

## Research



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# Anthropogenic environments exert variable selection on cranial capacity in mammals

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It is thought that behaviourally flexible species will be able to cope with novel and rapidly changing environments associated with human activity. However, it is unclear whether such environments are selecting for increases in behavioural plasticity, and whether some species show more pronounced evolutionary changes in plasticity. To test whether anthropogenic environments are selecting for increased behavioural plasticity within species, we measured variation in relative cranial capacity over time and space in 10 species of mammals. We predicted that urban populations would show greater cranial capacity than rural populations and that cranial capacity would increase over time in urban populations. Based on relevant theory, we also predicted that species capable of rapid population growth would show more pronounced evolutionary responses. We found that urban populations of two small mammal species had significantly greater cranial capacity than rural populations. In addition, species with higher fecundity showed more pronounced differentiation between urban and rural populations. Contrary to expectations, we found no increases in cranial capacity over time in urban populations—indeed, two species tended to have a decrease in cranial capacity over time in urban populations. Furthermore, rural populations of all insectivorous species measured showed significant increases in relative cranial capacity over time. Our results provide partial support for the hypothesis that urban environments select for increased behavioural plasticity, although this selection may be most pronounced early during the urban colonization process. Furthermore, these data also suggest that behavioural plasticity may be simultaneously favoured in rural environments, which are also changing because of human activity.

## 1. Introduction

From climate change to invasive species, humans are responsible for rapid and extreme environmental change, and biologists are increasingly interested in predicting how organisms will respond to such novel and rapidly changing environments [1,2]. Plasticity in the development and expression of behaviour allows animals to rapidly adjust to environmental variation [3,4], suggesting that species with high behavioural plasticity may cope best with human-induced rapid environmental change. Indeed, species with relatively larger brains are more likely to survive after introduction to a new region [5,6] or increase in abundance in the face of anthropogenic environmental changes [7]. The importance of behavioural plasticity for success in human-altered environments should be especially pronounced in cities, which represent some of the most extreme novel environments that organisms are faced with today [8]. Research suggests that species or lineages with relatively larger brains can better cope with urban and suburban environments [9,10] (but see [11,12]). Larger brains may facilitate innovative, novel behaviour that allows animals to survive in cities [13], such as exploiting new food resources, avoiding or ignoring novel predators [14–16], and adjusting signals in the face of noise [17,18].

While we have evidence that species with enhanced behavioural plasticity thrive in human-dominated areas, we know little about whether such environments are a significant selective force within species. Are urban populations of

animals adapting to increased demands on cognition? There is evidence that urban populations of some animals have adapted to pollutants [19], and have evolved differences in foraging morphology [20] and mobility [21,22], but it is unclear whether they are also adapting to the novel behavioural challenges associated with living near humans. Alternatively, it is possible that only those groups with relatively large brains can invade cities in the first place, such that selection on plasticity is stronger between species than within species. If animals are showing adaptive evolution of behavioural plasticity in anthropogenic environments, it would also be informative to know which species are showing the most pronounced evolutionary responses. Empirical and theoretical work suggest that both large population size and the potential for rapid population growth increase the likelihood that a species will show rapid evolutionary response to novel, anthropogenic environments, also known as 'evolutionary rescue' [23–28]. This mechanism suggests that species with high fecundity may show greater evolutionary changes in cognition in response to urban environments. At the same time, there is often thought to be a negative correlation between such 'fast' life-history traits and cognition [29,30], suggesting that such species may be unable to invade urban environments in the first place. Thus, it is an open question as to what life-history traits are associated with evolutionary changes in cognition in novel environments such as cities.

This research focused on the hypothesis that urban environments are selecting for increased behavioural plasticity by studying variation in cognition over time and space. We focused on mammals because skulls are readily available on a range of museum specimens, and external measures of skulls reflect relative cranial capacity [31], a commonly used proxy for overall cognitive abilities [32]. We compared variation in cranial capacity over a 100 year period in both rural and urban populations in Minnesota, a state where the majority of the human population (about 75%) have been concentrated in one large urban area (the Twin Cities) in recent history (about 150 years). We tested two predictions of the hypothesis that urban environments are selecting for increased cognition. First, we predicted that cranial capacity would be larger in urban populations relative to rural populations of the same species. Second, we predicted that cranial capacity would increase over time in response to increasing human development, but that this increase would be most pronounced in urban populations relative to rural populations. We tested one prediction of the hypothesis that evolutionary changes in cognition would be most pronounced in species capable of rapid population growth. In particular, we predicted that species with higher fecundity (more litters and greater litter size) would show more pronounced differences in cranial capacity between urban and rural populations.

## 2. Material and methods

### (a) Selection of specimens

From the database for University of Minnesota's Bell Museum mammal collection (more than 19 000 specimens), we tallied the total number of individuals of each species in urban and rural counties of Minnesota. We focused on Ramsey and Hennepin counties as our urban counties, but also included specimens

from Anoka, Dakota and Washington counties, if specimens were listed as collected in areas near population centres. We excluded specimens collected in or adjacent to other large metropolitan areas in Minnesota (in particular, Duluth and Rochester). We focused on species with at least 20 specimens available from urban areas, totalling 10 different species from several different families (see the electronic supplementary material).

We aimed to measure 40 specimens from each species (20 each from urban and rural populations). While making measurements, we eliminated damaged and incomplete skeletons, in addition to juvenile specimens, given that cranial capacity changes over development [33]. Thus, for some species, we ended up with fewer than the 20 individuals per population that we aimed to measure (see the electronic supplementary material). To control for variation in sample size across species, we ran power analyses for analyses that did not find significant differences between populations. In particular, we focused on the 'least significant number', or the sample size required for a statistically significant result, given the data structure is comparable for the larger sample. After testing our focal predictions that cranial capacity would vary between populations and over time, we added more specimens to the analysis to test some follow-up predictions (see the electronic supplementary material). In particular, we measured more specimens from rural populations to test whether observed changes in cranial capacity over time varied between lineages and between areas seeing more or less agricultural expansion.

### (b) Cranial capacity measurements

To estimate cranial capacity of specimens, three external measurements were recorded (length, height and width of the neurocranium). We used external neurocranium measurements used in past studies that are highly correlated with braincase volume in at least three orders of mammals [31,34,35]. The length was measured from the nasal/frontal suture to the top of the foramen magnum. The width was measured from the widest part of the parietal and squamosal bones. The height was measured from the basisphenoid to the highest point on the top of the cranium, excluding the sagittal crest when present. We used external neurocranium measurements because many of the museum specimens were small, old and fragile, and we did not want to damage the research specimens by using lead shot. All measurements were done by a single person (N.W.) using electronic digital callipers. Each measurement was performed once. All body measurements and additional information were recorded from each specimen's skin label. The complete dataset is available on Dryad (doi:10.5061/dryad.vn5sq).

To test for repeatability, several months after taking the original measurements, three specimens of each species were chosen randomly and re-measured. The difference between the two sets of measurements ranged from 3 to 9% (mean = 6%). We were interested in whether this repeatability may have influenced our analyses. For one of the smaller, more difficult species to measure (*Peromyscus leucopus*), we repeated all measurements three times (separated by at least 1 min). An ANOVA showed significant variation between individuals, despite the measurement error ( $R^2 = 0.97$ ,  $F_{49,100} = 74.6$ ,  $p < 0.0001$ ). However, measurements repeated within a day were more highly correlated (Spearman's  $\rho = 0.94$ ,  $p < 0.0001$ ) than those repeated across a several-month period (Spearman's  $\rho = 0.71$ ,  $p < 0.0001$ ). To test for the effects of low repeatability across months, we repeated the analyses reported below for *P. leucopus*, using mean cranial capacity as a function of both the original measurements and those repeated months later—despite the variation, we still found a significant effect of population on cranial capacity, controlling for year and body size (e.g. population effect:  $F_{1,46} = 5.28$ ,  $p = 0.02$ ). Taken together, these analyses of repeatability suggest that our results are conservative—there may be additional significant differences

between populations that we did not detect due to high variation across measurements.

We estimated relative cranial capacity as the product of our length, height and width neurocranium measurements, controlling for body size by including body size as a predictor in every statistical model constructed (see below for details). Past studies have found that the highest correlation between external neurocranium measurements and internal measurements of cranial capacity are linear combinations of length, width and height [31,34]. The relative importance of these three parameters for determining volumes varies between orders (depending on the shape of the head): for example, neurocranium length and width are highly correlated with cranial capacity in Artiodactyla, while height and width are highly correlated with cranial capacity in Carnivora [31,34]. However, our analyses make no direct comparisons of volume between species, only comparisons in volume over time and space within species, allowing us to focus on a simple product of the three neurocranial measures.

### (c) Controlling for body size and sex

We used total body length, tail length and hindfoot length (taken from skin measurements or measured by hand when absent) as a measure of body size. We ran a principal component analysis on these three variables for each species considered. In general, for all focal species, these variables were positively correlated and the first principal component (PC1) accounted for, on average, 58% of the variation. Results did not qualitatively change when other measures of body size were used (such as total length or hindfoot length alone). We controlled for body size by including this PC1 as a predictor variable in all statistical models constructed. The majority of species showed no significant variation in body size (PC1) across populations or over years, suggesting that temporal changes in body size [36] were not confounding the analysis. There were two exceptions to this observation—*Tamiasciurus hudsonicus*, which showed body size variation between populations, and *Myotis lucifugus*, which showed body size variation across years. To prevent this size variation from confounding our results, for these species, we included size-by-year or size-by-population interactions in models, where appropriate. We focused on this model-based method of controlling for body size because using ratios of cranial capacity to body size are wrought with interpretation issues [37]. However, because controlling for body size in different ways can lead to different conclusions about brain evolution [38], we repeated the analyses using the residuals of body size–cranial capacity regressions, and found no qualitative differences with reported results.

We did not include sex in our final analyses for two reasons. First, sex was unknown for 20% of specimens measured. Second, for those specimens where sex was known, there was no significant effect of sex on cranial capacity and the addition of sex into models did not qualitatively change the results.

### (d) Comparative analysis of life-history traits

We took life-history data typical for Minnesota populations of the species studied from Hazard [39]. Specifically, we took data on the highest number of offspring (per litter) and largest number of litters (per year) that were typical for a species. For instance, if a species was reported as having ‘generally 4–5 litters but sometimes 6 per year’, we recorded ‘5’ as the maximum litter number. We treat fecundity as a species-typical trait, and assume that it is the same across urban and rural populations. However, it is important to keep in mind that urban populations may have higher fecundity, although it is unclear whether this effect would vary across species.

We tested for effects of phylogeny on the relationship across species between life-history traits and cranial capacity differences between populations. Our phylogeny (see the electronic

supplementary material) was based on phylogenies for relationships between mammal orders [40,41], within Rodentia [42,43] and within murid rodents [44,45]. We used phylogenetic generalized least squares (PGLS) within R to estimate the effect of phylogeny [46,47]. Model selection, using sample-size-corrected Akaike’s information criterion (AICc), was used to determine the appropriateness of correcting for phylogeny. As detailed in the results, model selection implied analyses not corrected for phylogeny were more appropriate; however, both phylogenetically corrected and non-corrected analyses produced nearly identical results.

### (e) Statistical analyses

We used ANOVA for the majority of our analyses. Our focal analysis treated body size, year, population and a year-by-population interaction as independent variables, and cranial capacity as the dependent variable, run separately for each species. Because each population comparison represents an independent evolutionary event, we do not correct for multiple tests. In our expanded analyses of additional species (see the electronic supplementary material), we treated species, year (nested within species) and body size (nested within species) as our independent variables. All statistical analyses were performed in JMP v. 9.0 (SAS Institute, Cary, NC) apart from the PGLS, which was performed in R.

## 3. Results

### (a) Variation between populations

Of the 10 species measured, two showed significant differences in cranial capacity between rural and urban populations (table 1 and figure 1). Both white-footed mouse (*P. leucopus*) and meadow vole (*Microtus pennsylvanicus*) had larger cranial capacity (in a model controlling for body size) in urban relative to rural populations. Our dataset was limited by availability of specimens (in particular, urban specimens), so sample sizes were lower for some species (table 1; electronic supplementary material, figure S1). A power analysis suggested that if sufficient samples were present (up to 70 individuals), the observed differences between urban and rural populations would have also been significant for *Eptesicus fuscus* and *Sorex cinereus* (table 1)—these species also showed relatively larger cranial capacity in urban populations (figure 2).

We were interested in variation across species in the degree of difference in cranial capacity between urban and rural populations. We focused on the relative difference in cranial capacity between populations ((urban – rural)/(average urban and rural)) based on means that corrected for body size (least-squares means from models controlling for body size, reported in table 1). Using this metric, across all species measured, there was a significant tendency for urban populations to have relatively larger cranial capacity than rural populations (mean (s.e.) = 0.025 (0.009), *t*-test against a hypothesized mean of 0:  $t_9 = 2.79$ ,  $p = 0.02$ ). We then focused on whether fecundity of each species was correlated with the degree of differentiation in cranial capacity between populations. We tested whether it was appropriate to account for phylogenetic relationships across the 10 species. The AICc suggested that the model that ignored the effect of phylogeny was the best model ( $\Delta\text{AICc} = 8.5$  for model with lambda estimated as 0.67), although the results were virtually identical between models. The model uncorrected for phylogeny revealed a significant effect of litter size on the degree of differentiation of cranial

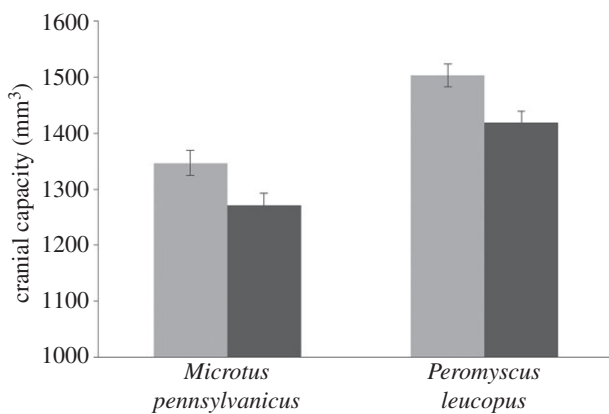


**Table 1.** Effect of year, population and body size on cranial capacity. Shown are results of ANOVAs ( $F$ -values) run for each of 10 species. Body size (the first principal component of a PCA on total body length, tail length and hindfoot length, run separately for each species), year, population (urban or rural) and a population-by-year interaction were treated as independent variables. Cranial capacity was measured as the product of the length, width and height of the braincase based on external measurements. Sample size ( $n$ ) for each analysis differed, so a power analysis was also run to determine the smallest sample size necessary to detect a significant difference between populations (LSN, least significant number). See figure 2 for unabbreviated scientific names of all species.

species	$n$ (LSN)	year	body size	population	pop. $\times$ year
<i>B. brevicauda</i>	37 (293)	0.61	6.51**	0.48	2.13
<i>C. gapperi</i>	33 (345)	0.17	0.24	0.37	0.64
<i>E. fuscus</i>	25 (70)	13.6***	9.53***	1.42	32.3***
<i>G. bursarius</i>	32 (14722)	0.07	53.6***	0.08	0.25
<i>M. lucifugus</i> <sup>a</sup>	27 (927)	0.12	0.69	0.12	5.03**
<i>M. pennsylvanicus</i>	36 (27)	2.35	11.1***	5.83**	0.02
<i>P. leucopus</i>	49 (25)	1.34	4.51**	8.51***	2.59
<i>S. carolinensis</i>	25 (378)	0.82	8.41***	0.26	2.63
<i>S. cinereus</i>	33 (57)	5.86**	0.25	2.33	0.64
<i>T. hudsonicus</i> <sup>a</sup>	38 (623)	4.59**	6.87**	0.24	1.56

<sup>a</sup>Fully factorial model run because body size varies with population and/or year (see Material and methods).

\* $p < 0.10$ , \*\* $p < 0.05$ , \*\*\* $p < 0.01$ .

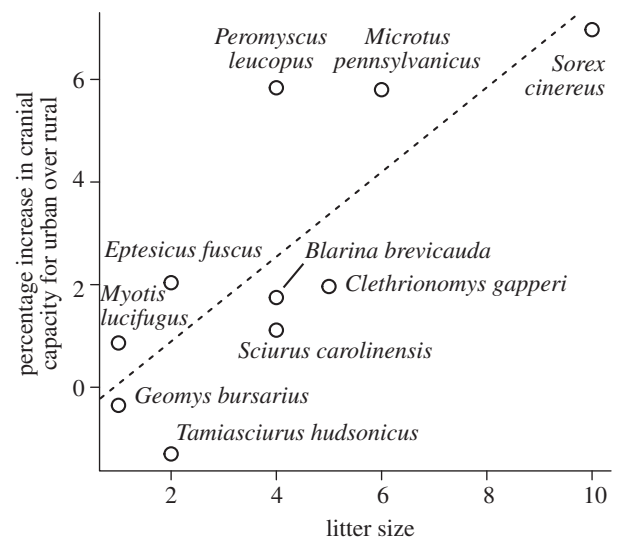


**Figure 1.** Variation between urban (light grey) and rural (dark grey) populations in cranial capacity. Shown are least-squares means from an ANOVA that included body size (the first principal component of a PCA on total body length, tail length and hindfoot length, run separately for each species), year, population (urban or rural) and a population-by-year interaction, run separately for each species (table 1).

capacity between urban and rural populations ( $F_{1,7} = 12.3$ ,  $p = 0.01$ ; figure 2), but no effect of litter number ( $F_{1,7} = 0.02$ ,  $p = 0.88$ ).

### (b) Variation over time

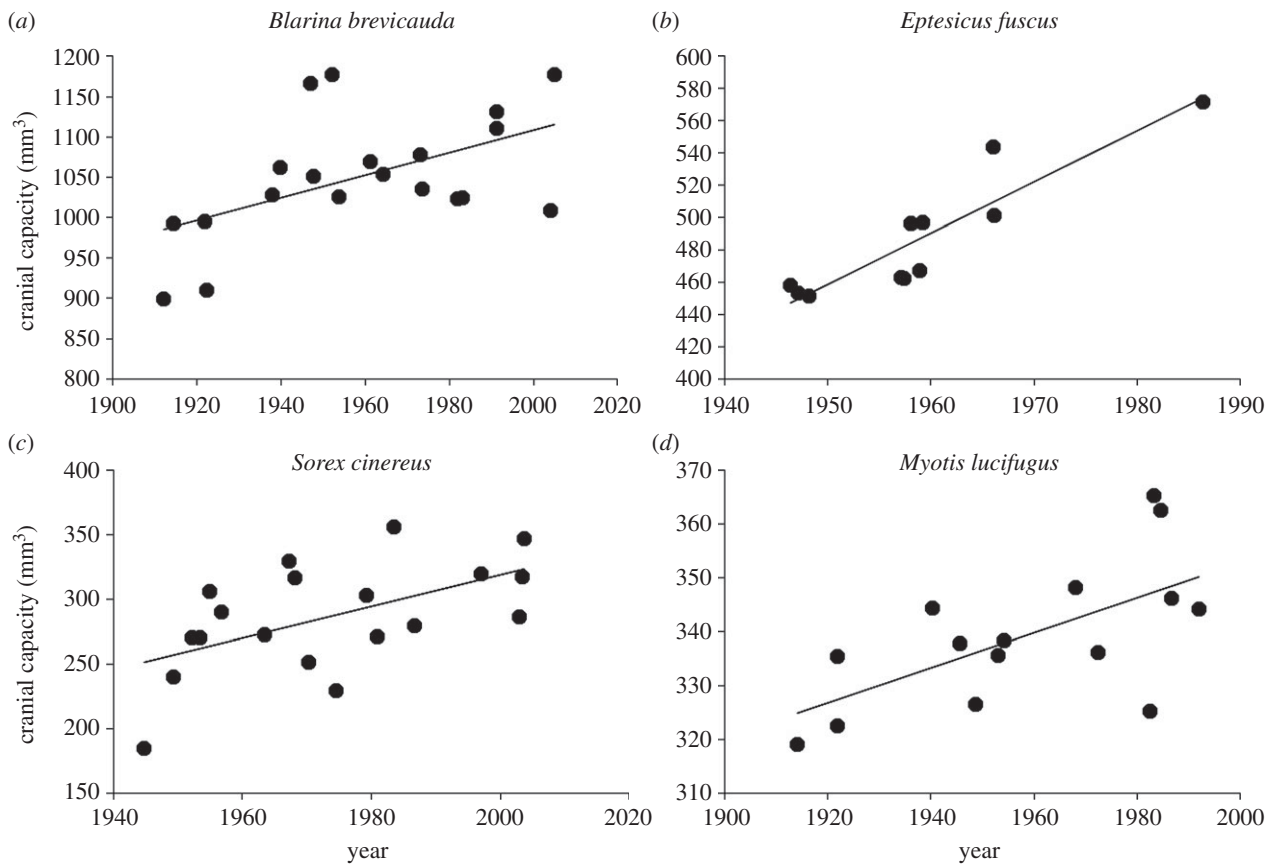
Given that several species showed significant year-by-population interactions for cranial capacity (table 1), we analysed the effects of year on cranial capacity separately for urban and rural populations, in models controlling for body size. There was no significant effect of year on cranial capacity for any urban population (table 2). Contrary to predictions, two species (*P. leucopus* and *E. fuscus*) showed marginally significant declines in cranial capacity over time in urban populations (table 2; electronic supplementary material, figure S2). Also contrary to expectations, rural populations



**Figure 2.** Variation in fecundity is correlated with degree of difference between rural and urban populations. Shown are the results of a model testing for effects of litter size and number on the relative difference in cranial capacity between rural and urban populations of a species. More positive values of the dependent variable indicate that urban populations have a greater cranial capacity than rural populations of the same species (based on least-squares means from a model that controlled for body size and year—see table 1). PGLS analysis indicated that phylogeny had little impact on the data, so data uncorrected for phylogenetic relationships are plotted.

of four species (two bats and two shrews) showed significant increases in cranial capacity over time (table 2 and figure 3). Additionally, *T. hudsonicus* showed marginally significant increases in relative cranial capacity over time in rural populations (table 2).

We found increases in relative cranial capacity in rural populations for all of the insect-feeding species we measured. We were interested in whether this unexpected pattern was a general trend across insect-feeding and carnivorous mammals.



**Figure 3.** Changes in cranial capacity over time in rural populations. Shown are leverage plots from ANOVAs that included body size (the first principal component of a PCA on total body length, tail length and hindfoot length, run separately for each species) and year, run separately for each species and population (table 2).

**Table 2.** Effect of year, population and body size on relative cranial capacity. Shown are results of ANOVAs ( $F$ -values) run for each of 10 species, for urban and rural populations separately. Body size (the first principal component of a PCA on total body length, tail length and hindfoot length, run separately for each species) and year were treated as independent variables. Cranial capacity was measured as the product of the length, width and height of the braincase based on external measurements. See figure 2 for unabbreviated scientific names of all species.

species	urban			rural		
	$n$	year	body size	$n$	year	body size
<i>B. brevicauda</i>	17	0.27	0.21	20	6.83**	9.35***
<i>C. gapperi</i>	17	0.53	0.26	22	0.15	0.02
<i>E. fuscus</i>	14	3.58*	9.91***	11	37.8***	0.36
<i>G. bursarius</i>	16	0.20	8.51**	16	0.05	44.1***
<i>M. lucifugus</i> <sup>a</sup>	13	0.64	1.03	15	7.24**	2.70
<i>M. pennsylvanicus</i>	18	1.58	11.8**	18	1.53	2.30
<i>P. leucopus</i>	25	3.62*	0.55	24	0.05	4.00*
<i>S. carolinensis</i>	14	0.51	3.67*	11	3.14	6.28**
<i>S. cinereus</i>	14	0.86	0.01	19	7.26**	0.37
<i>T. hudsonicus</i>	15	0.52	1.95	22	3.31*	0.63

<sup>a</sup>Year  $\times$  size interaction included in model because size varies with year (see Material and methods).

\* $p < 0.10$ , \*\* $p < 0.05$ , \*\*\* $p < 0.01$ .

To address this idea, we measured 171 additional rural-collected specimens, across five additional insectivore species (shrews and moles), four additional bat species, two additional

rodent species and two carnivore species for which enough specimens were available (see the electronic supplementary material for list of all included species). Across all insectivores,

**Table 3.** Effect of year on cranial capacity of rural populations of major clades measured. Shown are the results of four ANOVAs measuring the effect of species, year (nested within species) and body size (nested within species) on relative cranial capacity. Additional species measured are listed in the electronic supplementary material.

clade	<i>n</i> : individuals (species)	species	year (species)	size (species)
Insectivora	148 (7)	1662***	5.82***	8.91***
Chiroptera	60 (6)	270***	3.54***	0.44
Carnivora	31 (2)	1985***	9.85***	16.1***
Rodentia	140 (8)	1801***	1.18	21.9***

\* $p < 0.10$ , \*\* $p < 0.05$ , \*\*\* $p < 0.01$ .

bats and carnivorans, we found significant effects of year on cranial capacity for rural populations (table 3). However, no such patterns were detected among rodents.

We were interested in further exploring the unexpected observation that cranial capacity increased over time in several rural populations. We thought that large-scale conversion from native habitats to agriculture might also exert a selective force on cognition. To test this idea, we focused on measurements of 38 additional short-tailed shrews, collected from counties that differed in the extent to which they converted to agriculture, some of which converted to 75–100% agriculture over the last 150 years, and some that converted to less than 25% agriculture over the last 150 years. Contrary to the expectations of this follow-up hypothesis, non-agricultural populations showed a significant increase in relative cranial capacity over time (year:  $F_{1,14} = 6.02$ ,  $p = 0.02$ ; body size:  $F_{1,14} = 2.53$ ,  $p = 0.13$ ), while agricultural populations did not (year:  $F_{1,17} = 1.03$ ,  $p = 0.32$ ; total length:  $F_{1,17} = 11.2$ ,  $p = 0.004$ ). This suggests large-scale conversion to agriculture is not necessarily related to increased cranial capacity.

## 4. Discussion

### (a) Spatial variation in cranial capacity suggests cities sometimes select for cognition

This research sought to test the idea that rapid human-induced environmental change might select for increases in behavioural plasticity within species, not simply sorting of species that vary in behavioural plasticity. Our results provide some support for our first prediction: that, at least for some species, urban populations have relatively greater cranial capacity than rural populations (table 1 and figure 1). In particular, urban populations of two rodent species had roughly 6% greater cranial capacity in urban populations relative to rural populations in the same state. In addition, across all species measured, there was a significant tendency for urban populations to have larger cranial capacity when controlling for body size. These results are consistent with the idea that urban environments select for increased behavioural plasticity.

Studying patterns across 10 species allowed us to simultaneously test predictions about which species might show the most pronounced evolutionary changes in cognition. Both theory and empirical work suggest that population size and capacity for growth are important for evolutionary 'rescue' in response to the strong selection pressure imposed by novel environments such as cities [23–28]. Consistent with

this expectation, we found that variation across species in the number of offspring per litter was correlated with the degree of cranial capacity variation (figure 2). Species with higher reproductive rates had significantly greater cranial capacity in urban populations relative to rural populations than species with lower reproductive rates. This result also recalls a separate body of theory linking population size to evolutionary rate, because large populations can more effectively 'explore' a fitness landscape through mutational input, and are sometimes (but not always) more likely to cross fitness valleys [48,49]. However, given that fecundity does not necessarily translate into larger population sizes, its importance here may be due either to its effect on population growth rate or overall population size [23–28]. These results connecting fecundity to cranial capacity in urban populations echo previous research that found that the bird species successful in urban environments tend to be those with high annual fecundity [13]. Similarly, species with more generations since urbanization have been shown to have more fear acclimation towards humans, suggesting selection for reduced fear [50]. All of these studies are consistent with the idea that species capable of high reproduction may show more pronounced evolutionary responses to urban environments.

The results of this study combine with existing research to suggest that there are two distinct possible links between cognition and survival in urban environments. On the one hand, species with relatively greater neural investment are predisposed for survival in urban environments because they can learn to cope with novel conditions [9,10]. Owing to trade-offs between cognition and learning, these species may also be those with 'slow' life histories, consisting of delayed reproduction and lower fecundity [29,30,51]. On the other hand, species in urban areas may evolve increased cognition over many generations in that environment. In this case, species with higher fecundity should show more pronounced responses (figure 2).

### (b) Temporal variation in cranial capacity suggests rural environments may also be cognitively demanding

Contrary to our second prediction, we did not find increases in cranial capacity over time in urban environments. In fact, two species showed marginally significant declines in cranial capacity over time in urban populations (table 2; electronic supplementary material, figure S2). These unexpected results may have emerged out of two processes. First, it is possible that response to urbanization was rapid and that our time series missed the main selective events in the Twin Cities

area. Industry was already well developed in Minneapolis by 1860, and the population of the city was 200 000 by 1900 [52,53], whereas our earliest samples were from the 1920s and 1930s. Selection experiments on brain size have shown that significant differentiation can emerge after just two generations [54]. Second, it is possible that novel urban environments may only transiently select for increased cognition. While urban and suburban environments are quite extreme novel environments, they are somewhat predictable. For instance, many animals exploit novel, predictable resources such as bird feeders or garbage cans [55–56]. Given that brain tissue is costly [57], we might expect consolidation of behaviour appropriate for city living and a decrease in brain size over time following initial colonization of a novel but predictable environment—in other words, genetic assimilation of behaviour [3]. However, this interpretation is speculative and must be evaluated with more thorough time series.

An additional unexpected result was the finding that all insect-feeding species measured, two bats and two shrews, showed significant increases in cranial capacity over time in rural populations (table 2 and figure 3). Follow-up analyses revealed that this might be a general pattern for a range of insect-feeding and carnivorous species (table 3). This pattern does not seem to be driven by large-scale conversion to agriculture as it also occurred in rural areas with little conversion to agriculture. It is possible that rural environments may also be selecting for increased cognition, at least for certain species. Rural areas may be considered novel not just because of conversion to agriculture, but also because of extensive logging, recreational use and other human development. It is possible that development in rural areas requires increased movement to find enough food, and thus increased spatial memory. This might be especially pronounced in animals such as bats, where we already know spatial memory is important for feeding over wide areas and returning to their roost [58,59]—increased patchiness of food in rural areas may have forced bats to travel further, selecting for increased cognition. Regardless of the explanation, future research should consider the extent to which increased cognition is favoured in rural environments.

The present dataset cannot exclude the possibility that the observed variation in cranial capacity is due to variation in nutrition over time and space. Over the last 100 years, there have been major changes in the availability of once-limited nutrients such as nitrogen [60]. It is possible that improved nutrition of individual prey items has resulted in

developmental increases in cranial capacity [61,62]. Similarly, urban environments are also drastically different nutritionally than rural environments, and the body mass of animals living in association with humans has been increasing over the last several decades [63]. However, the fact that there were generally no increases in body size over time or in cities (see Material and methods) suggests that nutritional changes alone cannot explain our results.

### (c) Conclusions and future directions

In conclusion, our results provide some support of the hypothesis that urbanization selects for increased cognition, at least for a handful of species. In particular, highly fecund species show pronounced increases in cranial capacity in urban relative to nearby rural populations. The unexpected result that cranial capacity increases in size over time in rural populations suggests that selective or developmental conditions may also favour cognition in rural populations. Our results cannot determine the relative contribution of genetic or developmental differences between populations (and across years). However, given that several of the species studied are commonly used in the laboratory, it would be extremely interesting to follow up this research with a common garden experiment with urban and rural populations (e.g. *P. leucopus* or *M. pennsylvanicus*). Such a study on live specimens would also allow for behavioural tests of variation in cognition, instead of simply relying on a proxy for cognition (such as cranial capacity). Furthermore, given that these results are entirely correlational, the causal importance of novel, urban environments would be reinforced with an artificial selection experiment, even if over only a few generations [54]. In combination with previous research, this work reinforces the hypothesis that cognition will be important for survival of animals in novel environments such as cities, and possibly rural environments affected by human development. However, our results also suggest that increases in cranial capacity within species are not necessary for survival within urban environments.

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