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6 **Adaptive Lévy Processes and Area-restricted Search in Human Foraging**

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27

**28 Abstract**

29 A considerable amount of research has claimed that animals' foraging behaviors display  
30 movement lengths with power-law distributed tails, characteristic of Lévy flights and Lévy  
31 walks. Though these claims have recently come into question, the proposal that many  
32 animals forage using Lévy processes nonetheless remains. A Lévy process does not consider  
33 when or where resources are encountered, and samples movement lengths independently of  
34 past experience. However, Lévy processes too have come into question based on the  
35 observation that in patchy resource environments resource-sensitive foraging strategies, like  
36 area-restricted search, perform better than Lévy flights yet can still generate heavy-tailed  
37 distributions of movement lengths. To investigate these questions further, we tracked humans  
38 as they searched for hidden resources in an open-field virtual environment, with either patchy  
39 or dispersed resource distributions. Supporting previous research, for both conditions  
40 logarithmic binning methods were consistent with Lévy flights and rank-frequency  
41 methods—comparing alternative distributions using maximum likelihood methods—showed  
42 the strongest support for bounded power-law distributions (truncated Lévy flights).  
43 However, goodness-of-fit tests found that even bounded power-law distributions only  
44 accurately characterized movement behavior for 4 (out of 32) participants. Moreover, paths  
45 in the patchy environment (but not the dispersed environment) showed a transition to  
46 intensive search following resource encounters, characteristic of area-restricted search.  
47 Transferring paths between environments revealed that paths generated in the patchy  
48 environment were adapted to that environment. Our results suggest that though power-law  
49 distributions do not accurately reflect human search, Lévy processes may still describe  
50 movement in dispersed environments, but not in patchy environments—where search was  
51 area-restricted. Furthermore, our results indicate that search strategies cannot be inferred  
52 without knowing how organisms respond to resources—as both patched and dispersed  
53 conditions led to similar Lévy-like movement distributions.

## 54 **Introduction**

55 Numerous species have been proposed to display power-law distributed movement patterns  
56 when foraging [1-5]. Power-law distributed movement patterns are superdiffusive, with  
57 straight-line movement length,  $l$ , having probability distribution function  $P(l) \sim l^{-\mu}$ , with  $1 <$   
58  $\mu < 3$ . A common interpretation of power-law distributed movements is that they represent  
59 the outcome of Lévy walks (with probabilities based on duration) or Lévy flights (with  
60 probabilities based on distance traveled) [2,5,6]. When velocities are constant, we can  
61 consider these two synonymous, as we do here (and simply use the term Lévy flights). Both  
62 refer to scale-free random walks in which run duration or movement lengths are  
63 independently drawn from a probability distribution with a heavy power-law tail. Though the  
64 power-law distribution of movement lengths for many organisms has come into question [7],  
65 the processes which create animal paths are potentially still Lévy processes. We define a  
66 Lévy process with respect to foraging as a stochastic process in which increments are  
67 independently drawn and statistically identical for non-overlapping portions of the path [8].  
68 Examples of Lévy processes are Brownian motion, Lévy flights, Lévy walks, and Poisson  
69 processes. Because the underlying movement distributions do not change in response to  
70 resource encounters, Lévy processes imply that organisms do not use information about  
71 recent resource encounters to localize search in space.

72 In contrast to Lévy processes, patterns of extensive and intensive foraging in response  
73 to resource absence or presence, respectively, have also been widely observed across species  
74 [9-11]. This pattern of movement is called area-restricted (or area-concentrated) search.  
75 Area-restricted search requires memory in order to create local intensive searching around  
76 locations where resources have been found in the past. Moreover, area-restricted search is  
77 capable of generating distributions of movement lengths with heavy-tailed power-law  
78 distributions [12,13]. Though some work has been interpreted as suggesting that Lévy flights  
79 are optimal foraging strategies [14], these were not compared with alternative strategies like

80 area-restricted search. Comparisons of these foraging strategies in destructive foraging  
81 environments—where resources are not replaced—have found that when resource locations  
82 are spatially uncorrelated (distributed independently), ballistic foraging strategies are optimal,  
83 whereas when resource locations are spatially auto-correlated (distributed in clusters), then  
84 area-restricted search strategies are optimal [12-16].

85       Historically, the methodological difficulties associated with determining what generates  
86 a power-law distribution have led to considerable debate over which animals, if any, actually  
87 use Lévy processes [4,6,7,12,17,18]. In part, this argument has tried to address whether  
88 animals do Lévy flights by focusing on the statistical methodology used to identify the  
89 underlying distributions [4,7,16,17]. Still others have investigated behavioral mechanisms  
90 that can generate such distributions [12,13,19,20]. Here we take a different approach by  
91 focusing on the fact that a Lévy process samples from the same movement length distribution  
92 without regard to resource encounters, whereas area-restricted search strategies are processes  
93 that sample from different distributions depending on the time passage since last resource  
94 encounter [21-23]. Thus, our approach to identifying the underlying data generating process  
95 requires knowing exactly where resources are and how behavior changes in response to  
96 encountering them.

97       In the present study we focus on human foraging. Consistent with what has been shown  
98 for other animals, several studies have attempted to show that human movement patterns may  
99 be Lévy flights [2,24-26]. However, other studies have suggested that humans do not use  
100 Lévy flights, because—using maximum likelihood methods and goodness-of-fit tests—the  
101 observed distributions were found not to follow power-law distributions [7]. No previous  
102 studies have investigated the broader theoretical question of Lévy processes in humans, nor  
103 have previous studies investigated how human search may respond adaptively to the  
104 correlational structure of resource distributions.

105 Here we present an analysis of human foraging in a virtual environment, resembling a  
106 large open field. Using both clustered (patchy) and dispersed (non-patchy) resource  
107 distributions, we tracked individual search trajectories and resource encounters and asked to  
108 what extent paths were adapted to their specific sequence of resource encounters. Our aim  
109 was to determine how the movement lengths of human search trajectories are distributed and  
110 to address under what circumstances these distributions may represent Lévy processes or  
111 area-restricted search.

## 112 **Methods**

113 Participants ( $n=32$ ) searched in a circular virtual arena that contained hidden targets.  
114 The environment consisted of a textured ground plane resembling a large meadow and was  
115 surrounded by a fence, with large distal landmarks (e.g., mountains) to provide global  
116 orientation cues. There were no local cues, such as depressed grass, to signal where  
117 participants had been (Fig. 1A). Targets were either uniformly distributed (dispersed  
118 condition, Fig. 1B) or organized in patches (patched condition, Fig. 1C) in a between subjects  
119 design. People searched the virtual circular meadow (110m radius) displayed on three  
120 computer screens, representing 180° field of view. They did this using the arrow keys, which  
121 allowed them to either move forward or turn, but not both at the same time. The distance  
122 between two turns was defined as a movement length. 1440 items were randomly located: in  
123 the dispersed condition locations were independently and uniformly determined; in the  
124 patched condition, the centers of 24 patches were uniformly assigned, but non-overlapping,  
125 and 60 items were randomly located within 8.65 meters of the patch center. Participants  
126 heard a tone when they encountered an item (detected at a distance of 0.75 meters) and were  
127 required to search for and collect 90 items. The participants were randomly assigned to the  
128 two conditions, told to search for 90 items, with the search repeated 5 times for each  
129 participant. Participants were not told about the resource distribution. However, participants  
130 appear to have learned this rapidly, because behavior did not substantially vary over the 5

131 repeated foraging trials. We therefore report our analyses on the aggregated individual data  
132 over the 5 trails.

133 Statistical analyses used standard likelihood methods and Akaike weights to compare  
134 four statistical models: unbounded power-law, bounded power-law, unbounded exponential,  
135 and bounded exponential. Methods and code can be found in previous work [7,27]. For  
136 reference with past literature supporting Lévy flights, we also present results based on  
137 logarithmic binning [18,28]. In order to evaluate whether or not movements were  
138 independent of recent resource encounters, we compared observed turning with baseline  
139 turning following resource encounters. Baseline turning was measured by selecting random  
140 locations along the recorded trajectories and calculating the turning response as a function of  
141 the distance after these random locations (“Random dispersed” and “Random patched”). To  
142 establish whether or not paths were adapted to their environments, we compared paths across  
143 environments; paths observed in one resource distribution were simulated 100 times in the  
144 alternative resource distribution by rotating them using a uniform random sampling of the  
145 initial heading around  $360^\circ$ .

146

## 147 **Results**

148 Figure 2 presents rank/frequency plots of the data and the model fitting for the  
149 aggregated data from each condition and for each individual separately. Data are presented  
150 on logarithmic axes because a power-law distribution appears as a straight line on these axes.  
151 For the aggregated models (Fig. 2A, B), only the bounded power-law appears to fit the data  
152 with any degree of precision. The unbounded power-law overestimates the size of longer  
153 moves and the exponential fits underestimate these longer moves. For the individual data,  
154 model fits vary widely (Fig. 2C, D), with few individuals appearing to be well described by  
155 any statistical model.

156 Before we discuss the statistical tests associated with these distributions, we first  
157 present the results of logarithmic binning. For reference with previous literature  
158 [1,5,14,16,18,28-30], the insets of Figure 2A and 2B present the data using logarithmic  
159 binning methods. The slope for the patched condition was  $\mu = -1.45 \pm 0.40$  and for the  
160 dispersed condition was  $\mu = -1.23 \pm 0.31$ . These were not statistically different ( $P > .05$ ).  
161 Though necessary for an interpretation of Lévy flights, these results are far from sufficient.  
162 Moreover, the method of logarithmic binning has come under attack for multiple reasons and  
163 fails to compare alternative hypotheses [7,27].

164 Our statistical analyses thus used standard likelihood methods and Akaike weights to  
165 compare four statistical models based on the rank/frequency plots: unbounded power-law,  
166 bounded power-law, unbounded exponential, and bounded exponential. Table 1 presents the  
167 analyses based on aggregated data, providing the evidence ratios for the different models—  
168 which represent the Akaike weight of a model divided by the best fitting Akaike weight, such  
169 that the best fitting model has a value of 1.0 and other models have values  $> 1.0$ . Table 2  
170 presents the analyses based on individual data, showing the proportion of participants best fit  
171 by each model. For both aggregated and individual data, the bounded power-law model  
172 (truncated Lévy flight) was the best fitting model in all cases. We used a G-test (likelihood  
173 ratio test) to compare the bounded power-law with the data, with the null hypothesis that the  
174 data are consistent with this model [7]. Both aggregated data sets failed the goodness of fit  
175 test (Table 1) and all but two individuals in each condition failed the goodness of fit test  
176 (Table 2). This indicates that even the truncated Lévy flight—despite it being the best of the  
177 models we tested—still appears to poorly characterize human behavior.

178 In addition to the model fitting, we also found that the two conditions did not differ in  
179 mean movement length ( $M_{dispersed} = 43.2$ ,  $M_{patched} = 31.1$ ,  $t(30) = 1.35$ ,  $P = .19$ , two-tailed t-test),  
180 mean absolute turning angle ( $M = 53.8$ ,  $M = 52.5$ ,  $t(30) = 0.19$ ,  $P = .85$ , two-tailed t-test), or  
181 mean  $\mu$  associated with the best fitting bounded power-law model ( $M_{dispersed} = 1.06$ ,

182  $M_{patched}=1.16$ ,  $t(30)=-1.11$ ,  $P=.27$ , two-tailed t-test). These results lend themselves to two  
183 conclusions. Foremost, despite a strong apparent fit to power-law distributions when using  
184 logarithmic binning, the movement distributions are not well described by power-law  
185 distributions and therefore fail to meet a basic requirement of Lévy flights. Second, the two  
186 conditions do not appear to be significantly different from one another based on movement  
187 distributions alone, and are therefore potentially consistent with a common underlying search  
188 strategy (but see below).

189         The first conclusion is likely to come under some criticism. Only bounded power-laws  
190 are meaningful in natural systems, because “all power laws in nature have upper and lower  
191 cutoffs” (p. 41, [16]). Thus, realistically, we can expect true Lévy-like behaviors to be best  
192 characterized by truncated Lévy flights, especially if foragers stop when encountering items.  
193 Failures to fit bounded power-law distributions may simply reflect improper bounds, which  
194 may in this case be a function of, for example, human reaction times or different cognitive  
195 processes being used over very short or very long movement intervals. Despite failing the  
196 goodness of fit tests, because our data are statistically most consistent with truncated Lévy  
197 flights this may lead some readers to infer that the processes underlying the movement are  
198 indeed Lévy processes. But this is an unfounded inference. Even if the distributions were  
199 bounded power-law distributions, different behavioral processes (besides Lévy processes)  
200 can generate bounded power-law distributions. As noted in previous literature, inferences  
201 based on distributions alone are insufficient evidence to infer Lévy flights [12,13]. Ruling  
202 out such alternative explanations requires an analysis of movement based on where and when  
203 resources were encountered.

204         To address this issue, we compared turning angles following resource encounters for  
205 both patched and dispersed conditions with a baseline reference class of turning angles  
206 evaluated at random points along participants’ paths (Fig. 3). If individuals increase their  
207 turning angles above the baseline in response to encountering a resource item, this suggests



208 that movement lengths are not independently sampled, but reflect the participant's initiating  
209 intensive foraging. Indeed, following a resource encounter turning angles in the patchy  
210 environment were sharper than in the dispersed condition ( $M_{patched}=65.47^\circ$ ,  $M_{dispersed}=19.85^\circ$ )  
211 and sharper than turning angles taken relative to random points along the path ( $M_{random}$   
212  $_{patched}=29.79^\circ$ ). Thus, for the patched condition, the results support a transition to an intensive  
213 search following resource encounters, confirming area-restricted search. The observed  
214 turning angles for the dispersed condition were not different from their random reference  
215 class ( $M_{dispersed}=19.85^\circ$ ,  $M_{dispersed\_random}=16.89^\circ$ ), indicating insensitivity to resource  
216 encounters and consistent with a Lévy-flight-like process (possibly a truncated Lévy flight).

217 Was the area-restricted search in the patched condition associated with improved  
218 performance, as proposed in previous literature [12,13,16]? To establish whether increased  
219 turning following resource encounters was an adaptive change in search strategy, we asked  
220 how the paths produced in one environment would have performed had they been observed in  
221 the other environment (Fig. 4). Paths transferred from the dispersed environment to the  
222 patchy environment performed worse than paths originally generated in the patchy  
223 environment (observed - new:  $M_{dispersed}=-1.47$ ,  $SD=1.46$ ). However, paths transferred from  
224 the patchy environment to the dispersed environment did not perform differently than the  
225 original dispersed paths ( $M_{patched}=-0.31$ ,  $SD=2.84$ ). This is consistent with previous  
226 theoretical claims and demonstrates empirically that in patchy environments paths adapted to  
227 the spatially auto-correlated structure of the resource environment—responding to resource  
228 encounters with intensive search—are more efficient than a putative Lévy-flight-like process.  
229 However, in the spatially uncorrelated resource environment, information about resource  
230 locations was not provided by resource encounters and participants could efficiently utilize a  
231 random Lévy-like process.

## 232 Discussion

233           The present work follows Benhamou [12] in suggesting that the test for a Lévy flight  
234 requires two components: 1) an analysis of path distribution, and 2) evidence that the path is  
235 intrinsically generated and not a result of external resource encounters. Our results  
236 demonstrate that these two criteria are possibly met for humans foraging in dispersed,  
237 spatially uncorrelated resource environments—where we found movement lengths most  
238 consistent with a bounded power-law, though these failed the goodness of fit tests. These  
239 paths also showed no sensitivity to resource encounters, suggesting they may be consistent  
240 with Lévy processes. On the other hand, humans exposed to spatially auto-correlated  
241 resource environments, with resources distributed in patches, showed similarly distributed  
242 movement lengths but adapted their search to the structure of the environment by responding  
243 to resource encounters with increased turning, characteristic of area-restricted search.

244           The putative claim for Lévy flights in diverse categories of living organisms—ranging  
245 from T cells to hunter-gatherer foraging camps [1,2,5,6,31]—raises fundamental questions  
246 about the underlying generative processes driving these behaviors and the optimality of the  
247 resulting search. Our results offer potential inroads to future studies, as well as providing  
248 grounds for alternative explanations. In particular, putative Lévy flights may adapt to the  
249 resource structure of their environment by a change in the characteristic scale of their  
250 movement length distribution [6], movement distributions similar to bounded power-law  
251 distributions and possibly changes in movement length distributions may further arise as a  
252 result of adaptive changes in behavioral responses to encounters with resources. Because of  
253 the similar nature of the two movement length distributions in our two conditions, our results  
254 further warn against inferring behavior based on curve fitting.

255           In addition, when behavioral ecologists have investigated how animals respond to  
256 resources, area-restricted search has been observed in animals across the metazoan lineage  
257 (e.g., vertebrates and invertebrates) and typically involves similar neuromolecular  
258 mechanisms [32]. A common hypothesis when observing both shared traits and shared

259 mechanisms is that the trait existed in an ancestor common to the different species under  
260 study. In the case of metazoans, this species would have existed approximately 6 to 7  
261 hundred million years ago. This indicates that area-restricted search is likely to be an  
262 extremely common strategy for localizing search around patchy resources in space and  
263 should, at the least, represent an alternative hypothesis for comparison in future studies of  
264 Lévy-like movement patterns.

265       Finally, we note that the observed relationship between Lévy-flight-like processes and  
266 area-restricted search, in a single animal (i.e., humans), provides a foothold for further  
267 investigating the behavioral and neuromolecular mechanisms driving power-law distributed  
268 behavior across a wide range of species and environments [3,12,29,33,34]. This is in part  
269 because the neuromolecular mechanisms underlying behavioral changes in response to  
270 environmental rewards are well studied [10,35-37], which allows us to pose new questions  
271 for our understanding of the physiological and evolutionary origins of power-law distributed  
272 behavior patterns, specifically in terms of how they may be a response to resources.

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369

**Figure Legends**

370 Figure 1: The virtual foraging environment, resource distributions, and representative paths.  
 371 **A.** Participants' perspective during the task. One of the global landmarks (a mountain) is  
 372 visible in the distance. The number in the lower left hand corner is the number of resources  
 373 collected so far. **B.** The resource distribution in the dispersed environment with a path  
 374 generated by one participant. **C.** The resource distribution in the patchy environment with a  
 375 path generated by one participant.

376

377 Figure 2: Rank/frequency plots of aggregated and individual data along with model fits on  
 378 logarithmic axes. Black circles are movement lengths  $\geq x$ . The four model fits are power-  
 379 law (blue-straight line), bounded power-law (curved blue-dashed line), unbounded  
 380 exponential (curved red line), and bounded exponential (curved red-dashed line). **A.** The  
 381 aggregated data for the dispersed condition. The inset shows the results of logarithmic  
 382 binning with best fitting power-law. **B.** The aggregated data for the patched condition. The  
 383 inset shows the results of logarithmic binning with best fitting power-law. **C.** Data for each  
 384 individual in the dispersed condition. **D.** Data for each individual in the patched condition.

385

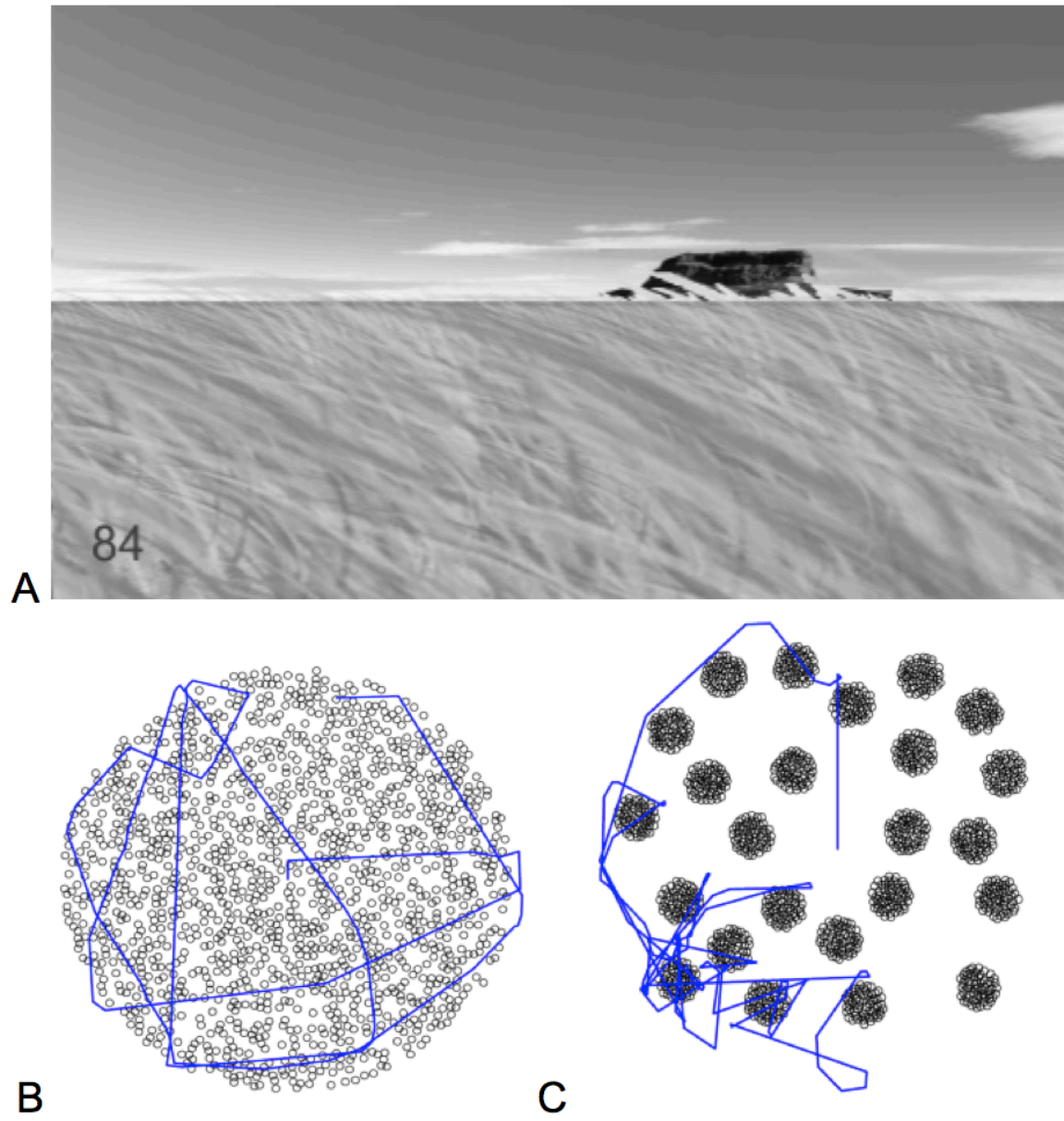
386 Figure 3: Turning angle as a function of distance after item encounter for the empirical data  
 387 ("Experiment dispersed" and "Experiment patched") and for random locations along the  
 388 trajectories ("Random dispersed" and "Random patched"). Participants in the patched  
 389 condition significantly increased turning in response to resource encounters relative to both  
 390 the dispersed condition ( $F(1,30)=5.31, P=.03$ , repeated measures analysis of variance) and  
 391 'random' baseline turning ( $F(1,15)=5.71, P=.03$ , repeated measures analysis of variance).  
 392 Turning angles in the dispersed condition were not different from the 'random' baseline  
 393 turning ( $F(1,15)=1.68, P=.21$ , repeated measures analysis of variance). Data show  
 394 mean $\pm$ sem.

395

396 Figure 4: Comparing path performance across environments. We compared path performance  
 397 by randomly simulating paths from the alternative environment using 100 simulated versions  
 398 of each observed path in the alternative resource distribution. Paths from the patched  
 399 condition simulated in the dispersed environment performed as well as dispersed paths in the  
 400 dispersed environment ( $t(15)=0.05, P=.97$ , two-tailed t-test). However, paths from the  
 401 dispersed environment simulated in the patchy environment were outperformed by the  
 402 original paths from the patchy environment ( $t(14)=-3.91, P=.002$ , two-tailed t-test).

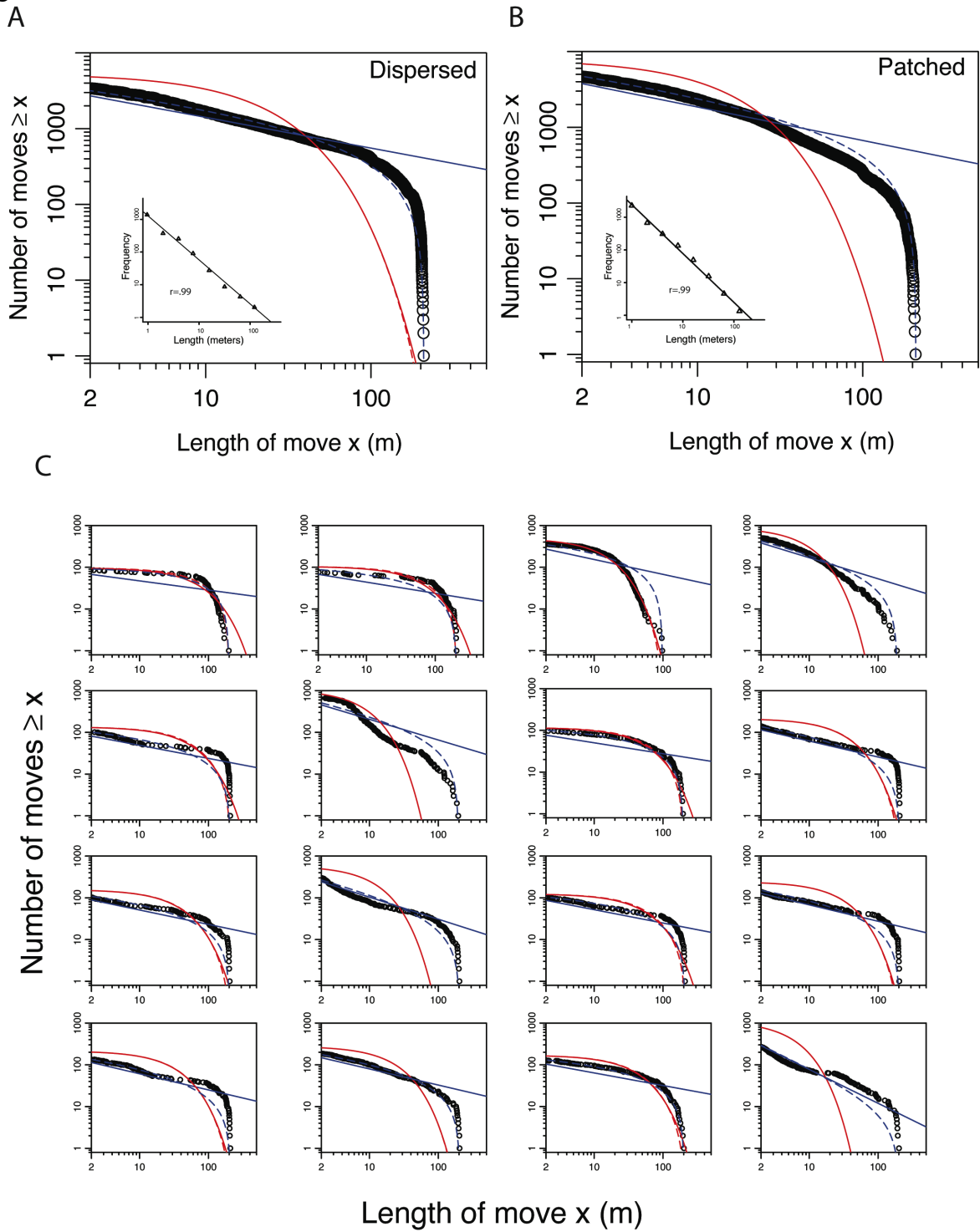


403  
404 **Figure 1.**



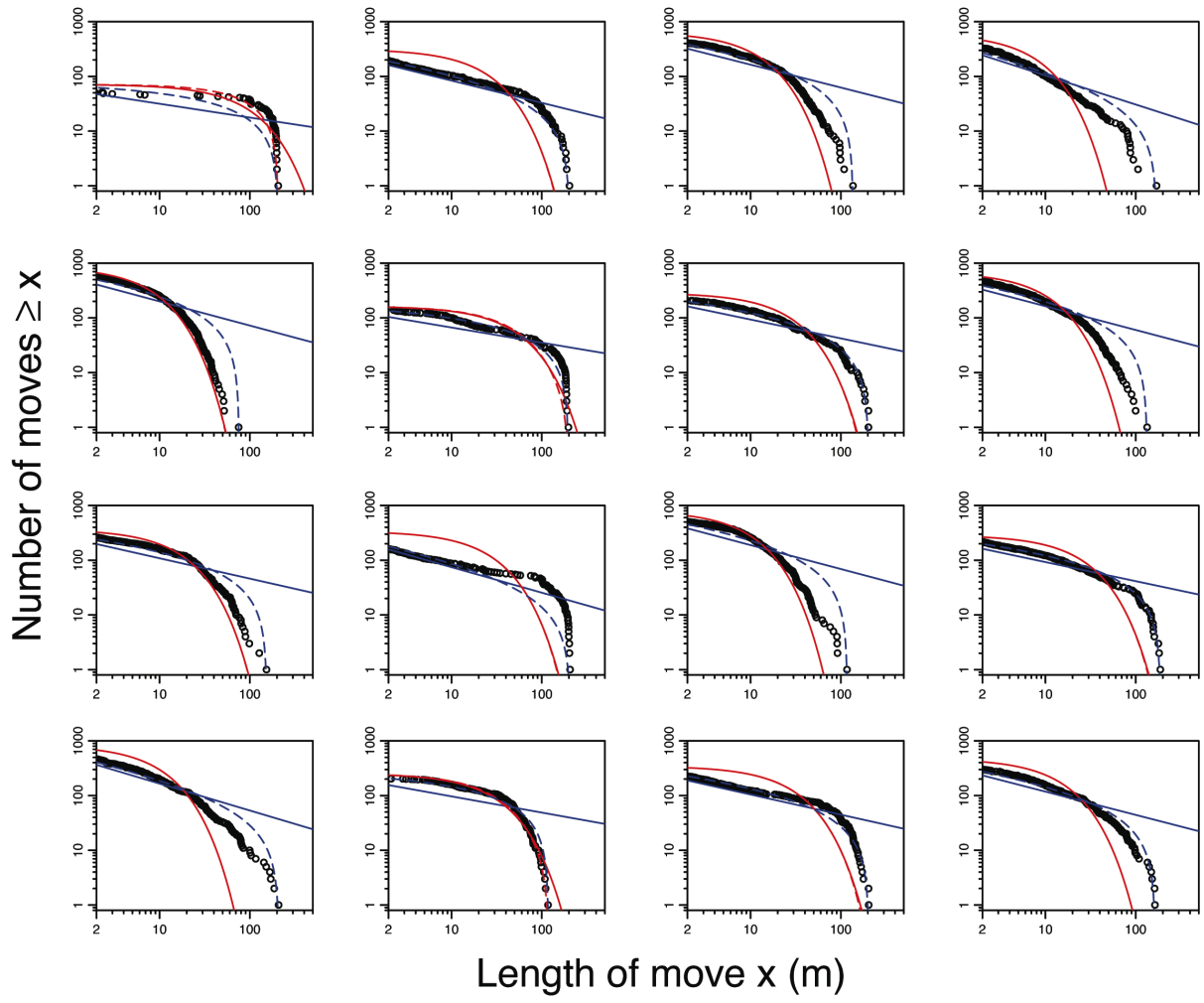
405

406 Figure 2.



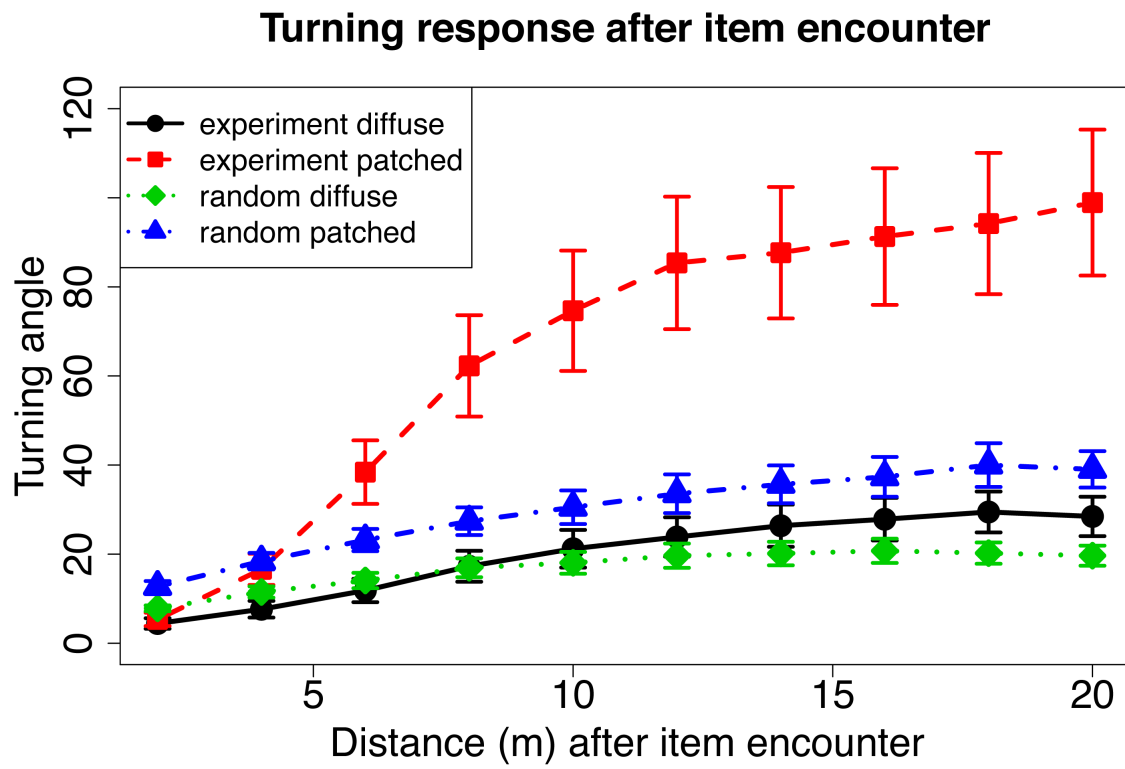
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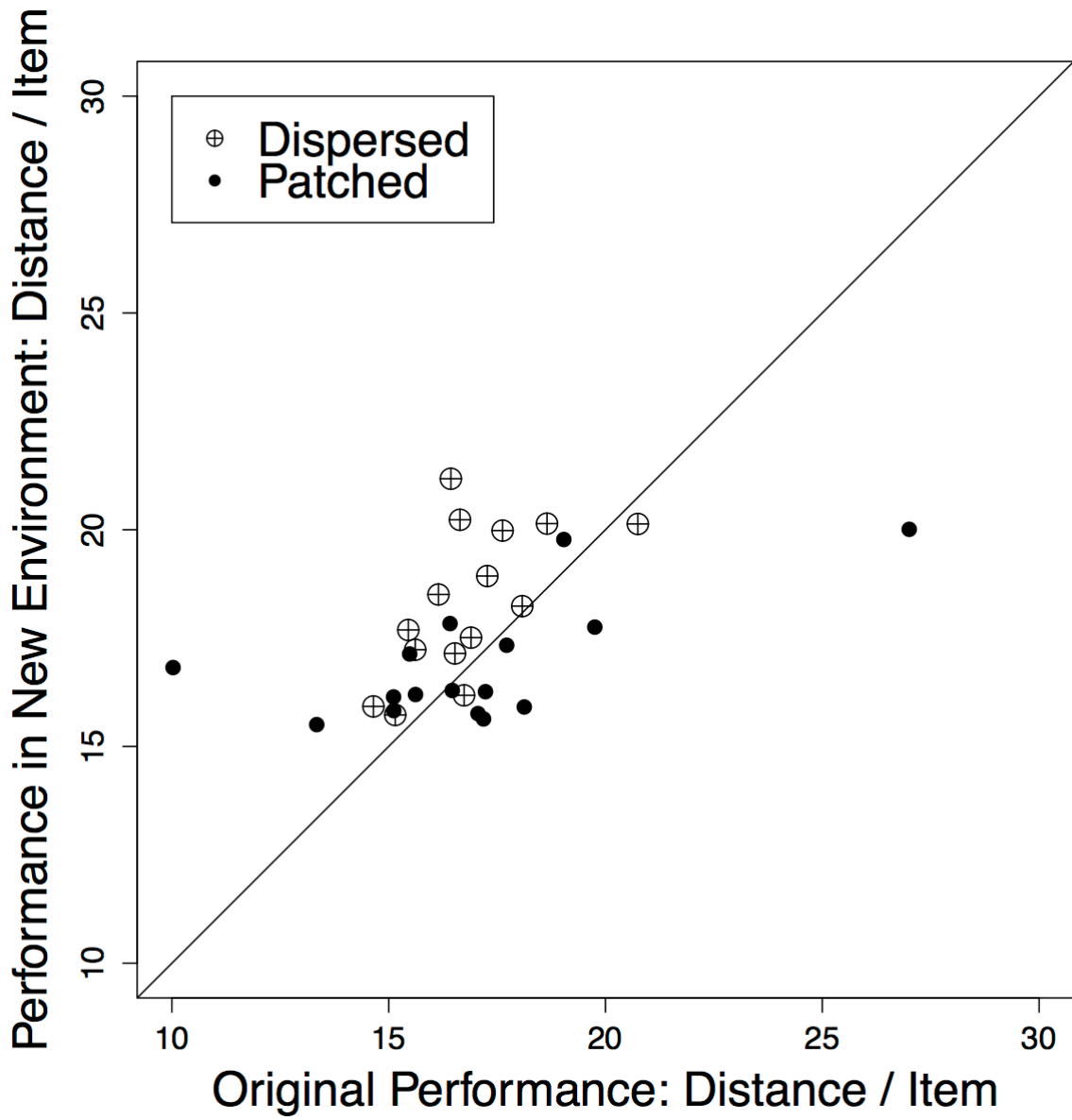
412 **Figure 3**



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415 **Figure 4**



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418 **Table 1: Model comparisons for aggregated data**

Aggregated	Evidence ratios				Best model's goodness of fit	
	PL	Exp	PLB	ExpB	$n$	$P$
Dispersed	$>10^{30}$	$>10^{30}$	<b>1.0</b>	$>10^{30}$	5210	0
Patched	$>10^{30}$	$>10^{30}$	<b>1.0</b>	$>10^{30}$	7688	0

419 Note: PL = power law, Exp = unbounded exponential, PLB = bounded power-law, ExpB =  
 420 bounded exponential.

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423 **Table 2: Model comparisons for individual data**

Individual	Proportion best fit by each model				Proportion with $P > .05$ for best model
	PL	Exp	PLB	ExpB	
Dispersed	0	0	<b>1.0</b>	0	.125
Patched	0	0	<b>1.0</b>	0	.125

424 Note: PL = power law, Exp = unbounded exponential, PLB = bounded power-law, ExpB =  
 425 bounded exponential.

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