

Memòria justificativa de recerca de les beques predoctorals per a la formació de personal investigador (FI)

La memòria justificativa consta de les dues parts que venen a continuació:

- 1.- Dades bàsiques i resums
- 2.- Memòria del treball (informe científic)

Tots els camps són obligatoris

1.- Dades bàsiques i resums

Títol del projecte ha de sintetitzar la temàtica científica del vostre document.

Behavioural Flexibility: evolutionary past and its role in a changing world

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Resum en la llengua del projecte (màxim 300 paraules)

A través de la historia de la vida, gran parte de los organismos han desarrollado estrategias para responder a un mundo en constante cambio. Hoy en día, las actividades humanas producen cambios ambientales a una velocidad sin precedentes, lo cual se traduce en grandes desafíos para la persistencia de biodiversidad. Esta investigación evalúa las respuesta de los animales a los cambios ambientales enfocándose en la flexibilidad del comportamiento como estrategia adaptativa. En una primera aproximación a una escala evolutiva, se otorgan evidencias del vínculo hasta ahora tenue entre la cognición e historias de vida, entregando un claro apoyo a la relación entre longevidad, vida reproductiva y el tamaño del cerebro en mamíferos. La longevidad es el centro de muchas hipótesis respecto a las ventajas de desarrollar un cerebro grande, como por ejemplo en la hipótesis del buffer cognitivo y las respuestas flexibles frente a nuevos ambientes. En un segundo nivel, se abordan factores extrínsecos e intrínsecos que podrían explicar las diferencias individuales en innovación, un componente clave en la flexibilidad del comportamiento. Por medio de una aproximación experimental, se evalúan potenciales escenarios que podrían conducir a consistentes diferencias individuales en uno de los principales factores subyacentes a la innovación (i.e. la motivación), y el potencial control endocrino sobre estos escenarios. Posteriormente, con el objetivo de evaluar la respuesta de los animales frente a los cambios ambientales actuales, se explora la respuesta de los animales frente a una de las actividades humanas mas disruptivas sobre los ecosistemas, la urbanización. Por medio de un análisis filogenético comparativo a nivel global en aves se abordan los mecanismos implicados en la pérdida de biodiversidad observada en ambientes urbanos. Los resultados entregan evidencias sobre la importancia de procesos de dispersión local junto con el papel clave de los rasgos de historia de vida, pero en un sentido diferente al clásicamente pensado. Finalmente por medio de una revisión bibliográfica se entregan evidencias teóricas y empíricas que respaldan el rol clave de la flexibilidad del comportamiento en confrontar los desafíos de una vida urbana. La integración de estos resultados muestra cómo el pasado evolutivo contribuye a hacer frente a los retos ambientales actuales, y pone de relieve posibles consecuencias ante un planeta más cambiante que nunca.

Resum en anglès(màxim 300 paraules)

Across the history of life, most of organisms have evolved proper strategies to respond to an ever-changing world. Nowadays, human-conducted environmental changes impose an unprecedented loss of biodiversity. This thesis assesses one of the key responses to actual environmental changes, behavior flexibility. In a first approximation by a phylogenetic comparative approach, strong evidences for the still tenuous link between cognition and life history is reported. The clearest support for the relationship between lifespan and brain size in mammals is showed. Lifespan is core to many hypotheses regarding the advantages of enlarged brains, like the cognitive buffer hypothesis to proper respond to novel environments. In a second level, it was explored for the drivers of innovation propensity, a key component of behavior flexibility. By mean of an experimental approach, the possible scenarios that may select for consistent individual differences in motivation, a major driver of innovation, were assessed. Consistent individual differences in motivation are reported, but heritability and endocrine control features suggest that mechanism may be different of those hypothesized. Later, to approach for the role of behavioral flexibility in changing environments, the behavior responses to one of the most disruptive effects of human activities on ecosystem, the urbanization, were assessed. First, using a global comparative analyses in birds communities across the world, it was showed the importance of local processes by random dispersal effects alongside habitat filtering to explain loss of biodiversity in urbanized environments. Some phylogenetic lineages appear more likely than others to thrive in urban environments, which is related to a future-returns strategy (i.e. low brood value) that allow for decrease the cost of delay reproduction and increase the opportunities to acquiring environmental information. Second, based on a literature review, theoretical and empirical evidences are reported for argue that behavioural flexibility is an important way to deal with urban environments. The integrations of these results shows how the evolutionary past has shaped the traits that contribute to deal with actual environmental challenges, and highlight the expected consequences in a rapid changing, human-dominated world.

2.- Memòria del treball (informe científic sense limitació de paraules). Pot incloure altres fitxers de qualsevol mena, no més grans de 10 MB cadascun d'ells.

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1. INTRODUCTION

Through the known history of life, environmental disruptions have impacted and changed the natural environments, however in the last five decades human activities has been changing the world at unprecedented pace (Millennium Ecosystem Assessment, 2005). The growing scale of human enterprises is the main responsible for the accelerated actual environmental changes, contributing to climate alterations, loss of biological diversity, eroding ecosystems around the globe (Ehrlich, 1995; Vitousek, 1997). Despite these fast human-conducted environmental disruptions, some organisms are doing better than ever. Uncovering the responses of species to environmental changes is challenge but a better understanding of how evolutionary history has shape behavioural responses and how these responses work in front of actual human-conducted environmental change may help us to mitigate the loss of biodiversity and manage organism that become pests with the global expansion of human population (Sih, Ferrari, & Harris, 2011; Sih, Stamps, Yang, McElreath, & Ramenofsky, 2010).

1.1 BEHAVIOUR FLEXIBILITY

The ability of an animal to adaptively modify their behaviour would provide an important adaptive potential to deal with environmental changes (Lefebvre, Reader, & Sol, 2004). Behavior flexibility facilitates the production of adaptive responses to a wide array of ecological challenges. For example, assist birds and mammals in the invasion of new environments (Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005) and predict bird population tendencies (Shultz et al. 2005). For one way, most of the variation among species in this traits is explained by cognitive abilities, as suggested by findings that brain size predict learning and propensity to innovate (Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Reader & Laland, 2002). On the other way, more simple cognitive process and temperament are related to innovation and learning variation within species (i.e. Cole et al. 2011, Sol et al. 2012), drivers factors that just in the last years has started to be studied. All above features and others still for unravelling contribute to the large variation that exist in behavioural flexibility among individuals, populations and species (Lefebvre et al., 2004; Lefebvre & Sol, 2008).

1.2 EVOLUTIONARY PAST

Evolutionary history has been important in shape traits that nowadays are effective for coping with changing environments, like behaviour flexibility and associated brain size (Sih et al., 2011). One of the hypotheses for the evolution of big brains involves the cognitive buffer hypothesis. That hypothesis take into account the balance between costs in time and energy to evolve big brains and the benefits provided in the form of longer reproductive life, compensating the enormous cost of evolve big brains. Although evidence exist for the basic tenets of cognitive buffer hypothesis, as big brained birds survival longer (Sol, Székely, Liker,

& Lefebvre, 2007), the link remain elusive in mammals and preclude us to generalize patterns.

1.3 INDIVIDUAL RESPONSES

Because important consequences on population dynamics and species evolution, the study of individual differences have acquired pivotal relevance in the last decade (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012). Behavioural flexibility in particular varies among individuals as consequences of underlying factors like temperament traits and other individual's features that remain to be elucidated. Species confronting human-induced rapid environmental changes (HIREC, sensu Sih et al. 2011) are under new selective pressures, thus understanding individual responses to actual environmental challenges may provide a way to understand evolutionary past and predict which individuals or species would be in disadvantage and what will be potential pest (Sih et al., 2011).

1.4 RAPID HUMAN-INDUCED ENVIRONMENTAL CHANGES (HIREC)

Habitat loss and fragmentation are the main types of human-induced environmental changes and urbanization is the most extreme example of this HIREC. Because the accelerate rate of human population growth coupled with the expansion of land for urbanization, understand the mechanisms involved in the organism responses to urbanization put enormous scientific challenges. Cities may allow an unique opportunity for comparative studies addressing the behaviour responses of animals as provide large scale examples (Anderies, Katti, & Shochat, 2007; Grimm et al., 2008). It is often assumed that urban species have adaptations to survive in such environments, yet the role of alternative processes has generally been under-appreciated. How species and individuals confront the challenges to live in these environments and the mechanisms involved, are questions that remain to be elucidate.

MAIN GOALS

This research has four main goals:

- (1) In light of the pivotal role of behavioral flexibility to generate adaptive responses to rapid environmental changes but yet poorly support for basic tenets of the cognitive buffer hypothesis, it was look to provide support for and generalize the evolutionary advantages of evolve big brains.
- (2) Behavior flexibility varies at individual level, but the drivers that promote individual variation in behavior flexibility are poorly knowed. There was assessed extrinsic and intrinsic promoters of innovation, one of the key components of behaviour flexibility.

- (3) To assess the processes that allow or preclude to live in urbanized environment. Taking birds as study models two hypothesized mechanisms, the dispersal-assembly and environmental filter hypotheses were assessed.
- (4) To assess for the role of behavior flexibility to confront urbanization. The relevant question was whether and how behavioral flexibility provides appropriate skills to organisms to confront urbanized environments.

2. METHODS

2.1 METHODS GOAL 1

Data

Lifespan

As an estimate of reproductive lifespan, information on maximum-recorded lifespan (in years) for 493 species of mammals was obtained from de Magalhaes et al. (2009; see references therein). We used two lifespan measures as dependent variables: 'lifespan' and 'reproductive lifespan' (see Barrickman et al. 2008).

Brain size

Data on brain mass for 493 species were compiled from published information from multiple sources (see Appendix I). Brain masses were either calculated from endocranial volumes or were whole brain masses that provides a reliable proxy of brain mass (Isler et al. 2008; Ashwell 2008; Finarelli and Flynn, 2009).

Body size

Larger species have larger brains, so it is necessary to estimate brain mass controlling for the allometric effect of body size. Body mass was obtained from the same sources as brain mass when available and complemented with published data as needed (Smith & Jungers, 1997).

Confounding Variables

We accounted for several factors that potentially can affect lifespan variation. Life history traits as gestation, weaning, age at first reproduction, litter size and litters per year were taken from published literature (Ernest, 2003; de Magalhaes et al., 2009; Bielby et al., 2007).

Geographic variables like maximum northern latitude (MNL) and maximum southern latitude (MSL) were gathered from breeding ranges published in the literature (Dorst & Dandelot, 1973; Strahan, 1995; Schilling et al., 1987; Mitchell-Jones et al., 1999; Kingdon, 1997; Folkens et al., 2002; Long, 2003; Patterson et al., 2003; Jackson, 2007; IUCN, 2008) and ecological variables like diet and habitat that were compiled from multiple sources (Long,

2003; Wilson & Reader, 2005; Jakson, 2007; Kingdon, 1997; Patterson et al. 2003; IUCN, 2008). Finally, both lifespan and reproductive lifespan scale allometrically with body size (Harvey & Clutton-Brock, 1985; Blumstein & Møller, 2008; this study) so it is relevant to examine whether brain mass correlates with lifespan when the body size effect is controlled for. To account for body size effects on lifespan, we estimated the residuals of a log-log regression of lifespan (or reproductive lifespan) against body size (termed 'residual lifespan' or 'residual reproductive lifespan', respectively).

Analyses

Closely-related taxa share many traits from common ancestors, thus species' traits cannot generally be treated as statistically independent points (Felsenstein, 1985). Lifespan values for species were modelled with a phylogenetic generalized least squares approach (PGLM) (Freckleton et al., 2002; Phillimore et al., 2006; Shultz & Dunbar, 2007). This method takes the phylogenetic variance/covariance matrix derived directly from the phylogenetic supertree of the species, and hence evaluates the association between variables taking into account the correlated error structure. PGLM analyses were conducted with R 2.7.0, (R Development Core Team, 2005), the R code kindly provided by R. P. Freckleton, and the phylogenetic hypothesis proposed by Bininda-Emonds et al. (2007, corrigendum 2008). Following Sol et al. (2008), a minimum adequate model (MAM) was constructed by means of a backward selection approach. Diagnostic plots were examined in order to check for outliers, heteroscedasticity, and non-normal errors.

2.2 METHODS GOAL 2

Study subjects

42 individuals of free-living feral pigeons from two populations over 57 km apart (Barcelona and Moià, Catalonia, Spain) were captured in February 2010. Upon capture biometric measures of each individual were taken and individuals were marked with a unique combination of colored plastic rings. Analyses were restricted to adult individuals (18 from Barcelona and 16 from Moià). Sexing of individuals was performed by observing courtship behavior (e.g. tail-dragging, bowing, driving, etc) (Johnston & Janiga, 1995) and breeding activity (i.e. egg laying and incubation).

General experimental procedure

Levels of motivation, aggressiveness, social dominance, motor and consumer innovation were quantified in a foraging context by exposing pigeons to four different tests. All tests were conducted in three periods from March 2010 to August 2011. All these experiments were videotaped and observations were made behind a curtain to avoid disturbing the animals. Finally, a cross-fostering breeding experiment was conducted from October 2010 until March

2011 (see below). All animal care, husbandry, and experimental procedures were approved by the Generalitat de Catalunya (0152S, Dept de Medi Ambient i Habitatge).

Motivation test- After the overnight fasting period, we approached a cage and put the habitual feeder (the same in all tests) with a seed mixture at the front of the cage. Latency to begin feeding after the disturbance was used as a measure of motivation (see Lefebvre et al. 1996; Bouchard et al. 2007; Sol et al. 2011).

Motor innovation - After the motivation test, we immediately replaced the feeder with an identical feeder covered with an opaque rigid cardboard lid and recorded the time the individual took to remove the lid and eat the food. If the individual did not solve the task after 20 min, it was considered to have failed to innovate. For individuals that did solve the task, the task was presented again two hours later to assess whether individuals had learnt how to solve the task. The latency from the first peck to the apparatus to open the lid was integrated with individual solve or not solve information, and both were the measure of motor innovation (i.e. probability of not solve across the experimental time, see analyses).

Consumer innovation test- As in the motor innovation test, the consumer innovation test started after the motivation test, when feeder with the familiar seed mixture was changed by an identical feeder containing an unfamiliar food. Both tests were conducted in consecutive days and individuals were left a maximum of 20 min to solve the task. The individual tendency to incorporate new food resources was measured as the latency to forage from the food within the feeder integrated with individual solve or not solve information (i.e. probability of not eat across the experimental time, see analyses).

Group observations of social dominance and aggressiveness- After an overnight fasting period of 15 hours, the habitual mix of seeds in a circular feeder (30 cm in diameter) was provided at the center of the habitual outdoor aviary. From four trials per group of the videos tapes, the dyadic proportions of wins and losses for each individual, the observed numbers of dyadic wins and losses in each group and total number of interactions between individuals were recorded. With this information the normalized David's scores was calculated (Devries, Stevens, Vervaecke, & de Vries, 2006). Aggressiveness of individuals was estimate as the total number of attacks initiated in each 20 min trial.

Cross-fostering experiment- Was based on 16 breeding pairs of pigeons in outdoor breeding aviaries (2 x 2 x 4 m.). Pigeons lay almost invariably clutches of two eggs (Johnston & Janiga, 1995), so one of the chicks was interchanged at 4 (+/-1) days of age with another from a different breeding couple. All chicks were individually marked using small plastic rings that were posteriorly replaced by plastic rings as the chicks grew up.

Corticosterone profile

Blood sampling- Corticosterone profile was quantified for each individual following the “capture restrain” protocol (J.C. Wingfield & Romero, 2001). The blood samples were stored in heparinized tubes and kept in a fridge with dry ice to be transported to the laboratory the same day, immediately after extraction.

Sample processing and Radioimmunoassay- The heparinized tubes were centrifuged in the laboratory at 3000 rpm for five minutes. Plasma was removed and stored at -20° C until Radioimmunoassay. To obtain corticosterone measures, hormone was extracted from plasma with ether and assayed by radioimmunoassay in duplicates based on Wingfield et al. (1992). The assays were conducted in the Institute of Animal Physiology at Autonomous University of Barcelona.

Statistical analyses

Behavioral tests

An intraclass correlation coefficient (ICC) was used to assess for individual consistency in the behavioral responses (Nakagawa & Schielzeth, 2010). To model motivation and innovation latencies, survival analysis were used (Bókony, Kulcsár, Tóth, & Liker, 2012; Dingemanse, Dochtermann, & Wright, 2010; Sol et al., 2012, 2011). To avoid co-linearity problems, the factors of Principal Component Analysis (PCA) was performed and used instead actual morphological variables in the models (i.e. high correlation of morphological variables). A model selection procedure based on $\Delta AICc$ was used to identify the best model or models. All analyses were performed by R software (R Development Core Team 2009). The packages irr (ICC), coxme (survival models) and MuMin (model selection) were used.

Parent-offspring resemblance (h^2)

Mother, father and mid-parent (i.e. average the absolute values of both parents) values of motivation, were regressed on mean chick values (Drent, Oers, & Noordwijk, 2003; Falconer & Mackay, 1996) by mean of generalized linear models (GLM) by the stats package. In a way to account for parental environment effects, we performed the same regression described above, but just for the foster group.

2.3 METHODS GOAL 3

Data base

We collected data from published studies and our own surveys on bird species abundance from urban to more naturalized habitats from 22 areas from all continents (See details in Fig. 1). To define the degree of urbanization, we followed Marzluff et al. (2001) and differentiated urbanized environments in “highly urbanized” environments (urban habitat, hereafter) and “moderately urbanized” environments (suburban habitat, hereafter). The

surrounding habitats considered as potential source of immigrants were rural and wildland environments. To obtain a measure that enables comparison we transformed abundances to densities expressing individuals per hectare (individuals/ha). The taxonomic representation of the base data consists of 842 avian native species from 121 families and 29 orders.

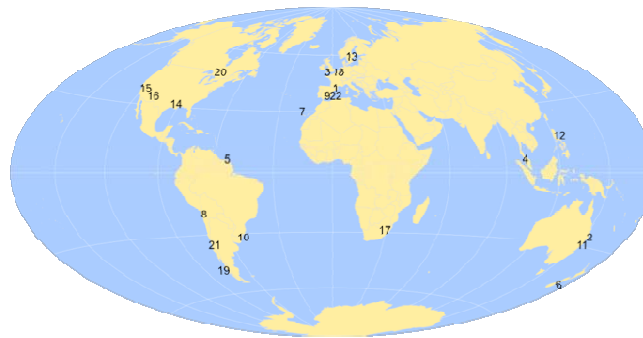


Figure 1. Worldwide location of the urbanization gradients. 1. Barcelona, 2. Brisbane, 3. Bristol, 4. Cameron Highlands, 5. Cayenne, 6. Dunedin, 7. La Palma, 8. La Paz, 9. Madrid, 10. Mar del Plata, 11. Newcastle, 12. Olongapo, 13. Orebro, 14. Oxford, 15. Palo Alto, 16. Phoenix, 17. Pretoria, 18. Rennes, 19. Santiago de Chile, 20. Toronto, 21. Valdivia, and 22. Valencia.

Life history data

Information for a set of life history traits was collected from published sources, including scientific journals, field guides and previously compiled datasets. The traits were: i. age at first breeding, in months; ii. clutch size, measured as the modal number of eggs per nest; iii. fecundity, computed as clutch size multiplied by the number of broods per year; iv. egg mass, in grams, v. incubation period, in days; vi. fledgling period, as the number of days the young birds stay in the nest from hatching to leaving the nest; vii. lifespan, based on the oldest record of an individual age in years; viii. developmental mode, classified in four stages (altricial, semialtricial, semiprecocial and precocial) following Stark & Ricklefs (1998); and ix. adult survival, as the mean annual survival rate (Liker & Székely, 2005). These variables were used to estimate the fast-slow continuum, the intrinsic rate of population growth (R_{max}), the brood value and generation time, as explained below. Following Bielby et al. (2007), we used a factor analysis to define variation in life history between species along the fast-slow continuum. The intrinsic rate of population increase (R_{max}) was estimated by solving Cole's (L. C. Cole, 1954) equation using a R script published in Sol et al. (2012). The variables included in the equation were fecundity, age at first breeding and lifespan. The value of current reproduction relative to the lifetime reproductive output of a species (henceforth, "brood value") was expressed as logarithm of $1/\text{total number of breeding attempts}$ (Sol et al 2012). Information on the following additional traits was obtained: i. body mass, measured in grams; ii. brain mass, in grams; iii. breeding habitat

generalism, quantified with Resniche package (De Cáceres, Sol, Lapiedra, & Legendre, 2011); iv. mating system (coded as polygamous vs. monogamous), v. parental care (uniparental, biparental, cooperative); vi. coloniality (solitary, facultative, semi-colonial, colonial); vii. migratory behavior (resident vs. migratory); viii. latitude of the census location; geographic range (degrees between the limits North and South of the species distribution) and brain size. Brain size relative to body size was used (Overington et al., 2009; Reader & Laland, 2002).

Data analysis

A quantitative measure of the tolerance of a species to urbanization was performed as the difference between its density in the urbanized environment (either in highly or moderately urbanized) and the density observed in the source environment (urbanization tolerance index, UTI) (Evans et al. 2011). Two types of UTIs were assessed; UTI_1 is the urbanization tolerance of one species in a highly urbanized area respect the surrounding, and UTI_2 is the urbanization tolerance of one species in a moderately urbanized area respect the surrounding environment. The logarithmically transformed (base 10) observed and expected values were used previous adding 1 to all values to ensure that indices of species that did not occur in one of the compared habitats could also be transformed. To assess whether some species were less or more abundant than expected by chance, we used community simulations. For each species, we created 999 random communities of the same size that observed in the urbanized community by randomly drawing (with replacement) individuals from a community in which each species occurred in the same proportion as in the source community. Based on the null distribution of abundances in all the random communities, avoiders, adapters and exploiters were identified. A species was considered an “avoider” if the observed abundance was equal or lower than the 2.5 percentile of the random abundances, an “exploiter” if this abundance was equal or higher than the 97.5 percentile and a “neutral” if it was observed as expected by chance. All response variable were modeled with generalized linear mixed models (GLMM, hereafter), using a Bayesian approximation in the R-package ‘MCMCglmm’ (Hadfield, 2009). The phylogeny, species, study location and sampling error were included as random factors. Repeatability and phylogenetic effects in the UTIs were estimated from their corresponding random errors (Hadfield & Nakagawa, 2010).

2.4 METHODS GOAL 4

For this goal the question was whether and how behavioural flexibility assists in the different stages through which a species passes to become an urban dweller?. To this purpose, a literature review was performed searching for studies that test for differences in behaviour among urban and non-urban individuals and species. Studies were assigned to represent

different stages of colonization of urban environments as defined by Evans et al (2011). The literature review was based on an initial search for published in the July 2012 edition of the Thomson Reuters "Web of knowledge", using key words like "BEHAVIOR+FITNESS+URBANIZATION" or "BEHAVIORAL CHANGES+SURVIVAL+ URBANIZATION"), and subsequent searches of studies cited in those papers. From a total of 153 papers found, the literature reviews and papers that did not provide evidence for a link between behavioural flexibility and urbanization (either negative, null or positive) were removed. Because the ecology of a species describes how plastic behaviours translate to population dynamics, we also discuss how two main ecological correlates of behavioural flexibility -life history and niche breadth- may affect the varying success of species in urbanized environments.

3. RESULTS

3.1 RESULTS GOAL 1

There was extensive variation both in brain mass and maximum lifespan across species (Fig. 1). Lifespan showed significant phylogenetic autocorrelation, with a lambda estimate close to 1 ($\lambda = 0.97$; $X^2 = 437.10$, $P < 0.0001$ that λ is 0; $X^2 = 10.89$, $P = 0.0009$ that λ is 1). We thus used a PGLM approach.

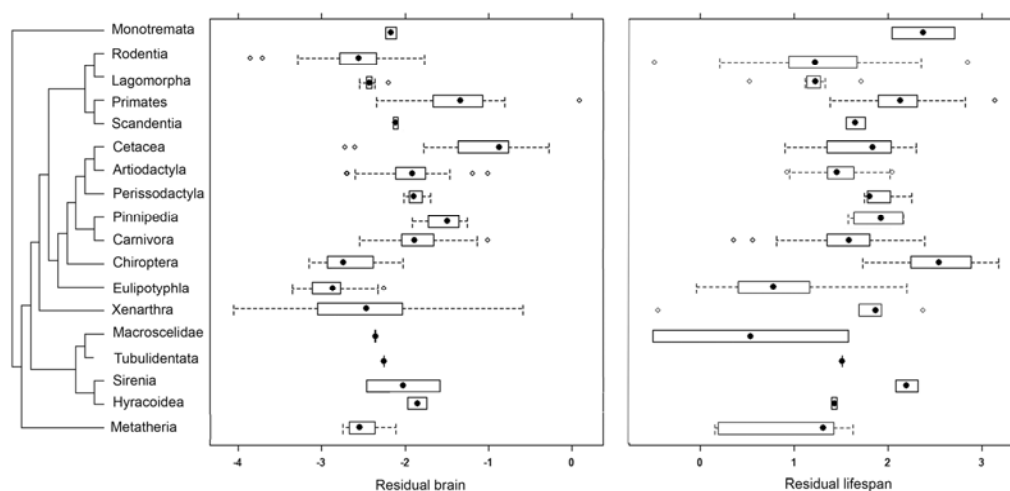


Figure 1. Box plots (median and 25 and 75% percentiles) of residual brain mass (accounting for body mass) and residual maximum lifespan (accounting for body mass) across mammalian orders, with phylogenetic relationships between taxa indicated on the left (phylogeny: Bininda-Emonds et al., 2008).

The relationship between residual brain mass and lifespan was positive and highly significant (partial regression coefficient \pm S.E., $b = 0.26 \pm 0.04$, $t_{486} = 5.37$, $P < 0.0001$). When the allometric effect of body mass on lifespan was incorporated in the analysis, the residuals of brain mass remained strongly associated with residuals of lifespan (PGLM: $b = 0.20 \pm 0.04$, $t_{486} = 4.26$, $P < 0.0001$) (see Figure 2).

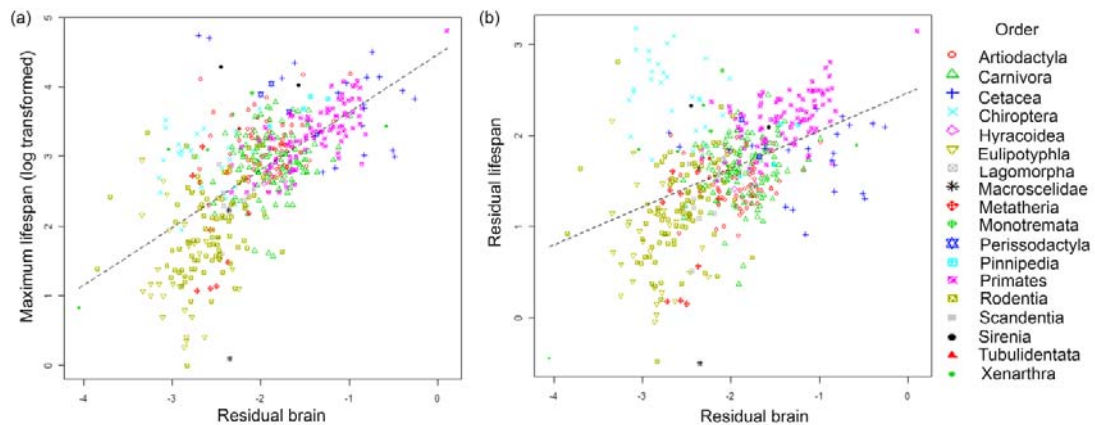


Figure 2. Relationship between residual brain size and maximum lifespan in 493 species of mammals (a) without (linear regression: $F_{4,486} = 176.9$, $R^2 = 0.59$, $P < 0.0001$) and (b) with control for the allometric effect of body size on lifespan (linear regression: $F_{4,486} = 36.67$, $R^2 = 0.22$, $P < 0.0001$). Equivalent results were obtained using PGLM analysis: a: $F_{5,491} = 57.17$, $R^2 = 0.31$, $P < 0.0001$; b: $F_{5,491} = 19.34$, $R^2 = 0.13$, $P < 0.0001$).

None of the ecological (i.e., basal metabolic rate, primary habitat, primary diet, feeding generalism or habitat breadth) and geographic variables (i.e. geographic range, mid latitude point or discontinuous distribution) evaluated were found to be significantly associated with lifespan in the MAM (PGLM: $P > 0.05$ in all variables), and did not alter the relationship between brain mass and lifespan. The MAM included age at first reproduction along with residual brain mass, lifespan measure (wild or captive), research effort (log transformed) and body mass (log transformed). Recorded lifespan was longer in captive animals, in better-studied species, in heavier species, and in species with an older age at first reproduction (Table 1).

Table 1. Minimum adequate PGLS model of lifespan for 384 mammalian species (adjusted r^2 = 0.42, for lifespan, 0.21, for residual lifespan, 0.35 for reproductive lifespan and 0.16 for residual reproductive lifespan).

| Predictors | Lifespan | | | | Residual lifespan | | | | Reproductive lifespan | | | | Residual reproductive lifespan | | | |
|---------------------------|----------|------|------|---------|-------------------|------|------|---------|-----------------------|------|------|---------|--------------------------------|------|------|---------|
| | b | se | t | P | b | se | t | P | b | se | t | P | b | se | t | P |
| Residual brain size | 0.17 | 0.05 | 3.4 | 0.0006 | 0.14 | 0.05 | 2.7 | 0.0006 | 0.19 | 0.1 | 3.2 | 0.001 | 0.15 | 0.1 | 2.6 | 0.009 |
| Age at first reproduction | 0.23 | 0.03 | 7.1 | <0.0001 | 0.23 | 0.03 | 7.2 | <0.0001 | 0.15 | 0.03 | 4.2 | 0.001 | 0.15 | 0.03 | 4.2 | <0.0001 |
| Body mass | 0.09 | 0.01 | 7.2 | <0.0001 | -0.10 | 0.01 | -4.0 | <0.0001 | 0.1 | 0.01 | 7.2 | <0.0001 | -0.03 | 0.01 | -2.6 | 0.0008 |
| Research effort | 0.03 | 0.01 | 3.6 | 0.0003 | 0.03 | 0.01 | 3.6 | 0.0004 | 0.03 | 0.01 | 3.7 | 0.0002 | 0.03 | 0.01 | 3.6 | 0.0003 |
| Origin lifespan data | -0.24 | 0.05 | -4.2 | <0.0001 | -0.30 | 0.05 | -4.5 | <0.0001 | -0.3 | 0.06 | -4.6 | <0.0001 | -0.3 | 0.1 | -4.8 | <0.0001 |

3.2 RESULTS GOAL 2

Is motivation driving innovation propensity?

An important proportion of individuals successfully solved the food innovation tasks (70% for the yellow rice task and 83% for the red lentils task) in line with previous studies (Sol et al., 2012), and highlight that most individuals are capable of adopting novel foods when they need so (Overington et al., 2009). Confirming also previous studies (Sherwin 2003, Overington et al. 2011, Bókony et al. 2012; but see Sol et al. 2012a), the probability of taste novel foods was primarily related to motivation (Best cox model: $z = 3.46$, $P < 0.001$). Regarding the motor innovation experiment, 53% of pigeons solved the task. In the same way, Overington et al. (2011) found that 55 % ($N = 36$) of carib grackles (*Q. mexicanus*) solving a novel motor task, and in a lesser extent 22 % of invasive common mynas ($N = 33$) (Sol et al., 2012). Pigeons were consistent in the performance over two consecutives trials of motor tasks ($ICC = 0.39$, 95% CI 0.06 - 0.76, $P < 0.0001$) and when comparing the time elapsed to open the lid between the first and the second trial of the motor innovation task, latency to solve decreased significantly ($z = 2.99$, $P < 0.01$), suggesting that individuals had learnt to solve the task (see figure 1) (Morand-Ferron, Cole, Rawles, & Quinn, 2011).

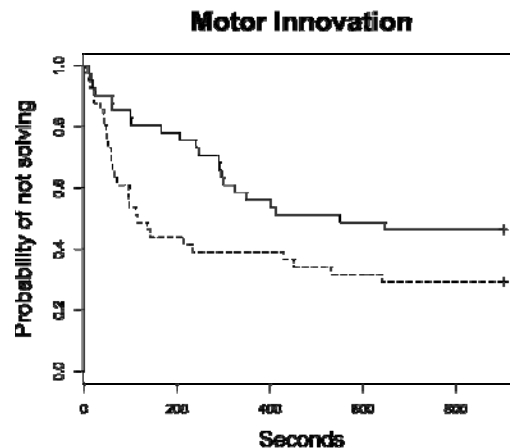


Figure 1. Differences in latency to solve the motor innovation test between the first and the second attempt. In the survival curves, solid lines represent the first attempt whereas the dashed line represents the second attempt. Only individuals solving the first test are included.

Unlike previous studies (Overington et al., 2011; Sol et al., 2012), motivation did not have any clear effect on motor innovation (Best cox model: $z = 1.42$, $P = 0.16$). Thus, we found mixed evidence for the influence of motivation on individuals' ability to innovate (i.e. positive influence on consumer innovation but not effect on motor innovation).

Is motivation a temperament trait?

There was individual consistency in the expression of motivation in the short-term, when we take the test performed in one elapsed day ($ICC = 0.71$, 95% CI, 0.49 - 0.85, $P < 0.001$, $N = 31$), but also when we analyze the tests after several fasting treatments, encompassing more than one year of captivity ($ICC = 0.32$, 95% CI, 0.15 - 0.53, $P < 0.001$, $N = 23$). This stable component was present in the two studied populations (Moià: $ICC = 0.23$, 95% CI, 0.05 - 0.53, $P < 0.01$, $N = 14$; Barcelona: $ICC = 0.52$, 95% CI, 0.25 - 0.82, $P < 0.001$, $N = 9$). These results are consistent with the observations of Sol et al. (2012) who found individual consistency (16%) for motivation in common mynas. Our results suggest that there may be a consistent individual basis underpinning motivation state in feral.

Are there individual differences in motivation as a function of variability of food opportunities?

The role of the environment:

Pigeons from the population with more stable food resources (Moià) have higher levels of motivation than those from the more variable and unpredictable population (Barcelona) (Cox model: $z = 2.38$; $P < 0.05$). Although factor 2 of the PCA as well as was retained, this was not significant ($z = -1.55$, $P = 0.12$) (See Figure 2).

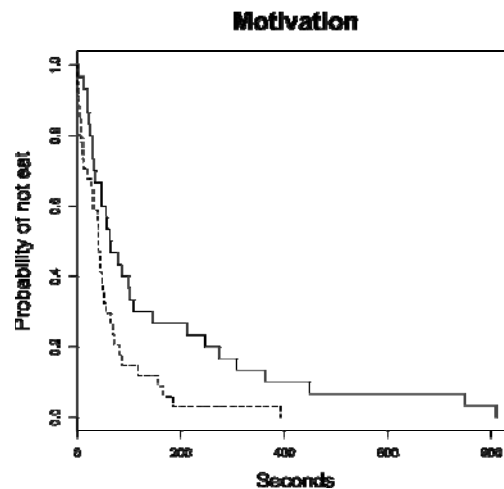


Figure 2. Latencies to eat in the motivation short-term test as function of uncertainties of food supplies in the population of origin. In the survival curves, solid lines represent pigeons from the more unstable food supplies (Barcelona), whereas the dashed line represents individuals from the more stable food supplies (Moià).

The role of social relationships

Feral pigeons showed consistent individual differences in the level of aggressiveness (ICC = 0.29, 95% CI, 0.12 - 0.49, $P < 0.001$, $N = 33$), indicating that this is a temperament trait (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For individuals from Barcelona, the best model for short-term motivation retained aggressiveness and factor 2 of the PCA, but factors are not significant ($P > 0.2$, for both). Likewise, taking motivation tests from all year of captivity, the best model retained again aggressiveness and morphology (i.e. factor 2 of the PCA). Although morphology was not accounting for motivation ($P > 0.1$), more aggressive pigeons tend to be more motivated, but not significant (Best cox model: $z = 1.66$, $P = 0.09$). In contrast to Barcelona, for the group of Moià, males (Best cox model: $z = 2.24$, $P < 0.05$) and smaller individuals (factor 1 of the PCA) (Best cox model: $z = 2.22$, $P < 0.05$) showed higher levels of motivation in the short-term period. The same pattern emerges in the long-term period of motivation (males $z = 2.89$, $P < 0.01$; smaller individuals, $z = 2.55$, $P < 0.05$).

There is a genetic component of motivation?

The parent–offspring resemblance analyses yielded no evidence for a genetic component of motivation ($P > 0.05$). Heritability may have been altered because of an increase in environmental variance under stressful conditions (Bitume et al., 2011), although it is unlikely that pigeons perceive captivity as a very stressful conditions.

Is baseline corticosterone involved in the phenotypic variation of motivation?

Individuals with high baseline corticosterone showed lower motivation levels (All best cox models: $z = -2.5$, $P < 0.05$). However, although best models accounting for long-term motivation consistently retained baseline corticosterone (see table 3), just morphology (i.e. component 2 of PCA) accounted for variation in motivation (Best cox model: $z = -2.91$, $P < 0.01$; i.e. individuals of long tail and long wings with short beak were more motivated). Thus, although the effect of corticosterone on motivation is evident in the short term of 6 months, one year later this effect is less clear. This is in line with those reported by Schoech et al. 2007, who found that in Florida scrub-jay (*Aphelocoma coerulescens*), individuals from an environment with variable and unpredictable food resources, even supplemented with food for a long time maintain high corticosterone concentration (Schoech, Bowman, Bridge, & Boughton, 2007).

3.3 RESULTS GOAL 3

In all the regions studied, the avian diversity declines with increased urbanization (Fig. 2a).

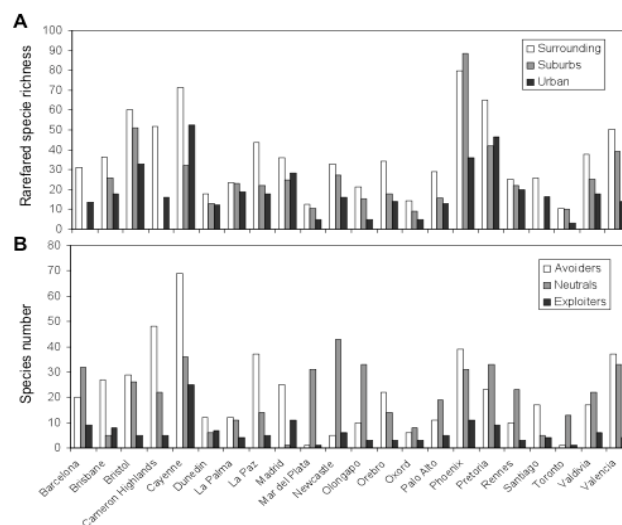


Figure 2. A. Decrease of species richness along the urbanization gradients. The values have been rarefied to take into differences in the number of individuals observed in each habitat. **B.** Number of species classified as avoiders, adapters and exploiters in each study region according to community simulations (see Methods for details).

In an attempt to understand this decrease, it was started by validating the dispersal-assembly hypothesis (Ostling 2005). As predicted by the hypothesis, species density in both moderately and highly urbanized environments co-varies with species density in the surroundings (Table 1).

The importance of immigration from surrounding habitats in building-up urban communities ("propagule pressure" hereafter) was further confirmed with the simulated communities, which indicate that the abundance of many species is close to what we would expect by random immigration (Fig. 2b).

Table 1. Relationship between species densities in surrounding and urbanized environments over two hypothetical models, accounting for differences in sampled method between studies.

| Fixed Terms | UTI ₁ | | | | UTI ₂ | | | |
|---|------------------------|----------|----------|--------|------------------------|----------|----------|--------|
| | Parameter Estimate (β) | Lower CI | Upper CI | P | Parameter Estimate (β) | Lower CI | Upper CI | P |
| Log ₁₀ Surrounding + 0.5 Plot ¹ | 0.47 | 0.41 | 0.52 | <0.001 | 0.68 | 0.62 | 0.73 | <0.001 |
| Transect ¹ | 0.06 | -0.18 | 0.33 | 0.620 | 0.08 | -0.18 | 0.34 | 0.52 |
| | 0.14 | -0.13 | 0.43 | 0.280 | 0.11 | -0.15 | 0.44 | 0.44 |
| Random Terms | | | | | | | | |
| Location variance | 0.01 | 0.00* | 0.03 | - | 0.02 | 0.00* | 0.06 | - |
| Phylogenetic variance | 0.27 | 0.15 | 0.04 | - | 0.13 | 0.02 | 0.26 | - |
| Species variance | 0.01 | 0.00* | 0.04 | - | 0.10 | 0.05 | 0.16 | - |
| Sampling error variance | 0.02 | 0.00* | 0.05 | - | 0.01 | 0.00* | 0.05 | - |
| Residual variation | 0.41 | 0.36 | 0.45 | - | 0.33 | 0.29 | 0.38 | - |

However, the simulations also reveal the existence of some species that are either less (i.e. urban avoiders) or more (i.e. urban exploiters) abundant than expected by chance (Fig. 2b). Further, the analyses of species occurring in several regions revealed that species are consistent in the way they respond to urbanization, with some being consistently classified as avoiders and others as exploiters (see Table 2). Avoiders tend to be more common than exploiters in all regions, implying that this non-random pattern accounts for part of the variation in biodiversity loss along the urbanization gradients. Thus, random dispersal does not seem to explain all the loss in species richness.

Table 2. Specie consistency in tolerance to different levels of urbanization, accounting for ecological and methodological differences between studies.

| | Model | R | Lower CI | Upper CI | DIC | N Species |
|-----------|------------------|------|----------|----------|----------|-----------|
| Without | UTI ₁ | 0.32 | 0.19 | 0.43 | -623.62 | 397 |
| phylogeny | UTI ₂ | 0.43 | 0.29 | 0.54 | -1184.59 | 336 |
| With | UTI ₁ | 0.50 | 0.34 | 0.62 | -417.73 | 344 |
| Phylogeny | UTI ₂ | 0.70 | 0.58 | 0.82 | -1003.63 | 294 |

Notes: 1000000 iterations with 500000 burning and thinning interval of 500.

Because closely-related species are expected to share many adaptations due to common ancestors, they should also show similar responses to urbanization. To test this prediction, the species tolerance to urbanization was quantified as the difference in their density (log-transformed) in the urbanized habitat and in the surrounding environment (Urbanization tolerance index, UTI), tackling thus the confounding effect of the propagule pressure. Assuming that individuals were free to choose among habitats and that they settle in those where their fitness was higher, a high UTI indicates that the species is an urban exploiter whereas a low UTI that it is an urban avoider. The results show evidence of phylogenetic heritability (sensu Hadfield & Nakagawa 2010) in all the UTIs, particularly when environmental alterations are more intense (UTI₁: $H^2 = 0.38$, CI= 0.26-0.51; UTI₂: $H^2 = 0.17$, CI = 0.06-0.40). The phylogenetic heritability is even higher when controlling by confounding factors (UTI₁: $H^2 = 0.63$, CI= 0.43-0.75; UTI₂: $H^2 = 0.52$, CI = 0.23-0.73), contradicting a previous study that failed to find similar evidence (Evans et al. 2011).

The finding that shared evolutionary history between species account for an important fraction of species variation in tolerance to urbanization points to the existence of adaptations that make some species more tolerant than others to urbanization. We consequently further examined the habitat filtering hypothesis by testing whether the tolerance to urbanization is associated with adaptive traits supposed to be useful to survive and reproduce in urbanized environments. The random-assembly hypothesis does not predict any trait–abundance connection. There have been proposed a variety of adaptations that may explain variation in tolerance to urbanization (See Table S1, supplementary Material). From all the traits considered (see Methods), our results reveal that urban exploiters can be distinguished from urban avoiders on the basis of their smaller brood value (MCMCglimm, posterior mean= -10.12, 95% CI from -16.472 to -5.099, n= 319) (Figure 3). A low brood value is found in species that prioritize future over current reproduction; the reproductive effort in these species is distributed into many attempts, whether in a same season or in different ones, rather than being allocated into a few reproductive events (Bókony et al., 2009). The effect of brood value holds when considering all other traits ($P < 0.001$ in all cases), including those previously shown to enhance tolerance to urbanization such as range size, residual brain size and habitat generalism

(Table 3; see Table S1 in Supplementary Information for references). On the contrary, there is no trait that allows distinguishing suburban adapters from suburban avoiders ($P > 0.1$ in all cases), indicating that the habitat filtering is less important when urban alterations are moderate.

Table 3. MCMCglmm modelling urbanization tolerance (i.e. urban avoiders vs. urban exploiters, $n = 305$ binary values) as a function of brood value, sampling method, habitat generalism and range size.

| | | Posterior Mean | Lower- 95% CI | Lower- 95% CI | Effect sampling | pMCMC |
|---------------------------|----------|-------------------|------------------|------------------|--------------------|--------|
| Brood value | | -12.76 | -24.23 | -4.65 | 8.15 | <0.001 |
| Sampling method | Grid | 0.00 | | | | |
| | Plot | 4.61 | 0.41 | 9.59 | 174.09 | 0.048 |
| | Transect | 7.20 | 2.26 | 14.26 | 32.68 | 0.032 |
| Spring habitat breadth | | 5.46 | -24.20 | 31.97 | 41.29 | 0.684 |
| Breeding range | | -0.89 | -4.33 | 1.93 | 25.53 | 0.594 |

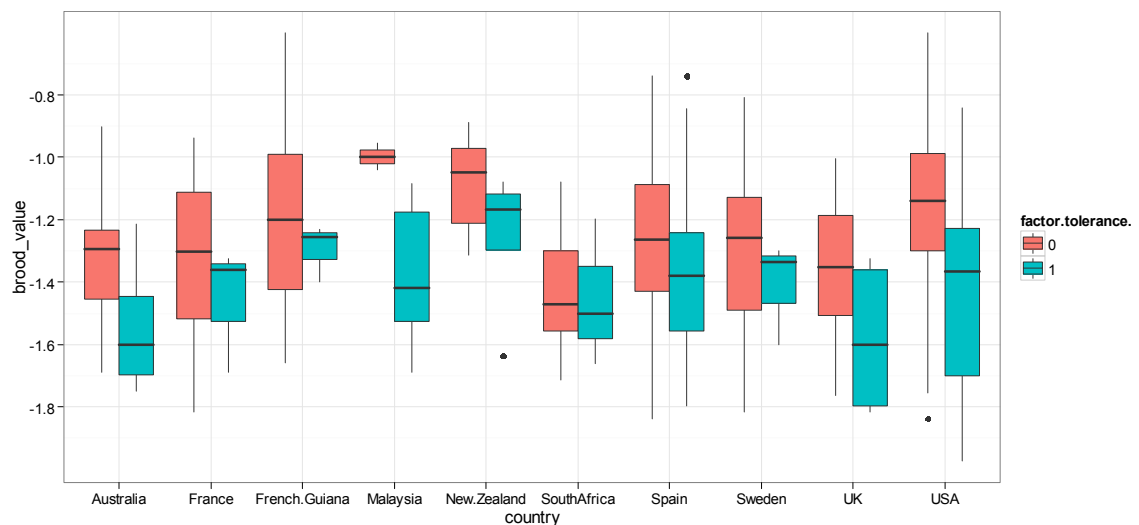


Figure 3. Differences in brood value between urban exploiters and avoiders. In legend, factor.tolerance; 0 = avoiders, 1 = exploiters.

3.4 RESULTS GOAL 4

Although influential in all stages of the colonization of urban habitats, behavioural flexibility appears to be particularly important during establishment, allowing among other things to better exploit novel resources, avoid disturbance by humans and communicate in noisy environments (see Figure 1). However, the paucity reporting fitness measures precludes to draw firm conclusions. Our understanding of the factors that allow the arrival to and population growth in urban habitats is even more deficient.

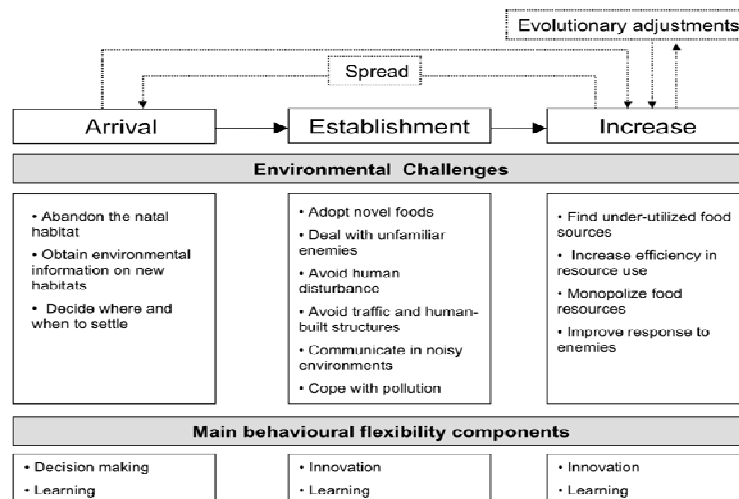


Figure 1. Schematic representation of the three main stages of the colonization of urban environments, with their environmental challenges and the main components of behavioural flexibility involved in dealing with them.

4. CONCLUSIONS

Evolutionary past

The evolved relationship between lifespan and brain size across evolutionary time scales provide indirect evidences on how cognitive process helps to the ability of the species to cope with actual environmental challenges. Evolve expensive big brains would provide ecological and evolutionary advantages that are traduced in a longer reproductive lifespan. The findings in this research provides a solid base from which a general theory on brain evolution can be developed, helping the integration of brain evolution within a life history framework and encouraging further research.

Individual differences

According to the data of feral pigeons, variability in innovation propensity is promoted by consistent individual differences in motivation (rather just cognitive mechanism). However this was only clear for consumer innovation. Although there are not evidences for a genetic component on motivation, endocrine mechanism mediated by corticosterone would promote physiological and behavioral adjusts to deal with changing environments.

Mechanisms to deal with urbanization

The importance of immigration from surrounding habitats in building-up urban communities was confirmed. The abundance of many bird species in urban environments is close to what we would expect by random immigration. Because in the wildland rare species dominate over abundant ones and because rare species are less likely to disperse by chance, the random dispersal of individuals itself predicts a decrease in species with the increase of urbanization. However, shared evolutionary history account for an important fraction of species variation in tolerance to urbanization. This point to the existence of adaptations that make some species more tolerant than others to urbanization. The strategy based on future reproductive returns (i.e. low brood value) is associated to establishment in highly urbanized habitats. This strategy can facilitate obtain information in the new environment and adjust behaviour by low costs of delay reproduction (Sol et al., 2012). A non-random distribution of urbanization tolerance across the tree of life has important consequences for conservation because the urbanization process should lead to a disproportionate loss of evolutionary history (Nee & May, 1997).

Role of behavioural flexibility to deal with urbanization

Theoretical and empirical evidences provide support for the pivotal role of behavioural flexibility to cope with challenges in urban environments. Although behavioural flexibility is influential in all stages of the colonization of urban habitats, it appears to be particularly important during the establishment stage, allow for better exploit novel resources, avoid disturbance by humans or communicate in noisy environments, among other urban challenges

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