



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES BIOMÉDICAS
BIOLOGÍA EVOLUTIVA

**¿BUSCADORES POR NATURALEZA? COMPARACIÓN DE LA CONDUCTA DE BÚSQUEDA
EN ESPACIOS ABIERTOS DE URBANITAS Y MIEMBROS DE COMUNIDADES DE
RECOLECTORES DE RECURSOS FORESTALES**

TESIS

(POR ARTÍCULO CIENTÍFICO)

HUMAN FORAGERS: SEARCHERS BY NATURE AND EXPERIENCE

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

CÉSAR FRANCISCO MAYA BERNAL

TUTOR PRINCIPAL DE TESIS: DR. MARCOS FRANCISCO ROSETTI SCIUTTO

INSTITUTO DE INVESTIGACIONES BIOMÉDICAS, UNAM

COMITÉ TUTOR: DR. GABRIEL ROLDÁN ROLDÁN

FACULTAD DE MEDICINA, UNAM

DR. LUIS PACHECO COBOS

FACULTAD DE BIOLOGÍA-XALAPA, UNIVERSIDAD VERACRUZANA

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Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **30 de abril del 2018** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Biología Evolutiva** del (la) alumno(a) **MAYA BERNAL CESAR FRANCISCO** con número de cuenta **307172129** por la modalidad de graduación de **tesis por artículo científico**, titulado: **"HUMAN FORAGERS: SEARCHERS BY NATURE AND EXPERIENCE"**, que es producto del proyecto realizado en la maestría que lleva por título **"¿Buscadores por naturaleza? Comparación de la conducta de búsqueda en espacios abiertos de urbanitas y miembros de comunidades de recolectores de recursos forestales"**, ambos realizados bajo la dirección del **DR. MARCOS FRANCISCO ROSETTI SCIUTTO**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 19 de junio del 2018


DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA



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Resumen

Diversos estudios de la conducta de forrajeo en humanos han mostrado la existencia de estrategias conductuales y de toma de decisiones que probablemente evolucionaron como adaptaciones al forrajeo y a una división de labores entre sexos. No obstante, el rol de la información adquirida durante el forrajeo (i.e. el aprendizaje) no ha sido suficientemente explorado, a pesar de que probablemente juega un papel importante en el proceso de toma de decisiones. Usando una novedosa tarea de búsqueda experimental en espacios abiertos, en este estudio exploramos los efectos de tres fuentes de información del ambiente en el desempeño y toma de decisiones de los participantes: (i) información obtenida directamente al realizar la búsqueda, (ii) información obtenida previo a la búsqueda a manera de un fragmento sucinto de información, que tenía la intención de simular experimentalmente información acerca del ambiente adquirida culturalmente, y (iii) información obtenida de la experiencia real en la búsqueda y recolección de recursos forestales con fines económicos. Encontramos que (i) la experiencia inmediata de búsqueda resultó en una rápida mejora del desempeño del principio al final de la tarea, dentro de un periodo de 2 minutos, (ii) la información proporcionada a los participantes antes de la tarea les permitió mejorar su desempeño de manera considerable desde el principio de la tarea, y (iii) la experiencia real de forrajeo mejoró el desempeño en menor medida y principalmente para las mujeres. Adicionalmente, la más grande mejora en el desempeño que mostraron los participantes que fueron previstos de información se vio reflejada en un cambio en el comportamiento que denotaba la expectativa de recursos agrupados. Es por todo esto, que sugerimos que nuestros resultados proporcionan evidencia en favor de la idea de mecanismos heurísticos en la toma de decisión, que evolucionaron como adaptaciones humanas al forrajeo, y que permiten que la información ambiental sea rápidamente incorporada en la toma de decisiones.

Abstract

Diverse studies of human foraging behavior have revealed behavioral and decision-making strategies that may have evolved as adaptations for foraging and for an associated division of labor between the sexes. Nevertheless, the role of information acquired during foraging (i.e. learning) has not been sufficiently explored, even though it probably plays an important part in shaping decision-making. Using a novel outdoor experimental search task we explored the effect of three sources of environmental information on participants' performance and decision-making: (i) information obtained directly from performing a search, (ii) information obtained prior to testing in the form of a distilled snippet of knowledge intended to experimentally simulate information culturally acquired about the environment, and (iii) information obtained from real-life experience of foraging for forest resources for economic gain. We found that (i) immediate searching experience improved performance from the beginning to the end of the short, 2-minute task, (ii) information priming improved performance notably from the very beginning of the task, and (iii) real-life foraging experience improved performance to a lesser extent and predominantly in women. Furthermore, the larger improvement in performance shown by information-primed participants was evidenced by a change in behavior denoting the expectation of clumped resources. We suggest that our results provide further evidence for the idea that heuristic mechanisms have evolved as adaptations in humans for foraging, allowing environmental information to be rapidly incorporated into decision-making.

1. Introducción

1.1. Toma de decisiones

La conducta animal está conformada de manera importante por eventos de toma de decisión, donde los organismos enfrentan situaciones en las que más de una acción, o respuesta a su ambiente, es posible. Por ejemplo, los abejorros, se ha observado que durante la búsqueda de alimento enfrentan situaciones con múltiples opciones, como qué ruta tomar y a qué velocidad ir (Klein et al. 2017), si usar la información proveniente de conspecíficos o sólo la del ambiente (Baracchi et al. 2018), o qué tipo de flores forrajear entre múltiples tipos (Muth et al. 2015), por mencionar algunas. La toma de decisiones puede tomar muchas formas, en diversos aspectos de la vida de los organismos, desde la elección de refugio, de pareja, de presas, hasta la decisión de en qué momento detener la búsqueda de recursos. Sin embargo, todas tienen dos aspectos en común: 1) el potencial de afectar la supervivencia y reproducción del organismo (McFarland 1977), y 2) un contexto de incertidumbre, donde no hay un conocimiento completo del ambiente (Dall et al. 2005).

Ejemplos de cómo la toma de decisiones afecta la supervivencia y reproducción de los organismos (i.e. adecuación) se pueden encontrar en virtualmente todos los seres vivos (Davies et al. 2012; McFarland 1977). Decisiones en la elección del sitio de forrajeo (Sigaud et al. 2017), del sitio de oviposición (Wood et al. 2018), o la elección de pareja (Weidt et al. 2008), afectan la adecuación de los organismos en mayor o menor medida.

Dado que muchas decisiones que un organismo puede tomar tienen el potencial de afectar su adecuación, se ha teorizado que los mecanismos biológicos que subyacen la toma de decisiones han pasado por procesos de evolución por selección natural y por ende son resultado del proceso evolutivo (Barkow et al. 1995; Gigerenzer et al. 2011; Hutchinson and Gigerenzer 2005). En consecuencia, mucha de la investigación al respecto de la toma de decisiones se ha enfocado en encontrar las estrategias óptimas a las que los animales podrían llegar por medio del proceso evolutivo: por ejemplo en el forrajeo (Pyke

et al. 1977), la elección de la presa correcta (de Boer et al. 2002) o el tiempo de permanencia en un parche de recursos (Charnov 1976).

Sin embargo, estos estudios consideran organismos que ya han pasado por un proceso de desarrollo en un ambiente determinado. De manera que evalúan el resultado de los componentes biológicos de la conducta en interacción con el ambiente donde se desarrolló. Por lo cual, resulta importante distinguir los elementos de la conducta que son resultado de la interacción con el ambiente para tener una perspectiva más estructurada de la misma.

1.2 Importancia del ambiente

La toma de decisiones no es ajena al ambiente, sin embargo, los organismos que la realizan sólo cuentan con conocimiento limitado de su ambiente, esto es, realizan decisiones en condiciones de incertidumbre (Dall et al. 2005; Gigerenzer et al. 2011). Enseguida después del auge de estudios sobre la optimización de la toma de decisiones, varios autores han notado la ausencia de la experiencia y el aprendizaje en estos estudios, y han recalcaron que no puede ser obviada (Dall et al. 2005; Kaplan 1992; McNamara and Houston 1985; Stephens 2007).

El aprendizaje forma parte importante de la conducta animal, y su importancia es evidente al tener en cuenta que los ambientes son cambiantes en menor o mayor medida. En ocasiones, estos cambios suceden en escalas temporales en las que la selección natural no puede responder en tiempo, por lo que un cambio inmediato es requerido, y el aprendizaje juega un papel indispensable en la adaptación local temporal y espacial (Mery 2013). De esta manera el aprendizaje refleja la importancia que tiene el evaluar el ambiente en todo momento para adaptarse a él.

1.3 La aproximación heurística

En el estudio de la toma de decisiones ha habido muchas aproximaciones a la capacidad de realizar inferencias *racionales* por parte de los animales (Gigerenzer et al. 1999). Desde los que consideraban que los organismos son capaces de tomar decisiones óptimas como si tuvieran la información, el tiempo y las capacidades computacionales que se requieren

para calcular la opción óptima (conocida como *racionalidad ilimitada*), hasta aquellos que consideran que los organismos toman decisiones con información incompleta, tiempo y capacidades de procesamiento de información limitados, sólo *racionales* dentro de un ambiente (conocidas como *heurísticas*).

La aproximación heurística propone que los organismos cuentan con mecanismos de inferencia simples y eficientes que, si bien no son óptimos, son suficientemente buenos para adaptarse a la estructura de información del ambiente, y que pueden resultar en una ventaja adaptativa dentro de los límites de las posibilidades biológicas de conocimiento y capacidad de procesamiento de los organismos al ignorar parte de la información en la toma de decisiones (Gigerenzer et al. 1999; Gigerenzer and Gaissmaier 2011). Varios ejemplos de estos mecanismos heurísticos se han sugerido y apoyado experimentalmente (Gigerenzer et al. 2011). Estos mecanismos serían el resultado del proceso evolutivo, y a su vez podrían construirse a partir de heurísticas existentes a través del aprendizaje (Todd and Gigerenzer 2000).

Entonces, si los mecanismos de toma de decisión son el producto de un proceso evolutivo, en dicho escenario se esperaría que todos los miembros de una especie compartan estos mecanismos, teniendo en consideración la existencia de variación, como con cada carácter biológico. Estos elementos compartidos, en humanos, se conocen como *universalidades* (Barkow et al. 1995; Norenzayan and Heine 2005), y se han estudiado en múltiples elementos de la conducta (Kappeler and Silk 2010).

1.4 El forrajeo como modelo de estudio

El forrajeo, definido como la búsqueda y obtención de recursos necesarios para la supervivencia de un organismo, como alimento, pareja, refugio, etcétera, es un muy buen ejemplo donde existen varios elementos de toma de decisión cuyos resultados tienen repercusiones directas en la supervivencia y reproducción (Bell 1991). Existen muchos elementos del forrajeo que pueden y han sido estudiados, siendo los más representativos la elección de sitio, de presas, y decisión de cambiar de parche de recursos, además de que han sido estudiados en diversas especies (Morgan et al. 2010).

Estudios sobre forrajeo se han concentrado en la importancia que tienen para la adecuación de los organismos, y a partir de ello han desarrollado un marco sobre estudios de optimización de la toma de decisiones como resultado del proceso evolutivo. El ejemplo más claro es la teoría del forrajeo óptimo (Pyke et al. 1977).

Sin embargo, como se mencionó arriba, el aprendizaje tiene un papel muy importante en la toma de decisiones en el forrajeo, y para el caso particular de la especie humana esto resulta más evidente por el papel que tiene el aprendizaje social en la adaptación de la especie (Boyd et al. 2011). Los humanos, al encontrarse distribuidos de manera global, se enfrentan a un amplio rango de condiciones ambientales, muy distintas y que cambian en el tiempo, sin embargo, la clave de su éxito se ha señalado como el aprendizaje social y la cultura, la capacidad de adquirir y transmitir grandes cantidades de conocimientos sobre un ambiente local y temporal, que permiten adaptar la toma de decisiones (Boyd et al. 2011).

Para el caso particular de la toma de decisiones en el forrajeo, pocos trabajos existen que apunten a la existencia de mecanismos heurísticos. Uno de los principales enfoques al respecto es el conocido *hot hand effect*, que se refiere al efecto positivo de eventos recientes sobre decisiones posteriores (Burns 2004; Scheibehenne et al. 2011; Wilke and Barrett 2009), y que se fundamenta en la expectativa de una distribución agregada para eventos seriales en el espacio y/o tiempo (e.g. como una racha), con su respectiva respuesta conductual, que refleja una propiedad estadística de la distribución de muchos recursos en el ambiente (Taylor 1961). Diversos estudios al respecto han encontrado evidencia a favor de la existencia de este fenómeno (Kerster et al. 2016; Wilke et al. 2014), que podría encontrarse de manera universal y ser producto de la adaptación al forrajeo.

1.5 Objetivo

Este estudio lo desarrollamos con el objetivo de investigar la posible existencia de mecanismos de toma de decisiones *universales* en la conducta de búsqueda en humanos, así como investigar la importancia de la experiencia y el aprendizaje, a través de observación conductual en una tarea experimental de forrajeo.

2. Sobre el artículo.

Human foragers: Searchers by nature and experience

Enviado a la revista *Human Nature*.

2.1 Title page

Human foragers: searchers by nature and experience

César Maya^a, Marcos F. Rosetti^{a|}, Luis Pacheco-Cobos^b, Robyn Hudson^a

^aInstituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, Mexico City, Mexico

^bFacultad de Biología, Universidad Veracruzana, Xalapa, Veracruz, Mexico

Corresponding authors: Marcos F. Rosetti; *email addresses:* rosetti_m@yahoo.com

ORCID numbers

César Maya: 0000-0003-1279-498X; Marcos F. Rosetti: 0000-0002-4607-8984; Robyn Hudson: 0000-0002-5526-9555

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2.2 Abstract

Purpose: Diverse studies of human foraging behavior have revealed behavioral and decision-making strategies that may have evolved as adaptations for foraging and for an associated division of labor between the sexes. Here, we explore the role of information acquired during foraging in shaping decision-making.

Methods: Using a novel outdoor experimental search task we explored the effect of three sources of information on participants' performance and decision-making: (i) information obtained directly from performing a search, (ii) information obtained prior to testing in the form of a distilled snippet of knowledge intended to experimentally simulate information acquired culturally about the environment, and (iii) information obtained from real-life experience of foraging for natural resources for economic gain.

Results: We found that (i) immediate searching experience improved performance from the beginning to the end of the short, 2-minute task, (ii) information priming improved performance notably from the very beginning of the task, and (iii) real-life foraging experience improved performance to a lesser extent and predominantly in women.

Furthermore, the larger improvement in performance shown by information-primed participants was evidenced by a change in behavior denoting the expectation of clumped resources.

Conclusions: We suggest that our results provide further evidence for the idea that heuristic mechanisms have evolved as adaptations in humans for foraging, allowing environmental information to be rapidly incorporated into decision-making.

Keywords: Foraging behavior; Decision-making; Environmental information; Sex differences; Heuristics; Mexico

2.3 Introduction

Human foraging has been studied from a wide range of perspectives often considering an evolutionary viewpoint, yet remains a topic rich with questions regarding fundamental aspects of our behavior. Detailed descriptions of the foraging behavior of hunter-gatherer populations (Berbesque et al. 2016; Hill et al. 1987), as well as those of people living in rural contexts and relying importantly on gathering activities (de Boer et al. 2002; Lee and Brewis 2009; Pacheco-Cobos et al. 2010; Sosis 2002; Thomas 2007), have focused on the identification of behavioral patterns in natural contexts, recognizing the importance that environmental factors may have when evaluating these behaviors. Using a different approach, computer-based tests have been used to evaluate foraging in highly controlled situations, which provide the possibility of closely exploring aspects of foraging such as changes in the decision process (Hutchinson et al. 2008; Neave et al. 2005; Wolfe 2013; Zhang et al. 2015) or in the underlying cognitive mechanisms (De Lillo et al. 2014; Ehinger and Wolfe 2016; Krasnow et al. 2011). While such approaches have been essential in describing the cognitive patterns relevant to foraging, there is a limit in the extent to which these findings can be extrapolated to realistic situations. Thus, a third approach consisting in simulating natural environments aims to mimic the spatial characteristics of the environment in which foraging takes place (e.g. large open areas, caloric expense) while being able to manipulate variables experimentally (New et al. 2007; Rosetti et al. 2015; Smith et al. 2010). While these studies report patterns of foraging behavior consistent with those obtained from observations of hunter-gatherers, they can be far less demanding to conduct. In addition, computer-based tasks can be economical, but testing in realistic

situations provides richer behavioral descriptions than virtual set-ups. Indeed, differences in performance observed between virtual and realistic situations highlight the importance of the physical environment in shaping behavior, and thus the need to approach behavioral testing in experimental conditions using biologically relevant setups (Gilchrist et al. 2001; Rosetti et al. 2017). Despite the aforementioned differences between methodological approaches to the study of human foraging behavior, salient, consistent behavioral patterns have been found regarding theoretical models of searching (Constantino and Daw 2015; Thomas 2007; Wolfe 2013), sex differences in foraging strategies (Krasnow et al. 2011; Neave et al. 2005; Pacheco-Cobos et al. 2010; Rosetti et al. 2015; Silverman et al. 2007), and the decision-making underlying these patterns (Hutchinson et al. 2008; Wilke and Barrett 2009).

For humans, as for other animals, foraging success is strongly tied to decision-making and context. Animals' foraging bouts involve a range of decisions: when to start foraging, what to forage for, where, how, for how long, and so on (Bell 1991). Because of the impact that decision-making has on an animal's survival and reproduction, it is expected that evolution by natural selection has adapted decision processes to optimize the outcome (McFarland 1977), exemplified, for instance by the optimal foraging theory (for a review of its formulation see Pyke et al. 1977). However, as has been more recently emphasized, animals have to forage under constraints of time and limited information, probably applying a heuristic approach, that is, ecologically efficient decision mechanisms specifically adapted to exploit information in the environment that may result in an adaptive advantage (Gigerenzer et al. 1999). Following this approach, recent studies of

human foraging suggest that some of our decision processes may have evolved as adaptations to a foraging lifestyle, as the expectation of aggregated outcomes in sequences of events (Scheibehenne et al. 2011; Wilke and Barrett 2009), and are particularly tuned to detecting and using relevant environmental information (Zhang et al. 2015).

Adapted, ecologically rational behavioral responses are probably not only a direct consequence of evolution through natural selection, but can also arise indirectly through individual and social learning, as well as from the integration of simpler existing heuristic mechanisms into new, more complex ones (Todd and Gigerenzer 2000). Regarding human foraging behavior, research has focused particularly on the assumption of evolved behavioral adaptations for foraging in patchy environments (Wilke and Barrett 2009), and on the division of labor between sexes in hunter-gatherers (Silverman et al. 2007). However, many authors have noted the importance of gathering environmental information (i.e. learning) to achieve a successful outcome (Dall et al. 2005; Kolling and Akam 2017; McNamara and Houston 1985). This is of particular relevance in humans because social learning is considered an important form of human behavioral adaptation (Boyd et al. 2011), for instance, Koster and Venegas (2012) found that knowledge of prey choice among Arang Dak, in lowland Nicaragua, is due to social learning to the degree that less experienced hunters are familiar with the same information. Thus, human foraging behavior seems to be the result of the convergence of the operation of endogenous, evolved decision-making processes, the acquisition of environmental information through learning, and culturally transmitted knowledge. Dissecting out the influence of each of these could help us better understand how each shapes decision-making.

In this study we aimed to investigate how two elements of human foraging behavior (related to and presumably the result of evolved decision-making processes), namely searching success and associated decision-making, can be influenced by different conditions of acquiring environmental information. For this, we designed a large-scale search task that takes place in an outdoor arena and incorporates several of the physical constraints of searching in a patchy environment, while allowing us to control for the environmental information available to the searcher. In three experiments, we evaluated the effect of three forms of environmental information acquisition on searching performance and decision-making. We present and discuss the results in four sections. In the first three, we report the effect on performance of (i) information directly acquired while performing the search task, (ii) of information priming by the experimenter that was intended to simulate socially transmitted knowledge of the environment, and (iii) of information obtained from real-life experience of foraging for natural resources. Lastly, (iv) we compare the effect of the three forms of environmental information acquisition on decision-making during the search task.

2.4 General methods

2.4.1 Task setup

The task, modified from Rosetti et al. (2015), was designed to test the behavioral outcome of decision-making while searching in a patchy environment over a large outdoor area. We arranged a series of small, opaque cones (8 cm high, 7.5 cm diameter) over a flat cement area (basketball court, 15 m x 28 m), so as to form five patches of 30 cones each.

Each patch was made up of cones of the same color and each patch was colored differently to distinguish it as a distinct unit for searchers and experimenters. Each patch covered a circular area approximately 1.2 m in diameter. Within each patch, six golf balls were placed beneath the cones in a nearest neighbor fashion, close to each other (Fig. 1). The position of the cluster of balls in each patch was randomly determined and the same arrangement was used for all tests.

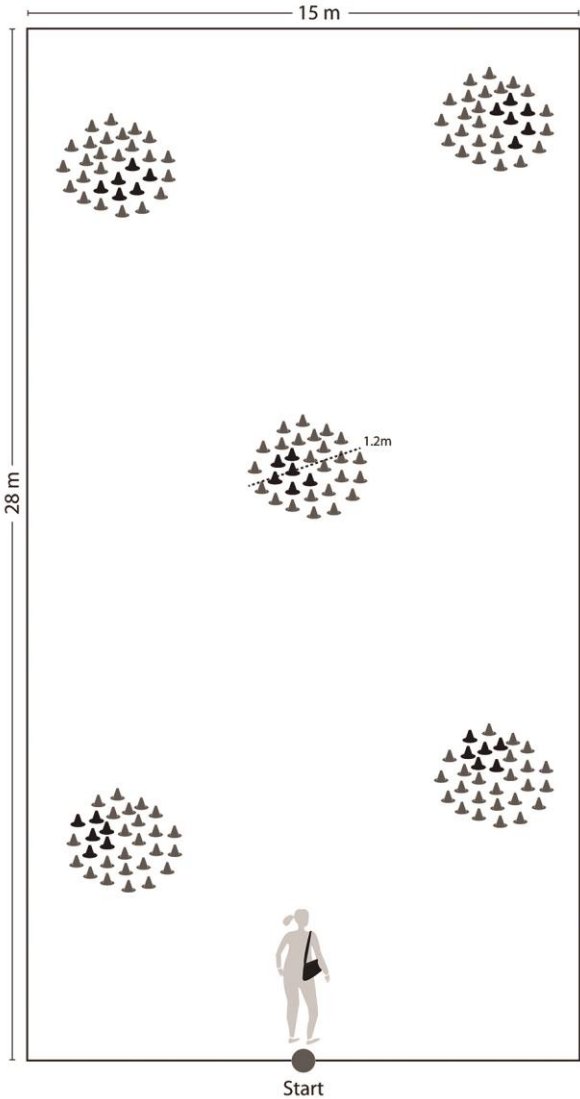


Fig. 1 Search arena. Arena dimensions and the spatial arrangement of each group of cones (patch) and hidden balls (black cones) are shown

2.4.2 Search task

Three experimental conditions were implemented using independent groups of participants. In all conditions there was a 2-minute time restriction, established in pilot tests, to limit the number of patches participants could visit, thereby forcing their decision to stay on or to leave a patch. Participants received a cloth bag in which to place any balls they found. They were instructed to locate as many balls as possible within 2 minutes, to avoid lifting simultaneously more than one cone, and to leave the cones upright. Additional instructions are described for each of the experiments below. Participants were fitted with a bike helmet with an attached GoPro wide-angle camera (Hero 4, Go Pro Inc, California, United States), allowing us to record the searching process from a first-person perspective and to code behavior with high resolution.

2.4.3 Questionnaire

After the search task, participants filled out a questionnaire in which we collected personal information (sex and age) and search experience (scored as had/did not have, frequency of visits to wild areas in search of natural resources, and motive). The questionnaire also included two questions probing participants' understanding of basic probability: 1) if you throw a die, (i) the chance of getting a two, and (ii) the chance of getting a six (scored as both correct/incorrect), and 2) choosing from a set of three diagrams

of cone patches the option that more closely resembled the pattern in which the balls were hidden in the actual test (see Fig.1 in supplementary material).

2.4.4 Ethics approval

This study was approved by the Internal Review Board for Research on Human Beings of the *Instituto de Investigaciones Biomédicas* at the *Universidad Nacional Autónoma de México*. Informed consent was obtained from participants before the start of testing.

2.4.5 Behavioral analysis

Videos from each trial were coded using *Behavioral Observation Research Interactive Software* (BORIS; Friard and Gamba 2016) into a sequence containing the time that each cone was lifted, that a ball was collected, and the time of arrival at and leaving a patch. From this, we calculated for each participant the number of patches visited, the number of cones lifted, the number of balls collected, and the time spent in each patch.

2.4.6 Statistical analysis

All descriptive statistics are given as means \pm SD. Comparisons between general descriptors of performance among conditions (i.e. number of collected balls, inspected cones and number of patches visited) were done using *t*-tests and effect sizes were calculated with Cohen's *d*.

In order to test specific hypotheses about performance, generalized linear and linear mixed models (GLMs and GLMMs, respectively) were fitted using R (version 3.3.2; R

Core Team 2016) and functions from the *lme4* package (Bates et al. 2015). Several models, addressing different hypothesis, were developed. First, to assess differences in general performance between conditions we performed a GLM to evaluate how the number of successes (cones lifted with a ball beneath) and the number of failures (cones lifted with no ball beneath) (binomial response variable) was influenced by the experimental condition, sex of participant, number of patches visited, and their interactions (fixed variables). Secondly, to evaluate the change in performance (response variables: successes and failures), in relation to the participants' progress through successive patches (fixed variable), we fitted GLMMs with participant ID as random variable and each condition as a different model. For this, we only considered the first five patches visited as less than 10% of participants re-visited patches. Thirdly, we developed GLMs to evaluate the relation between the results of the questionnaire and performance (response variables: successes and failures), accounting for the ability of participants to recognize the distribution pattern, previous experience of searching for natural resources, and practical knowledge of probability (fixed variables), each on one model and with its interaction with condition. We chose these response variables (i.e. successes and failures) rather than the collection rate (balls collected per number of cones lifted) as the response variables in a binomial model so as to consider the differential effort that may be concealed by the collection rate; e.g. lifting 30 cones and finding six balls has the same collection rate as lifting five cones and finding one ball (see participants' variation in execution in Fig.2 through 7 in supplementary material). In all cases significance was calculated using the *lmerTest* package (Kuznetsova

et al. 2017), and multiple comparisons were calculated using *multcomp* (Hothorn et al. 2016) and *lmeans* (Lenth 2017) packages.

2.5 Experiment 1: Effect of immediate experience on search performance

Studies of searching behavior have showed that humans can rapidly gather and implement novel environmental information regarding their performance (e.g. target location; Kerster et al. 2016; Smith et al. 2010), which is also the case for baboons when facing a novel environment (Marshall et al. 2013). Among the evolved adaptations to foraging that have been suggested to exist in humans, we can find positive recency, which is the expectation of clumped sequences in space or time (Burns 2004; Scheibehenne et al. 2011; Wilke and Barrett 2009). Thus, in a first baseline (BL) condition, we aimed to identify the effect of immediate experience on searching by investigating whether participants' performance improves as they move through successive patches.

2.5.1 Methods

Participants ($N = 71$, 49% men, mean age 20.99 years, SD 2.19) were recruited on a university campus in Mexico City, Mexico, and were directly invited to participate in the experiment. All were urbanites who reported little or no experience of searching for natural resources. For those reporting experience (42 %), this was at a frequency of about once a year and solely for recreational, not economic, purposes. They were tested in the setup described in Section 2, and were instructed to collect as many balls as possible within the two-minute test time but given no information as to the number or distribution of the balls.

2.5.2 Results and discussion

Participants appeared to be engaged by the searching task, rapidly lifting cones at a mean rate of 0.93, SD 0.26 per second. All participants visited more than half the total number of patches, with 66% of participants finding more than half the balls (i.e. 15; Table 1).

Table 1
General performance in the three searching conditions

Condition	Visited patches		Inspected cones		Collected balls	
	mean	SD	mean	SD	mean	SD
BL	4.46	1.08	87.97	22.29	16.54	5.05
INFO	4.44	0.85	72.49	17.98	19.79	4.83
EXP	4.60	1.13	87.73	30.84	18.16	6.97

Table 2
Summary of the generalized mixed model for the performance by patches
Performance ~ Patch + (1|Participant) in the three search conditions

Condition	Patch	Estimate	SE	z value	P*
BL	1	-1.589	0.074	-21.453	<0.001
	2	-1.460	0.094	1.361	0.173
	3	-1.359	0.094	2.433	0.015
	4	-1.365	0.104	2.134	0.032
	5	-1.263	0.138	2.360	0.018
INFO	1	-0.976	0.071	-13.739	<0.001
	2	-1.024	0.094	-0.513	0.607
	3	-0.879	0.094	1.030	0.303
	4	-0.947	0.099	0.294	0.769
	5	-0.627	0.139	2.505	0.012
EXP	1	-1.414	0.086	-16.304	<0.001
	2	-1.312	0.107	0.949	0.343
	3	-1.167	0.108	2.272	0.023
	4	-1.303	0.130	0.850	0.395
	5	-1.282	0.188	0.702	0.483

* Significance reflects the following comparisons: We compared mean correlation rate in the first patch to 0, and subsequently, we compared the mean correlation rate of patches two through five to the mean correlation rate of the first patch.

Performance improved as participants advanced from patch to patch, with performance by patch three being significantly greater than for patch one (Table 2). Performance was not significantly different for the number of patches visited, and no significant differences for sex were found (Table 3).

Table 3
Summary of the generalized model describing Performance ~ Condition:Sex + Visited Patches, and the multiple comparisons for each factor in the three search conditions.

	Estimate	SE	z value	P
<i>Condition, $\chi^2 = 117.71$ df = 2 p < 2e-16</i>				
BL – INFO	-0.488	0.045	-10.666	< 0.001
BL – EXP	-0.116	0.048	-2.393	0.044
INFO – EXP	0.371	0.048	7.633	< 0.001
<i>Visited patches, $\chi^2 = 0.88$ df = 1 p = 0.347</i>				
	0.019	0.020	0.941	0.346
<i>Sex, $\chi^2 = 3.60$ df = 1 p = 0.057</i>				
Men – Women	-0.083	0.039	-2.119	0.034
<i>Sex:Condition, $\chi^2 = 10.34$ df = 2 p = 0.005</i>				
BL				
M – W	-0.112	0.065	-1.715	0.086
INFO				
M – W	0.083	0.064	1.287	0.198
EXP				
M – W	-0.220	0.072	-3.042	0.002

Additionally, we found that participants who at the end of the test correctly identified the diagram showing the distribution that matched the pattern in which the balls were hidden had a higher performance than those who did not (GLMM: recognized vs. did not recognize, $\Delta b = 0.30$, $SE = 0.070$, $z = 4.248$, $p < 0.001$). When comparing participants according to their previous experience of foraging or their proficiency in probability, we did not observe a relation with searching performance.

Based on these results, we suggest that the behavior of the urbanites in this study may have reflected a capacity to rapidly detect distribution patterns. Participants significantly improved their performance as they advanced from patch to patch, reflecting their ability to rapidly gather relevant information as they advanced in the task, apparently learning statistical properties of the distribution of the balls (i.e. that they were arranged in clusters), as has been observed in other studies of target location (Geng and Behrmann 2002; Smith et al. 2010). This was supported by the better search performance of participants who at the end of the tests correctly identified the diagram corresponding to the actual arrangement of the balls.

2.6 Experiment 2: Effect of information priming on performance

Applying the information obtained while searching (e.g. slowing down when a local change in resource density is detected) is perhaps the most computationally simple form of behavioral reaction (Wajnberg et al. 2013). However, a much more dramatic form of information transmission that impacts foraging has to do with culture (Horner et al. 2006). For instance, Ladio and Lozada (2003) described how Mapuche groups still make use of culturally appreciated forest resources despite the high costs of long travel from the steppe, their actual place of residence. Similarly, Sosis (2002) describes how Ifaluk fishermen kept visiting far away patches with suboptimal returns instead of more optimal ones for reasons that could be considered to be culturally transmitted but were not further investigated. In order to test this rapid, accurate transmission of information, we developed a condition (INFO) in which participants were primed with a snippet of information prior to the test. Such priming was intended to simulate distilled and factual knowledge of the foraging

environment, with the aim of evaluating to what extent this form of information would modify performance of the task.

2.6.1 Methods

As in the previous BL condition, participants ($N = 67$, 46% men, mean age 21.46, SD 2.31 years) were recruited on the same university campus in Mexico City, Mexico, and were directly invited to participate in the experiment. Also as in BL, some participants (57%) reported to engage in recreational collection of natural resources approximately once a year. In addition to general instructions on the task, participants received the following snippet of information: “*If you find a ball, it is likely that there are other balls nearby*”.

2.6.2 Results and discussion

Participants lifted cones at a mean rate of 0.78, SD 0.21 per second. When compared to BL (Table 1), t tests revealed that participants in INFO visited a similar number of patches ($t(132.21) = 0.10, p = 0.918$), while inspecting significantly fewer cones ($t(132.82) = 4.50, p = 1e-05$, Cohen’s $d = 0.76$) but collecting more balls ($t(135.97) = -3.85, p < 0.001$, Cohen’s $d = 0.65$), suggesting a positive effect on searching of the information priming they had received. Compared to BL, performance in INFO was significantly better since the very first patch (Fig. 2). This performance did not change as participants advanced from patch one to patch four (Table 2). In addition, similar to BL, performance was not significantly different for the number of patches that participants visited nor between sexes (Table 3).

Furthermore, we found that participants who correctly identified the distribution that matched the pattern in which the balls were hidden showed a higher performance than those who did not (GLMM: recognized vs. did not recognize, $\Delta b = 0.21$, $SE = 0.085$, $z = 2.577$, $p = 0.009$). In addition, participants reporting previous foraging experience had a significantly higher performance (GLMM: experienced vs. inexperienced, $\Delta b = 0.167$, $SE = 0.065$, $z = 2.567$, $p = 0.010$). Proficiency in probability showed no relation to searching performance.

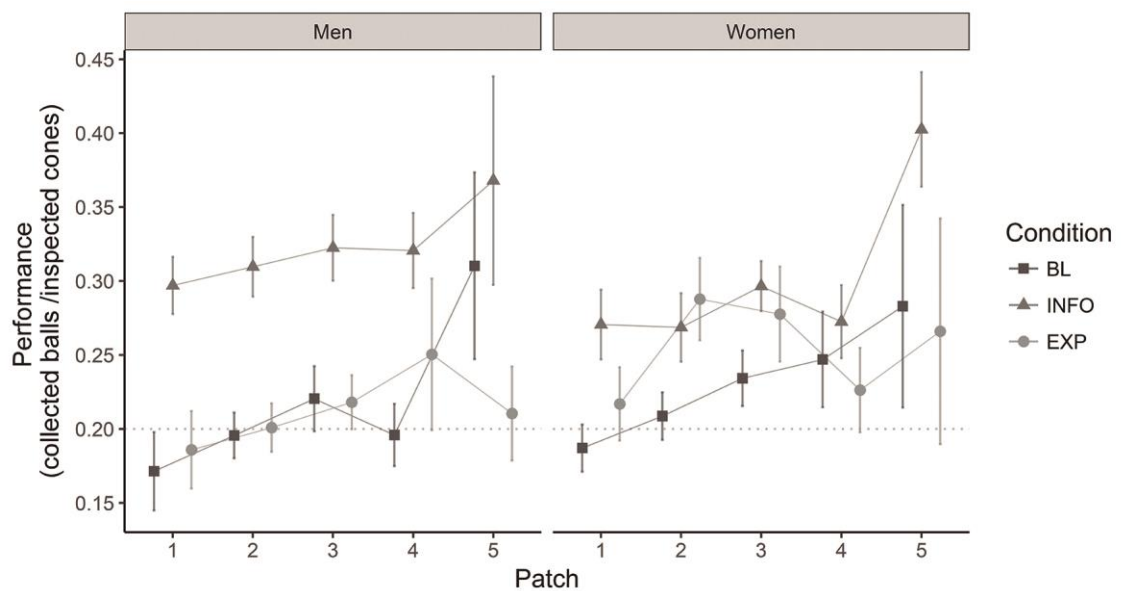


Fig. 2 Performance in the search task for each experimental condition and according to participants' sex. The dotted line at $y = 0.20$ represents the environment richness of each patch consisting in six balls each under one of 30 cones = 0.2. Patch number reflects the sequence in which patches were visited, not particular patches. BL = baseline condition, INFO = information condition, EXP = experienced foragers. Means \pm SE are shown

In INFO, we could observe the importance that even scanty knowledge of the distribution of resources had on the foraging performance of participants who had little to no experience in foraging for natural resources. We observed a clear improvement in performance from the very beginning of the search task compared to BL, which may not be surprising considering the importance of socially transmitted information in foraging (Koster et al. 2016; Koster and Venegas 2012; Scalise Sugiyama 2001). Additionally, although we did not observe an increase in performance as participants advanced from patch to patch, the value of the first patch was almost twice as large as that of the first patch in BL. This suggests information had a certain ceiling effect, rapidly reaching and maintaining high performance. In addition, we found that those who correctly identified the distribution of balls at the end of the test had a higher performance, showing that despite being primed some participants did not internalize the information snippet as well as others. A particularly tantalizing result was that those participants in INFO (but not in BL) who reported went on foraging trips (however infrequently), performed significantly better. This suggests that information might be better exploited by those with experience, turning information acquisition into decision-making.

2.7 Experiment 3: Effect of real-life foraging experience on performance

Lastly, information can also be obtained empirically, that is, acquired through repeatedly foraging in the same environment. For instance, Chipeniuk (1995) showed that foraging experience during childhood is a good predictor of the capacity to assess biodiversity, while Bock (2005) reports on how skill learning and strength are both relevant to children in order to become proficient foragers at each developmental stage.

Thus, we conducted a third experiment (EXP) in which the task was as in BL but where we tested participants with considerable real-life experience in searching for natural resources, hypothesizing that they might be able to apply their knowledge when evaluated in the searching task.

2.7.1 Methods

Participants were university students from a mountainous rural region neighboring the municipality of Zongolica, in the state of Veracruz, Mexico, who reported undertaking weekly foraging trips in search of natural resources of economic relevance (mainly firewood, coffee, fungi, or edible and medicinal plants), and thus substantially greater than that reported by the urbanites tested in BL and INFO. Previous research in the area has focused on ethnobiological reports on the collection and use of forest resources of economic relevance (Escamilla-Prado et al. 2012; Weimann and Heinrich 1998)(insects, medicinal plants, coffee). We directly invited participants ($N = 53$, 47% men, mean age 20.85, SD 1.89 years) to take part in the experiment while visiting their university campus. The experimental procedure was the same as for Experiment 1 (BL).

2.7.2 Results and discussion

Participants lifted cones at a mean rate of 0.91, SD 0.31 per second. Their execution of the task, as shown by t tests, was similar to the participants in BL (Table 1): they visited a similar number of patches ($t(109.20) = -0.68, p = 0.491$), lifted a similar number of cones ($t(90.28) = 0.04, p = 0.962$) and collected a similar number of balls ($t(90.42) = -1.43, p = 0.155$). Performance by patch three was significantly greater than that of patch one (Table

2). Moreover, in this condition, the difference between sexes was significant, women had a higher performance than men (Table 3), and when considering sex between conditions, only women in EXP differed from BL (GLM: BL vs. EXP, $\Delta b = -0.17$, $SE = 0.067$, $z = -2.545$, $p = 0.029$).

Again, we found that participants who correctly identified the pattern in which the balls were hidden had a higher collection rate than those who did not (GLMM: recognized vs. did not recognize, $\Delta b = 0.25$, $SE = 0.084$, $z = 3.048$, $p = 0.002$). Proficiency in probability showed no relation to searching performance.

These results suggest that previous experience with foraging for natural resources may improve foraging performance in a novel experimental environment, but only to a limited extent. Compared to participants in BL, those in EXP had a significantly higher performance but only for women. Previous experience in foraging has been associated with a stronger expectation of clumped resources, as Wilke and Barrett (2009) found when testing the expectation of aggregation in sequences of events (i.e. positive recency) among Shuar hunter-horticulturalists and undergraduate students (encounter of fruits and coin tosses). In our study, participants' previous experience might explain the somewhat better performance observed in EXP compared to BL (Table 3).

The unexpectedly large disparity in performance between EXP and INFO conditions (INFO > EXP; Fig. 2) may reflect the nonspecific foraging experience that the EXP participants in this study reported in the questionnaire, ranging from forest environments to crop fields. The task presented here was inspired by our observations of

foraging for fungi by rural Mexicans (Pacheco-Cobos et al. 2010), but other types of resources could have very different patterns of distribution and/or degrees of conspicuity or clumping (cf. Rosetti et al. 2010). For example, firewood (often collected from fallen trees) is usually rather conspicuous and once a patch is located, its large abundance may not require intensive searching, whereas looking for harvestable vegetables in crop fields must be performed by systematically walking along the furrows in order to avoid damaging unharvested plants.

We also found that women outperformed men in the searching task. This suggests that while both sexes may engage in an equal amount of foraging, women's searching strategies (i.e. more conservative, see Pacheco-Cobos et al. 2010) may result in a better capture of information about the nature of resource distribution which they may in turn be able to translate to a novel task such as the present one. Sex differences in search strategy are further discussed in the next section. It may also be noted that participants without foraging experience (BL) quickly performed equally well as EXP. When comparing conditions by patch, significant differences between BL and EXP disappear and their estimated differences decrease from 0.19 in patch 1 to 0.02 in patch 5; see Table 1 in supplementary material). Thus, even though previous experience is important for foraging performance because of the information acquired, when faced with a novel environment women may have a slight advantage.

Again, probability proficiency was unrelated to performance, suggesting that foraging decisions, as with many other heuristic processes, do not require an explicit

understanding of probability (Gigerenzer et al. 1999). Further studies should help corroborate and identify what type of experience and how much is sufficient to modify heuristic mechanisms underlying foraging in humans.

2.8 Effects of information acquisition on decision-making

Elements underlying a foraging outcome include an animal's decision-making (Bell, 1991). Because animals have to perform under time constraints and with limited information, it has been suggested that they have heuristic decision mechanisms that are specifically adapted to exploit the information in the environment available to them (Gigerenzer et al., 1999). One example of this is positive recency, or the expectation of clumped resources in space or time (Burns, 2004). In this sense, while heuristic mechanisms may be shaped by natural selection they can be calibrated by environmental information. For instance, Wilke and Barret (2009) found that knowledge of independent events may weaken the expectation of positive recency. Thus, by combining the observations of performance in the three experimental conditions described above, we aimed to investigate how the different forms of information acquisition shaped participants' decision-making.

2.8.1 Methods

For this, we re-analyzed the choice made by the searchers after lifting each cone by dichotomizing their subsequent choice of cone as one nearby or one further away (Fig. 3a). We hypothesized that improvement in performance across patches as a result of receiving information from the experimenter or derived from foraging experience would be reflected

in a change in searching strategy, going from systematic lifting of cones so as to deplete a patch (Fig. 3b) to lifting cones clearly aimed at locating and collecting the items clumped within the patch (Fig. 3c). In order to code searching strategy, we used a dichotomous distance categorization for each cone to the following one: nearest-neighbor cones (1C) and more than one cone away (2C+; Figure 3a). For each participants' searched patch, we calculated the *proportion of 1C moves after inspecting an empty cone* (PXC) and the *proportion of 1C moves after collecting a ball* (PXB). From these, we obtained the change in proportion of 1C moves (*change after collection*), calculated as the difference between PXB minus PXC, which allows us to identify searching strategies: a depleting systematic strategy, that shows no difference between PXB and PXC (*change after collection* ≈ 0), a strategy aimed at locating and collecting clumped resources, that has a PXB higher than its PXC (*change after collection* > 0), and the opposite strategy aimed at locating and collecting dispersed resources, that has a PXB lower than its PXC (*change after collection* < 0).

Following the statistical criteria described in Section 2.6, we fitted GLMMs to assess decision-making. We tested how the change in participants' decisions from picking up an empty cone (PXC) to finding a ball (PXB) (*change after collection*; fixed variable) influenced the number of successes and failures in each patch (response variables), considering participants' ID as a random variable. We also fitted a LMM to evaluate the possible relation of condition, sex, recognition of the distribution pattern, and its interactions (fixed variables) on decision making (*change after collection*, response

variables), as suggested by differences in performance discussed above, considering as random variable participants' ID.

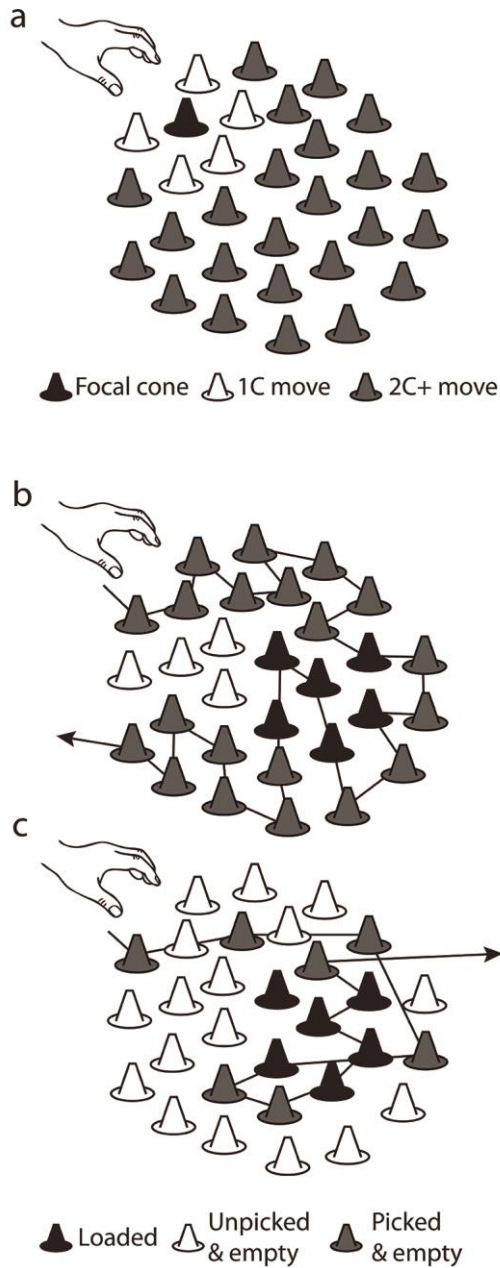


Fig. 3 Search decisions within patches. (a) Categorization of search decisions within patches from one (focal) cone to the next cone lifted as either a nearest (1C move) or distant (2C+) cone. (b, c) Hypothetical difference in participants' decisions to lift cones in patches when they lack information (b), or when they have information (c), either recently acquired, via information priming, or from real-life foraging

2.8.2 Results and discussion

The change in proportion of 1C moves after collecting a ball (*change after collection* = PXB - PXC) was a significant predictor of performance in the task ($b = 0.740$, $SE = 0.09$, $z = 8.2$, $p < 0.001$). The positive relation between *change after collection* and performance indicates that participants who often picked distant cones (i.e. 2C+ moves) after empty ones and switched to near cones (i.e. 1C moves) after collections did better in the task, because it paid to search close when finding a ball in this patchy environment (cf. Fig. 3c).

Table 4
Summary of the generalized mixed model describing
Change after collection ~ Condition:Sex + Condition:Recognition + Sex:Recognition +
(1|ID),
and the multiple comparisons for each factor.

	Estimate	SE	t value	p
Condition, $\chi^2 = 39.96$ df = 2 p < 0.001				
BL – INFO	-0.226	0.036	-6.258	< 0.001
BL – EXP	-0.080	0.035	-2.258	0.064
INFO – EXP	0.146	0.039	3.673	< 0.001
Sex, $\chi^2 = 7.59$ df = 1 p = 0.005				
Men – Women	-0.076	0.030	-2.528	0.012
Recognition, $\chi^2 = 16.49$ df = 1 p < 0.001				
No – Yes	-0.110	0.030	-3.650	< 0.001
Sex:Condition, $\chi^2 = 5.78$ df = 2 p = 0.055				
BL: M – W	-0.128	0.043	-2.942	0.003
INFO: M – W	0.011	0.048	0.231	0.818
EXP: M – W	-0.110	0.052	-2.100	0.037
Recognition:Condition, $\chi^2 = 2.84$ df = 2 p = 0.241				
BL: No – Yes	-0.175	0.045	-3.890	< 0.001
INFO: No – Yes	-0.057	0.056	-1.024	0.307
EXP: No – Yes	-0.099	0.056	-1.763	0.079
Recognition:Sex, $\chi^2 = 0.01$ df = 1 p = 0.909				
Men: No – Yes	-0.114	0.043	-2.616	0.009
Women: No – Yes	-0.107	0.041	-2.560	0.011

We set out with the intent of evaluating whether detecting a ball would trigger a behavioral response evidencing the expectation of clumped resources. We found that positive recency increased in men and women in INFO, and to a lesser degree in women in BL and EXP (Fig. 4a, Table 4). Remarkably, men in BL and EXP showed in fact a negative recency after collections, that is, an expectation of resources more distantly distributed. In addition, we observed that experience in foraging (EXP) slightly increased positive recency in women and decreased negative recency in men. Finally, we found a similar increment in negative recency in both BL and EXP for subjects who did not recognize the pattern (Fig. 4b).

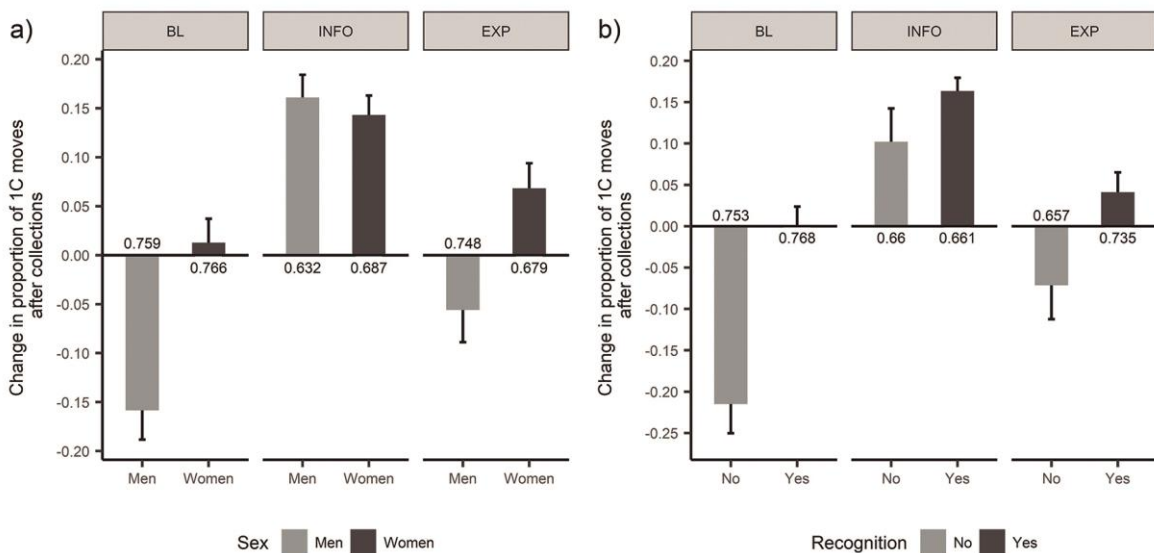


Fig. 4 Change in the proportion of 1C moves after collection (PXB – PXC, see text for interpretation) by (a) sex and condition, and (b) recognition of the distribution pattern of balls and condition. Proportions of 1C moves after empty cones (PXC) are shown near zero value with the intention to state the reference point for the change in each group

Studies where women show better object location memory (Neave et al., 2005; New et al., 2007) or men better three-dimensional mental rotation (Silverman et al., 2007), have often been used to support the notion that division of labor was conducive to sex differences in spatial abilities. While in this work we did not evaluate spatial abilities, we did find a difference in how spatial information impacted on decision making. The tendency for men to show negative recency may be linked to differential foraging strategies. Women may choose to focus on more stable strategies and thus opting for positive recency even when lacking information, while men may choose riskier strategies and thus opt for negative recency. Since the distribution was always patchy, women's strategy did indeed pay off with them getting better scores in EXP and marginally in BL. This could be in fact experimentally tested in the future using our test, combining patches of cones with clustered and dispersed targets. This finding is similar to the results of the study by Krasnow et al. (2011), where they observed a female advantage for gathering-specific location memory although men, when motivated, could improve their location memory. Since we found this in BL and EXP, sex differences in foraging heuristics may be deeply rooted in our hunter-gatherer evolutionary past and thus might be universals (Norenzayan & Heine, 2005).

Differently to BL and EXP, in INFO we observed an increase in positive recency for both men and women. Even though the information priming was brief and unspecific (only giving a general idea of the clumped distribution of balls and not the number of balls or the distance between them), the implementation of this information into decision-making by participants was immediate and observable in the increase in collection rate from the

very first patch visited, reflecting a readiness, and even by humans inexperienced in foraging, to implement ecologically relevant information into their searching strategies. In this sense, the information snippet that we provided did influence the heuristic decision-making, thus raising questions as to what type of information or how much information may positively modify foraging decisions. Moreover, we found that information priming not only modified participants' searching strategy but did so in a similar manner for men and women. Thus, having reliable information may create a ceiling effect in decision making and masking differences in strategy between the sexes. A similar conclusion was reached in a study of chacma baboons, where personality-dependent decisions were present only when information cues were unreliable (Carter, Marshall, Heinsohn, & Cowlshaw, 2013).

Together, the results of the three experimental conditions presented here support the existence of basic, possibly universal, heuristic mechanisms underlying foraging behavior that quickly incorporate environmental information, whether this comes from directly transmitted knowledge (INFO), through interaction with the environment throughout life (EXP), or while experiencing a novel searching environment (BL).

2.9 General discussion

From the experimental conditions implemented in this study, we aimed to evaluate the influence of three forms of experience in searching performance and decision-making: (i) In BL, we intended to evaluate the searching behavior of urbanites, who had little to no experience of foraging for natural resources and were faced with a novel searching

environment where they could only gather information during a brief search. (ii) In INFO, we intended to simulate the effect of culturally transmitted knowledge by supplying a small snippet of information about resource distribution (in this case, patchiness) on searching behavior of urbanites. And (iii) in EXP, we intended to evaluate the possible role of real-life foraging experience on the searching behavior of regular foragers, who were faced with a novel searching environment with a resource distribution intended to simulate that found in nature for some resources (Taylor, 1961), and where they had the possibility to translate their experience to the new experimental environment. For each of these aims we found empirical support derived from participants' performance as well as their responses to the questionnaire.

Regarding the experimental search task, we consider that its current configuration, which involved a large open area and greater energetic cost to participants than is usual in most laboratory settings (cf. Rosetti et al., 2017), shows potential for further studies of human foraging behavior and decision-making. This task involves a low cost, easily implemented setup, which can be mounted in almost any location, as we were able to do in two distant urban and rural regions. This task can also be readily modified to experimentally explore a variety of questions relating to human foraging behavior; e.g. including monetary rewards to explore the influence of motivation, modifying time limits to explore the effect of time constraints, using different forms of information priming, modifying patch and resource distribution and quality, and so on. Similar searching tasks have been used to explore decision-making involving potential cognitive dysfunction associated with psychiatric psychopathology (Pellicano et al., 2011; Rosetti et al., 2016).

This opens a range of possibilities to explore human foraging behavior hypotheses, from evolutionary, ecological, cognitive, and even psychopathological points of view.

In conclusion, we implemented a novel searching task that allowed us to explore the role of experience in searching performance and decision-making in a simulated foraging context. Immediate experience during the search was rapidly incorporated into the searching behavior of human participants with little to no experience of foraging for natural resources to improve their performance. Even minimal information priming about the pattern of resource distribution effectively modified decision making of the participants, tuning their decisions to the expectation of clumped resources, almost immediately improving their performance. And foraging experience of diverse natural resources, we suggest, slightly tunes heuristic information-gathering and implementation into decision-making, better adapting humans to foraging. Additionally, this searching task proved useful by providing a more realistic, yet experimental, method with which to approach the study of the effect of several variables on the decision-making mechanisms involved in human searching behavior, thereby hopefully contributing to an increased understanding of the cognitive processes underpinning such a central aspect of human behavior.

2.10 Compliance with Ethical Standards

All authors declare that they have no conflict of interest. All procedures performed here were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable

ethical standards. Informed consent was obtained from all individual participants included in the study.

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3. Discusión

3.1. Adaptación de la toma de decisiones

Debido a la importancia que tiene la obtención de alimento, pareja u otros recursos en la adecuación de los organismos, es de esperar que estos cuenten con adaptaciones específicas a sus condiciones de forrajeo. Existen ejemplos de adaptaciones morfológicas y fisiológicas al forrajeo (Raubenheimer 2010), pero el estudio de adaptaciones conductuales es igualmente importante (Bell 1991). Ejemplo de posibles adaptaciones al forrajeo en humanos son el efecto de expectativa de eventos agregados (i.e. el *hot hand effect*), que se ha sugerido como un mecanismo de toma de decisión que resulta favorable en la búsqueda de recursos que tienen una distribución agregada (Scheibehenne et al. 2011; Wilke and Barrett 2009), o las diferencias entre sexos en las habilidades espaciales y la memoria de localización (Neave et al. 2005; New et al. 2007; Silverman et al. 2007), que se ha propuesto son el producto de nuestra evolución reciente como cazadores-recolectores, donde hubo una división de labores entre sexos que a su vez dio lugar a una especialización a tareas de forrajeo. Otro patrón de diferencias entre sexos encontrados en la conducta de búsqueda hace referencia a las trayectorias de búsqueda (Pacheco-Cobos et al. 2010; Rosetti et al. 2015), donde los hombres recorren trayectorias más largas para encontrar la misma cantidad de recursos que las mujeres.

Nuestro estudio replica algunos de estos hallazgos, como la expectativa de distribuciones agrupadas de los recursos o la diferencia entre sexos en las decisiones de búsqueda. Y de manera específica, se suma con la observación de diferencias entre sexos en el grado de agrupación que se espera en la distribución de los recursos (i.e. movimientos dentro de los parches en las condiciones BL y EXP del estudio), lo cual es acorde con lo que sugieren Pacheco-Cobos et al. (2010) respecto a diferencias en las decisiones de búsqueda entre sexos, apuntando a un posible origen en la división de labores.

3.1.1. El papel de la evolución: Cazadores-recolectores

El ambiente que se piensa ha tenido mayor influencia en la evolución de las adaptaciones cognitivas presentes actualmente en la especie humana (i.e. *tool box* cognitivo), ha sido el

pleistoceno, periodo en el que existimos como cazadores-recolectores (Capriles et al. 2016; Pawlik et al. 2014), ya que los cambios ambientales que hemos enfrentado en los últimos 12 a 10 mil años a partir de la domesticación de especies de plantas y animales es muy reciente en nuestra historia evolutiva (Gowdy and Krall 2014). Durante el pleistoceno, se sugiere, se desarrollaron nuestras adaptaciones específicas a ese estilo de vida, particularmente la división de labores y la especialización en distintas tareas, por un lado las mujeres desarrollando características para una recolección más eficiente, mientras que los hombres, por otro lado, para ser mejores cazadores (Lombardo and Deaner 2018; Silverman et al. 2007). Sin embargo, a pesar de estas posibles adaptaciones morfológicas y conductuales al forrajeo, unas de las principales adaptaciones humanas, que se considera son las responsables del éxito de la especie, son el aprendizaje social y la acumulación de la cultura (Boyd et al. 2011), lo cual nos permite adquirir y transmitir conocimiento entre conspecíficos, de generación en generación o entre pares, acumulando conocimiento y experiencia a través de generaciones. Por lo que resulta un elemento del aprendizaje que no puede ser descartado cuando se estudia el forrajeo en humanos.

3.1.2. El papel del desarrollo y la información: El caso de la cultura

Investigaciones sobre el forrajeo en humanos han hecho hincapié en el desarrollo de las habilidades físicas y cognitivas requeridas para dicha actividad en poblaciones de cazadores recolectores (Bock 2005; Lew-Levy et al. 2017). Estas habilidades de forrajeo, adaptadas a ambientes particulares, se adquieren gracias a la experiencia y a la transmisión cultural. En este sentido, los resultados de nuestro estudio sugieren que los humanos tenemos la capacidad de implementar un pequeño fragmento de información del ambiente transmitida socialmente (i.e. el patrón de distribución del recurso buscado, condición experimental INFO), de manera inmediata, y aplicarlo con efectos favorables en la conducta de búsqueda desde el primer momento. Este hallazgo apunta a la importancia que la información transmitida de manera cultural tiene para el forrajeo en humanos. No obstante, preguntas como *¿qué otro tipo de información, además de la distribución espacial del recurso buscado, puede tomar una persona de su ambiente para favorecer su*

desempeño? y *¿qué elementos de su toma de decisiones durante el forrajeo, si alguno, no pueden ser modificados?* quedan en gran medida abiertas a investigación. Así mismo, en el presente estudio observamos diferencias entre hombres y mujeres en las decisiones de búsqueda dentro de los parches, que eran anuladas cuando los sujetos contaban con información (i.e. condición INFO). Por lo cual, al investigar la existencia de mecanismos de toma de decisiones *universales* en la conducta de búsqueda en humanos, se debe tener en cuenta que, de existir, estos pueden ser hasta cierto grado sensibles a componentes de información, experiencia y aprendizaje, como parte de su naturaleza misma (Norenzayan and Heine 2005).

3.2. La existencia de universalidades en el forrajeo

Si bien el concepto de *universalidades* goza de reconocimiento y tiene fundamentos evolutivos (Kappeler and Silk 2010), es importante considerar que es un concepto difícil de demostrar, principalmente por limitaciones metodológicas (siendo una importante el hecho de que todos los seres humanos pasan por un proceso de culturalización particular). Por ello, se ha sugerido que existen diferentes tipos de *universalidades* (Norenzayan and Heine 2005) con base en el grado de accesibilidad con la que se pueden usar por todos los individuos, la herramienta cognitiva utilizada, y la función, puesto que puede cambiar su función dependiendo de la población, o una misma función puede ser realizada con diferentes herramientas. El *hot hand effect* podría ser una universalidad, probablemente producto de la historia evolutiva. La diferencia entre sexos en habilidades cognitivas y estrategias de búsqueda podrían así mismo ser parte de adaptaciones al forrajeo. Sin embargo, dada la gran importancia que tiene la culturalización en la especie humana, no podemos descartar con certeza que nuestros resultados de diferencias entre sexos no se traten de un producto de las diferencias culturales presentes entre los sexos en las sociedades occidentales donde se han realizado estos estudios. Aunque, consideramos que la probabilidad de que sea universal es factible, y podría ser posteriormente corroborada controlando con diferencias culturales mayores.

4. Conclusiones

En este estudio abordamos la búsqueda de patrones conductuales que apuntaran a la existencia de mecanismos de tomas de decisión heurísticos y universales en la especie humana. Usamos una aproximación experimental, con tres condiciones, 1) de adquisición y uso de información del ambiente de manera directa, 2) de adquisición de información del ambiente a manera de transmisión cultural y 3) de experiencia en forrajeo de recursos forestales. En estas, evaluamos el papel de tres formas de adquisición de experiencia en la toma de decisiones, mientras que de manera simultánea buscamos patrones conductuales que apuntaran a universalidades en la misma. Gracias a la capacidad de observación de la prueba que desarrollamos, observamos la importancia que tiene la información del ambiente para el desempeño y la toma de decisiones, así como los diferentes efectos que tienen diferentes fuentes de información, y concluimos que los humanos tenemos la capacidad inmediata para procesar e implementar determinada información ambiental obtenida por diferentes medios (e.g. como los patrones de distribución de los recursos), de manera favorable, dentro de un ambiente de búsqueda, siendo la transmisión cultural la que tuvo el efecto más marcado e inmediato, en contraste con la información adquirida a través de la experiencia pasada e inmediata, que igualmente tuvo un efecto positivo pero menos marcado. Así mismo, concluimos que, de ser mecanismos universales, las diferencias entre sexos en las decisiones de búsqueda pueden pasar a segundo plano si la información del ambiente así lo precisa, permitiendo una mejor adaptación a la búsqueda dentro de un ambiente local.

La toma de decisiones dentro de la conducta de forrajeo tiene repercusiones directas en la supervivencia y reproducción de los organismos, por lo que se espera una adaptación precisa al ambiente. Esta adaptación es hasta cierto grado posible gracias a mecanismos de inferencia que son producto de la evolución (i.e. *heurísticas*), mientras que su ejecución puede ganar precisión gracias a la plasticidad que representa el aprendizaje, que también es resultado del proceso evolutivo. Nuestro estudio contribuye a conocer la injerencia de distintas formas de información, resultados de la experiencia y el aprendizaje, sobre los mecanismos heurísticos de toma de decisiones.

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2.15. Supplementary material

Human foragers: Searchers by nature and experience

Human Nature

César Maya^a, Marcos F. Rosetti^a, Luis Pacheco-Cobos^b, Robyn Hudson^a

^aInstituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, Mexico City, Mexico

^bFacultad de Biología, Universidad Veracruzana, Xalapa, Veracruz, Mexico

Corresponding authors: César Maya, Marcos F. Rosetti; email addresses: cpaco_cir@hotmail.com; rosetti_m@yahoo.com



Fig. 1 Diagrams of the three possible distribution of the balls within the patches that were presented to participants as part of the questionnaire. Order of presentation was balanced across participants

BL data for men

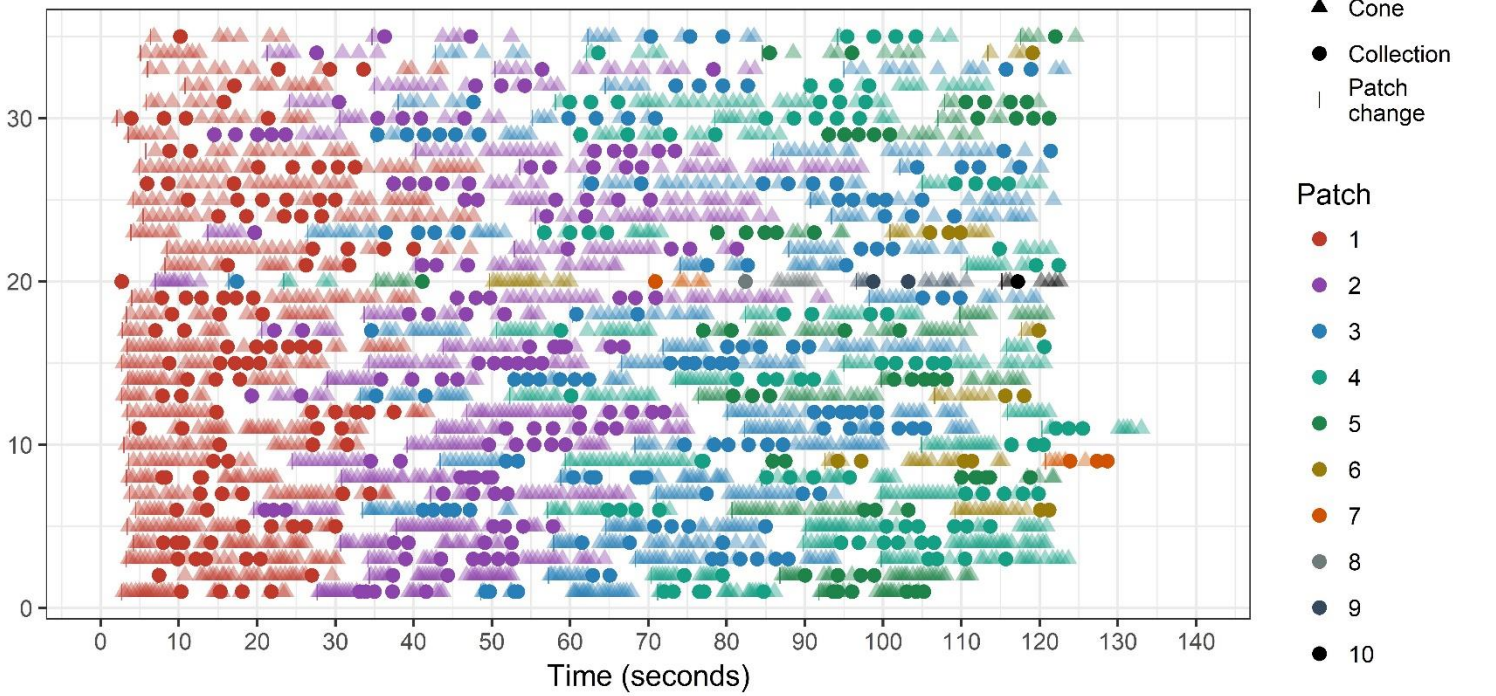


Fig. 2 Detailed performance of men in BL. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

BL data for women

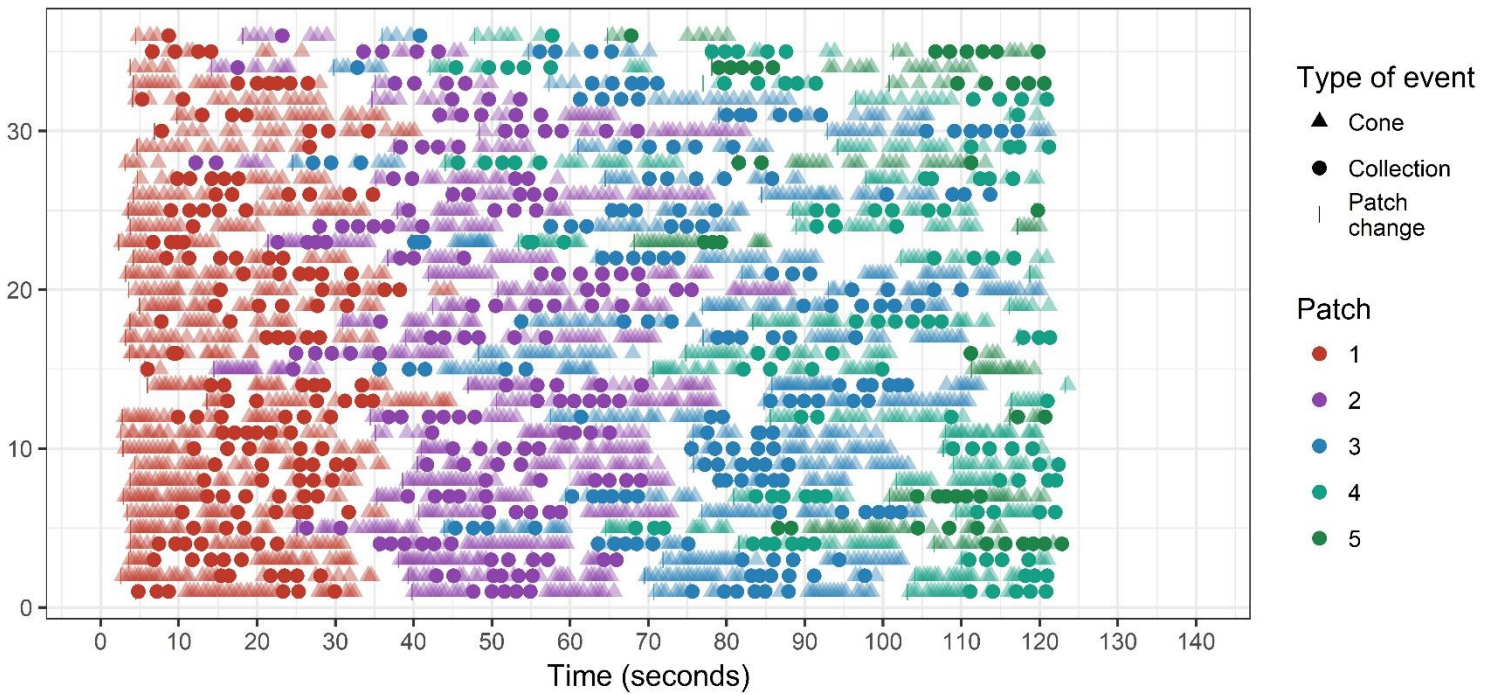


Fig. 3 Detailed performance of women in BL. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

INFO data for men

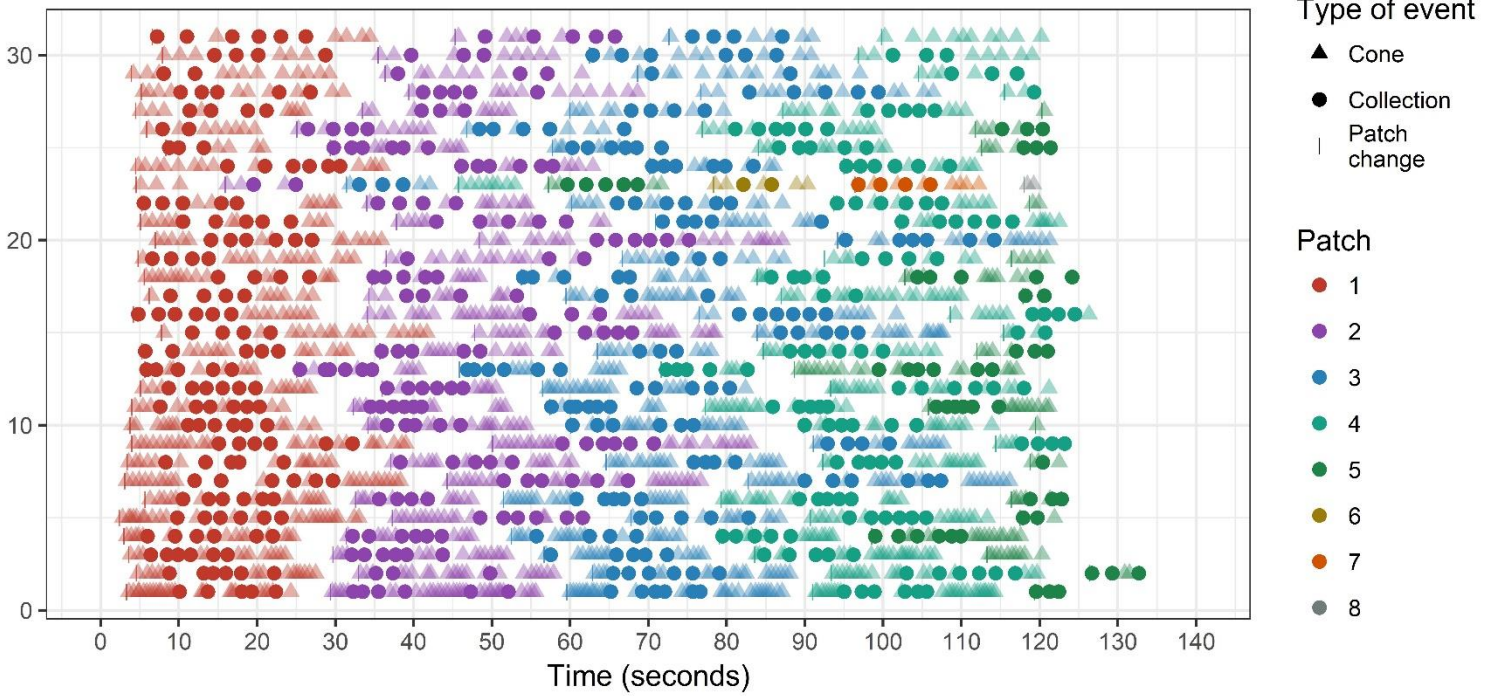


Fig. 4 Detailed performance of men in INFO. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

INFO data for women

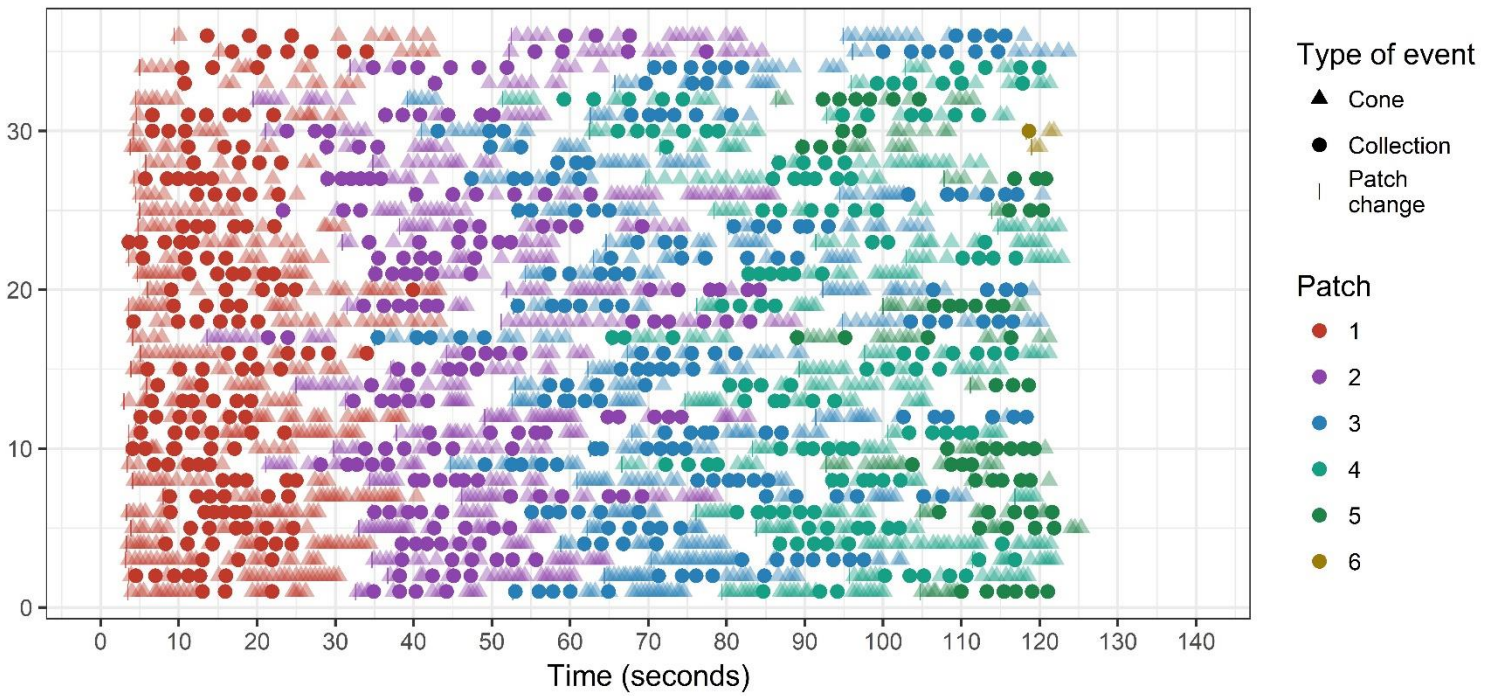


Fig. 5 Detailed performance of women in INFO. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

EXP data for men

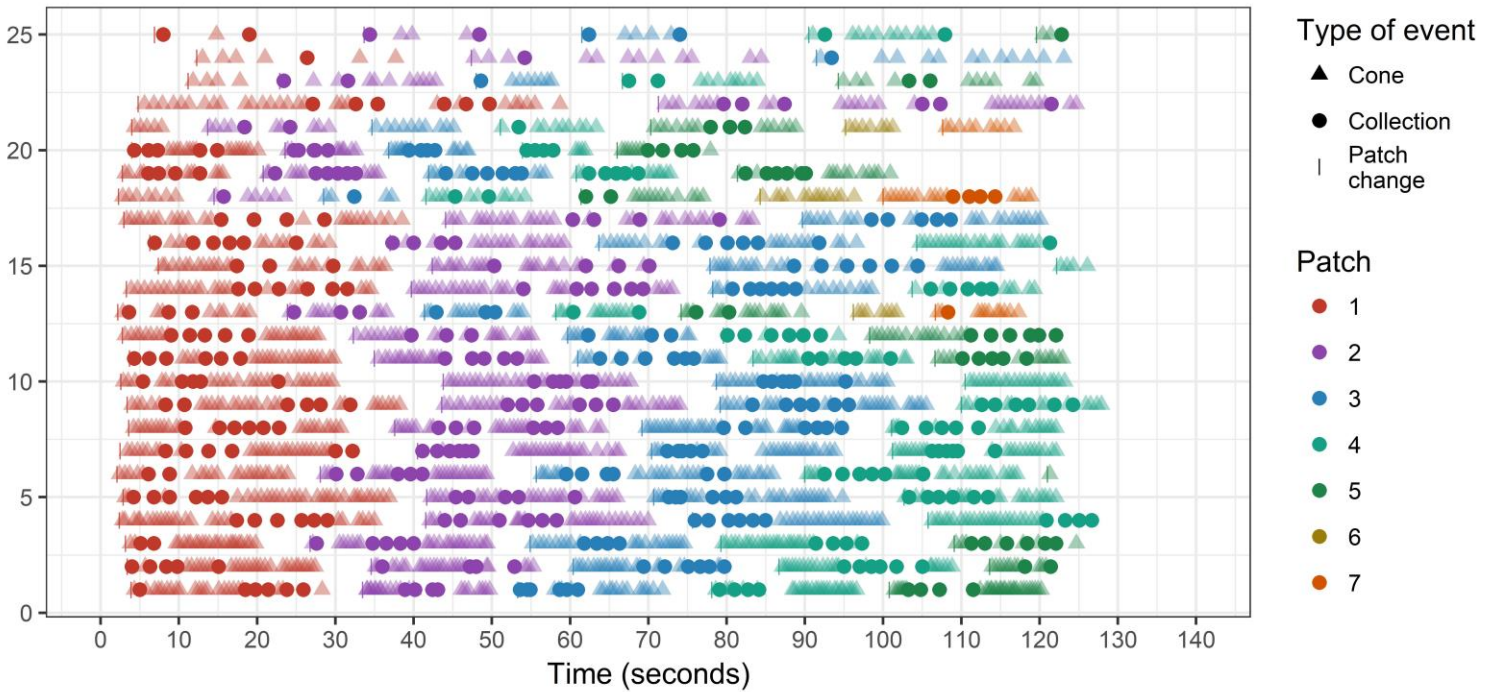


Fig. 6 Detailed performance of men in EXP. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

EXP data for women

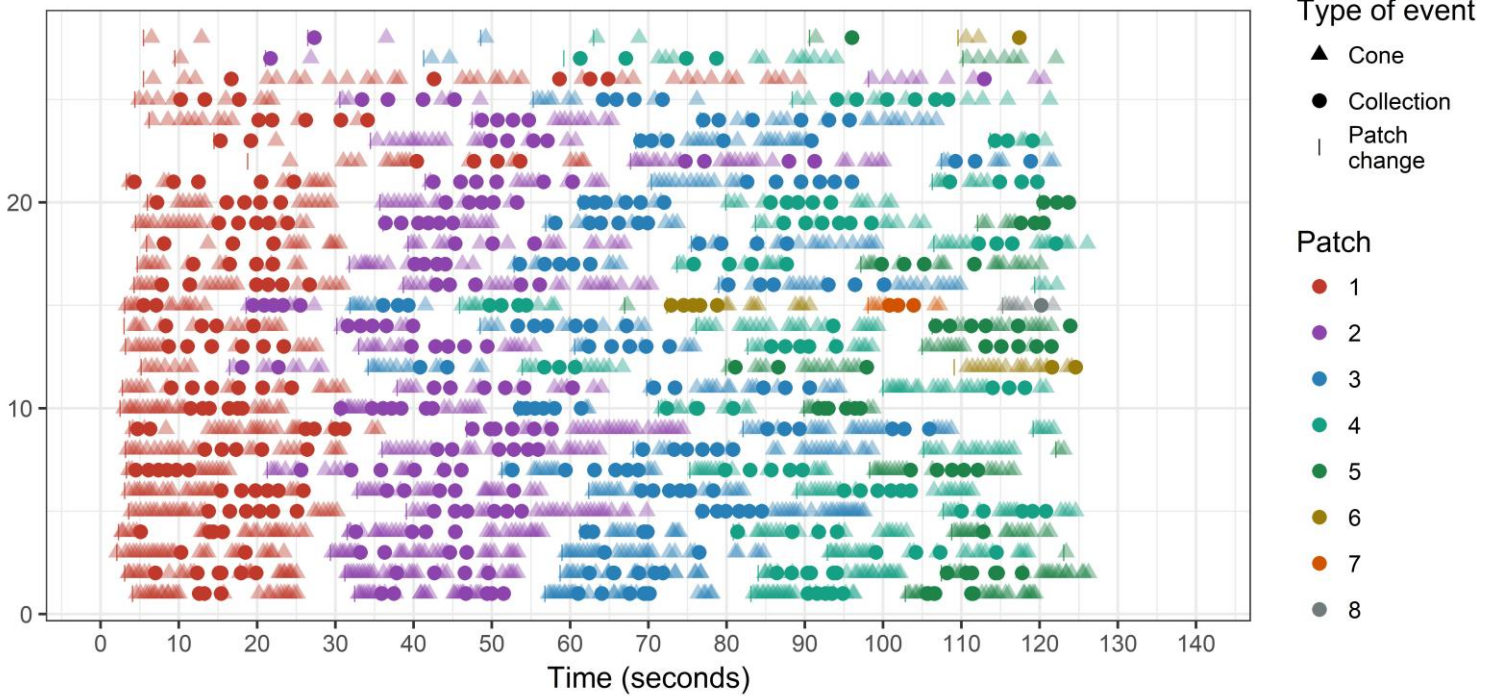


Fig. 7 Detailed performance of women in EXP. Each line in the y axis represents one participant, and they are arranged from zero onwards from the greater amount of moves to the smaller one

Table 1

*Multiple comparisons of the generalized mixed model for the performance by patches
Performance ~ Patch*Condition + (1|Participant) in the three search conditions*

Comparison	Estimate	SE	z value	p
Patch 1				
BL – INFO	-0.599	0.105	-5.687	<0.001
BL – EXP	-0.191	0.113	-1.691	0.208
INFO – EXP	0.407	0.112	3.622	<0.001
Patch 2				
BL – INFO	-0.413	0.103	-3.981	<0.001
BL – EXP	-0.114	0.112	-1.020	0.563
INFO – EXP	0.298	0.112	2.652	0.021
Patch 3				
BL – INFO	-0.457	0.103	-4.402	<0.001
BL – EXP	-0.194	0.112	-1.726	0.195
INFO – EXP	0.262	0.112	2.330	0.051
Patch 4				
BL – INFO	-0.369	0.118	-3.105	0.005
BL – EXP	-0.029	0.144	-0.204	0.977
INFO – EXP	0.339	0.141	2.410	0.041
Patch 5				
BL – INFO	-0.564	0.190	-2.965	0.008
BL – EXP	-0.020	0.242	-0.085	0.996
INFO – EXP	0.543	0.238	2.276	0.058