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

Significance statement

Animals exhibit individual personalities, but how they are shaped is unknown. By employing controlled manipulations on new-born bat pups and GPS-tracking them outdoors as adults, we reveal that the early life conditions bats are exposed to have a significant impact on their foraging behavior as adults. We moreover show that the original individual predispositions of the bats do not predict their behavior. These findings enhance our understanding of the developmental factors that shape animal behavior and emphasize the vital importance of environmental enrichment during early life stages.

Introduction:

Anyone who has ever observed animals knows that individuals 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 such as 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 pools 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 and outdoors foraging. Specifically, we examined whether exposure to an enriched environment as pups, affects the bats' behavior as measured in the lab and 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 behavioral 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 foraging box experimental setup was designed to assess the innate personality traits in bats which we could then use as parameters when trying to explain their foraging outdoors. Repeated measurements were used to confirm that the traits met the criteria for personality, such as consistency over time. 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. Importantly, bats in both colonies were raised in large social groups of similar size. 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). Post-enrichment and post-release trials were conducted to assess whether early life experiences had an effect on the development of bat personality and in order to identify persistent personality traits that can be used as a proxy of the individual innate predispositions. 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 scored 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 form a triangle (Figure 1B) – reminiscent of a pareto front [23] – suggesting a trade-off between the different traits. The three vertices of the triangle (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). These results did not change also when examining the enriched and impoverished colonies separately. To compute an integrative measurement of personality, we ran a PCA analysis on the data from trials 1 and 5. We found a significant Pearson correlation ($P=0.03$, $r=0.58$, Supplementary figure S1) between the individuals' scores on PC1 in trials 1 and 5 suggesting that this measure captures a persistent representation of behavior that takes both boldness and exploration into account (the activity weight was very low).

Notably all three personality traits exhibited significant correlations in the two baseline trials suggesting that indeed they capture behavioral tendencies (Figure 2).

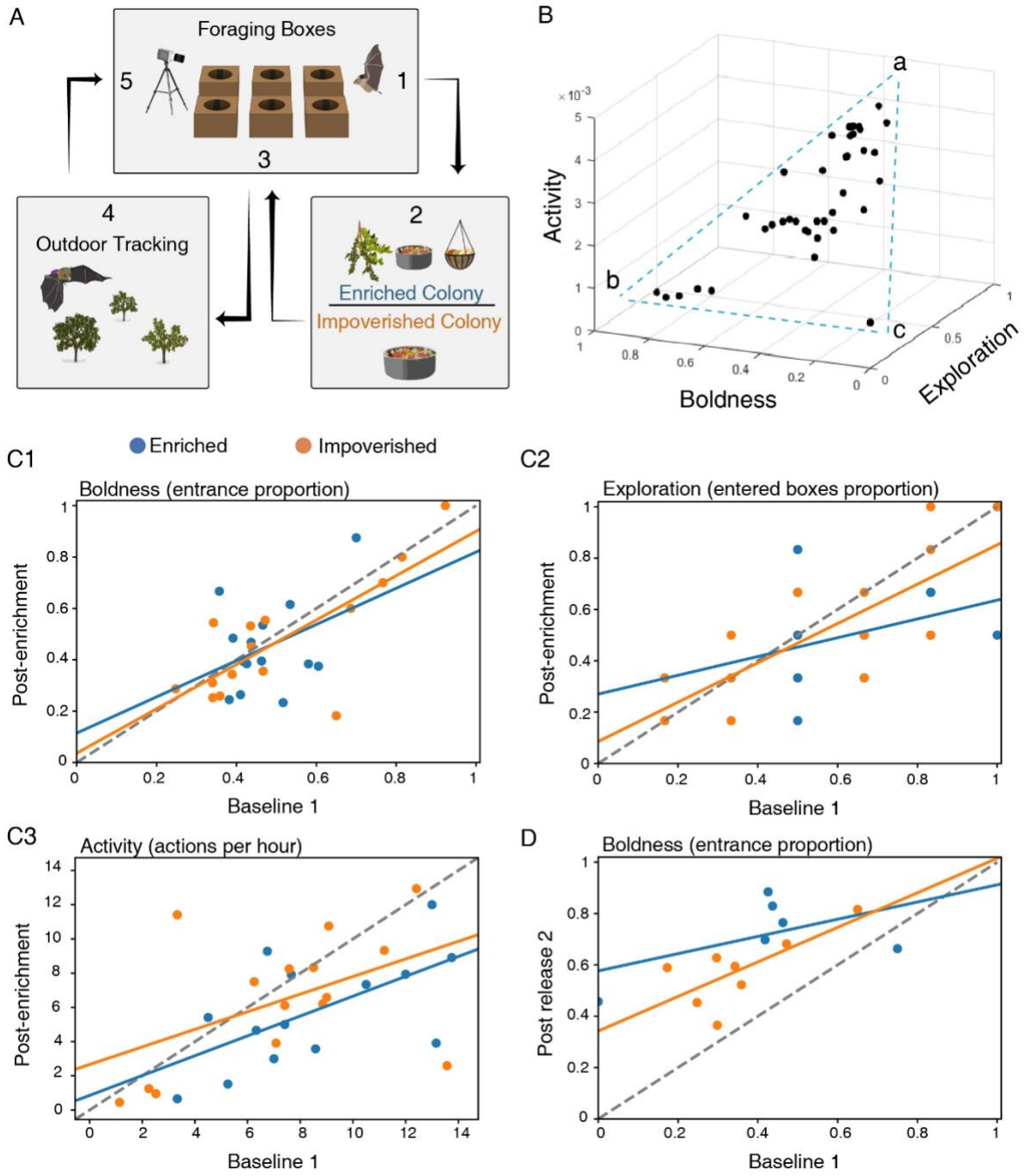

Figure 1. Assessing personality in the laboratory. (A) Schematic illustration of the experiments. **(B)** A 3D plot of the three behavioral traits, estimated during Trial 1. **(C1-3)** Behavioral traits were consistent over time. The behavioral traits of the first and third (post-enrichment) trial are presented. Positive correlations were found for all three behavioral traits over a period of more than 10 weeks. For the enriched (blue lines), the impoverished (orange lines), and both environments together (not shown), 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 temporal dynamics of boldness and exploration revealed similar patterns: both increased between the first two consecutive baseline trials (Figure 2). Following the enrichment condition (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 ($P < 1.9e-07$, see discussion). A mixed-effect Generalized Linear Model (GLMM) was used, with the behavioral traits set as the response variable, trial number (1 or 5) as a fixed factor, and bat ID as a random effect (see Table 2). While exploration showed a fairly similar pattern. Activity, in contrast, 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). An individual-level comparison between the first and last trial is presented in Figure 2C

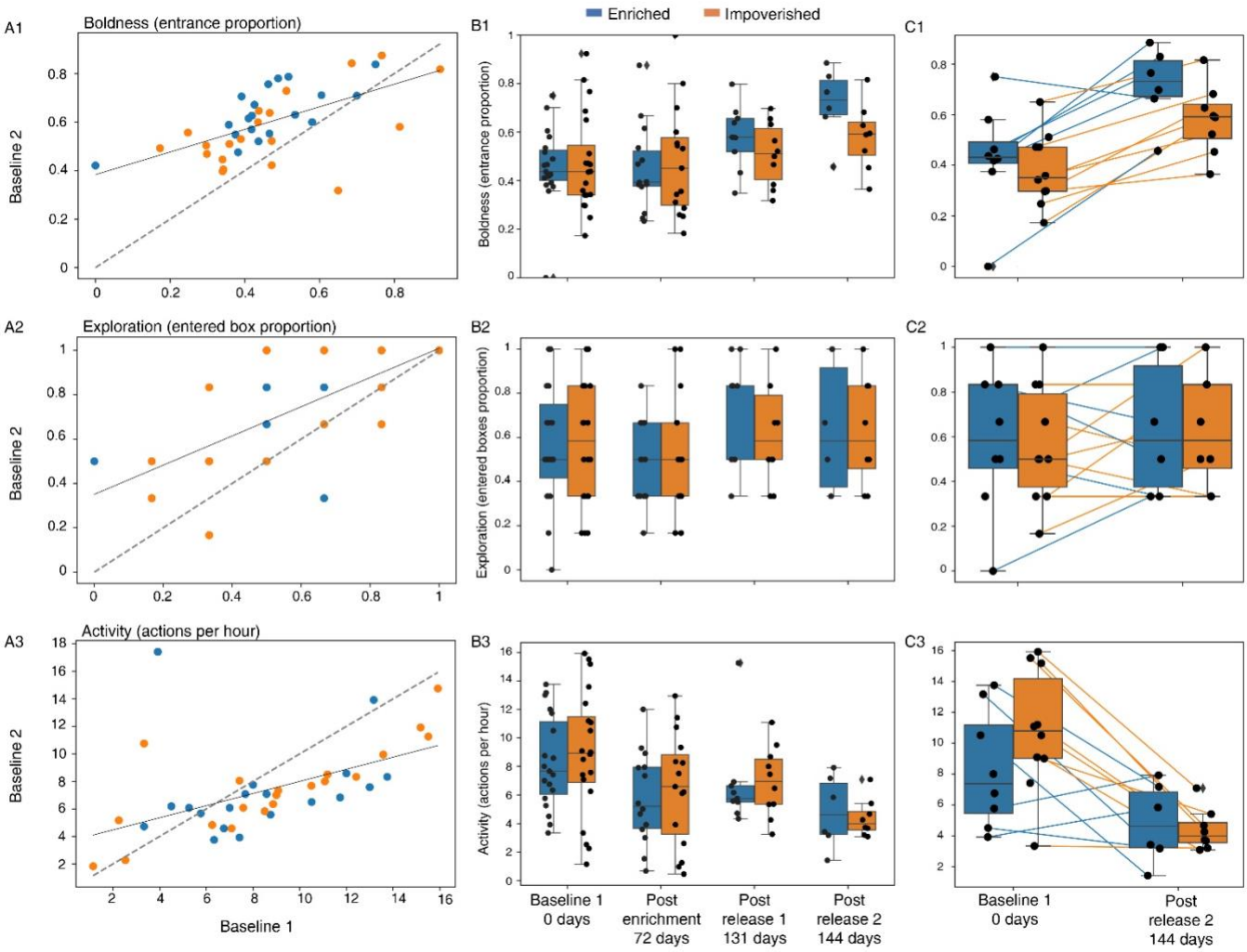

Figure 2. Personality measurements over time. (A) The behavioral traits of the first and second baseline trials, performed in two consecutive nights, are presented. Positive correlations were found for all three behavioral. Boldness (Pearson r=0.59, p=5.8e-05) **(A1)**; exploration (Pearson r=0.70, p=5.3e-07) **(A2)**; and activity (Pearson r=0.52, p=0.0005) **(A3)**.
Dashed line represents the Y=X line.
(B) Box plots depicting the bats' behavior across the five trials according to three traits: Boldness **(B1)**, exploration **(B2),** and activity levels **(B3)**. **(C)** Paired box plots show individual bat values in the first trial (baseline 1) and the fifth trial (post-release 144 days apart on average) for each trait: Boldness **(C1)**, exploration **(C2)**, and activity levels **(C3)**. Lines connect repeated measurements from the same individual, illustrating within-individual behavioral changes over time. The number of bats participated in each trial is given in Methods, Table 8. In the baseline trials, no significant differences were found between the two environmental conditions (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 S2 also shows the indication. 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.

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 response parameter, the trial number and the interaction between trial number and the environmental condition as fixed factors, and bat ID as a random effect). The interaction between trial and environmental condition 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 ~ trial + (1 | bat ID)

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)
response ~ 1 + Trial*EnvironmentalCondition + (1 | bat ID)

Response	AIC	BIC	LogLikelihood	Deviance				
Boldness	-100.5	-82.807	56.25	-112.5				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.448	0.0444	10.078	137	3.266e-1	0.36	0.536
	Environmental condition Impoverished	0.007	0.061	0.117	137	0.906	-0.115	0.129
	Trial number	0.038	0.014	2.744	137	0.006	0.010	0.066
	Environmental condition Impoverished:Trial	-0.011	0.019	-0.58	137	0.561	-0.049	0.026
Response	AIC	BIC	LogLikelihood	Deviance				
Exploration	-0.46128	17.231	6.230	-12.461				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.625	0.066	9.467	137	1.13e-16	0.494	0.755
	Environmental condition Impoverished	-0.010	0.092	-0.112	137	0.910	-0.192	0.171
	Trial number	-0.003	0.019	-0.182	137	0.855	-0.041	0.034
	Environmental condition Impoverished:Trial	0.0030.006	0.025	0.247	137	0.804	-0.043	0.054
Response	AIC	BIC	LogLikelihood	Deviance				
Activity	-1586	-1568.3	799.01	-1598				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	0.002	0.0002	11.017	137	1.319e-2	0.002	0.003
	Environmental condition Impoverished	0.0002	0.0003	0.908	137	0.365	-30e-5	0.0009
	Trial number	-0.0002	7.292e-05	-3.273	97	0.001	-30e-3	-9.e-05
	Environmental condition Impoverished:Trial	-9.2e-05	9.640e-05	-0.959	137	0.338	-20e-5	9.8e-05

206 ***Outdoor foraging behavior***

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

215 The enriched bats significantly differed from the impoverished bats in all these movement
216 parameters (Figure 3 and Figures S3-S4). Specifically, they spent significantly more time out
217 foraging every night (3.5±1.9 vs. 2.8±1.8 hours), flew farther from the colony (1.3±1.8 vs.
218 0.8±1.13 km), and explored larger areas (7.82±6.72 vs. 3.39±3.86 km^2); all values represent
219 the Mean±SD for the entire study period (19 bats). In this analysis we included all bats and
220 averaged according to the number of nights we recorded per bat. Examining of the data after
221 15-20 nights outside where all bats have been out for a similar period (n=17 bats with data)
222 the pattern was the same and the values were: 4.02±1.19 vs. 2.8±0.75 hours, 1.66±1.77 vs.
223 0.6±0.28 km, 2.34±2.71 vs. 0.23±0.23 km^2.

224 To assess the relative effects of experience (i.e., enriched/impoverished) on foraging and to
225 compare it to the bats' original predisposition, we ran a GLMM, with their original
226 predisposition (Trial 1) and environment (enriched / impoverished) as fixed factors. We ran
227 this analysis two times using either boldness or the PC1 score that accounted for both
228 boldness and exploration of Trial 1 as a proxy for the bats' innate predisposition, because
229 these had been examined before the bats were exposed to the different environments.

230 The analysis revealed that the environment in which the bats were reared was more important
231 than their original predisposition for explaining their outdoor foraging behavior. While the
232 effect of predisposition was not significant, the enriched environment significantly correlated
233 with spending more time outside, flying to a significantly larger maximal foraging distance,
234 and exploring a larger area ($P<0.028$, $P<0.01$, and $P<0.02$, respectively). GLMM was used (see
235 Table 4a-b, with environmental condition as the predisposition and experience as fixed

factors). A model that includes an interaction between the predisposed boldness, exploration, or activity and the environmental condition, showed a worse fit (higher AIC). The bats' experience (represented by the number of nights they spent foraging until the day of the assessment), also had a significant positive effect, increasing the nightly foraging time and the maximal distance (P<0.0006, and P<0.004; GLMM for the time spent outside and the maximal nightly distance respectively, Table 4a-b). The bats' age (days from birth) did not have a significant effect. However, the proportion of nights that bats spent foraging outside the roost was not significantly associated with environmental condition, nor was it influenced by sex or age (P=0.95, see Supplementary Table S2).

We also tested the correlation between the behavioral traits measured in the wild and found a significant positive correlation only between the maximal distance and the area the bat expolred, (Pearson correlation test; Table 5).

Table 4a. GLMM results for outdoors measurements with the first boldness as predisposition. The lines depicting results for the environmental and the predisposition effects are highlighted in green and blue respectively.
response ~ 1 + Environmental_condition + Baseline_boldness + Sex + Age + Days_spent_outside + (1 | Bat_ID)

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 spent outside until assessment 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 spent outside until assessment day	10.982	3.868	2.838	710	0.004	3.386	18576
Response	AIC	BIC	Loglikelihood	Deviance				
Explored area	116.55	123.68	-50.277	100.55				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	-4.310	6.312	-0.682	12	0.507	-18.065	9.444
	Environmental condition Impoverished	-5.286	2.081	-2.539	12	0.025	-9.821	-0.750
	Boldness of the first baseline	7.746	6.454	1.200	12	0.253	-6.315	21.809
	Bat sex Male	-2.354	2.260	-1.041	12	0.318	-7.279	2.570
	Bat latest age	0.001	0.022	0.068	12	0.946	-0.047	0.050
	Total amount of nights the bat spent outside	0.183	0.074	2.466	12	0.029	0.021	0.346

Table 4b. GLMM results for outdoors measurements with the baseline trial PC1 as predisposition. The lines depicting results for the environmental and the predisposition effects are highlighted in green and blue respectively.
response ~ 1 + Environmental_condition + Baseline_PC1 + Sex + Age + Days_spent_outside + (1 | Bat_ID)

Response	AIC	BIC	Loglikelihood	Deviance				
Time spent outside	8636.9	8673.5	-4310.4	8620.9				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	161.22	66.908	2.409	710	0.016	29.864	292.58
	Environmental condition Impoverished	-58.829	26.251	-2.241	710	0.025	-110.37	-7.289
	PC1 of the first baseline	0.619	54.32	0.011	710	0.990	-106.03	107.27
	Bat sex Male	-7.650	26.159	-0.292	710	0.770	-59.01	43.708
	Bat age	0.084	0.242	0.347	710	0.727	-0.391	0.559
	Number of days spent outside until assessment day	1.347	0.379	3.547	710	0.0004	0.601	2.093
Response	AIC	BIC	Loglikelihood	Deviance				
Maximum distance per night	12438	12474	-6210.9	12422				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper

	Intercept	1434.7	594.15	2.414	710	0.015	268.2	2601.2
	Environmental condition Impoverished	-580.89	226.37	-2.566	710	0.010	-1025.3	-136.46
	PC1 of the first baseline	-365.17	460.75	-0.792	710	0.428	-1269.8	539.43
	Bat sex Male	-318.9	225.1	-1.416	710	0.157	-760.83	123.03
	Bat age	-1.108	2.121	-0.522	710	0.601	-5.274	3.057
	Number of days spent outside until assessment day	11.783	4.107	2.868	710	0.004	3.718	19.847
Response	AIC	BIC	Loglikelihood	Deviance				
Explored area	117.82	124.94	-50.909	101.82				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	1.331	5.878	0.226	12	0.824	-11.476	14.139
	Environmental condition Impoverished	-5.544	2.154	-2.573	12	0.024	-10.239	-0.849
	PC1 of the first baseline	-1.518	4.323	-0.351	12	0.731	-10.939	7.902
	Bat sex Male	-1.712	2.274	-0.752	12	0.465	-6.668	3.242
	Bat latest age	-0.005	0.025	-0.217	12	0.831	-0.061	0.050
	Total amount of nights the bat spent outside	0.174	0.077	2.243	12	0.044	0.005	0.343

Table 5. Pearson correlation test results

	Pearson r value	Pearson P value
Time spent out vs maximal distance	0.28	0.23
Time spent out vs explored area	0.21	0.38
Maximal distance vs explored area	0.82	<1.269e-05

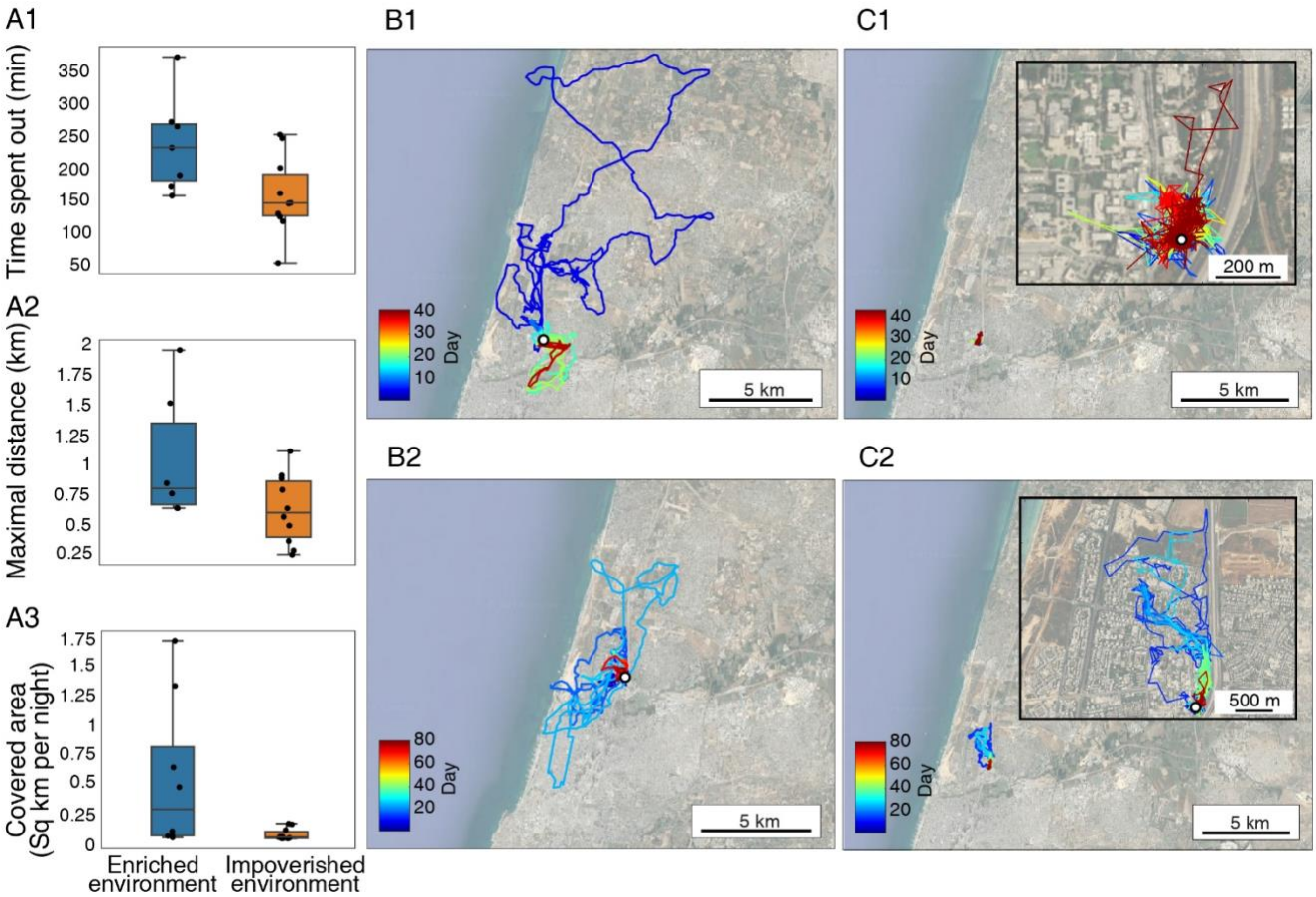

Figure 3. Early environmental exposure affects outdoor foraging behavior. (A1) Time spent by the bats outside the colony each night (in minutes). **(A2)**. Distance to the furthest point from the colony per night. **(A3)** The area explored by the bats. The data for each bat were estimated for the period between its 15th and 20th day outdoors (n=17 bats). 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, each representing a different measured season (B1,B2); **(C)** Individuals raised in the impoverished colony, data shown for two individuals, each representing a different measured season (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. More examples of individual bat movement maps are presented in Figure S3.

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. Preliminary results suggest that these differences may persist throughout the bat's lifetime; however, additional data must be analyzed to determine the long-term effects. 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. Importantly, all personality traits exhibited significant correlations in the two baseline trials suggesting that indeed they capture behavioral tendencies whose values might change with experience, while individual relations remain similar over time. Moreover, it is possible that a different set of personality traits would 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.

The observed behavioral changes in the enriched bats may be the result of increased learning opportunities and enhanced problem-solving abilities driven by early-life exposure to a more dynamic environment. The enriched environment likely provided the bats with more varied experiences, allowing them to practice and refine their foraging and exploratory behaviors. These additional opportunities for learning could have contributed to the increased boldness

and exploratory traits observed in the enriched bats. By encountering a more complex environment, these bats may have developed greater behavioral flexibility, enabling them to adapt more efficiently to novel situations in the wild.

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 2). This decrease in activity reflects familiar pups' behavior, which usually becomes less frenetic over time.

The enriched bats were significantly bolder in Trial 5 (Figure 2). This could be a real difference indicating an interesting interaction (positive feedback) between the early exposure to an enriched environment with the more exploratory outdoors behavior. That is, the more exploratory tendency of the enriched bats made them even bolder over time. However, we could not overrule the possibility that the difference in trial 5 was a result of a post-selection bias generated by the tendency of bolder individuals in the enriched condition to remain in our colony until the end of the study, while many of the bolder ones from the impoverished condition left the colony earlier and probably moved to other colonies. This tendency can be seen in Figure 2 when examining only the bats that had remained until the last trial (Figure 2C1 – and Figure S2 - see the difference in boldness in trial 2 when only examining the bats that remained in the colony). More research is needed to tell apart these two explanations.

346 ***Outdoor tracking***

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

352 Interestingly, we found no significant correlation between the time bats spent outside and the
353 maximal distance they flew per night. This finding suggests that spending more time outdoors
354 does not necessarily reflect longer foraging journeys; some bats may have remained near the
355 roost despite prolonged activity. This distinction highlights the importance of measuring
356 multiple behavioral dimensions, as time spent outside alone may not accurately capture the
357 spatial scale of foraging behavior.

358 Research conducted by Egert-Berg et al. (2021), focusing on the foraging behavior of Egyptian
359 fruit bats in the wild, demonstrated that bats that roost in cities display more exploratory
360 behavior than bats that roost in rural habitats. Our current study suggests how such
361 differences in behavior could arise as a result of early-life exposure to an enriched
362 environment such as that in the urban environment, which is much more diverse and dynamic
363 than the rural environment. Urban roosting bats encounter more types of food and must
364 practice more diverse skills to obtain it, like the bats in our enriched colony. Our findings can
365 thus explain how bats and other animals with early exposure to the urban environment
366 become more exploratory. Although fruit-bat pups tend to be more active than adults, it is
367 possible that such adaptations can also be acquired by the adults as well.

368 The lack of correlation found between the indoor and outdoor behaviors emphasizes the
369 significance of assessing behavior in the bats' natural habitat to obtain more reliable and
370 meaningful results. While measuring personality traits, particularly boldness and exploration,
371 in a small captive setup clearly assesses some aspects of personality, translating these to
372 behavior in the real world may be limited. It is possible that other behavioral traits measured
373 indoors, such as neophobia or decision-making under uncertainty, might have shown stronger
374 associations with outdoor behavior. Although some studies have found an indoor/outdoor
375 correlation in other animals (see [25]) , our findings highlight the importance of choosing

behavioral traits that are ecologically relevant, and suggest that the traits we measured may not have captured the dimensions most predictive of natural behavior.

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.

382 **Methods:**

383 ***Ethical statement***

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

387 ***Experimental animals***

388 The experiment was conducted on young Egyptian fruit bats. A total of 40 bats were captured
389 from three wild colonies (Herzliya, Beit Guvrin, and Tinshemet; Table 6) between the years
390 2019-2021 and housed in the Zoological Garden at Tel Aviv University. We captured pregnant
391 females or females with young pups before their volant stage, to ensure that the pups would
392 be naïve and without previous individual flight experience. Of the 40 bats in the study, 21
393 were born in our lab and 19 were captured at a very young age together with their mothers,
394 before they could fly independently. To avoid an origin bias, bats from all colonies were
395 divided equally and housed in two identical rooms (~2.5x2x2.5m^3, Table 6), maintained at a
396 controlled temperature of 24-26°C and a light cycle approximately matching the times of
397 sunrise/sunset. The bats' diet in both environments comprised seasonal mixed fruits
398 (watermelon, apples, melons, and bananas *ad lib*).

399 Upon arrival, the bats' weight and forearm were measured and documented. Each mother-
400 pup pair was bleached with a unique mark, and each bat was also tagged with a subcutaneous
401 electronic RFID chip. All bats were measured and checked regularly every 2-3 weeks to make
402 sure they were healthy. Three individuals were removed from the experiment: two due to
403 injury (broken wings), and one due to weight loss (>10% loss of their previous body weight).

404 ***Environmental conditions***

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

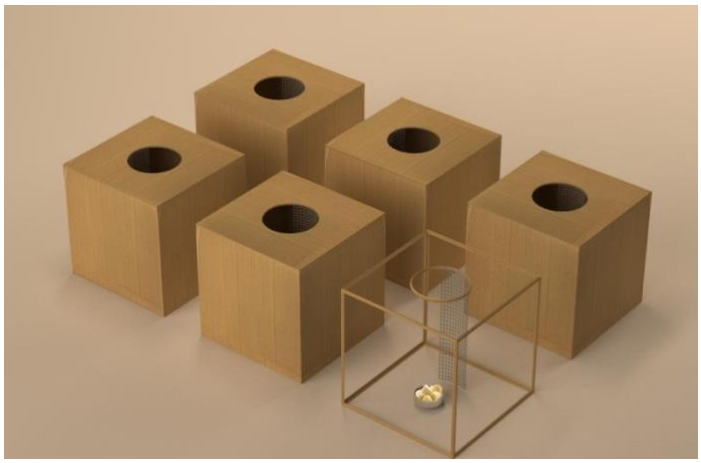

Figure 4. Experimental set-up schematic. Each bat is placed in a tent with 6 foraging boxes

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).

445 **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

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

450 ***Personality after foraging in the wild***

451 Bats that routinely exited the open colony to forage and returned were twice tested again in
452 the foraging box experiment: 2-3 weeks following their first exit (Trial 4, post-release 1), and
453 5-6 weeks following their first exit (Trial 5, post-release 2). A total of 19 bats were tested for
454 these trials (see Table 8).

455 **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

456
457 ***Behavioral analysis***

458 Each bat's actions during the foraging box experiment were documented based on video
459 recordings by two independent observers. In cases of disagreement, a third observer

compared the two and made the final judgement. The identified actions comprised: landing on or entering the carrying bag in which the bats had been introduced into the room; landing; entering the food boxes; collecting food; or flying around to explore the environment.

Similar to our previous study [10], we then calculated the following personality traits:

Boldness/Risk-taking: boldness can be defined in several ways [28]. We measured it as the proportion of times the bat entered the boxes out of the total number of landings and entering with or without collecting food from the boxes. A previous study has shown that entering boxes placed on the ground is a risky behavior that a bat generally avoids [10].

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

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

Statistical analysis of the behavioral trials

To verify that there were no behavioral differences between the two groups prior to applying our environmental conditions, we compared the baseline trials between the two environmental conditions (Table S1). We used mixed-effect general linear model (GLMM) implemented in MATLAB R2019, with the traits set as the response variable, the environmental condition and trial number (baseline 1 or 2) set as fixed factors, and bat ID set as random effect (n=39, Table 8).

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

To assess the impact of the environmental condition on each behavioral trait, we employed GLMMs. We used the behavioral trait as the response 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.

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 [29].

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 [30]. 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: For each bat, we calculated the maximum distance from the colony for each night. We then computed the 95th percentile of these nightly maximum distances and used it as a threshold radius. Using the colony as the center point, we excluded all GPS locations falling beyond this radius. A convex hull was then calculated from the remaining points to estimate the core area utilized by each bat.

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 response 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

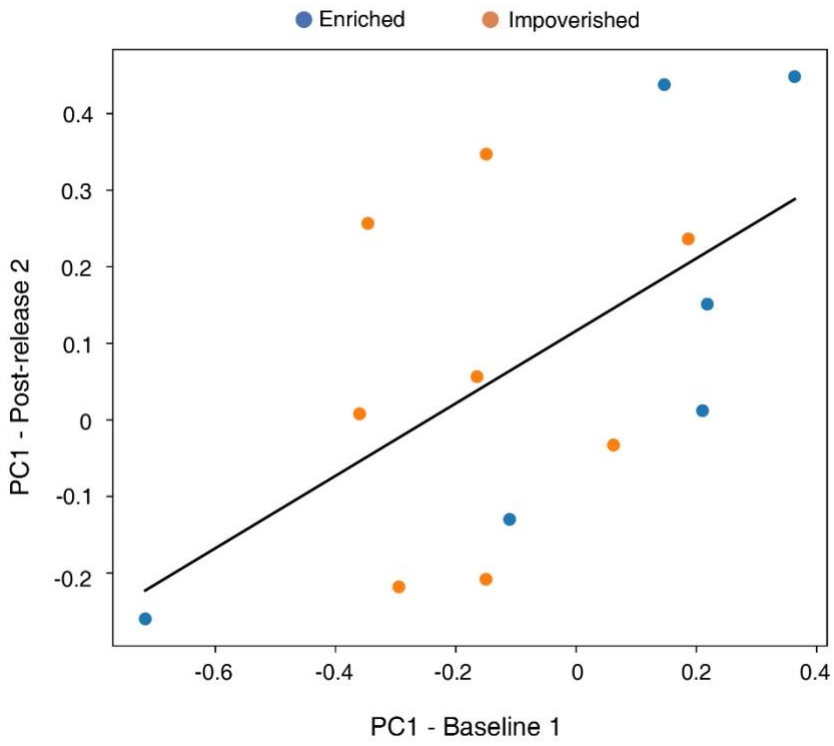


Figure S1. PCA analysis for trial 1 (baseline) and 5 (post-release 2); positive correlation was found between the individual scores on PC1 (Pearson correlation P=0.03, r=0.58)

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

response ~ 1 + Environmental_condition + Trial_number + (1| Bat_ID)'

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

Table S2. GLMM results for proportion of nights foraging outside the roost (%).

DaysOutProportion ~ 1 + EnvironmentalCondition + Sex + Age + (1|Bat_ID)
With Y ~ Binomial (TotalExperimentDays) and link=logit

Response	AIC	BIC	LogLikelihood	Deviance				
Proportion of Nights Outside	-207.95	-185.13	108.97	-217.95				
	Fixed effects coefficients (95% CIs)							
	Name	Estimate	SE	tStat	DF	P value	Lower	Upper
	Intercept	1.315	0.419	3.134	705	0.001	0.491	2.139
	Environmental condition_Impoverished	0.024	0.399	0.061	705	0.951	-0.760	0.808
	Sex_M	0.323	0.393	0.820	705	0.412	-0.450	1.096
	Age	6.77e-05	0.0003	0.179	705	0.857	-0.0006	0.0008

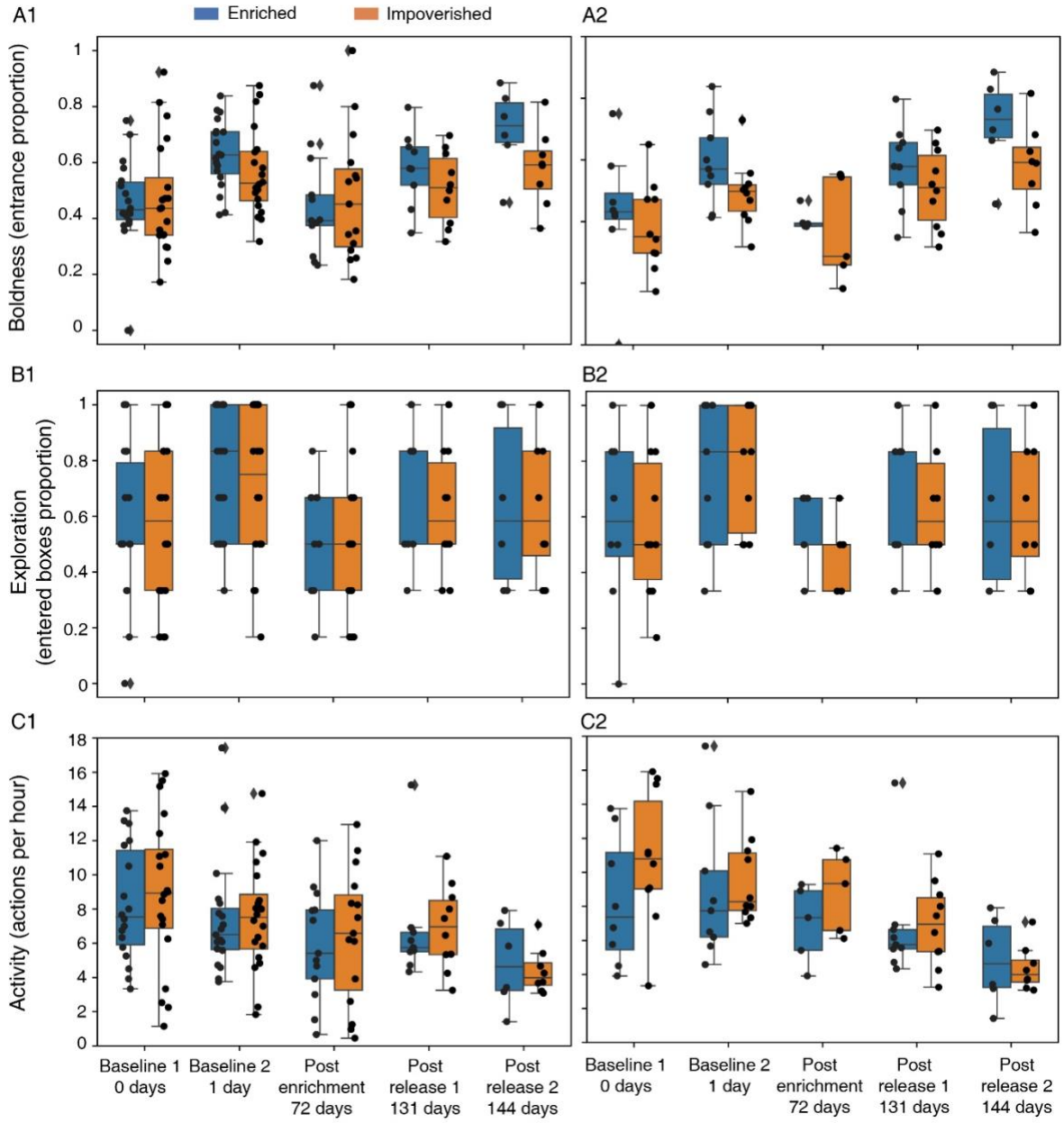


Figure S2. Full bat behavioral traits over time. Box plots depicting the bats' behavior across the five trials according to three traits: Boldness (A), exploration (B), and activity levels (C). The experimental phase and

the time in days from the day of the first trial are depicted on the X-axis. Box plots show the 25% and 75% percentiles. Medians and whiskers based on 1.5 IQR are shown. A1, B1, and C1 represent all bats tested, while A2, B2, and C2 represent only the bats that were tracked outdoors using GPS devices.

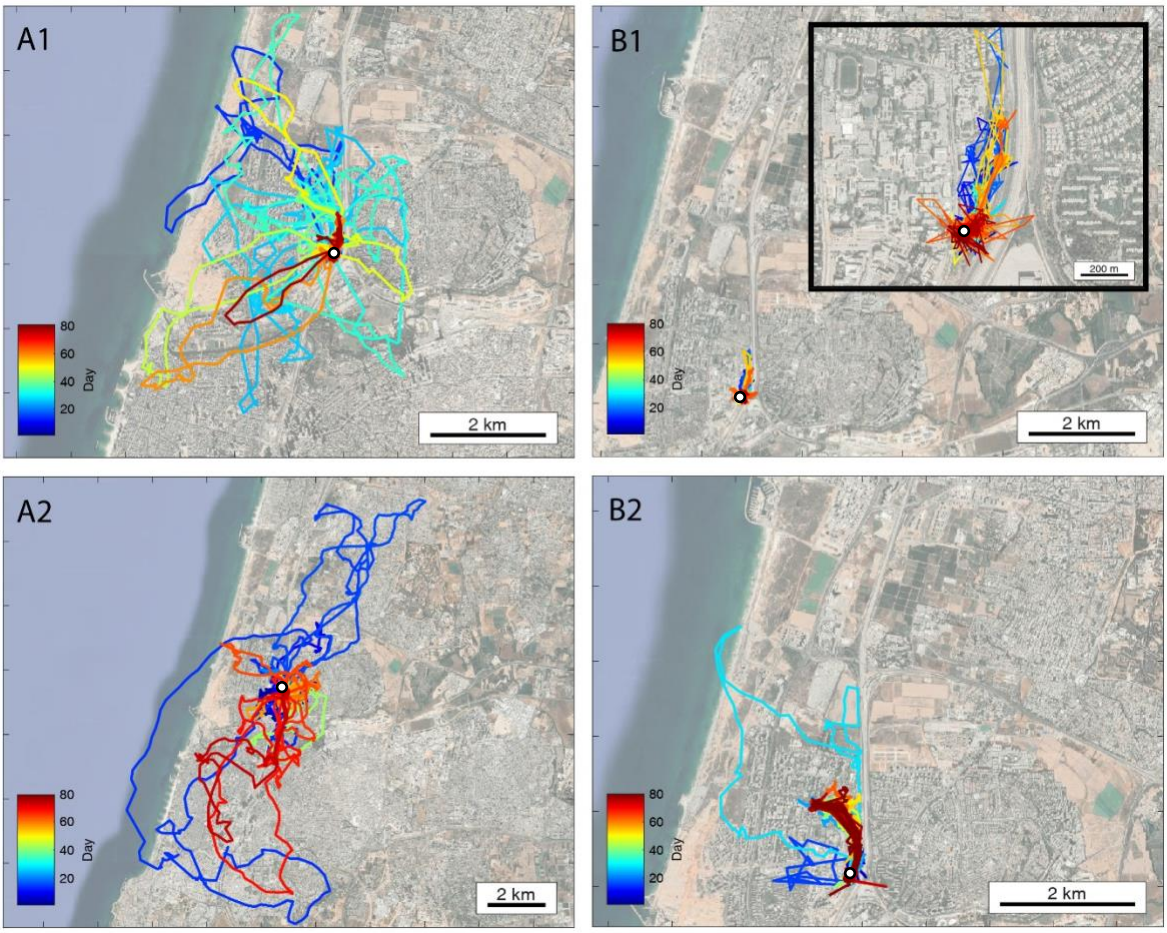
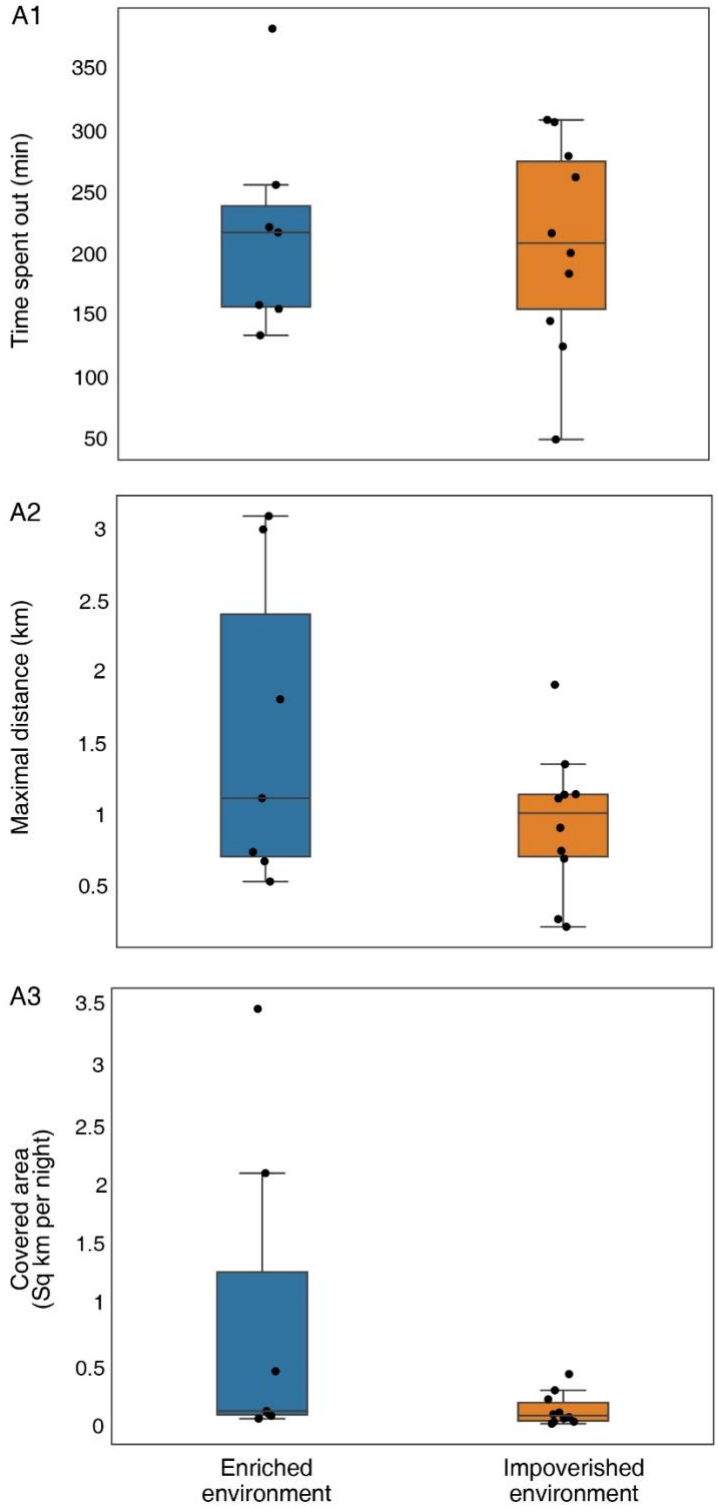


Figure S3. Early environmental exposure affects outdoor foraging behavior. The complete movement of four individuals - two from each colony. **(A)** Individuals raised in the enriched colony, data shown for two individuals (A1,A2); **(B)** Individuals raised in the impoverished colony, data shown for two individuals (B1,B2). Colors depict time in days. The open colony is marked by a white circle. Insert in B1 zooms-in on the tracks.



576

577 **Figure S4. Early environmental exposure affects outdoor foraging behavior. (A1)** Time spent by the
578 bats outside the colony each night (in minutes). **(A2)**. Distance to the furthest point from the colony
579 per night. **(A3)** The area explored by the bats. The data for each bat were estimated for the period
580 between its 21st and 26th day outdoors (n=17 bats). Median and whiskers based on 1.5 IQR are shown.

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