



The effect of urbanization on innovation in spotted hyenas

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Abstract

Urbanization represents a dramatic form of evolutionary novelty in the landscapes inhabited by many extant animals. The Cognitive Buffer Hypothesis suggests that innovation, the process by which animals solve novel problems or use novel behaviors, may be key for many animals when adapting to novel environments. If innovation is especially beneficial in urban environments, then we would expect urban animals to be more innovative than their non-urban counterparts. However, studies comparing innovative problem-solving between urban and rural habitats have produced mixed results. Here, we hypothesized that these findings result from comparing only two levels of urbanization when related research suggests that the stage of invasion of urban habitats likely has a strong effect on demand for innovation, with demand being highest during early establishment in a novel environment. To test this hypothesis, we assessed innovation in three locations where spotted hyenas experienced varying degrees of urbanization. Spotted hyenas are relatively innovative compared to other carnivores and, although many large carnivores in Africa are endangered, spotted hyenas remain abundant both inside and outside protected areas. We measured innovation with a multi-access puzzle box with four different doors through which hyenas could obtain a food reward. We predicted that hyenas in a transitional, rapidly urbanizing habitat would be more innovative, measured by the number of unique doors opened, than those in rural or fully urban habitats. Contrary to our predictions, hyenas in the rural habitat were the most innovative. These results challenge the idea that the evolutionary novelty associated with urbanization favors greater innovativeness.

Keywords Urbanization · Innovation · Spotted hyenas · Problem-solving · Cognitive buffer hypothesis

Introduction

Urbanization is one of the most extreme, yet most common, forms of human-induced rapid environmental change. Urbanization dramatically changes natural habitats and presents a host of novel challenges for wildlife from finding

food or shelter to avoiding novel sources of mortality (Sih 2013; Sol et al. 2013; Griffin et al. 2017). To survive in an increasingly urbanized world, animals must respond adaptively to these novel challenges or face extinction (Sol et al. 2013).

The Cognitive Buffer Hypothesis (CBH) suggests that innovation, the process of solving novel problems or using novel behaviors to solve familiar problems (Reader et al. 2016), can buffer the negative effects of environmental change, including change created by urbanization (Sol 2009). Support for the CBH comes from research showing that bird species with the highest innovation rates are the likeliest to invade novel or variable environments successfully (Sol et al. 2002, 2005, 2016). However, results from studies comparing innovativeness between urban and non-urban habitats or species have been mixed; a few studies have shown better innovative problem-solving in urban animals (Audet et al. 2016; Preiszner et al. 2017; Griffin et al. 2017), but many others have had ambiguous results or shown no difference between animals living in urban and

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non-urban habitats (birds: Kark et al. 2007; Møller 2009; Papp et al. 2014; Griffin et al. 2017; Prasher et al. 2019; lizards: Kang et al. 2017). Thus, it is currently unclear whether innovative problem-solving represents an adaptive response to urbanization. However, research suggests that selection on innovation almost certainly depends on the stage of invasion, such that demand for innovativeness may be strongest during the initial invasion and colonization when exposure to novelty is high, but subsequently decreases after a species becomes established in a novel environment (Wright et al. 2010; Snell-Rood and Wick 2013; Griffin et al. 2017). Studies on urbanization often compare only two levels of urbanization and both the stage or degree of urbanization at urban sites and types of non-urban sites assessed vary considerably across studies, which might explain these mixed results.

To further investigate the relationship between innovation and urbanization, we tested innovation in spotted hyenas (*Crocuta crocuta*) living in three different locations representing three different stages of urbanization: stable rural, transitional, and stable urban. Spotted hyenas are the most abundant large carnivores in sub-Saharan Africa, where they inhabit almost every ecosystem, including highly urban ones (Holekamp and Dloniak 2010; Yirga et al. 2013; Baynes-Rock 2015). Hyenas are relatively innovative compared both to other Hyaenids and to members of other carnivore species (Holekamp et al. 2015; Benson-Amram et al. 2016). In addition, previous research with spotted hyenas has shown a high degree of intraspecific variation in innovativeness (Benson-Amram and Holekamp 2012), and has also found that innovativeness is a repeatable trait across time and context (Johnson-Ulrich et al. 2020), which makes spotted hyenas ideal for examining which environments favor the greatest expression of innovation.

Hyenas in both the rural and urban locations have had many generations to adjust to their environments, so these environments should theoretically pose much less novel or unpredictable challenges for hyenas than do the challenges posed by the rapid change being experienced by hyenas in the transitional location. Therefore, the CBH predicts that hyenas in the transitional location should express much higher levels of innovativeness than those in the rural and urban locations. We tested innovation in substantial numbers of hyenas inhabiting all three locations to test this prediction of the CBH.

Methods

Study locations

We tested free-ranging hyenas in three locations between June 2016 and November 2017. The first location where we tested spotted hyenas was near the center of a protected area,

the Maasai Mara National Reserve (hereafter “the Reserve”) in Kenya. In this area of the Reserve, human activity in the form of tourism, cattle grazing, and poaching has been minimized via strict management since the year 2000. Thus, hyenas in this ‘rural’ location inhabited a relatively stable and pristine environment with little novelty. In fact, environmental conditions in this part of the Reserve have evidently changed very little since the late Pleistocene (Steele 2013).

The second location in which we tested hyenas was also located in the Reserve, but along its northern boundary, where the home range of the tested hyenas included the burgeoning town of Talek, situated immediately north of the Reserve boundary (Green et al. 2018). Over the last two decades, this ‘transitional’ location has seen a rapid increase in building construction, livestock grazing, pastoralist activity, and tourism (Boydston et al. 2003; Pangle and Holekamp 2010; Green et al. 2018). In the Reserve, one hyena generation is approximately 6.23 ± 3.00 years, so urbanization has only been increasing for about three generations. Telemetry data indicated that, in addition to foraging inside the Reserve, hyenas living in the transitional location regularly use Talek town and surrounding areas to forage on trash and livestock (Green and Holekamp 2019). Thus, the transitional location was shifting rapidly from rural to urban, where hyenas were currently experiencing changes associated with the early stages of colonization of, or adaptation to, a novel habitat.

The third location in which we tested hyenas was the city of Mek’ele, Ethiopia. Mek’ele boasts a large population of fully urbanized hyenas; these hyenas den in some of the only remaining undisturbed forest within city limits, church yards on the edges of the city, and commute into the city each evening to forage on trash and livestock remains. Most people in northern Ethiopia believe that spotted hyenas eat evil spirits, so the presence of hyenas is tolerated (Abay et al. 2010; Yirga et al. 2013). Spotted hyenas have occupied cities in northern Ethiopia for several hundred years (Gade 2006), so this ‘urban’ location represents a relatively stable urban habitat for hyenas.

Study subjects

All individuals were identified by their unique spot patterns, scarring, and ear damage. Hyenas live in large, stable social groups called ‘clans.’ Spotted hyenas in Reserve clans have been observed as part of a long-term research project since 1988, such that we have detailed information about rank, kinship, age and demographic status for every subject. Dates of birth were estimated by the appearance of the natal coat when cubs first appeared above ground, and all cubs were sexed based on the morphology of the erect phallus. In Ethiopia, we were able to sex individuals both by the morphology of the erect phallus, when visible, and

in adult females by signs of sexual maturity and reproductive activity, such as engorged nipples or a torn phallus. In Ethiopia, we distinguished between two age classes, adults and subadults, based on body size, morphology, pelage length, and signs of sexual maturity in females. Because we could only assign hyenas to one of these two age classes in Ethiopia, we also binned all Reserve hyenas into adult and subadult age classes; we classified subadults as hyenas who were less than two years old and adults as hyenas who were more than two years because two years is the age at which spotted hyenas reach reproductive maturity (Glickman et al. 1992). In the Reserve, we tested hyenas from two clans in both the rural and transitional locations for a total of four clans in Kenya. In Ethiopia, clan membership was unknown, but testing was conducted at only two sites that were less than a kilometer apart. Subject sampling heavily overlapped between these two sites, which suggested to us that all these hyenas belonged to a single clan. However, it is possible that clan structure is different in Mek'ele hyenas than in natural populations (Schramme 2015).

Test apparatus

We tested innovation using a multi-access box (MAB). Like other innovative problem-solving paradigms or 'puzzle boxes', a MAB tests innovation in the context of extractive foraging (Auersperg et al. 2011). Unlike single-access puzzle boxes, however, MABs typically have multiple entry points, each of which requires unique cognitive skills (Auersperg et al. 2011), unique motor behaviors (Manrique et al. 2013; Johnson-Ulrich et al. 2018), and/or sequential learning (Huebner and Fichtel 2015). The MAB design used in the present study was previously used to test innovation in captive spotted hyenas (Johnson-Ulrich et al. 2018). This MAB was a square galvanized steel box weighing approximately 36 kg and measuring approximately 41 × 41 × 41 cm (length × width × height). It had four different doors on each vertical face that all provided access to a common interior and each door required subjects to use a different motor behavior. Thus, we were able to measure each subject's ability to innovate up to four different times with the four doors, which were as follows: (1) the push door: this was a door 30.5 × 28 cm with a hinge on the side that could be pushed inwards to open. (2) The sliding door: this was a door 30.5 × 28 cm with protruding flanges that could be pushed or pulled sideways to slide open. (3) The pull door: this was a door 30.5 × 28 cm with a hinge on the bottom that could be pulled outwards and downwards to open by grasping a doorknob near the top of the door. (4) The drawer: this was a drawer 10 cm in height that was flush against the bottom of the MAB and took up the entirety of the floor of the MAB; it could be pulled outwards to open. Magnets were used to create mild resistance on all doors to ensure that they would

not accidentally fall open; subjects were required to actively interact with the MAB to retrieve the food. All doors could be accessed using either snout and jaws or paws. The top of the MAB was removable for familiarization trials. The MAB had multiple 2.5 cm circular holes cut on every side except the bottom so that subjects could smell the food inside during trials. All four doors could be blocked by bolting them shut such that blocked doors could still be manipulated by subjects but would not open to allow food retrieval.

Test procedure

In the Reserve, subjects were tested during daily observation periods from 0600 and 1030 or 1700 to 1830 h—the daylight hours during which hyenas were most active there. In Ethiopia, the hyenas were largely nocturnal; therefore, all testing was done between 1800 and 2300 h—the hours in which hyenas left their daytime resting sites and traveled around the city to forage. Research vehicles were used as mobile blinds in all three locations to shield researchers from view when deploying the MAB. The MAB was presented opportunistically to hyenas whenever they were found in suitable testing conditions. The MAB was baited with approximately 200 g of either goat or beef muscle, skin, or offal depending on what was locally available. During some trials full cream milk powder was also used in addition to, or in place of, meat. The MAB was deployed approximately 20 m away from subjects and the research vehicle was then moved to a distance of approximately 20 m from the MAB. All trials were videotaped. Trials were initiated when a hyena came within 5 m of the MAB. We ended a trial if a hyena retrieved the bait or if all hyenas present moved at least 5 m away from the MAB for more than 5 min, moved at least 100 m away from the MAB, or laid down for 5 min without standing up and without contacting the MAB. Average trial duration was 8.85 ± 10.18 min (median = 5 min, range = 0.25–6.43 min, $N = 846$ trials; see Supplementary Material Table S1 for trial duration grouped by location).

While all hyenas present within 5 m were recorded, hyenas were only considered to have participated in a trial if they made contact with the MAB, and only participating hyenas were given a score for success (opening a door) or failure (failing to open a door) in any given trial. If the bait was retrieved and consumed, the MAB was rebaited for consecutive trials. Prior to testing, hyenas were given familiarization trials in which the MAB was baited but its top was removed and left open. We aimed to give every hyena two familiarization trials prior to being given the option to participate in test trials. On average, hyenas were given 1.31 ± 1.63 (median = 1, range = 0–9, $N = 352$ subjects) familiarization trials prior to being presented with their first test trial, but only fed from the MAB in 0.46 ± 9.94 (median = 0, range = 0–7, $N = 352$ subjects) familiarization

trials prior to being presented with their first test trial (see Supplementary Material Table S1 for descriptive statistics on familiarization trials grouped by location).

We conducted testing in four different phases for each hyena. During the first phase, all four doors were accessible to the subject. Once a hyena used a door to obtain the bait in three out of four consecutive test trials, the hyena was considered to have learned that door, and the hyena progressed to phase two. In phase two, the door learned in phase one was bolted shut, and the subject was required to use one of the three other doors still available to retrieve the bait. In phase three, the doors learned in phases one and two were bolted shut. In phase four, the doors learned in phases one, two, and three were bolted shut. Subjects were given the opportunity to participate in trials until they either learned all four doors by completing all four phases or they scored five consecutive failures.

The MAB was deployed preferentially to groups of fewer than 5 hyenas, but there was some variability in group sizes because hyenas could freely come and go during presentation of the MAB. Hyena societies are marked by a high degree of fission–fusion dynamics, such that the numbers and identities of individuals within subgroups changes hourly (Smith et al. 2008). Thus subgroup membership was almost never the same across multiple deployments of the MAB and 76.6% to 84.9% of hyenas in the Reserve had at least one opportunity to participate in a trial. Of those that had at least one opportunity, 75.3%–82.9% participated in at least one trial by making contact with the MAB.

When we presented the MAB to more than one hyena, we configured the MAB for the hyena on the most advanced phase of testing because these hyenas were the most likely to participate in the trial. Overall, there were only five trials total in which a hyena solved the MAB during the ‘wrong’ phase of testing by joining a trial where we had configured the MAB for a group mate rather than itself. We also included up to two additional pieces of bait (up to 600 g) during group trials to ensure that the solver was always able to retrieve at least one piece of bait. Familiarization trials were recorded for hyenas that came within 5 m of the MAB after a hyena had solved it.

Measuring innovation

We scored innovativeness as the number of unique doors, from zero to four, that a hyena opened. Hyenas that participated in fewer than five trials, none of which were successful, were not included in our analysis and were not counted among our 89 subjects. We used a cut-off of at least five trials because the highest trial number in which a hyena ever solved the MAB for the first time was its fourth trial. No hyena ever solved the MAB after failing to do so for

more than four consecutive trials. Therefore, we were confident that hyenas who failed to solve the MAB across five consecutive trials had sufficiently demonstrated a lack of innovativeness. Previously, we found that innovativeness was significantly repeatable within individual hyenas who had solved the MAB at least once (Johnson-Ulrich et al. 2020) and we, therefore, included all hyenas with at least one successful trial in this analysis. Furthermore, most hyenas subsequently demonstrated learning of each solution by opening the same door repeatedly across three out of four consecutive trials (average percent of doors learned out of doors opened = 55.67%, SD = 45.12%, median = 75%, range = 0–1).

Of the 89 hyenas that reached the criteria for inclusion in the innovation analysis, only ten hyenas were included in the dataset with incomplete data; these hyenas failed to reach criterion for ending testing before the end of the study period (see Test Procedure). However, all ten of these hyenas had solved the MAB on at least one occasion so their scores represent the minimum innovation score they might have obtained. Because our dataset was zero-inflated (the average innovation score for our 89 subjects was only 0.73 ± 1.39), removing their data would bias each location average downwards to a greater extent than would including their incomplete scores.

Statistical analysis

Before analyzing overall innovation rates, we first analyzed the factors influencing participation, problem-solving success, and latency to solve across individual trials using generalized linear mixed models (GLMMs) with the package ‘glmmTMB’ (Brooks et al. 2017) in the statistical program R (R Core Team 2019). In the participation model, the response variable was a binary variable indicating whether or not a hyena made contact with the MAB after approaching to at least 5 m. In the problem-solving model the response variable was a binary variable indicating whether a hyena solved or failed to solve the MAB after making contact with it. In the latency to solve model, the response variable was the latency in seconds from first contact to opening the MAB. Latency to solve is frequently used as an estimate problem-solving efficiency or innovativeness (Chow et al. 2016; Johnson-Ulrich et al. 2018). We used binomial distributions with a logit link function for the participation and problem-solving model and a generalized Poisson distribution with a log link function for the latency to solve model. In all three models, we included fixed effects of bait type and quality to investigate whether bait had an effect on response to the MAB. We included trial number and prior number of times a hyena fed from the MAB to control for previous experience. In our latency model, trial number was highly collinear with phase number; therefore, we did not include

trial number in the latency model. We included body condition (gaunt, normal, fat and obese) to control for any proximate effects of hunger or satiety. Body condition reflects how recently a hyena has eaten and was measured the same way as ‘belly size’ is in other carnivores (Caro 1994; Pusey and Packer 1994). We included the number of other hyenas present within 5 m to control for any social effects, and phase of testing to control for MAB set-up. Phase was included as a binary variable (familiarization vs test phase) in the participation model and an ordered numeric variable (Phase 1–4) in the problem-solving model and latency model. Trial duration was included as a control variable; hyenas had more opportunity to participate when trials were longer (Participation Model) and hyenas that solved the MAB (Problem-solving Model) typically had shorter trials than hyenas that failed to solve as a result of our test protocol where trials were only ended if bait was consumed, if a hyena left a 5 m radius around the MAB for at least five minutes, or if a hyena did not interact with the MAB for at least five minutes. Because trial duration was slightly correlated with latency to solve, it was excluded from the latency model. We also included a random effect of subject ID in the participation and problem-solving models. We did not include a random effect of subject ID in the final latency to solve model because it explained zero variance and resulted in poor model fit. We initially included a random effect for clan identity to control for any clan level socio-ecological variation that might affect innovation independently from urbanization. However, the amount of variation explained by clan was negligible, so we removed it from all final models. The reference condition for the categorical variable ‘Body condition’ was ‘normal’ and the reference condition for the categorical variable ‘Location’ was ‘Transitional’. Bait variables were all included as independent binary variables because more than one condition could apply to any given trial. We also created participation and problem-solving models that included sex, rank, and clan size but because these variables were missing for hyenas from the urban location our sample size was greatly reduced. Ultimately neither sex, rank, nor clan size was significant in these models, and overall results were largely unchanged (Participation GLMM Sex: Odds ratio = 0.74, $P = 0.28$, Rank: Odds ratio = 1.31, $P = 0.26$, Clan size: Odds ratio = 0.99, $P = 0.57$; Problem-solving GLMM Sex: Odds ratio = 4.22, $P = 0.36$, Rank: Odds ratio = 0.92, $P = 0.96$, Clan size: Odds ratio = 0.93, $P = 0.25$).

We used a generalized linear mixed model (GLMMs) to compare innovation scores among our three locations. The dependent variable was innovation score and the independent variables were location and age class. We included age class because previous research on problem-solving in hyenas found some behavioral differences in the way subadult and adult hyenas interacted with a similar puzzle box (Benson-Amram and Holekamp 2012). Like the participation

and problem-solving models, we initially included a random effect for clan identity, but the amount of variation explained by clan was negligible so we removed it from our final model. Like the participation and problem-solving models we did not include sex or rank in the innovation model because these variables were unknown for subjects from the urban location. However, when comparing hyenas between only transitional and rural locations, neither sex nor rank had large effect sizes nor were they statistically significant (Innovation GLMM Sex: Odds ratio = 1.39, $P = 0.47$, Rank: Odds ratio = 1.10, $P = 0.79$). Main results for the variable ‘location’ were unchanged regardless of the inclusion of age class, sex, or rank. We used the R package ‘Performance’ to check for collinearity and overdispersion, and we used the R package ‘Dharma’ to examine the distribution of our residuals. Because our response variable was a count of innovations learned by each hyena, in our initial model we used the Poisson family (link = log). However, this model had significant overdispersion. Therefore, we re-analyzed the same model using a generalized Poisson distribution to account for overdispersion (overdispersion parameter = 3.25).

Results

Participation

We collected data from 490 hyenas in 846 trials for a total of 3344 observations of hyena behavior within trials. The average number of hyenas present within 5 m of the MAB over the entire duration of a trial \pm standard deviation was 3.95 ± 4.16 (median = 2, range = 1–32, $N = 846$ trials). Of hyenas that approached to at least 5 m, the average number of hyenas that actually contacted the MAB (participated) during a trial was 2.26 ± 2.91 (median = 1, range = 0–28, $N = 846$ trials). This amounted to an average of $54.5\% \pm 38.8\%$ of hyenas present participating out of those that approached to at least 5 m. Participation was lower in the urban location ($32.6\% \pm 40.0\%$, $N = 374$ trials), than in the transitional ($69.2\% \pm 28.5\%$, $N = 211$ trials) and rural ($74.0\% \pm 26.6\%$, $N = 261$ trials) locations (Table 1). The type of bait used also had significant effects on participation; hyenas were more likely to participate in trials where the MAB was baited with milk powder and less likely to participate in trials when the MAB was baited with dried meat (Table 1). Participation was also affected by prior experience, measured as trial number and prior number of times a hyena fed from the MAB. Subadult hyenas were more likely than adults to participate in trials, which is similar to previous findings in hyenas (Benson-Amram and Holekamp 2012) and other animals that have found that juveniles tend to be more bold or exploratory than older animals (Kummer and Goodall 1985; Reader and Laland 2003; Biondi et al. 2010;

Table 1 Model output for the factors influencing participation, trial success, and latency to solve the MAB

Variable name	Participation model ^a			Problem-solving model ^b			Latency model ^c		
	Odds Ratio	<i>z</i>	<i>P</i>	Odds Ratio	<i>z</i>	<i>P</i>	Odds Ratio	<i>z</i>	<i>P</i>
Bait type—Milk powder	1.87	3.49	<0.001^d	1.04	0.06	0.95	0.86	− 0.51	0.61
Bait type—Bone	1.10	0.65	0.52	0.61	− 1.24	0.21	1.00	− 0.01	0.99
Bait type—Meat	1.24	1.23	0.22	1.19	0.29	0.77	0.80	− 1.20	0.23
Bait type—Offal	1.12	0.64	0.52	0.42	− 1.41	0.16	0.63	− 2.28	0.02
Bait quality—Rotten	1.08	0.42	0.67	1.48	0.76	0.45	1.14	0.64	0.52
Bait quality—Dried	0.55	− 2.79	0.01	0.44	− 1.30	0.19	0.78	− 1.49	0.14
Phase of testing ^e	0.73	− 2.69	0.01	0.16	− 4.13	<0.001	1.60	3.56	<0.001
Trial number	0.97	− 3.16	0.001	1.04	0.55	0.58	—	—	—
Prior # of feeds	1.29	4.06	<0.001	1.62	1.89	0.06	0.97	− 0.69	0.49
Body condition—Fat	1.38	1.87	0.06	0.43	− 1.48	0.14	1.42	1.98	0.05
Body condition—Gaunt	1.02	0.04	0.97	0.00	0.00	1.00	NA	NA	NA
Location—Urban	0.26	− 4.05	<0.001	0.06	− 1.02	0.31	1.21	0.46	0.64
Location—Rural	2.14	2.76	0.01	3.87	0.95	0.34	0.51	− 4.29	<0.001
Age Class—Subadult	3.37	5.30	<0.001	0.86	− 0.12	0.91	0.86	− 1.13	0.26
Number of hyenas	0.97	− 2.62	0.01	0.95	− 1.19	0.23	1.00	0.30	0.76
Trial duration	1.00	4.21	<0.001	1.00	− 3.65	<0.001	—	—	—

^aSample sizes for the participation model were: $n=2857$ observations and $N=343$ subjects. This sample includes every hyena that ever approached within 5 m of the MAB. Adjusted and conditional ICC values for subject ID (random effect) were 0.41 and 0.33, respectively

^bSample sizes for the problem-solving model were: $n=1040$ observations and $N=212$ subjects. This sample includes every hyena that ever contacted the MAB. Sample sizes may be slightly smaller than sample sizes for descriptive statistics because observations or individuals with missing data were excluded from models. Adjusted and conditional ICC values for subject ID (random effect) were 0.94 and 0.84, respectively

^cSample sizes for the latency to solve model were: $n=197$ observations and $N=24$ subjects. This sample includes every trial where a hyena successfully opened the MAB. Subject ID was removed as a random effect from this model because it explained zero variance and ICC values could not be computed

^dBolded values indicate significance at $\alpha=0.05$

^eEstimates for phase of testing in the problem-solving model is for a quadratic term

Thornton and Samson 2012). Larger group size, measured as the number of other hyenas present within 5 m, slightly decreased the odds of participation. This result likely reflects a low level of social interference where larger groups might be more likely to contain a hyena of higher rank than the focal hyena which may reduce the likelihood of that hyena approaching the MAB. Surprisingly, body condition, which is a reliable indicator of how recently a hyena has fed, did not affect participation. Finally, location had a positive effect on the likelihood of participation in the rural location and a negative effect on the likelihood of participation in the urban location relative to our transitional location.

Problem-solving

Hyenas that participated in test trials were given a score for either solving or failing to solve the MAB. Ultimately, we collected problem-solving data from 212 subjects in 460 trials for a total of 1040 observations. In the problem-solving model, only phase of testing and trial duration had significant effects on the likelihood of solving the MAB (Table 1).

Phase of testing had a quadratic effect where hyenas were most likely to solve the MAB during Phase 2 and less likely to solve the MAB on Phase 1, 3, or 4. This effect is likely a result of our test protocol where only successful hyenas progressed to Phase 2, biasing our sample towards hyenas that were likely to continue to be successful. However, Phases 3 and 4 subsequently increase in difficulty because more doors to the MAB are blocked, which decreases the likelihood of a successful trial. However, the amount of variation explained by fixed effects was very small in this model. Instead, subject ID explained nearly all of the variation in the likelihood of solving the MAB (conditional intraclass correlation coefficient (ICC)=0.84). This high ICC suggests that there were repeatable individual differences in the likelihood of solving the box which is consistent with our earlier analysis of the repeatability of innovative problem-solving in hyenas (Johnson-Ulrich et al. 2020). Interestingly, location had no effect on the likelihood of solving the MAB and is likely related to the low overall success rate across trials (mean=0.18, SD=0.38) and variable success rate even among hyenas that solved the MAB at least once (mean=0.61, SD=0.49).

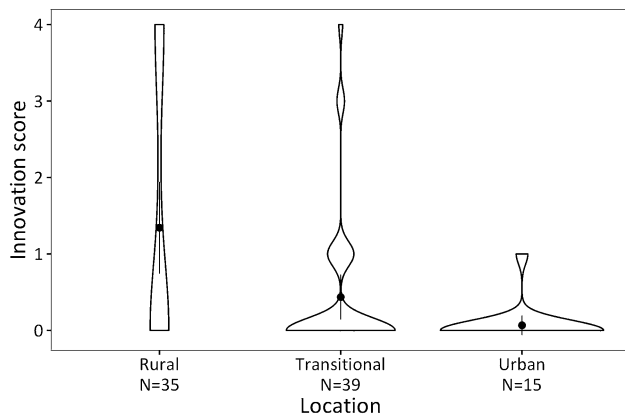


Fig. 1 Violin plots display the kernel probability density of each innovation score for hyenas in each location. Black dots in the center of each violin plot show the mean score for each location and bars show the 95% confidence intervals for each mean. *N* indicates the number of hyenas that received scores in each location

Latency to solve

Hyenas that solved the MAB were given a score for their latency to solve the MAB after first making contact with it. Twenty-four hyenas ultimately solved the MAB at least once and most did so more than once resulting in a total of 197 trials where a hyena solved the MAB. Bait type had a significant effect on latency; when the MAB was baited with offal hyenas were significantly faster to solve the MAB. Similar to our results for the problem-solving model, phase of testing also had a significant effect on latency; hyenas were slower to solve the MAB on later phases of testing (Table 1) which again suggests that later of phases of testing, when previously learned doors were blocked, were more difficult for hyenas. Body condition also significantly affected latency, fat hyenas were slower to solve the MAB relative to hyenas in normal body condition. Finally, location significantly affected latency to solve; hyenas living in the rural location were, on average, 51% quicker at solving the MAB than hyenas in the transitional location (Table 1).

Innovativeness

Of the 212 hyenas that participated in test trials, 89 participated in enough trials to be assigned an innovation score (See “Methods”: Measuring Innovation). We collected data on innovativeness from 35 hyenas in the rural location, 39 in the transitional location, and 15 in the urban location. Of the 89 tested individuals, 34 were adults and 55 were subadults, 45 were females, 32 were males, and 12 were of unknown sex. On average, hyenas earned an innovation score of 0.73 ± 1.39 (median = 0, range = 0–4). Contrary to our expectations we found that hyenas in the rural location

were significantly more innovative than those in the transitional location (GLMM: Odds ratio = 2.42, $\beta = 0.88$, $z = 2.18$, $P = 0.029$; Fig. 1; Supplementary Table 2). Furthermore, hyenas in the urban location were not significantly different from those in the transitional location (GLMM: Odds ratio = 0.22, $\beta = -1.53$, $z = -1.46$, $P = 0.145$; Supplementary Table 2) and hyenas in the urban location were significantly less innovative than those in the rural location (Post hoc contrast: Odds ratio = 0.09, $\beta = -2.41$, $t = -2.32$, $P = 0.023$). Age class had no significant effect on innovation scores (GLMM: Odds ratio = 0.64, $\beta = -0.44$, $z = -1.14$, $P = 0.253$; Supplementary Table 2), so age affected participation but not innovation among participants. These average innovation scores appear to be driven by both the ratio of innovative hyenas present in each location (Rural: 40%, $N = 35$ hyenas; Transitional: 25.6%, $N = 39$ hyenas; Urban: 6.67%, $N = 15$ hyenas) and innovation scores among hyenas that opened at least one door (Rural: 3.36 doors, $N = 14$ hyenas; Transitional: 1.7 doors, $N = 10$ hyenas; Urban: 1 door, $N = 1$ hyena).

Discussion

Our results failed to support the prediction of the CBH that average innovation scores would be highest in the transitional location. Instead, we found that average innovation scores were significantly higher for hyenas in the rural location than hyenas in the transitional location, and we found that average innovation scores from transitional and urban locations did not differ significantly from one another. In addition, there was little variation in problem-solving success rates among our three locations which suggests that high innovation scores likely reflect higher flexibility in opening doors that require unique motor actions rather than high solve rates. Furthermore, successful hyenas in the rural location were significantly faster at problem-solving than successful hyenas in the transitional location. In sum, more innovative hyenas were faster and more flexible solvers than less innovative hyenas. Overall, these results challenge the CBH's assertion that environmental change, such as that created by urbanization, favors innovativeness.

Recent research offers two possible explanations for our results. First, it may be that environmental change only favors specific types of innovativeness. In the present study, we measured innovation in an extractive foraging context and it is possible that environmental change favors innovative behaviors under different contexts (e.g., Liebl and Martin 2014).

Second, recent phylogenetic analyses of the evolution of larger avian brains have challenged the notion that environmental change selects for innovativeness. Brain size is

correlated with innovation rates in birds (Sol et al. 2005) and these studies suggest that larger brains may predate the invasion of variable habitats (Sayol et al. 2016; Fristoe et al. 2017). Thus, the causality implied by the CBH may be reversed, such that large brains might facilitate the invasion of variable environments instead of variable environments selecting for the evolution of large brains. Likewise, spotted hyenas are relatively innovative compared to other carnivores and it may be that their relatively high level of innovativeness historically facilitated their adaption to a wide variety of habitats in sub-Saharan Africa, including urban ones. However, this leaves unanswered the questions of which environmental variables favored the evolution of large brains in the original habitats of the bird species mentioned above, and why hyenas in our rural location have significantly higher innovation scores than hyenas in the transitional and urban locations. If hyenas' high baseline level of innovativeness exapted them for urbanization or if environmental change only favors innovation outside of a foraging context, we would have predicted no differences in innovation scores among our three study locations. Below, we briefly outline potential individual, physiological, or environmental variables that might mediate the relationship we observed between urbanization and innovation.

Individual mediators

Although there are some exceptions (Griffin et al. 2017; Biondi et al. 2020; Brooks et al. 2020; Jarjour et al. 2020), many studies have found that animals in cities are bolder and less neophobic, and that these personality traits might also affect cognition (Griffin et al. 2015; Dougherty and Guillette 2018). Previous work in these locations found that hyenas in the transitional location were less neophobic towards novel objects than hyenas in the rural location (Greenberg and Holekamp 2017). However, transitional hyenas were also less bold when feeding from inside a novel box, and were less likely to take risks when approaching a mock intruder than hyenas in the rural location (Greenberg and Holekamp 2017; Turner et al. 2020). Personality traits have also been linked to learning and problem-solving abilities in captive spotted hyenas (Johnson-Ulrich et al. 2018) and other animals (Dougherty and Guillette 2018). We found significant differences in participation among our three locations; hyenas in the rural location were much more likely to contact the MAB on any given trial than were hyenas in transitional or urban locations, which may reflect individual differences in boldness (Table 1). Thus, it is plausible that greater boldness among rural hyenas led to higher participation rates. However, we excluded subjects in all three study locations that failed to participate from our analysis of innovation, which should have controlled for the effect of boldness on innovation. Ultimately, further research is needed to directly

compare hyena personality and innovative problem-solving ability among these three locations.

Physiological mediators

Internal factors such as hunger or stress can also affect problem-solving (McEwen and Sapolsky 1995; Morand-Ferron et al. 2016). Some research suggests that body condition can influence participation in cognitive tasks (van Horik et al. 2017); however, we found no effect of body condition on participation or problem-solving in the present study. Anthropogenic disturbance can increase stress levels in animals (Partecke et al. 2006; Van Meter et al. 2009; Hammond et al. 2019), and stress generally has negative impacts on cognitive abilities (McEwen and Sapolsky 1995). Although previous research has found higher fecal glucocorticoid metabolites, a marker for stress, in spotted hyenas exposed to anthropogenic disturbance than in hyenas inhabiting undisturbed areas (Van Meter et al. 2009), hyena populations in the urban location have been established in northern Ethiopia for hundreds of generations, so it would be surprising not to find an attenuated stress response to anthropogenic activity in this location (Partecke et al. 2006; Atwell et al. 2012; Iglesias-Carrasco et al. 2020).

Environmental mediators

In addition to hunger levels, the immediate availability or lack of availability of food in the external environment may also influence the expression of innovation. Research investigating how either limited or abundant resources can promote innovation have yielded only mixed support for the idea that necessity, created by resource limitations, promotes innovation (Griffin and Guez 2014; Reader et al. 2016). On the other hand, the hypothesis that abundant resources, by increasing energy or time available to animals, can promote innovation has been well supported (Kummer and Goodall 1985; Benson-Amram et al. 2013; Reader et al. 2016). Although hyenas primarily scavenge in the urban location and hunt in the rural location, it is currently unclear how food abundance varies among the three locations. However, 28.96% of hyenas were classified as fat in the urban location compared to only 10.45% and 10.47% in the transitional and rural locations, respectively; this might suggest that food abundance was greater in the urban area. However, the 'spare time' hypothesis would have predicted that greater food abundance in the urban location would promote higher innovativeness, and the 'necessity' hypothesis would have predicted equal levels of innovativeness in the transitional and rural locations; neither of these is what we observed. Furthermore, the fact that location was not a significant predictor of trial success, after controlling for subject ID, suggests that the immediate proximate environmental conditions

under which trials were conducted explains little variation in the probability of solving the MAB. Instead, subject ID explained most of the variation in trial success (Table 1: conditional ICC = 0.84). Thus, it appears likely that difference in average innovation scores among the three locations was a result of the three locations containing significantly different ratios of innovative and non-innovative hyenas. This variation might be a result of genetic variation, but the transitional location has only been experiencing urbanization for two or three hyena generations, which allows insufficient time for much genetic change to have occurred. Instead, we strongly suspect developmental effects might explain the observed variation in innovativeness among hyenas in the three locations.

Exposure to more cognitive challenges generally results in greater cognitive development across animals (Diamond et al. 1964; Kotrschal and Taborsky 2010; Rojas-ferrer et al. 2020), so performance on cognitive tasks is often assumed to reflect cognitive demands in that environment. For hyenas, urbanization may offer more opportunities than challenges per se because scavenging from open trash dumps is most likely far less challenging than hunting wild prey. Hyenas in both Kenyan locations hunt and kill at least 90% of the prey in their diet (Holekamp et al. 1997), but hyenas in the transitional location increasingly feed on livestock (Green et al. 2018). In the urban location, “hunting” in the form of livestock depredation accounts for only 11% to 15% of total diet of hyenas, with the remainder being scavenged (Abay et al. 2010). Within mammalian carnivores, hunting behavior and a diet of vertebrate prey have been associated with larger overall brain size (Swanson et al. 2012), so it is possible that the reduced demand for hunting wild prey in our transitional and urban locations due to the presence of anthropogenic food sources is associated with reduced innovativeness in our study locations. Indeed, innovation scores likely also reflect an individual’s motor diversity because each door required a different motor action to open and innovation scores measured the number of unique doors a hyena opened. Many studies have found a key role for motor diversity in foraging innovations (Diquelou et al. 2015; Johnson-Ulrich et al. 2018) and it is plausible that hunting requires a great deal more motor flexibility than scavenging does (e.g., Hyaenidae: Holekamp et al. 2015). We suggest that investigating a link between hunting and motor diversity might be a promising avenue for future research.

Other environmental factors likely to vary among our three study locations that might create cognitive challenges include differential social demands (Schramme 2015) and differential threats of intraguild predation by lions. For example, lion abundance is considerably greater in our rural location than in our transitional location (Green et al. 2018), and lions do not occur at all in the urban area. Competition with lions is among the chief causes of mortality

in hyenas, and earlier versions of the CBH emphasize a key role of larger brains for avoiding any mortality causing events, not just those caused by novelty (Deaner et al. 2003). The social intelligence hypothesis suggests that large brains and enhanced cognitive abilities are a result of social challenges (Dunbar and Shultz 2007), and previous research on hyena cognition have found strong effects of social factors on the development of cognitive abilities (Johnson-Ulrich and Holekamp 2020). Although we found no effect of overall group size on the likelihood of solving the MAB in the transitional and rural locations, it is possible that other differences in social group structure among the three locations, such as weaker social cohesion (Schramme 2015; Belton et al. 2018), could influence innovativeness.

Finally, the similar levels of innovativeness expressed by hyenas in the transitional and urban location also suggests that the transitional location might not actually represent the “early colonization” stage of urbanization and instead, might be better characterized as a fully urban location. Even just two decades of gradually increasing urbanization (around 3 hyena generations) could have been enough time for hyenas to have behaviorally adapted to an altered environment via plasticity or microevolutionary processes. This would also suggest that even hyenas living mostly inside a protected area are experiencing environmental conditions akin to a fully urban one.

Conclusions

We found that hyenas in the rural location were significantly more innovative than hyenas in a transitional or fully urban location. This result challenges the prediction of the CBH that novel or changing environments should favor innovativeness. Instead, our results support the suggestion that how animals respond to urbanization is likely to be related to their adaptive match with urban environments (Griffin et al. 2017). Although cities are evolutionarily novel to all animals, including humans, they might not actually pose any novel challenges for spotted hyenas, and may in fact reduce the demand for innovation. In future, identifying the variables that mediate expression of innovation in animals across an urbanization gradient may shed light on the kind of environment that originally favored the evolution of innovativeness.

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Author contributions LJU and KEH conceived the project. LJU and KEH designed the methodology. LJU, GY, RLS, and KEH collected data. LJU and KEH analyzed the data and wrote the manuscript. GY and RLS edited the manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available in the Knowledge Network for Biocomplexity (KNB) repository, [<https://doi.org/10.5063/9C6VTD>].

Compliance with ethical standards

Conflicts of interest The authors report no conflicts of interest or competing interests relevant to the content of this article.

Ethics statement This work was conducted under research permit no. NACOSTI/P/16/35513/10422, issued by the Kenyan National Commission on Science, Technology and Innovation. The data collection procedure followed here was also approved by the Michigan State University Institutional Animal Care and Use Committee (IACUC): AUF #04/16–050-00. All research procedures were designed to adhere to the American Society of Mammalogists (ASM) Guidelines for the use of wild mammals in research and education (Sikes 2016) and to the Association for the Study of Animal Behaviour (ASAB) Ethics Committee and the Animal Behaviour Society (ABS) Animal Care Committee Guidelines for the treatment of animals in behavioral research and teaching (2017). Subjects in all locations are habituated to the presence vehicles and vehicles served as mobile blinds to hide researchers from view during deployment and collection of the MAB. Hyena participation in trials with the MAB was entirely voluntary, but encouraged with the use of bait. Researchers took care to remain at least 5 m from hyenas when collecting the MAB, and the MAB was not collected until all hyenas had moved at least 5 m away. However, hyenas regularly approached stationary vehicles at much closer distances.

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