Early experience affects foraging behavior of wild fruit-bats more than their original behavioral predispositions

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Abstract

There are immense consistent inter-individual differences in animal behavior. While many studies have documented such behavioral differences, often referred to as individual personalities, little research has focused on the underlying causes and on determining whether they are innate or based on individual experience. Moreover, most studies on animal personalities have described consistent differences in behavior under laboratory conditions. We aimed to examine the impact of the early experienced environment on individual animal behavior, and to compare it to that of the individual's original genetic predisposition. Additionally, we explored the correlation between personality traits measured indoors and the animal's outdoor behavior. We studied Egyptian fruit bats, in which vast behavioral variability and plasticity have already been demonstrated. We raised bats in a captive colony under either enriched or impoverished environments and assessed their personality under controlled laboratory conditions. We then released the bats into the wild and tracked their foraging using GPS. Bats that had experienced an enriched environment during early life displayed increasing boldness and exploratory behavior when foraging outdoors, demonstrating how early-life experience can affect adult behavior. The individuals' original predispositions did not predict their later foraging behavior. Our findings shed new light on the interplay between innate and experienced-based effects on individual behavior.

Key words: Fruit bats, personality, GPS, behavior, early life experience

Introduction:

Anyone who has ever observed animals knows that individual persistently differ in their behavior. These behavioral tendencies, enable distinguishing individuals from one another and remain consistent over time and across various situations, have been termed “animal personalities” [1]. While some opposition exists regarding the use of this term [2], it is nonetheless commonly employed [3,4], and we use it here to describe a set of behavioral traits that remain consistent within individuals over time and across contexts [1].

Personality traits have been extensively documented in various taxa [1,5,6]. They are typically assessed through the measurement of proxies for behavioral traits like boldness, activity, and exploration [7]. However, while individual personality differences have been observed in numerous species [5,6,8,9], only a limited number of studies have investigated the underlying factors that contribute to their emergence.

Broadly speaking, the ontogeny of an animal's personality can be affected by its genetic predisposition and by its individual experience. To date, only a few studies have explored how individual personality develops, and how the interplay between genetic factors, maternal effects, and early experiences or environmental effects shape personality [1,6,10–12]. In the few studies that did so, the effects of these factors have been observed exclusively in captive settings [12–16]. For instance, researchers found differences in personality traits, such as boldness and exploration, in guinea pigs raised in captivity under different photoperiods simulating spring or autumn conditions [11]. Similarly, intertidal gobies reared in different habitat complexities have shown differences in spatial learning laboratory experiments: gobies that developed in complex rock pool demonstrated faster learning abilities compared to those raised in homogenous sandy shores [15].

Only a handful of studies have examined behavioral traits under both captive and natural conditions. One such experiment showed that the foraging behavior of birds in captivity was consistent with their behavior in the field. For example, the exploratory tendencies in captivity were correlated with seeking new feeding sites in the wild [17]. There is also a scarcity of hypothesis-driven experiments that employ specific manipulations to investigate the ontogeny of personality. In this study, we aimed to elucidate the roles of genetic

predisposition and early life experience on free-foraging fruit-bat personality using a controlled manipulation.

Egyptian fruit bats have been shown to exhibit immense individual differences both in indoor personality tests [18] and when foraging in the wild [19]. These bats have also been shown to exhibit environmentally dependent behavioral plasticity. Specifically, the same individual fruit-bats were much more exploratory when foraging in urban environments than when foraging in rural environments [10,20]. Moreover, fruit-bats that roost in cities were shown to be even more exploratory than rural fruit-bats that commute into cities, suggesting that the environment might have an additive effect on their behavior.

In this study, we performed a controlled manipulation to determine whether the environment that young bat pups experience can affect their personality. Specifically, we examined whether exposure to an enriched environment as pups affects the bats' behavior when they later forage in the wild as adults. Living in enriched or dynamically changing environments has been linked in multiple species to many behaviors, including increased risk-taking and boldness [10,21,22]. Maturation in an enriched environment can also affect learning capabilities, as noted above regarding gobies [15], and motor performance as demonstrated in laboratory rats [13].

In our study, we manipulated the extent of environmental enrichment experienced by juvenile fruit-bats in a captive environment and examined the correlation between this early experience and their foraging behavior in the wild several months later. We compared the effects of experience to the bats' original predisposition, estimated when they were naïve pups (~4 months old; prior to any manipulation). We also examined personality traits over a prolonged period to confirm their individual behavioral consistency, and we explored the relationship between the personality traits observed in captivity and the outdoor foraging behavior. We hypothesized that both early-life experience and original predisposition would interact in shaping individual personalities.

Results:

Assessing Personality in the lab: To assess bats' personality, we ran young bats through the multiple-foraging box paradigm, which was developed in our lab and has been shown to measure behavioral variability along multiple axes [10]. A total of 40 bats participated in the foraging box experiments, which were repeated a maximum of five times per individual over a period of almost five months (Figure 1A, see Methods). The experiment comprised baseline trials for each bat on two consecutive nights, upon the bats reaching an average age of 4.1±1.4 months (trials 1-2; Mean±STD). Subsequently, we randomly divided the bats into two colonies, each exposed to different environmental conditions. Both colonies were provided with the same basic diet sufficient for all bats in the colony. The ***enriched colony*** underwent frequent changes in their surroundings for a period of ~10 weeks, through the introduction of various enrichments that forced the bats to practice trial and error to obtain (Methods). While the ***control impoverished colony*** was exposed to a stable environment with minimal changes. A post-enrichment boxes trial was performed immediately after this period (Trial 3, on average 72 days after the previous). Finally, two post-release boxes trials were performed after the bats were released into our open colony and could freely forage in the wild and explore their natural environment (Trials 4-5, average 45 and 58 days after their release into the wild). We used these trials to assess proxies of the three above-noted behavioral traits: boldness, exploration, and activity. To assess the behavioral traits during the foraging box experiments, we measured the bats' actions. Specifically, we recorded how many times they approached and took food from a foraging box, the number of different boxes they explored (i.e., landed on), and the total number of actions they performed during the night (Figure 1A and see Methods).

When plotting the three behavioral traits (boldness, exploration, and activity) in 3D they seem to be form a triangle (Figure 1B) – reminiscent of a pareto front [23] – suggesting a trade-off between the different traits. The three vertices (often referred to as the archetypes when analyzing a pareto front) represent individuals that exhibit: (a) high exploration, high activity, and medium-low boldness. (b) high boldness, low activity, and low exploration. and (c) low boldness, low activity, and low exploration (very few bats). These three archetypes suggest a trade-off between boldness on the one hand, and activity and exploration on the other hand.

For all three behavioral traits, we found a significant positive correlation between baseline (Trial 1) and the post-enrichment trial (Trial 3) examined on average 72 days apart. A significant positive correlation was also found between bats' boldness during the baseline (Trial 1) and the second post-release trial (Trial 5), examined on average 144 days apart. These findings suggest that these behavioral traits, and especially boldness, remain consistent at least throughout the bat's early life (Figure 1 C1-3, Pearson correlation test: $r=0.66$ $P<9.7e-0.5$, $r=0.66$ $P<9.1e-0.5$, and $r=0.51$ $P<0.004$; for Trials 1-3 for boldness, exploration and activity respectively, and $r=0.6$ $P<0.021$, for Trials 1-5 boldness, Table 1). This was also the case when examining the enriched and impoverished colonies separately.

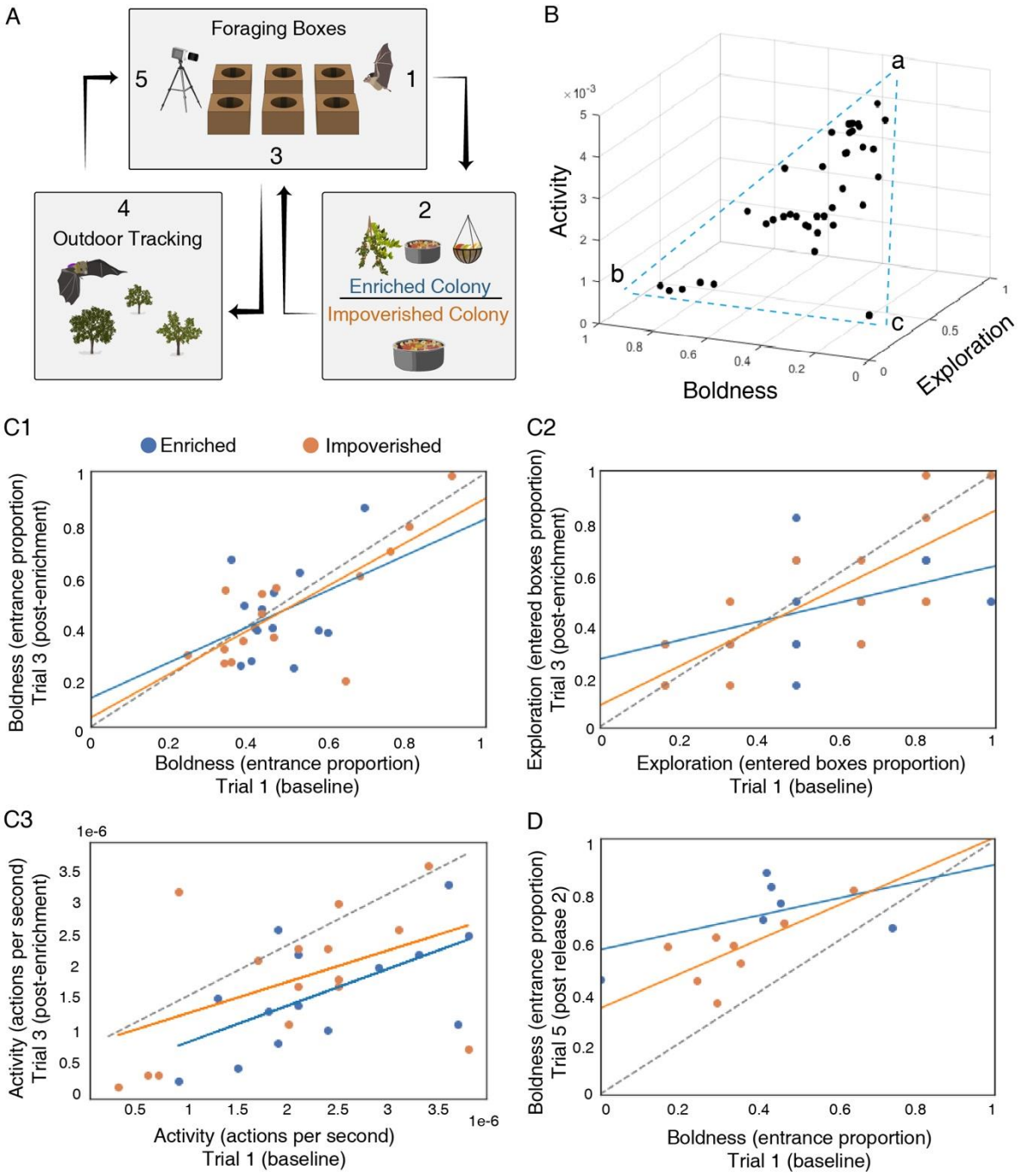

Figure 1. Assessing personality in the laboratory. (A) Schematic illustration of the experiments. **(B)** A 3D plot of the three behavioral traits, estimated during Trial 1. **(C1-3)** Behavioral traits were consistent over time. The behavioral traits of the first and third (post-enrichment) trial are presented. Positive correlations were found for all three behavioral traits over a period of more than 10 weeks. For the enriched, the impoverished, and both environments together, respectively: **(C1)** Boldness; **(C2)** exploration; and **(C3)** activity. **(D)** Boldness of the first and fifth (post-release 2) trial. Dashed line represents the Y=X line.

Table 1. Pearson's correlation test

	Boldness 1-3	Exploration 1-3	Activity 1-3	Boldness 1-5
Pearson r value	0.66	0.66	0.51	0.6
Pearson p value	<9.7e-05	9.1e-0.5	0.004	0.021

The overall patterns of boldness and exploration revealed similar patterns (Figure 2): both increased between the first two consecutive baseline trials (Figure S1). Following the enrichment treatment (i.e., in Trial 3) they decreased back to the level of the first baseline and then increased again in the two post-release trials (4-5). Boldness was significantly higher in the last trial compared to in the first one ($P < 1.9e-07$, mixed effect Generalized Linear Model – GLMM with the behavioral traits as the explained parameter, the trial number (1 or 5) as fixed factor and bat ID as a random effect, Table 2), while exploration showed a fairly similar pattern. Activity, in contras showed a different pattern. It decreased continuously throughout the trials and was significantly lower in the last trial compared to in the first one ($P < 0.0001$, GLMM as above).

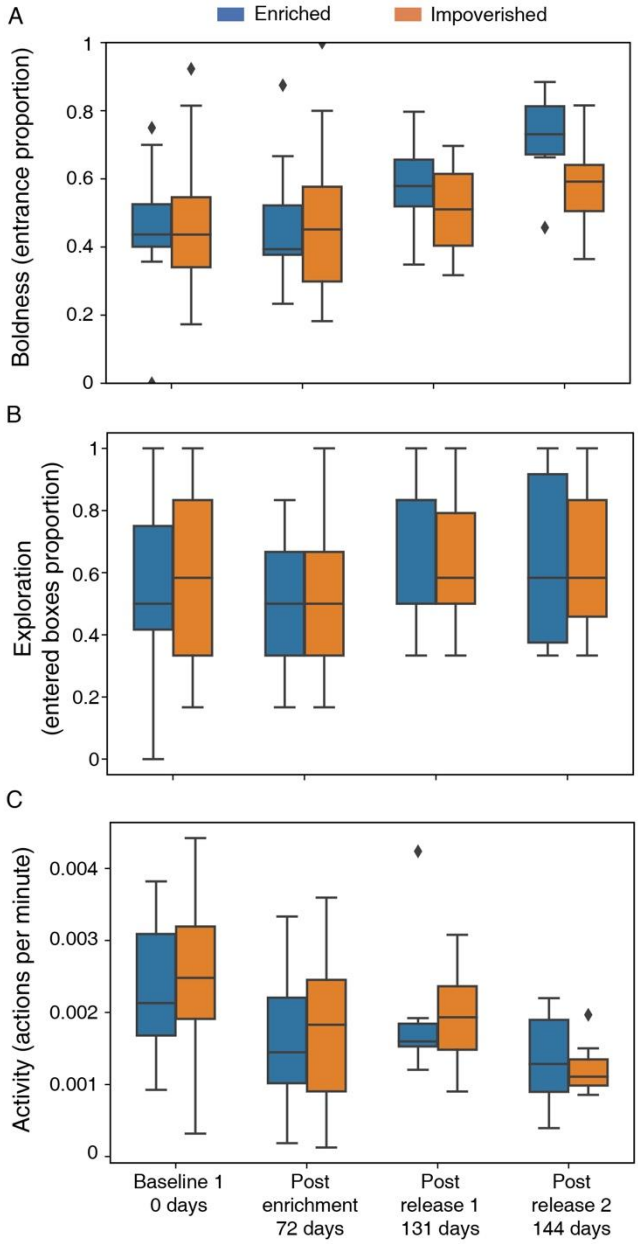

Figure 2. Bat behavioral traits over time. Box plots depicting the bats' behavior across the five trials according to three traits: Boldness **(A)**, exploration **(B),** and activity levels **(C)**. The experimental phase and the time in days from the day of the first trial are depicted on the X-axis. Box plots show the 25% and 75% percentile. Medians and whiskers based on 1.5 IQR are shown. The number of bats participating in each trial is given in the Methods, Table 8. In the baseline trials, no significant differences were found between the two treatment groups (enriched / impoverished) for any of the three behavioral traits we measured (P = 0.62, P = 0.84, P = 0.72 for boldness, exploration, and activity levels, respectively, n=40, Table S1). Figure S1 also shows the indicating. Results of baseline 2 performed one day after baseline 1 (indicating habituation to the setup).

Despite the above-reported changes in behavior over time, the environment that the animals experienced as juveniles (enriched or impoverished) did not have a significant effect on their personality as measured in the lab (GLMM - with the behavioral traits set as the explained

parameter, the trial number (excluding Trial 2) and the interaction between trial number and the enrichment treatment as fixed factors, and bat ID as a random effect). The interaction between trial and treatment was not significant (Table 3). When examining only Trials 4-5, i.e., following their release into nature, the enriched bats were observed to be significantly bolder than the non-enriched bats (P=0.003, GLMM as above). However, this seems like a result of post-selection resulting from which bats remained in our colony and could be tested (see Discussion).

Table 2. mixed GLM results for the comparison between trials 1 and 5

Response	AIC	BIC	LogLikelihood	Deviance				
Boldness	-36.379	-28.498	22.189	-44.379				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.408	0.031	13.16	51	5.03e-18	0.346	0.471
	Trial number	0.056	0.009	6.02	51	1.902e-07	0.037	0.075
Response	AIC	BIC	LogLikelihood	Deviance				
Exploration	12.074	19.956	-2.037	4.074				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.545	0.049	11.02	51	4.248e-15	0.446	0.644
	Trial number	0.018	0.016	1.157	51	0.252	-0.013	-0.013
Response	AIC	BIC	LogLikelihood	Deviance				
Activity	-580.34	-572.46	294.17	-588.34				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.002	0.0001	13.737	51	9.050e-19	0.002	0.003
	Trial number	-0.0002	7.135e-05	-4.065	51	0.0001	-0.0004	-0.0001

Table 3. mixed GLM results for all tested trials (1-5), excluding trial 2

Response	AIC	BIC	LogLikelihood	Deviance				
Boldness	-65.459	-49.768	38.729	-77.459				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.375	0.048	7.708	97	1.11e-1	0.279	0.472
	Environmental condition Impoverished	0.043	0.067	0.637	97	0.525	-0.091	0.177
	Trial number	0.049	0.014	3.443	97	0.0008	0.020	0.077
	Environmental condition Impoverished:Trial	-0.016	0.019	-0.842	97	0.401	-0.054	0.022
Response	AIC	BIC	LogLikelihood	Deviance				
Exploration	-1.849	13.842	6.924	-13.849				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.532	0.068	7.807	97	6.87e-1	0.396	0.667
	Environmental condition Impoverished	0.001	0.094	0.019	97	0.984	-0.186	0.19
	Trial number	0.009	0.018	0.532	97	0.804	-0.043	0.056
	Environmental condition Impoverished:Trial	0.006	0.025	0.247	97	0.804	-0.043	0.056
Response	AIC	BIC	LogLikelihood	Deviance				
Activity	-1126.4	-1110.7	569.2	-1138.4				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.002	0.0002	9.791	97	3.79e-1	0.002	0.003
	Environmental condition Impoverished	0.003	0.0003	1.072	97	0.285	-30e-5	0.001
	Trial number	-0.0002	7.292e-05	-3.273	97	0.001	-30e-3	-9.e-05
	Environmental condition Impoverished:Trial	-0.0001	9.887e-05	-1.197	97	0.234	-30e-5	7.7e-05

168 ***Outdoor foraging behavior***

169 After releasing the bats into our open colony, in which they were free to fly out, we tracked
170 them using GPS devices as they explored the world for the first time and foraged in their
171 natural environment. We analyzed data from 19 bats, obtaining data from 39.2±17.0
172 (Mean±SD) foraging nights per bat on average, accounting for 72.5±8.3% (Mean±SD) of the
173 individuals' foraging nights. We used the following movement parameters as representatives
174 of the bats' outdoor behavior: the total nightly time spent foraging as a proxy for activity; the
175 explored area as a proxy for exploration; and the maximal distance from the colony as a proxy
176 for boldness (see Methods).

177 The enriched bats significantly differed from the impoverished bats in all these movement
178 parameters (Figure 3). Specifically, they spent significantly more time out foraging every night
179 (3.5±1.9 vs. 2.8±1.8 hours), flew farther from the colony (1.3±1.8 vs. 0.8±1.13 km), and
180 explored larger areas (10.3±7.1 vs. 2.4±0.8 km^2); all values represent the Mean±SD for the
181 entire study period (19 bats). Examination of the data after 15-20 nights outside (all bats have
182 been out for a similar period; n=17 bats with data) the pattern was the same and the values
183 were: 4.02±1.19 vs. 2.8±0.75 hours, 1.66±1.77 vs. 0.6±0.28 km (only exploration was assessed
184 for the entire period).

185 To assess the relative effects of experience (i.e., enriched/impoverished) on foraging and to
186 compare it to the bats' original predisposition, we ran a GLMM, with their original
187 predisposition (Trial 1) and environment (enriched / impoverished) as fixed factors, and the
188 bats' boldness/exploration/or activity estimates in Trial 1 as a proxy for their innate
189 predisposition, because these had been examined before the bats were exposed to the
190 different environments.

191 The analysis revealed that the environment in which the bats were reared was more important
192 than their original predisposition for explaining their outdoor foraging behavior. While the
193 effect of predisposition was not significant, the enriched environment significantly correlated
194 with spending more time outside, flying to a significantly larger maximal foraging distance,
195 and exploring a larger area ($P<0.04$, $P<0.02$, and $P<0.001$, respectively, GLMM and see Table
196 4a-c, with the environmental condition as the predisposition and the experience as fixed
197 factors. A model that includes an interaction between the predisposed boldness, exploration,

198 or activity and the environmental treatment, showed a worse fit (higher AIC). The bats'
199 experience (represented by the number of nights they spent foraging until the day of the
200 assessment), also had a significant positive effect, increasing the nightly foraging time and the
201 maximal distance (P<0.0006, and P<0.004; GLMM for the time spent outside and the maximal
202 nightly distance respectively, Table 4a-c). The bats' age (days from birth) did not have a
203 significant effect.

204 We also tested the correlation between the behavioral traits measured in the wild and found
205 a significant positive correlation between all the traits but with a limited explained variance,
206 suggesting that they represent different behavioral aspects (Pearson correlation test; Table 5).
207

208 **Table 4a.** GLMM results for outdoors measurements with the first boldness as
209 predisposition.

Response	AIC	BIC	LogLikelihood	Deviance				
Time spent outside	8638.2	8674.8	-4311.1	8622.2				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	185.42	74.081	2.469	710	0.013	38.014	332.83
	Environmental condition Impoverished	-57.736	26.374	-2.189	710	0.028	-109.52	-5.956
	Boldness of the first baseline	-32.783	78.474	-0.417	710	0.676	-186.85	121.29
	Bat sex Male	-9.0905	26.014	-0.349	710	0.726	-60.163	41.982
	Bat age	0.029	0.217	0.135	710	0.892	-0.397	0.456
	Number of days sepnt outside until assasment day	1.416	0.351	4.028	710	6.1e-05	0.726	2.106
Response	AIC	BIC	LogLikelihood	Deviance				
Maximum distance per night	12437	12474	-6210.7	12421				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	1543.2	651.67	2.368	710	0.018	263.73	2822.6
	Environmental condition Impoverished	-591.24	228.02	-2.592	710	0.009	-1038.9	-143.57
	Boldness of the first baseline	-550.64	649.03	-0.848	710	0.396	-1824.9	723.6
	Bat sex Male	-262	224.84	-1.165	710	0.244	-703.43	179.42
	Bat age	-0.705	1.888	-0.372	710	0.708	-4.414	3.002

	Number of days sepnt outside until assasment day	10.982	3.868	2.838	710	0.004	3.386	18576
Response	AIC	BIC	LogLikelihood	Deviance				
Explored area	115.75	122.87	-49.875	99.749				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	13.021	6.173	2.109	12	0.056	-0.428	26.472
	Environmental condition Impoverished	-8.664	2.035	-4.256	12	0.001	-13.100	-4.229
	Boldness of the first baseline	-4.375	6.311	-0.693	12	0.501	-18.126	9.375
	Bat sex Male	-0.340	2.210	-0.154	12	0.880	-5.157	4.475
	Bat latest age	-0.030	0.021	-1.374	12	0.194	-0.077	0.017
	Total amount of nights the bat spent outside	0.157	0.072	2.155	12	0.052	-0.001	0.315

Table 4b. GLMM results for outdoors measurements with the first exploration as predisposition

Response	AIC	BIC	LogLikelihood	Deviance				
Time spent outside	8638.3	8674.9	-4311.2	8622.3				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	150.46	94.662	1.589	710	0.112	-35.395	336.31
	Environmental condition Impoverished	-54.536	27.037	-2.017	710	0.044	-107.62	-1.454
	Exploration of the first baseline	12.267	57.784	0.212	710	0.831	-101.18	125.72
	Bat sex Male	-9.138	27.2	-0.335	710	0.736	-62.54	44.263
	Bat age	0.085	0.253	0.338	710	0.734	-0.411	0.582
	Number of days sepnt outside until assasment day	1.346	0.391	3.437	710	0.0006	0.577	2.116
Response	AIC	BIC	LogLikelihood	Deviance				
Maximum distance per night	12438	12475	-6211	12422				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	1212.7	841.79	1.440	710	0.150	-440.04	2865.3
	Environmental condition Impoverished	-559.99	236.37	-2.369	710	0.018	-1024.1	-95.913

	Exploration of the first baseline	2.282	495.25	0.004	710	0.996	-970.04	974.61
	Bat sex Male	-293.2	236.43	-1.240	710	0.215	-757.38	170.98
	Bat age	-0.254	2.244	-0.113	710	0.909	-4.662	4.152
	Number of days sepnt outside until assasment day	10.533	4.220	2.495	710	0.012	2.246	18.819
Response	AIC	BIC	LogLikelihood	Deviance				
Explored area	116.22	123.34	-50.111	100.22				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	10.701	8.132	1.315	12	0.212	-7.017	28.419
	Environmental condition Impoverished	-8.578	2.142	-4.004	12	0.001	-13.246	-3.911
	Exploration of the first baseline	-0.217	4.555	-0.047	12	0.962	-10.142	9.708
	Bat sex Male	-0.813	2.288	-0.355	12	0.728	-5.799	4.172
	Bat latest age	-0.028	0.026	-1.095	12	0.294	-0.086	0.028
	Total amount of nights the bat spent outside	0.166	0.076	2.171	12	0.050	-0.0005	0.033

Table 4c. GLMM results for outdoors measurements with the first activity as predisposition

Response	AIC	BIC	LogLikelihood	Deviance				
Time spent outside	8638	8674.6	-4311	8622				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	144.04	70.124	2.054	710	0.040	6.363	281.71
	Environmental condition Impoverished	-59.582	26.619	-2.238	710	0.025	-111.84	-7.320
	Activity levels of the first baseline	7523	13220	0.569	710	0.569	-18432	33478
	Bat sex Male	-4.216	28.018	-0.150	710	0.880	-59.225	50.792
	Bat age	0.057	0.206	0.277	710	0.781	-0.348	0.463
	Number of days sepnt outside until assasment day	1.374	0.342	4.010	710	6.7e-05	0701	2.026
Response	AIC	BIC	LogLikelihood	Deviance				
	12435	12472	-6209.6	12419				

Maximum distance per night	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	618.48	596.04	1.037	710	0.299	-551.74	1788.7
	Environmental condition Impoverished	-647.23	219.58	-2.947	710	0.003	-1078.3	-216.13
	Activity levels of the first baseline	1.88e+05	1.09e+05	1.722	710	0.085	4e+05	400900
	Bat sex Male	-103.57	237.1	-0.436	710	0.662	-569.06	361.93
	Bat age	-0.077	1.713	-0.045	710	0.963	-3.441	3.286
	Number of days sepnt outside until assasment day	9.831	3.774	2.604	710	0.009	2.420	17.242
Response	AIC	BIC	LogLikelihood	Deviance				
Explored area	116.17	123.3	-50.087	100.17				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	9.217	7.259	1.269	12	0.228	-6.599	25.035
	Environmental condition Impoverished	-8.555	2.053	-4.167	12	0.001	-13.029	-4.082
	Activity levels of the first baseline	299.990	1360.300	0.220	12	0.829	-2663.800	3263.7
	Bat sex Male	-0.321	2.975	-0.107	12	0.915	-6.803	6.161
	Bat latest age	-0.025	0.026	-0.958	12	0.356	-0.822	0.031
	Total amount of nights the bat spent outside	0.150	0.099	1.516	12	0.155	-0.6570	0.367

Table 5. Pearson correlation test results

	Pearson r value	Pearson P value
Time spent out vs maximal distance	0.24	<2.72e-11
Time spent out vs explored area	0.09	<0.009
Maximal distance vs explored area	0.2	<3.15e-8

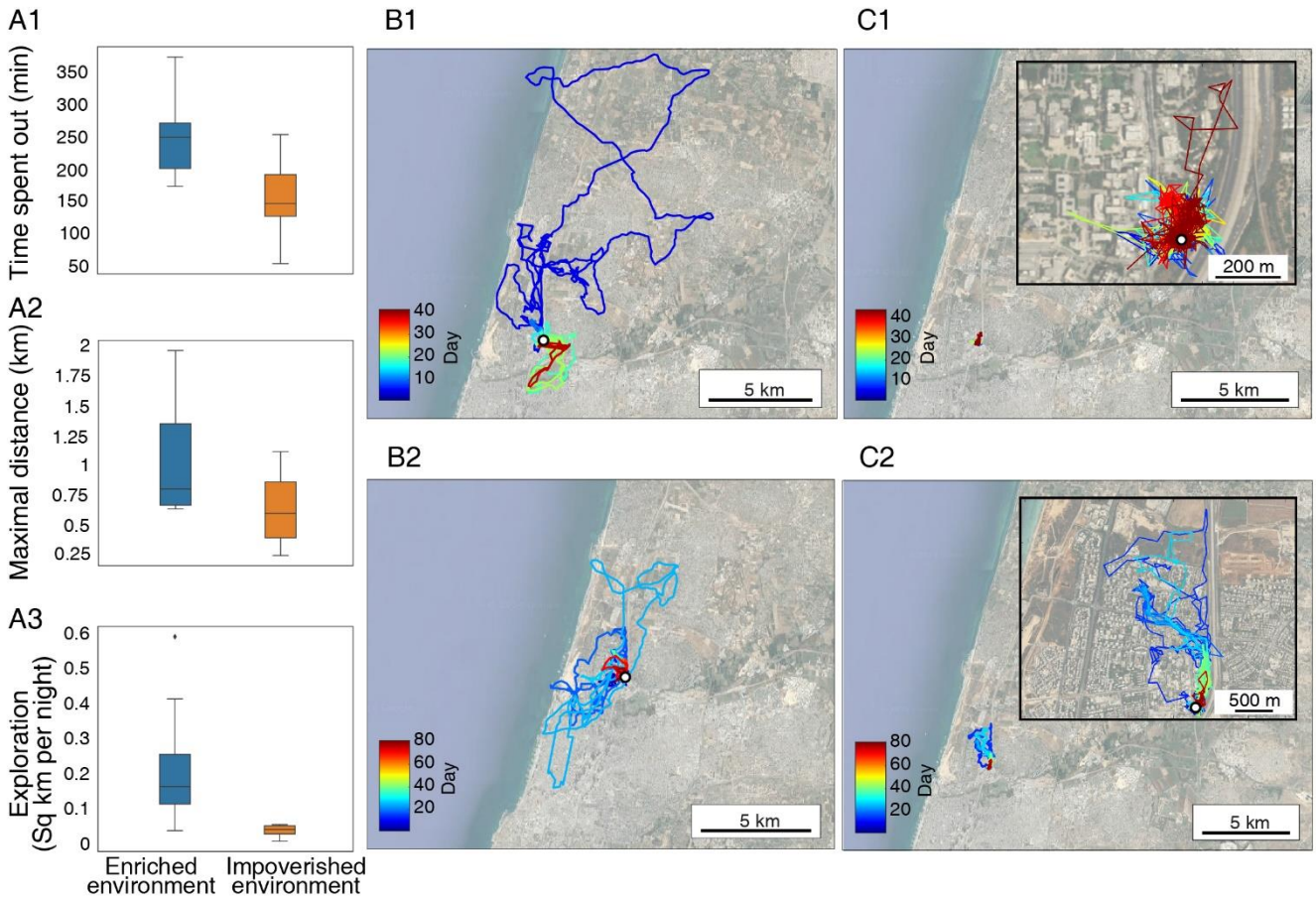

Figure 3. Early environmental exposure affects outdoor foraging behavior. (A1) Time spent by the bats outside the colony each night (in minutes). **(A2)**. Distance to the furthest point from the colony per night. **(A3)** The area explored by the bats. The data for foraging time and distance for each bat were estimated for the period between its 15th and 20th day outdoors (n=17 bats). The exploration data are for the entire season. Median and whiskers based on 1.5 IQR are shown. **(B-C)** The complete movement of four individuals - two from each colony. **(B)** Individuals raised in the enriched colony, data shown for two individuals (B1,B2); **(C)** Individuals raised in the impoverished colony, data shown for two individuals (C1,C2). Colors depict time in days. The open colony is marked by a white circle. Insert in C1-2 zooms-in on the tracks. All maps present the entire movement of four individual bats.

Lastly, we compared the foraging behavior outdoors to the behavioral personality traits measured in the indoor foraging task (assessed ~two weeks following their release into the open colony - Trial 4). There was no significant correlation between indoor personality and any of the outdoor foraging characteristics. (Pearson correlation test, P>0.05 for all comparisons).

Discussion

Intra-specific inter-individual behavioral differences have been documented in many species[5,6,8], but very few studies have explored the processes leading to these differences. In

this study, we used a controlled manipulation to examine the effects of the early-life environment to which juvenile fruit-bats had been exposed on their adult behavior.

We demonstrate that early exposure to an enriched environment seems to affect the foraging behavior of bats in the wild. Bats that were exposed early on to an enriched environment were bolder (i.e., flew farther from home), and were more exploratory. Moreover, their early exposure was a better predictor of their foraging behavior than their individual behavioral predisposition that had been measured indoors before they had any experience of the outside world. We assessed the bats' predispositions at a very young age, as soon as they could fly but before they had a chance to gain any experience. These dispositions are thus likely innate, but we note that they might also have been shaped by maternal effects (e.g., by hormonal transfer, see [10]) in addition to genetics. Moreover, it is possible that a different set of personality traits might have predicted outdoor behavior better than those we used here although we should note that we chose personality traits commonly used in such studies.

Our findings are in line with the findings from previous research of other organisms that showed that individuals raised in enriched environments [12,13,15,16] exhibited higher levels of boldness and exploratory behavior. Moreover, studies have shown that exposure to enriched environments enhances motor skills in animals [13]; and growing up in complex environments has been associated with improved learning abilities and with the utilization of multiple cues for obtaining rewards [15]. Notably, unlike any previous study, our experimental paradigm allowed us to examine the animals' behavior in their natural habitat following manipulation of their environment early on in life.

Indoor behavior

In contrast to the outdoor behavior, the behavioral traits that we assessed in controlled indoor experiments were not affected by the early environmental enrichment, i.e., enriched bats did not become bolder or more exploratory under laboratory conditions. When examining the bats' behavioral traits across the five trials, we found that boldness and exploration demonstrated a similar temporal dynamics, increasing between consecutive trials that were performed closely to one another in time and decreasing following a prolonged period since the previous trial (Figure 2). This pattern indicates that despite the bats' initial habituation to the set-up, following a period of no exposure to the set-up, the bats' boldness (or exploration)

again reduced, probably due to some sort of sensitization to the set-up. The bats maintained their within-individual tendencies while doing so, suggesting that indeed boldness (and to a lesser degree exploration) were good measures of consistent personality. It is possible that a different measure of exploration (one that does not suffer from a ceiling effect like the one we used here) might have shown more consistency over time. Activity in contrasts continuously (and significantly) showed a different pattern decreasing over time independently of the time elapsed between trials (Figure 3). This decrease in activity reflects familiar bat pups' behavior, which usually becomes less frenetic over time.

The enriched bats were significantly bolder in Trial 5 (Figure 2), but we suspect this was a result of a post-selection bias generated by a greater number of bold individuals in the enriched treatment having remained in our colony until the end of the study, while many of the bolder ones from the impoverished treatment left the colony earlier and probably moved to other colonies. This difference (which was likely random) can be seen in Figure 2 when examining only the bats that had remained until the last trial (Figure 2A2). However, this post-treatment selection is probably not what drove the effect we observed outdoors, as there was no correlation between the indoor and outdoor behaviors.

Outdoor tracking

The enriched bats spent significantly more time foraging outdoors, exhibited greater flight distances, and were more exploratory compared to the impoverished bats. These differences could result in actual differences in foraging success. As fruit bats must constantly keep track of an ever-changing landscape of resources (fruit trees)[24], being exploratory might pose an advantage for such individuals, especially in a rapidly changing urban environment.

Research conducted by Egert-Berg et al. (2021), focusing on the foraging behavior of Egyptian fruit bats in the wild, demonstrated that bats that roost in cities display more exploratory behavior than bats that roost in rural habitats. Our current study suggests how such differences in behavior could arise as a result of early-life exposure to an enriched environment such as that in the urban environment, which is much more diverse and dynamic than the rural environment. Urban roosting bats encounter more types of food and must practice more diverse skills to obtain it, like the bats in our enriched colony. Our findings can thus explain how bats and other animals with early exposure to the urban environment

become more exploratory. Although fruit-bat pups tend to be more active than adults, it is possible that such adaptations can also be acquired by the adults as well.

The lack of correlation found between the indoor and outdoor behaviors emphasizes the significance of assessing behavior in the bats' natural habitat to obtain more reliable and meaningful results. While measuring personality traits, particularly boldness and exploration, in a small captive setup clearly assesses some aspects of personality, translating these to behavior in the real world could be problematic (although some studies have found an indoor/outdoor correlation in other animals; see [25]).

Overall, our study provides evidence of the profound impact of early life environmental conditions on the behavior of the adult bats. These findings contribute to our understanding of the developmental factors that shape animal behavior and highlight the importance of environmental enrichment during the early life stage.

Methods:

Ethical statement

Experiments were approved by the TAU IACUC; permit number: 04-18-030. Capture of Egyptian fruit bats for the research was approved by the Israel National Park Authority, permit number 2020/42646.

Experimental animals

The experiment was conducted on young Egyptian fruit bats. A total of 40 bats were captured from three wild colonies (Herzliya, Beit Guvrin, and Tinshemet; Table 6) between the years 2019-2021 and housed in the Zoological Garden at Tel Aviv University. We captured pregnant females or females with young pups before their volant stage, to ensure that the pups would be naïve and without previous individual flight experience. Of the 40 bats in the study, 21 were born in our lab and 19 were captured at a very young age together with their mothers, before they could fly independently. To avoid an origin bias, bats from all colonies were divided equally and housed in two identical rooms (~2.5x2x2.5m^3, Table 6), maintained at a controlled temperature of 24-26°C and a light cycle approximately matching the times of sunrise/sunset. The bats' diet in both environments comprised seasonal mixed fruits (watermelon, apples, melons, and bananas *ad lib*).

Upon arrival, the bats' weight and forearm were measured and documented. Each mother-pup pair was bleached with a unique mark, and each bat was also tagged with a subcutaneous electronic RFID chip. All bats were measured and checked regularly to make sure they were healthy. Three individuals were removed from the experiment: two due to injury (broken wings), and one due to weight loss (>10% loss of their weight previous body weight).

Environmental conditions

While both colonies were provided with the same basic conditions and food, the bats in the "enriched" environment regularly experienced varying environmental enrichment three times a week, including changing the number and shape of food bowls, hanging food baskets from the ceiling, playback of vocalizations recorded from a larger colony, and adding rope ladders or ropes hanging from the ceiling. In the "impoverished" environment the animals

experienced a dull environment with no variation in conditions throughout the study period. They received their food in one bowl, while nothing was hung from the ceiling and no other enrichment was provided.

Table 6. Egyptian Fruit bat pups were captured with their mothers in rural and urban colonies and then divided between two experimental conditions, enriched and impoverished.

Season	Environmental condition	Colony ID	Coordinates	Number of pairs
1 (2019-2020)	Enriched	Tinshemet	31°59'43.2"N 34°57'19.2"E	1
		Beit Guvrin	31°36'45.8"N 34°53'41.7"E	1
		Herzliya	32°10'18.4"N 34°48'51.1"E	4
	Impoverished	Tinshemet	31°59'43.2"N 34°57'19.2"E	1
		Beit Guvrin	31°36'45.8"N 34°53'41.7"E	1
		Herzliya	32°10'18.4"N 34°48'51.1"E	3
2 (2020-2021)	Enriched	Beit Guvrin	31°36'45.8"N 34°53'41.7"E	5
		Herzliya	32°10'18.4"N 34°48'51.1"E	9
	Impoverished	Beit Guvrin	31°36'45.8"N 34°53'41.7"E	5
		Herzliya	32°10'18.4"N 34°48'51.1"E	10

Defining baseline personality in juveniles – the foraging box experiment

As juveniles (55-281 days old), the young bats participated in a foraging box experiment to examine a set of personality traits in a captive setting [10]. The experimental set-up consisted of an indoor tent (3.9x2.7x1.9 m^3), with six evenly spaced black plastic boxes placed on the floor (i.e. foraging box, 64x38x40 cm^3). Each box had a round hole in its lid (10 cm diameter) with a mesh ladder leading down to a food bowl, containing sufficient amount of food for the bat for

an entire night, to prevent the bat from selecting another box simply because the first one is empty (figure 4).

The exposure phase. Bats are social animals [26,27]. To reduce the stress of being alone in a new environment before the first trial, a group of 4-5 pups from the same environment was placed in the tent overnight (16:00-8:00) for a session of exposure. Each of the six boxes contained an amount of food sufficient for all of the bats taking part in the exposure.

The Experiment. Following this one night of introduction, each pup (n=39, see Table 8) was placed alone in an open carrying bag (35x26x30 cm^3) inside the flight tent with the six foraging boxes (described above) for a full night. Each food bowl offered an amount of food that was enough for the full night, containing 25 pieces of fruit (with a total weight of 150 g) and 50 ml mango nectar. The experiment took place two nights in a row to determine behavioral consistency. The experiment was recorded using an IR video camera (Sony HDRCX730, Sony FDR-AX53), together with one infrared light (Methaphase Technologies Inc-ISO-14- IR-24) placed inside the tent.

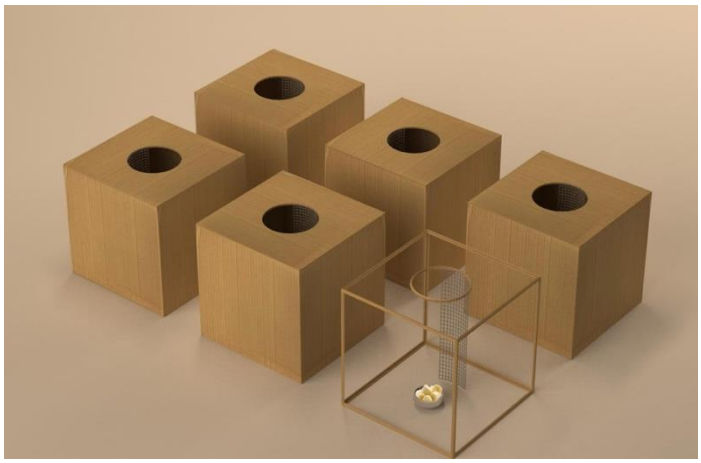

Figure 4. Experimental set-up schematic. Each bat is placed in a tent with 6 foraging boxes

The environmental enrichment began only after all the bats in the enriched room had completed the baseline experiments (see Table 7 for the full time-line of the experiment). Both groups then experienced the (enriched/impoverished) environment for at least two months before moving on to the next stage the open colony, from which the bats are free to fly in and out as they choose (see details below).

375 **Table 7.** Full time-line of the experiment

	October-December				December-June	
2019-2020	Baseline Trials N=11	Environmental enrichment		Release to open colony	Tracking bats using GPS devices N=10	Post release trials N=9
2020-2021	Baseline Trials N=29	Environmental enrichment	Post-enrichment trial N=29	Release to open colony	Tracking bats using GPS devices N=11	Post release trials N=10

376 During the second season (year 2020-21), following the exposure to the environmental
377 conditions, all bats (n=29, Table 8) underwent an additional night in the foraging box
378 experiment to evaluate the effect of the enriched environment. This additional trial took place
379 prior to their transfer to the open colony and is termed the "post-enrichment trial".

380 ***Personality after foraging in the wild***

381 Bats that routinely exited the open colony to forage and returned were twice tested again in
382 the foraging box experiment: 2-3 weeks following their first exit, and 5-6 weeks following their
383 first exit. A total of 19 bats were tested for these trials (see Table 8).

384 **Table 8.** Number of bats that participated in each of the trials

	Environmental condition	Baseline (both 1+2)	Post-enrichment trial	Post release trials (4+5)
Season 1	Enriched	6	-	4
	Impoverished	5	-	5
Season 2	Enriched	13	14	5
	Impoverished	15	15	5
Total number of bats		39	29	19

385
386 ***Behavioral analysis***

387 Each bat's actions during the foraging box experiment were documented based on video
388 recordings by two independent observers. In cases of disagreement, a third observer
389 compared the two and made the final judgement. The identified actions comprised: landing

390 on or entering the carrying bag in which the bats had been introduced into the room; landing;
391 entering the food boxes; collecting food; or flying around to explore the environment.

392 Similar to our previous study [28], we then calculated the following personality traits:

393 **Boldness/Risk-taking:** boldness can be defined in several ways [29]. We measured it as the
394 proportion of times the bat entered the boxes out of the total number of landings, entering
395 and collecting for from the boxes. A previous study has shown that entering boxes placed on
396 the ground is a risky behavior that a bat generally avoids [28].

397 **Exploration:** the exploratory index was calculated as the number of individual foraging boxes
398 the bat visited (i.e., 0-6). Note that each box contained enough food for the entire night
399 eliminating the need for it to visit more than one box.

400 **Activity:** activity level was defined as the number of interactions with the boxes (landings and
401 entries) normalized by the total time in the experiment (i.e., after the bat had left the carrying
402 bag for the first time).

403 ***Statistical analysis of the behavioral trials***

404 To verify that there were no behavioral differences prior to applying our treatment, we
405 compared the baseline trials between the two colony conditions (Table S1). We used mixed-
406 effect general linear model (GLMM), with the traits set as the response variable, the
407 environmental condition and trial number (baseline 1 or 2) set as fixed factors, and bat ID set
408 as random effect (n=39, Table 8).

409 We use the term "personality" to encompass a set of behavioral traits that exhibit consistency
410 within individuals over time and across various contexts [1]. To evaluate the consistency of the
411 measured behavioral traits, we conducted a comparison between the bats' first trial (baseline
412 1) and the trial conducted following their exposure to the different environmental conditions
413 (post-enrichment trial). These analyses incorporated only the individuals from the second
414 measuring season, because we only ran the post-enrichment measurement during the second
415 season.

416 To assess the impact of the environmental condition on each behavioral trait, we employed
417 GLMMs. We used the behavioral trait as the explained parameter, the tested environmental

condition (i.e., enriched or impoverished), trial number (1-5), and the interaction between environmental conditions and trial number as fixed factors. Bat ID was set as a random effect. We excluded the behavioral data collected during the second baseline.

Analyzing the bats' outdoor foraging behavior

Following the captive stage described above, bats were transferred to our open colony, an Egyptian fruit bat colony, representing a natural urban roost where bats can exit nightly to forage in the wild and return to roost in our fully monitored day-roost (or move to a different roost). Food is provided in the roost every evening. This system allows us to continuously monitor the bats' natural behaviors within and outside the roost [30].

The bats were released in groups of 4-6 individuals (et an average age of 218.92±56.8 days) from the same experimental colony (either the enriched or impoverished environment), alternately between these two environmental conditions. Each bat was fitted with an on-board GPS device (Vesper, ASD inc.) following its 2nd foraging night in the wild, in order to monitor most of the navigational history of all individuals. The device was coated using Parafilm (Heathrow Scientific) and duct tape, and was attached to the bats using a chain necklace covered with heat-shrink (see full details in [31]. The mean weight mounted on the bats was 6 gr, accounting for 5.6% ± 0.6% of the bats' weight. The GPS was programmed to start recording a few hours before sunset and stopped at 6:00AM, collecting GPS locations every 30 seconds.

These data allowed us to assess various parameters extracted from the individuals' natural foraging behavior, which served as proxies for their exploratory and activity tendencies. Specifically, we measured the:

Maximum flying distance: Defined as the distance to the furthest point from the open colony that the bat reached on every night outside.

Time spent outdoors: Defined as the total time the bat spent outside the colony on a given night. Nights when a bat did not leave the colony (6.2 days per bat on average) were not included in the analysis.

The explored area was estimated as follows: The area used by all bats during both seasons was divided into a grid of equal sized squares (1.0x0.85km^2). We then counted the number of

squares traversed by each bat throughout the whole season and calculated the average number of squares that a bat traversed every night.

Statistics: To examine the influence of the environmental condition (i.e., enriched or impoverished), we used GLMs for each of the three outdoor traits, with the traits set as the explained parameter. Environmental condition, bat age and sex, and the number of nights the bat spent outside until the assessment day were set as a fixed effect. For the explored area analysis, the total number of days the bat spent outside during the entire tracking period and the bat's age at the last time of measuring were set as fixed effects. For the maximum distance and the time spent outdoors, we used data from each night the bat was outside. Explored area receiving only one (seasonal) measurement for each bat.

Captivity and outdoor comparison

We sought to demonstrate the effectiveness of our captive setup by comparing the individual's behavior in both indoor and outdoor settings. To achieve this, we analyzed the Pearson correlation between the first post-release trial and the average of the subsequent five days of outdoor measurements using Pearson correlation test. In addition, we tested the correlation between the individual’s first post-release trial and the average of its subsequent 20 days outdoor measurements.

Author contribution: A.R., Y.Y., and L.H. Conceived and designed the research. A.R, R.A and N.G. collected the data. A.R., A.G., and X.C. analyzed the data. A.R. and Y.Y. wrote the manuscript. A.G. reviewed and edited the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare that they have no competing interests.

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Availability of data and materials: The datasets generated and analyzed during the current study are available on Mendeley Data: DOI: 10.17632/wh7c636y3t.1

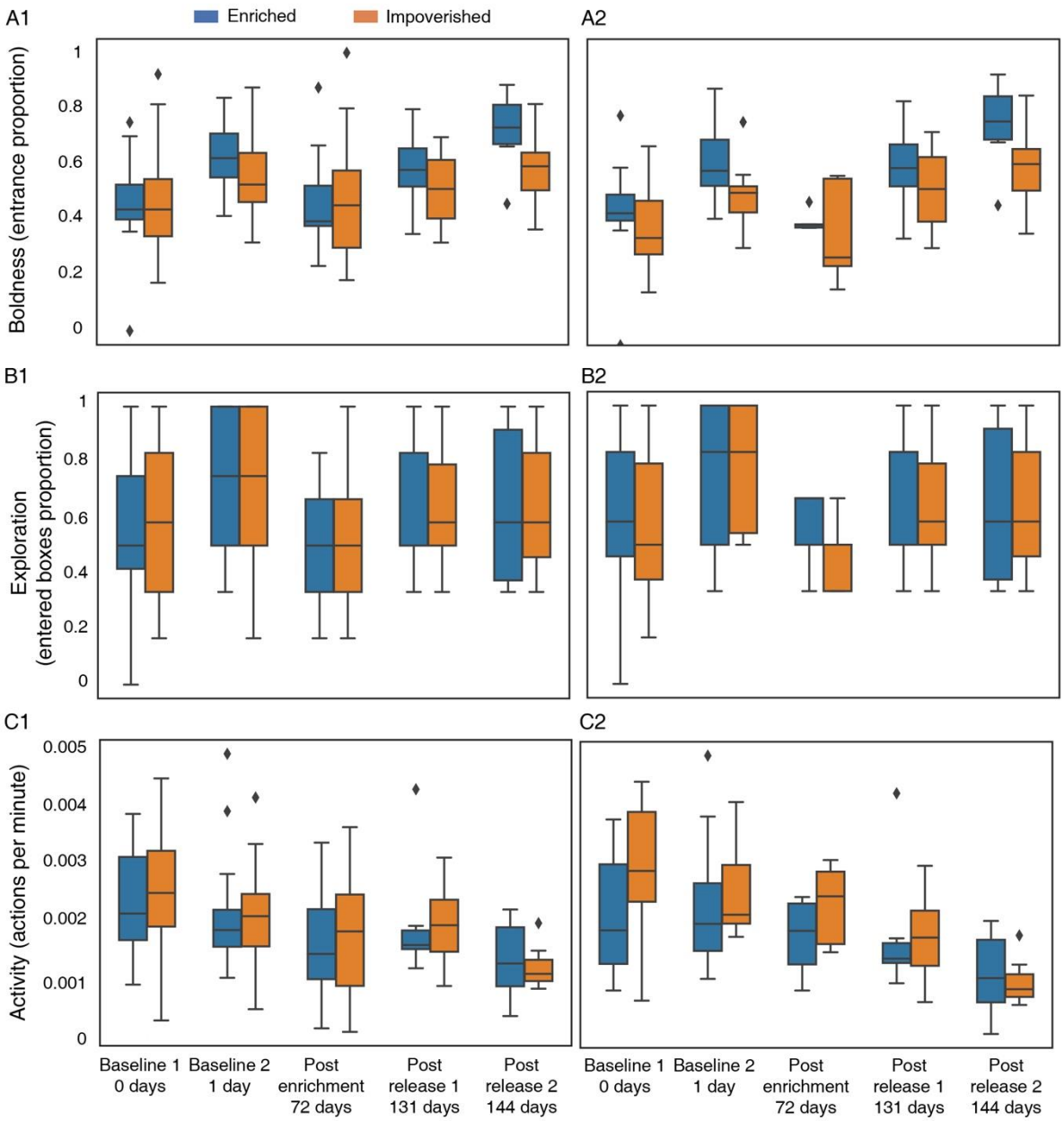
Supplementary

Table S1. Mixed GLM results for baseline trials of two environmental conditions

Response	AIC	BIC	LogLikelihood	Deviance				
Boldness (N=40)	-74.127	-62.28	42.064	-84.127				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.340	0.047	7.244	76	3.031e-10	0.246	0.434
	Environmental condition	-0.022	0.044	-0.497	76	0.620	-0.110	0.066
	Trial number (1 or 2)	0.133	0.023	5.776	76	1.581e-07	0.087	0.178
Response	AIC	BIC	LogLikelihood	Deviance				
Boldness (N=19)	-30.614	-22.559	20.307	-40.614				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.303	0.071	4.239	34	0.0001	0.157	0.448
	Environmental condition Impoverished	-0.071	0.055	-1.303	34	0.201	-0.184	0.04
	Trial number (1 or 2)	0.137	0.038	3.59	34	0.001	0.059	0.215
Response	AIC	BIC	LogLikelihood	Deviance				
Exploration (N=40)	-8.551	3.295	9.275	-18.551				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.416	0.071	5.854	76	1.145e-07	0.274	0.558
	Environmental condition	-0.014	0.074	-0.199	76	0.842	-0.163	0.133
	Trial number (1 or 2)	0.160	0.031	5.111	76	2.312e-06	0.097	0.222
Response	AIC	BIC	LogLikelihood	Deviance				
Exploration (N=19)	6.103	14.158	1.948	-3.896				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.392	0.113	3.444	34	0.001	0.161	0.623
	Environmental condition Impoverished	-0.003	0.103	-0.033	34	0.973	-0.213	0.206
	Trial number (1 or 2)	0.190	0.055	3.463	34	0.001	0.078	0.302
Response	AIC	BIC	LogLikelihood	Deviance				
Activity level (N=40)	-874.680	-862.840	442.360	-884.680				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper

	Intercept	0.002	0.0002	8.993	76	1.371e-13	0.002	0.003
	Environmental condition	0.000	0.0002	0.358	76	0.721	-0.0004	0.0006
	Trial number (1 or 2)	-0.000	0.0001	-2.175	76	0.032	-0.0006	-2.78e-05
Response	AIC	BIC	LogLikelihood	Deviance				
Activity level (N=19)	-399.320	-391.270	204.660	-409.320				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.002	0.0005	5.118	34	1.205e-05	0.001	0.003
	Environmental condition	0.000	0.0003	1.186	34	0.243	-0.0002	0.001
	Trial number (1 or 2)	-0.000	0.0002	-0.419	34	0.677	-0.0006	0.0004

489 Figure S1. **Full bat behavioral traits over time**



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