a). Further, the amount of time that rats spent in one patch was influenced both by the local reward schedule, and by the reward schedule of the un-occupied patch (fig. 3b). When the opposite patch reward schedule was more advantageous than that of the current patch (i.e. higher initial rate or slower depletion rate), rats reduced the amount of time they spent in the current patch relative to situations when both patches had identical schedules. Similarly, if the opposite patch had a less favorable reward schedule than the current patch, rats increased their allocation of time to the current patch. These results indicate that rats integrated multiple independent sources of cost and benefit information in a manner broadly consistent with the predictions of theoretical foraging models.

Interestingly, we observed clear sex differences in patch residence times, with female rats systematically exiting patches earlier than male rats. This difference was consistent across conditions: female rats showed numerically lower residence times compared to male rats in every session type that we tested (fig. 3c). Female and male rats were similarly sensitive to local patch and opposite patch reward schedules (fig. 3d).

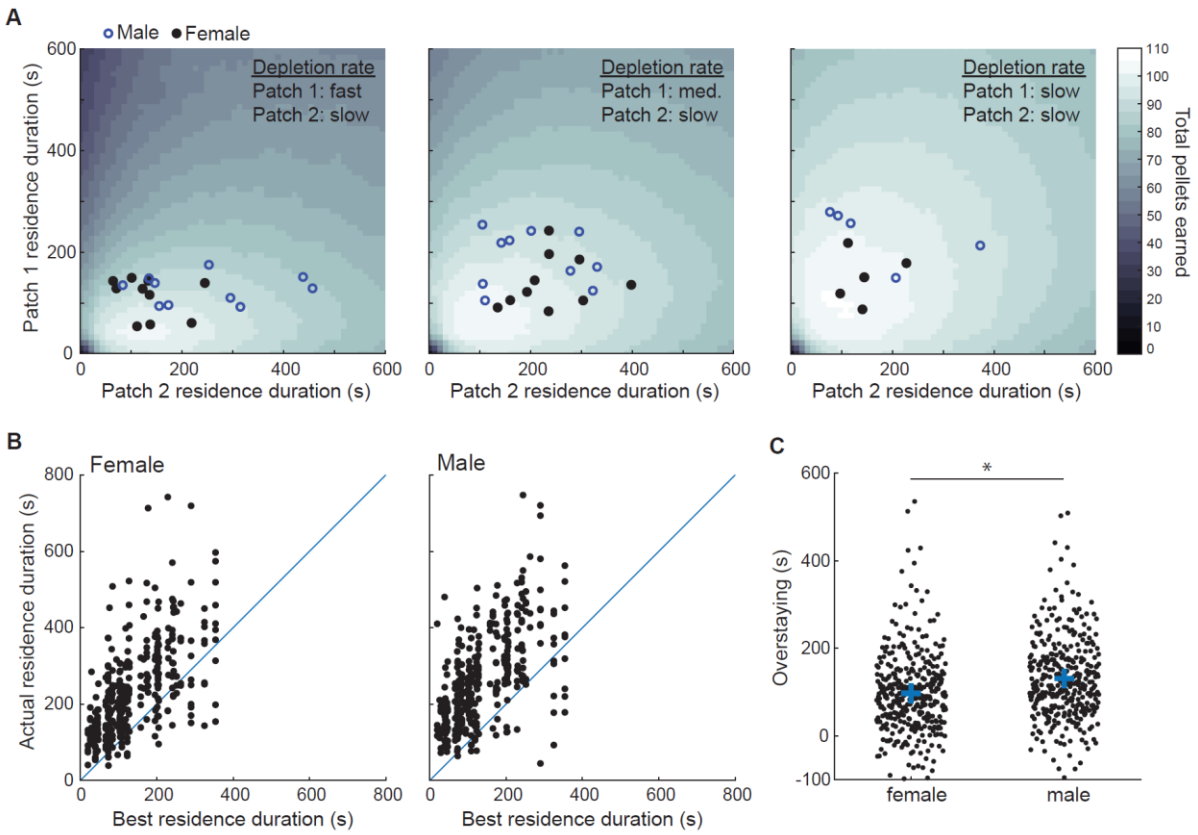

Figure 4. Rats overharvested patches. (A) In each panel, the heat map depicts food earnings resulting from each behavioral strategy (i.e. each pair of patch residence durations) as determined by simulations. Results for three sessions are shown, with patch 1 depletion rate ranging from fast to slow, and all other task parameters fixed (travel time = 60 s; patch 2 depletion rate = slow). Data points depict observed rat behavior for sessions with matching parameters; each point represents behavior from one session. (B) Observed patch residence duration is plotted against the patch residence duration that earned the greatest amount of food in simulations; each point depicts one patch in one behavioral session. (C) Overstaying (the difference between the simulation-determined food intake-maximizing residence duration and the observed residence duration) is aggregated by sex. Each point depicts one patch in one behavioral session. Blue crosses depict the mean for each distribution. Positive values indicate that residence durations exceeded the best durations determined by simulation. Overstaying was significantly greater in male rats.

We used linear mixed-effect models to quantify how task parameters and subject-specific factors were related to patch residence duration. Fixed effects in the model included sex, reward schedule parameters (initial reward rate, patch depletion rate) for both the currently-occupied and opposite patches, travel time, and the physical location (left or right) of the patch. Subject identity was included as a random effect. Travel time and reward schedule parameters exerted significant effects on patch residence duration in the directions predicted by classical models of foraging behavior (table one). Sex was a significant predictor of residence duration, consistent with the results shown in figure three. The physical location of patches within the apparatus did not significantly affect residence duration. Though we initially tested a version of the model that included all two-way interactions between predictors, none were found to be significant, so interaction terms were not included in the final model.

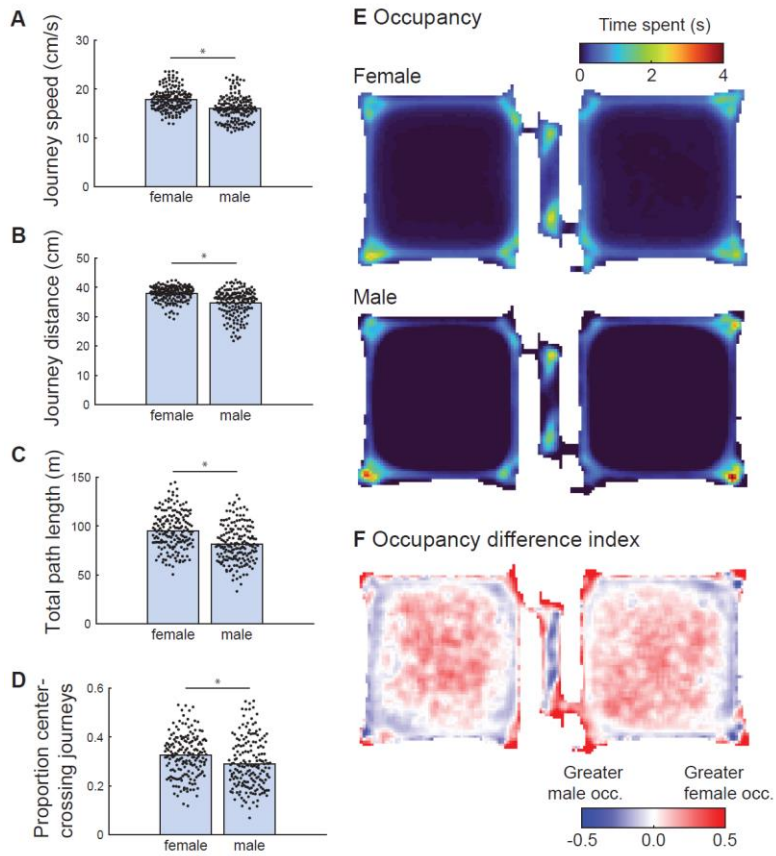

Figure 5. Sex differences in movement. (A) Average movement speed during journeys—discrete bouts of movement—was greater for female rats. Each data point shows average journey speed for one session; bars depict group means. (B) The distance travelled per journey was greater for female rats. Each data point shows average journey distance for one session; bars depict group means. (C) Total distance travelled per session (computed without segmenting data into discrete journeys) was greater for female rats. Each data point shows total distance travelled for one session; bars depict group means. (D) A fraction of female rat's trajectories crossed through the center of the open field foraging patches. Each data point shows the fraction of total journeys within one session that passed within 15 cm of the patch's center. (E) Heat maps show the amount of time female (top) and male (bottom) rats spent at different locations on the apparatus, averaged over all subjects and all sessions. (F) Heat maps show the occupancy difference index, the relative difference in time spent at each location between male and female rats. Red marks locations where females spent more time on average than males, blue indicates locations where males spent a greater amount of time on average than females, while white denotes locations with similar occupancy between males and females.

Rats overharvested patches.

We used numerical simulations to determine the patch residence durations that resulted in the greatest food earnings for each session type. Assuming a fixed residence duration for each visit to a patch, we computed the rate of reward associated with all possible combinations of patch one and patch two residence durations. In figure 4a, lighter and darker colors indicate higher or lower average reward rates across combinations of patch residence durations in three example session types. Observed residence durations for male and female rats are also plotted. Rats' behavior generally tracked regions of strategy space associated with the high rates of reward. However, both male and female rats systematically chose patch residence durations longer than the rate-maximizing residence durations determined by simulation. Across all sessions, rats' chosen residence durations were strongly correlated with ($r = 0.58$, $p = 1.48 \times 10^{-66}$, $n = 718$ patch residence times, Pearson's correlation; fig. 4b), but systematically greater than, rate-maximizing residence durations ($t_{717} = 28.10$, $p = 9.55 \times 10^{-118}$; one-sample t-test; fig. 4c). Though both male and female rats overharvested patches, by leaving patches earlier than male rats, female rats more closely

approximated the rate-maximizing strategy. Consistent with this, female rats earned slightly more food pellets per session compared to male rats (55.1 vs. 51.1 pellets; $t_{357} = 2.24$; $p = 0.02$; two-sample t-test).

Sex differences in movement patterns do not fully explain sex differences in foraging.

Previous work has shown that male and female rats move through and interact with open spaces differently (e.g. Bishnoi et al., 2021; Hyde & Jerussi, 1983; Osterlund Oltmanns et al., 2021; Stöhr et al., 1998). Consistent with this, we observed differences between male and female rats in several movement properties. Following previous approaches (Drai et al., 2000; Eilam & Golani, 1989), we segmented position-tracking data into discrete journeys—bouts of continuous locomotion bounded by periods of little or no movement—and computed average journey properties for each behavioral session. Female rats travelled more quickly on journeys (fig. 5a; $p = 2.52 \times 10^{-13}$; $t_{357} = 7.61$; two-sample t-test), and thereby covered a greater distance on average with each bout of movement (fig. 5b; $p = 2.62 \times 10^{-14}$; $z_{357} = 7.62$; rank sum test). Consistent with these differences in individual journeys, female rats travelled a greater total distance per session during than male rats (fig. 5c; $p = 2.12 \times 10^{-11}$; $t_{357} = 6.91$; two-sample t-test). The spatial distribution of behavior also differed between male and female rats. Female rats made significantly more journeys that crossed near the center of foraging patches (fig. 5d-f; $t_{357} = 3.45$; $p = 6.24 \times 10^{-3}$). Indeed, examining time spent at each location across the apparatus by male and female rats revealed a tendency for male rats to spend relatively greater amounts of time along the perimeter of the foraging patches, and female rats to spend relatively greater time

We wondered whether basal differences in movement could account for the sex differences in foraging decisions we observed. For instance, if rats moved randomly within patches until they encountered the door to the travel corridor and exited the patch, rats with a higher average running speed would reach doors more quickly and therefore exit patches earlier. This account predicts that variation in running speed should systematically affect patch residence duration, with faster running speeds resulting in shorter residence durations.

For individual visits to patches across all subjects and sessions ($n = 2464$ patch visits), we computed rats' mean running speed while in the patch and fit a linear model to assess how well running speed, sex, and their interaction predicted patch residence duration. The model revealed significant effects of running speed ($\beta = -19.16$; $p = 1.34 \times 10^{-30}$), sex ($\beta = -159.73$; $p = 8.29 \times 10^{-22}$), and the interaction of running speed and sex ($\beta = 18.00$; $p = 2.35 \times 10^{-17}$). These results indicate that while running speed and sex both influenced how long rats remained in patches, the effect of sex was substantially larger. However, the significant interaction term indicates that the nature of the relationship between running speed and residence duration differed for males and females. Indeed, running speed and residence duration were negatively correlated in male rats ($r = -0.31$; $p = 1.25 \times 10^{-26}$; Pearson's correlation), while there was no evidence of a similar relationship in female rats ($r = -0.03$; $p = 0.36$; Pearson's correlation). These findings suggest a nuanced relationship between running speed, sex, and patch-leaving decisions: male rat that moved more quickly also tended to leave patches earlier, but the fact that female rats ran faster on average than male rats does not account for their tendency to abandon patches earlier.

Discussion

Efficient foraging requires a careful accounting of costs and benefits, and in natural settings information about these factors must be learned directly from experience. We developed a

behavioral task for the laboratory that mimics key aspects of this scenario in a controlled setting. Rats learned the local reward statistics assigned to spatially-distinct foraging patches and the travel time penalty associated with switching between them. Using this knowledge, rats adjusted the amount of time they allocated to each foraging location, paralleling—though not perfectly matching—the patch residence durations that maximized food earnings. These results show that the task elicited flexible, context-sensitive foraging behavior from rats.

Overstaying and patch foraging.

As in previous studies of patch foraging involving a range of species, rats in our study consistently chose residence times longer than those predicted by food intake rate maximization models (Cash-Padgett & Hayden, 2020; Cassini et al., 1990; Constantino & Daw, 2015; Hayden et al., 2011; Kane et al., 2019; Nonacs, 2001). Many possible explanations have been proposed for this overharvesting phenomenon, and it is probably driven by a combination of different factors (Kendall & Wikenheiser, 2022). Perhaps the most general explanation—and one not exclusive of various other causes—is that rats were optimizing more than food earnings. In most scenarios foragers must consider many other factors while searching for food, including predation risk (Choi & Kim, 2010; Ydenberg & Dill, 1986), potential competitive or affiliative interactions with conspecifics (Li et al., 2012; Nagy et al., 2020; Whishaw, 1988; Whishaw & Tomie, 1988), energy expenditures (Hart et al., 2017), and opportunities for incidental learning about aspects of their environments (Wang & Hayden, 2021). Foraging strategies that balance these and other factors might depart from the predictions of rate maximization but nevertheless perform well in real-world scenarios. Future experiments that manipulate food availability alongside important non-food factors will be important for understanding the behavioral and neural mechanisms of the complex multi-objective optimization problem that natural foraging entails.

Sex differences in foraging decisions.

Female rats left patches earlier than male rats across all task conditions (fig. 3), and our regression analysis indicated that sex differences in running speed accounted for only a small portion of this effect. This suggests that a yet unidentified sex difference drives divergent patch-leaving decisions. Gonadal hormones—acting over the course of development or on a shorter timescale—are clear candidate mechanisms for orchestrating sex differences in decision making. Indeed, a recent study of intertemporal choice in rats (Hernandez et al., 2020) reported robust sex differences that were controlled by circulating testosterone levels. When choosing between a small amount of food delivered quickly and a larger amount of food available after a delay, male rats preferred the “larger-later” option, while female rats opted for the “smaller-sooner” selection. However, reducing testosterone levels in male rats shifted their preference toward the smaller-sooner choice, while reducing ovarian hormones in female rats did not alter their preferences. Interestingly, previous work has found that temporal preferences measured on intertemporal choice tasks are predictive of patch-leaving decisions (Kane et al., 2019), with a tendency to favor immediate vs. delayed rewards in the intertemporal scenario corresponding to overharvesting patches in the foraging scenario. Integrating these two lines of work, one might predict that female rats would be especially prone to overstaying—the opposite of what we observed. However the different strains of rats used here (Long-Evans) and in Hernandez et al.’s (2020) work (Fisher-Brown Norway hybrid) could also impact the relationship between sex and intertemporal choice. More work investigating how sex, strain, and hormones interact on foraging and intertemporal choice tasks would clearly be fruitful.

Our results add to the growing list of sex differences in rodent decision making studies that may point to differences in the way that male and female rats weigh the threat of aversive outcomes against opportunities to earn food. For instance, Pellman and colleagues (2017) arranged for a previously-safe foraging patch to unpredictably deliver foot shocks during some foraging bouts. Male rats responded by reducing their total number of visits to the patch, but lengthening the duration of their visits. In contrast, female rats simply visited the now-risky patch less frequently, and eventually lost body mass as a result. In a similar vein, Orsini and colleagues (2016) measured rats' preferences between a large food reward that was sometimes accompanied by a shock and a smaller amount of food that carried no risk of shock, and found that female rats had a stronger preference for the smaller and safer option compared with male rats. Indeed, even a simulated predator cue (Zambetti et al., 2019) had a stronger impact on food-seeking behavior in female rats despite the absence of any actual painful outcome.

Along these lines, our result is consistent with female rats adopting a strategy that reduces the amount of time spent in the open-field foraging patches, thereby reducing predation risk. However, given that the average difference in residence times between male and female rats was relatively modest, it is unclear whether the protective effect such a strategy might confer would be of practical importance. Further, it remains unclear why male rats would not seek to minimize their risk of predation in the same way. Future work combining theoretical and experimental approaches will be critical to identifying the adaptive basis (if any) of the sex differences reported here.

Limitations and future directions.

The patch-leaving task introduced here complements other approaches to studying decision making and foraging behavior in rodents, and is particularly amenable to electrophysiological studies as the structure of the task closely follows classic designs used to investigate spatial representations in the brain (Muller & Kubie, 1987). Nevertheless, future studies using this approach could improve and expand on the work reported here. Task conditions in which the difference in food earnings for good and bad foraging strategies was larger would help rule out satisficing, the use of a "good enough" but not optimal strategy, as an explanation of overstaying. Similarly, a "closed economy", in which subjects earned their entire allotment of food by performing the task, would test whether rats were simply not energetically challenged enough to incentivize discovering and implementing better foraging strategies. Relaxing certain elements of the task structure would make the foraging scenario more realistic. For instance, foragers in the wild are not constrained to visit patches in a rigid sequence, but rather take advantage of known regularities in resource distribution and other environmental factors to plan advantageous foraging trajectories (Janmaat et al., 2006, 2014; Rudebeck & Izquierdo, 2022). A free-choice version of the patch task would afford this possibility (Hall-McMaster et al., 2021). Instantaneous repletion of patches is also unrealistic, and future experiments could examine whether rats are sensitive to rates of patch depletion and the rates at which patches replenish. Finally, foraging on our task was largely passive, requiring only that rats occupied one of the two foraging patches. Consequently, interesting questions regarding search strategies rats might use to localize spatially-distributed food items, the effort and cognitive costs of search, and related issues were not addressed. These factors could be included in future versions of the task with suitable modification.

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Author contributions

MG and AMW designed the study. MG and SG collected the data. MG, SG, and AMW analyzed the data. AMW drafted the manuscript, with input and edits from MG and SG.

Declaration of interests

The authors declare no competing interests.

Figure legends

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Tables

Table 1. Regression analysis of patch residence durations.

Effect	Estimate	*SE*	95% CI		*p*
			LL	*UL*	
Intercept	-3.19×10^{-16}	0.03	-0.06	0.06	0.99
Depletion rate, current patch	-0.20	0.03	-0.26	-0.15	9.40×10^{-12}
Depletion rate, opposite patch	0.10	0.03	0.05	0.16	4.51×10^{-4}
Initial rate, current patch	0.13	0.02	0.08	0.19	5.27×10^{-6}
Initial rate, opposite patch	-0.09	0.03	-0.14	-0.03	3.37×10^{-3}
Travel time	0.55	0.02	0.49	0.60	6.00×10^{-64}
Sex (female = 1)	-0.13	0.03	-0.19	-0.72	1.14×10^{-5}
Side (left = 1)	-0.03	0.03	-0.10	0.01	0.14

LL, lower limit of confidence interval; UL, upper limit of confidence interval; SE, standard error

Methods

Subjects. Long-Evans rats (n = 10, five female) weighing 200-300 g and aged 10-12 weeks were purchased from Charles River. We did not track levels of circulating sex hormones in either male or female rats. All procedures followed the NIH Guide for the Care and Use of Laboratory Animals and were approved by the Chancellor's Animal Research Committee at the University of California, Los Angeles.

Apparatus. The test apparatus consisted of two square-shaped open field arenas (77 cm) connected to one another by a corridor (25 × 77 cm). At each end of the corridor, 12 cm openings could be blocked by doors actuated by stepper motors. Large extra-maze cues were visible from the foraging patches, allowing rats to orient themselves in space and discriminate between foraging locations. An infrared video camera (OptiTrack Flex 3) mounted overhead interfaced with video tracking software (Blackrock Neuromotive) to measure rats' location in real time at 30 Hz. Two 40-mg food pellet dispensers (Med Associates) were positioned above each foraging patch to ensure an even distribution of food pellets across the foraging arenas. The behavioral task was controlled by custom Matlab (Mathworks) code. Behavioral events and video tracking data were timestamped by an electrophysiology recording system (Blackrock Cereplex direct).

Behavioral task. Rats were handled 10-15 minutes per day for a week before behavioral testing began to acclimate them to contact with experimenters. During the week of handling, rats were also habituated to the behavioral apparatus by allowing them to explore it for approximately 10 minutes per day with all doors open, and with sucrose pellets scattered randomly throughout the two foraging locations. Following handling and apparatus habituation, rats performed one 30-minute task session each day. At the beginning of each session rats were placed in the travel corridor with doors to both patches closed. When the programmed travel delay for that session elapsed, one of the two patch doors was randomly selected to open, and the rat was free to enter the patch and begin foraging. While rats occupied a foraging patch, food pellets (40 mg, 100% sucrose; Bioserv) were delivered following the time-based reward schedule assigned to the patch in that session. Rats could choose to abandon their current foraging patch at any time by entering the travel corridor and approaching within 10 cm of the door to the opposite patch; this caused the door to the previous patch to close, confining the rat to the travel corridor for the travel time assigned to that session. When the travel time elapsed, the door to the next patch opened. Rats were forced to visit patches in an alternation pattern, though there was no minimum amount of time rats were required to remain within a patch. Food pellets were not delivered to either patch while rats were in the travel corridor.

Reward schedules. Patch reward schedules were parameterized by an initial inter-pellet interval (which set the rate of reward when rats first entered the patch), and an exponential time constant (which determined how quickly inter-pellet interval increased while rats remained within the patch). These parameters defined food pellet delivery rate as a function of patch residence duration. The precise time of individual pellet deliveries was determined by drawing a latency from a Gaussian distribution with mean equivalent to the reciprocal of the current rate of reward and a standard deviation of four seconds. In this way, the cumulative number of pellets earned for a given residence time matched the functions plotted in figure 1b on average, but the precise timing of pellet deliveries was unpredictable on successive visits to the same patch. Reward schedules were generated using three values for initial inter-pellet interval (10, 15, and 20 s, corresponding to high, medium, and low initial reward rates), and three values for the time constant that set the

rate at which inter-pellet interval increased (and reward rate correspondingly decreased) over time (100 s, 300 s, and 600 s, corresponding to fast, medium, and slow patch depletion rates). Three reward schedules were constructed by fixing depletion rate at medium and setting initial rate to high, medium, and low; an additional three schedules were constructed by fixing initial reward rate to medium and setting depletion rate to range fast, medium, and slow (fig. 1b).

Testing sequence. After handling, rats performed five training sessions with short travel time, medium depletion rate, and medium initial rate. By the fifth training session all rats were reliably switching between patches multiple times within each sessions and were deemed ready to begin the task sequence. Behavioral sessions were constructed by assigning reward schedules to each of the patches, and choosing a travel time; these assignments remained fixed for the duration of the session. We tested all assignments of the depletion rate and initial reward rate schedules to the physical patch locations with both long (60 s) and short (0 s) travel times (fig. 2c). Rats progressed through the sequence of sessions in a block-wise fashion, with half of rats first completing the depletion rate sessions and the other half first completing the initial rate sessions. Within each block, the order of sessions was randomized. This design resulted in the depletion rate and initial rate blocks each comprising 18 sessions, for a total of 36 sessions per rat, and 360 sessions for the entire cohort of 10 rats. Two sessions from the depletion rate block (from two different rats) were discarded due to errors in saving data that were not discovered until after the experiment was complete. One rat was inadvertently tested on the same set of session parameters from the initial rate block twice; there was no principled reason to prefer one of these sessions over the other, so both were included in the final data set. Together, a total of 359 sessions (181 initial rate manipulation sessions, 178 depletion rate manipulation sessions) were included for analysis.

Data analysis. All data analyses were conducted in Matlab (2021a). Patch residence time was computed for each patch in each session as the median duration of visits to the patch in question. The start time of a patch visit was taken to be the moment when the rat's center of mass crossed from the travel corridor to the foraging patch. The end time of visits was taken to be the moment that rats approached the door to the opposite patch and triggered the travel time phase of the task. Visits to a patch that were interrupted by the end of the session were not included in the calculation of patch residence time because there was no way of knowing how much longer the rat would have remained in the patch.

All regression models reported here were linear mixed effects models that were fit using the Matlab function *fitlme*. For the model assessing how task parameters and subject factors affected patch residence time (table 1), fixed effects were initial patch reward rate, patch depletion rate, and travel time (coded as continuous variables), as well as sex and patch location (coded as categorical variables; females and left patch coded as "one"). Subject identity was included as a random effect and coded as a categorical variable. The values for initial patch reward rate were entered as the reciprocal of the initial inter-pellet interval of the patch, while the values for patch depletion rate were entered as the reciprocal of the patch time constant. We standardized regressors to facilitate comparison of effect sizes. We also tested a version of the model that included the predictors described above, as well as every pairwise interaction between predictors. However, none of the interaction terms were significant, so we excluded interactions from the model reported here to maximize the accuracy of coefficient estimates.

For the model examining the influence of running speed on patch residence duration, fixed effects were mean running speed within the patch (a continuous variable), sex (a categorical variable;

females coded as “one”), and their interaction. Because the interaction was significant in this case, we retained it for the model reported in the text. Subject identity was included as a categorical random effect.

*Determining rate-maximizing patch residence time*s. A behavioral strategy on the task comprised the set of patch one and patch two residence durations. We considered only fixed, deterministic strategies as there was no way for rats to predict the stochasticity of the reward schedules, and therefore no way in which choosing a different residence duration on successive visits to the same patch could produce a better outcome than consistently applying the correct deterministic strategy. For each pair of residence durations (ranging from 0 – 600 s in one second increments) we used numerical simulations to compute the associated food pellet earnings. Simulations began with the session time set to zero seconds; as in the actual behavioral task, the first event to occur was the programmed travel duration, so session time was incremented by that amount. Next, one patch was randomly selected to be the first available to the simulated agent. For each simulated patch visit, food pellet delivery times were calculated according to the reward schedule assigned to the patch as described above, and any pellets delivered before the agent’s residence duration for that patch elapsed were added to the agent’s total earnings. The session time was then incremented by the patch residence duration and the travel time assigned to that session, and the agent then moved on to the second patch. The programmed travel delay for the short travel time was zero seconds; however, rats were not able to transit the travel corridor instantaneously. The average transit time across all short travel time sessions was approximately 5 s, so for simulations of sessions with a short travel time the session time was incremented by 5 s when rats switched patches. Simulations continued in this way until the session time reached 30 minutes, the duration of actual behavioral sessions. Using this method, we computed the rate of reward over the strategy space of patch one and patch two residence times (fig 4a). Each pair of residence durations was simulated 500 times for each session type, and earnings were averaged across simulations. The resulting rate maps were smoothed by 1 second in each direction, and the peak pixel was taken to be the rate-maximizing behavioral strategy for that session type. For the figure showing behavior and model-predicted reward rate (fig. 4a), we included data from symmetrical sessions (i.e. sessions involving the same the same two reward schedules and differing only in which schedule was assigned to the left or right patch) when possible, as there was no significant effect of position within the apparatus.

Journeys & movement statistics. Artifacts in video tracking data (i.e. large jumps in position) were removed and corrected by interpolation. Following previously-described approaches, we segmented position-tracking data into continuous bouts of movement (journeys) and periods with little or no sustained movement. Periods when rats were confined to the travel corridor were not included in this analysis as movement was limited by the confines of the corridor. The onset of a journey was defined as the moment running speed exceeded 5 cm/s, and the journey terminated when running speed fell below 5 cm/s. The distance travelled on each journey detected in this way was computed by summing the rat’s displacement between successive tracking points; very short journeys (total distance < 20 cm) were excluded from analysis. Features of the remaining journeys (average running speed, distance travelled, distance to center of patch) were computed. We categorized journeys as center crossing if the rat approached within 15 cm of the center of the patch arena at any point on the journey. Independent of journeys, we computed the total distance travelled in each session while foraging in the patches (total path length) by summing the distance between successive positions, excluding intervals when the rat was in the travel corridor.

To examine the distribution of behavior over space we divided the apparatus into 1 cm bins and determined how long rats spent at each location in each session. These plots were averaged across sessions separately for male and female rats (fig. 5E). We used the average male and female occupancy to compute the occupancy difference index for each location on the apparatus (fig. 5F). Occupancy difference index was defined as the difference of female and male average occupancy divided by the sum of male and female average occupancy for each location; in this way, values near zero indicated relatively equivalent male and female occupancy, while positive (negative) values indicated proportionately greater time spent at a location by female (male) rats.

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Figure 1

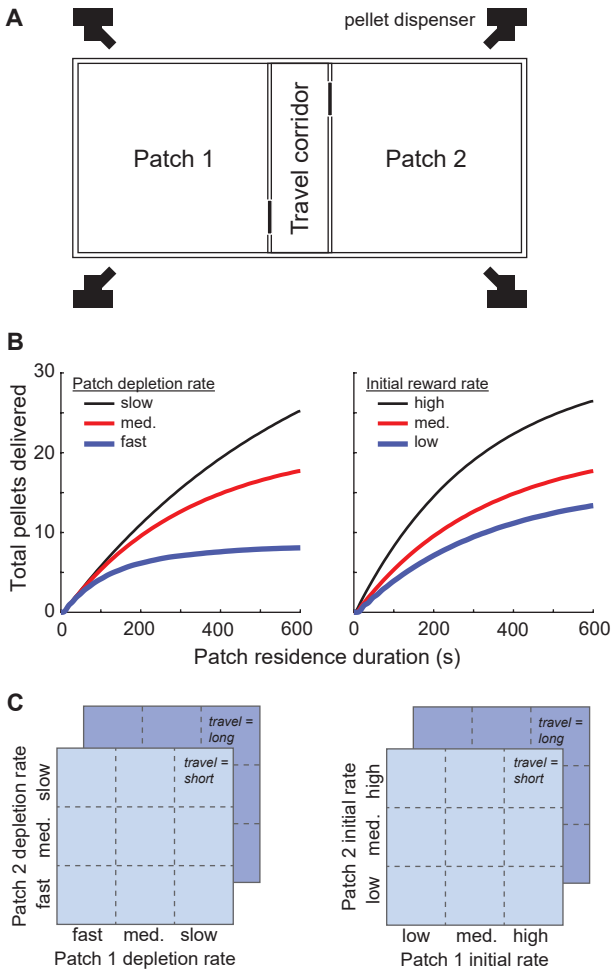

A
pellet dispenser
Patch 1
Travel corridor
Patch 2
B
Total pellets delivered
Patch depletion rate
slow
med.
fast
Initial reward rate
high
med.
low
0
10
20
30
0
200
400
600
Patch residence duration (s)
C
travel = long
travel = short
Patch 2 depletion rate
slow
med.
fast
fast
med.
slow
Patch 1 depletion rate
Patch 2 initial rate
high
med.
low
low
med.
high
Patch 1 initial rate

Figure 2

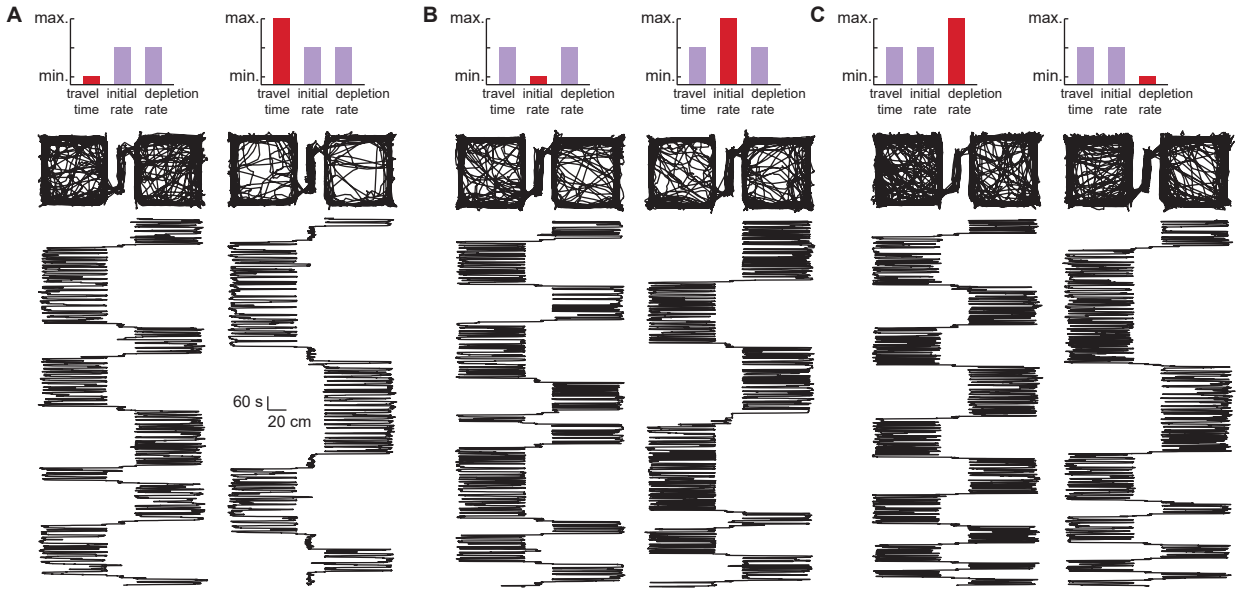

A
max.
min.
travel time
initial rate
depletion rate
max.
min.
travel time
initial rate
depletion rate
60 s
20 cm
B
max.
min.
travel time
initial rate
depletion rate
max.
min.
travel time
initial rate
depletion rate
C
max.
min.
travel time
initial rate
depletion rate
max.
min.
travel time
initial rate
depletion rate

Figure 3

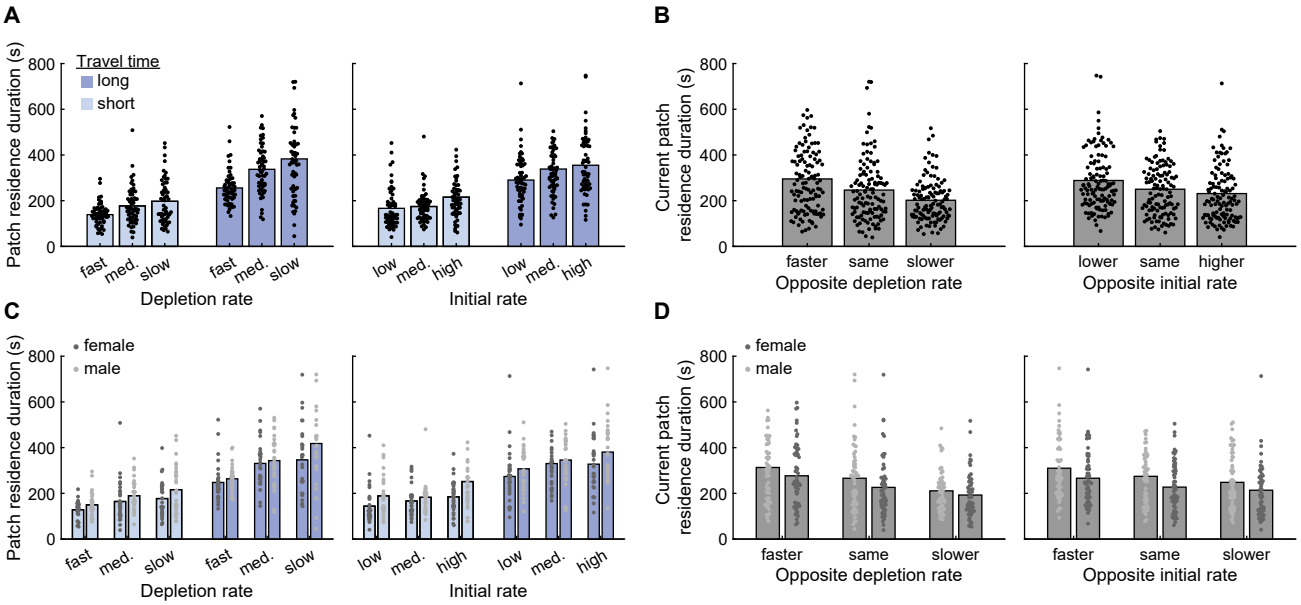

A
Travel time
long
short
Patch residence duration (s)
800
600
400
200
0
fast
med.
slow
fast
med.
slow
Depletion rate
low
med.
high
low
med.
high
Initial rate
B
Current patch residence duration (s)
faster
same
slower
Opposite depletion rate
lower
same
higher
Opposite initial rate
C
female
male
D

Figure 4

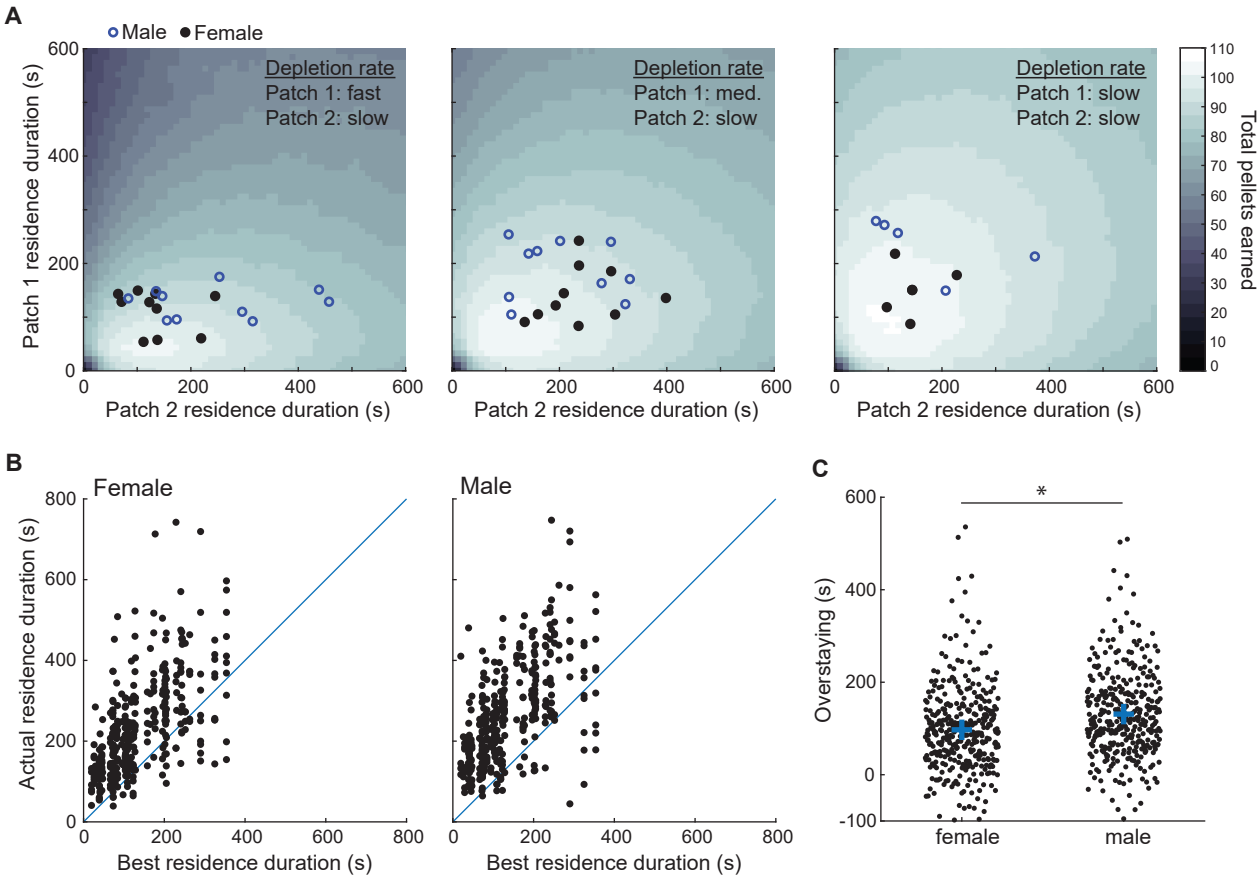
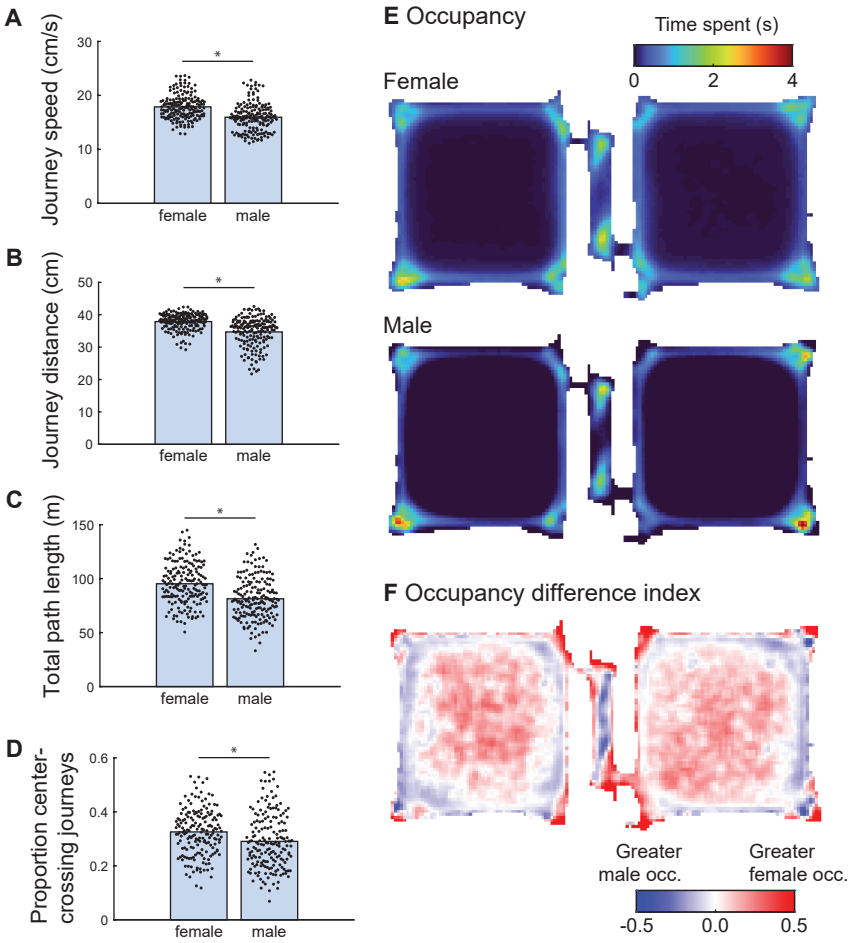

A
Male
Female
Depletion rate
Patch 1: fast
Patch 2: slow
Depletion rate
Patch 1: med.
Patch 2: slow
Depletion rate
Patch 1: slow
Patch 2: slow
Patch 1 residence duration (s)
Patch 2 residence duration (s)
Total pellets earned
B
Female
Male
Actual residence duration (s)
Best residence duration (s)
C
Overstaying (s)
*
female
male

Figure 5


A
Journey speed (cm/s)
30
20
10
0
*
female
male
B
Journey distance (cm)
50
40
30
20
10
0
*
female
male
C
Total path length (m)
150
100
50
0
*
female
male
D
Proportion center-crossing journeys
0.6
0.4
0.2
0
*
female
male
E Occupancy
Time spent (s)
0
2
4
Female
Male
F Occupancy difference index
Greater male occ.
Greater female occ.
-0.5
0.0
0.5