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ORIGINAL ARTICLE

Risk-taking behavior, urbanization and the pace of life in birds

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Abstract

Despite growing appreciation of the importance of considering a pace-of-life syndrome (POLS) perspective to understand how animals interact with their environment, studies relating behavior to life history under altered environmental conditions are still rare. By means of a comparative analysis of flight initiation distances (i.e., the distance at which an animal takes flight when a human being is approaching) across > 300 bird species distributed worldwide, we document here the existence of a POLS predicted by theory where slow-lived species tend to be more risk-averse than fast-lived species. This syndrome largely emerges from the influence of body mass, and is highly dependent on the environmental context. Accordingly, the POLS structure vanishes in urbanized environments due to slow-lived species adjusting their flight distances based on the perception of risk. While it is unclear whether changes in POLS reflect plastic and/or evolutionary adjustments, our findings highlight the need to integrate behavior into life history theory to fully understand how animals tolerate human-induced environmental changes.

Significance statement

Animals can often respond to changing environmental conditions by adjusting their behavior. However, the degree to which different species can modify their behavior depends on their life history strategy and on the environmental context. Species-specific perception of risk is a conspicuous example of adjustable behavior tightly associated with life history strategy. While there is a general tendency of higher risk aversion in rural than city-dwelling birds, it is dependent on the species' life history strategy. Slow-lived species are more prone to adjust their flight initiation distances based on the perception of risk, allowing humans to approach closer in urban than rural environments. Behavior must therefore be taken into account together with life history to reliably assess species' vulnerability at the face of ongoing environmental change.

Keywords Life history theory · Phenotypic plasticity · Human-induced rapid environmental changes · Learning

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Introduction

Behavior is widely considered one of the main mechanisms through which animals cope with changes in the environment (Bogert 1949; Klopfer 1962; Mayr 1965). Unlike other phenotypic features, behavior can often be rapidly modified to solve new ecological problems, thus contributing to reduce the uncertainties and adaptive mismatches that arise when environmental conditions change (Huey et al. 2003; Price et al. 2003; Estrada et al. 2016; Sol and Maspons 2016). A growing number of studies has for instance documented that animals living in urban environments differ in behaviors related to resource use, disturbance avoidance, and communication from those inhabiting little urbanized environments (reviewed in Shochat et al. 2006; Evans et al. 2012; Lowry et al. 2013; Sol et al. 2013). Evidence is also accumulating that these behavioral differences primarily reflect plastic adjustments, although some may also result either from selection or from a non-random sorting of individuals by behaviors that affect colonization success (reviewed in Sol et al. 2013).

Despite the plastic nature of most behaviors, some animals exhibit strong consistencies in how they behave across time and contexts (reviewed in Sih et al. 2004; Réale et al. 2007). These behavioral consistencies are expressed among individuals within species, as well as among individuals of distinct species (e.g., Møller 1994; Verbeek et al. 1994; Koolhaas et al. 1999; Gosling 2001; Greenberg 2003; Sih et al. 2004; Réale et al. 2007). An example is a behavioral syndrome where some animals are risk-averse whereas others are risk-prone across a range of situations regardless the actual risks (Sih et al. 2004, 2012). This syndrome has attracted considerable interest of behavioral ecologists because the inability of individuals to adjust their behavior to the actual level of risk can entail important costs, such as greater exposure to predators, reduced foraging opportunities and increased energetic expenditure (Sih et al. 2004, 2012). However, the reasons why some animals readily adjust their behavior in response to novel situations while others persist with their behavior, even when maladaptive, remains unresolved (Sih et al. 2004). Recently, it has been suggested that the striking consistencies in risk-taking behavior observed across individuals of a given species, but not in members of other species, can be understood if we consider behavior and life history as dimensions of a same pace-of-life syndrome (POLS) (Wolf et al. 2007; Réale et al. 2010).

The POLS theory argues that animals experiencing different environmental conditions should diverge in a suite of behavioral and physiological traits according to their life history (Ricklefs and Wikelski 2002; Tieleman et al. 2005; Hau et al. 2010; Réale et al. 2010). A central premise of this theory is the existence of a fast-slow continuum of life history variation (FS hereafter), which reflects the impossibility to simultaneously maximize survival and fecundity (Stearns 1983; Saether 1988). The FS aligns organisms along a pace-of-life (POL) axis from a "highly reproductive" (fast-lived) strategy at one end to a "survival" (slow-lived) strategy at the other end. As slow-lived animals prioritize future over current reproduction (Stearns 2000), they should generally be more risk-averse compared to those at the fast extreme (Martin et al. 2000; Wolf et al. 2007; Hau et al. 2010; Møller and Garamszegi 2012; Møller and Liang 2013). In contrast, fast-lived animals should prioritize behaviors that enhance current reproductive effort, even when doing so involves taking some risks. Therefore, the POLS theory explicitly verbalizes the classic idea that selection should favor behaviors ensuring higher adult survival in slow-lived animals and behaviors that enhance reproductive effort in fast-lived animals.

Despite the existence of theoretical predictions, empirical support for the existence of a risk-taking POLS is currently scarce (Hille and Cooper 2014; Charmantier et al. 2017). A number of factors may indeed prevent the detection of such a POLS. One is the extent to which risk-taking behaviors can be modified by learning. Slow-lived species have less cognitive and time constrains to gather new environmental information and accommodate their behavior accordingly by means of learning (van Schaik and Deaner 2003; Sol 2009a; Sih and Giudice 2012; Sol et al. 2016). If plastically modifying FID depends on the position of the animal in the fast-slow continuum, the POLS may vanish in contexts where the perception of risk is low.

Another factor that makes the demonstration of POLS challenging is the low heritability of life history traits (Price and Schulter 1991). The analysis of individual variation within populations is fundamental to disentangle the importance of plasticity and genetic processes, as well as being of interest in itself (Reale et al. 2007). However, the low heritability of life history traits reduces the likelihood of detecting POLS at the individual level. An obvious alternative is to examine POLS across populations or species, as they have had more opportunities to diverge in behavioral and life history traits, yet such a level of analysis is more rarely used.

Here, we investigate if risk-taking behaviors are a defining part of a POLS syndrome in birds, and ask to what extent the syndrome can be relaxed according to the environmental conditions. We focus on behavioral and life history differences across species exposed to contrasting degrees of human disturbances. Our measure of risk-taking behavior is the flight initiation distance (FID), defined as the distance at which an individual takes flight when approached by a human. Previous work in birds has shown that FID within and across species is shorter in urbanized than in non-urbanized environments (Møller 2008; Carrete and Tella 2011; Sol et al. 2012a), indicating that the perception of risk is context-dependent. We take advantage of these previous findings to address two main expectations of POLS theory regarding risk-taking behavior. The first is the expectation that slow-lived species should exhibit longer FID than fast-lived species when the perception of risk is high. Although FID has been found to be positively related to certain vital rates in birds, like fecundity (Blumstein 2006; Møller and Garamszegi 2012), the fast-slow continuum is better characterized in the context of the full life cycle of a species (Adler et al. 2014). We operationally defined the continuum as the combination of life history traits that better predicts the fecundity-survival trade-off (Caswell 2000; Oli and Dobson 2003; Oli 2004). We then used information on > 11,000 measures of FID belonging to > 300 avian species to ask whether flight distances vary depending on the position of the species in the fast-slow continuum. To this purpose, we used phylogenetic Bayesian mixed models that allow the integration of species-level information generated by observations of multiple individuals. As theoretical and empirical evidence suggests that both the fast-slow continuum (Stearns 1992) and FID (Møller 2015) are positively correlated with body size, we also examined whether body size may be one of the factors underlying the FID-FS association.

The second expectation of POLS theory is that slow-lived species can better accommodate their FID to the perception of risk than fast-lived species. This expectation derives from the supposed higher behavioral plasticity of slow-lived species (Sol 2009b), which would allow them to habituate faster to human presence, and from constraints in fast-lived species to adopt risk-averse strategies due to the need to prioritize reproduction. We validated this prediction by investigating how FIDs change between urban and rural habitats as a function of the position of the species in the fast-slow continuum, again using phylogenetic Bayesian mixed models. Following suggestions that behavioral differences between urban and non-urban birds might be linked to brain size and learning capabilities (Kark et al. 2007; Maklakov et al. 2011; Sol et al. 2011), we also verified whether a larger brain size contributes to explain why slow-lived species should be better able to accommodate FID to risk perception (Sol 2009a, b).

Material and methods

Measuring FID

A total of 11,863 FID observations were recorded by one of the authors (APM) during February–September 2006–2014, using a standard experimental field procedure (Hediger 1934; Hemmingsen 1951; Blumstein 2006). All estimates were collected blindly with respect to the hypotheses being tested here, thereby preventing any conscious or unconscious bias. The observations were made in an area of 100 km^2 in Orsay (48° 42’ N, 2° 11′ E, France), 800 km^2 in Northern Jutland (57° 12’ N, 10° 00′ E, Denmark), 500 km^2 in Oslo (59° 54’ N, 10° 45′ E, Norway), and 500 km^2 on Hainan Island (19° 12’ N, 109° 42′ E, Southern China). In most regions, observations were carried out in both urban habitats (i.e., areas with multistory buildings, single-family houses, roads, and urban parks) and rural habitats (i.e., open farmland and woodland lacking continuous urbanized areas). Therefore, our distinction between urban and rural habitats essentially separates environments very frequented by humans from those less frequented.

To record FIDs, the observer located an individual bird with binoculars and subsequently moved at a normal walking speed towards the individual, while counting the number of steps (which approximately equals the number of meters (Møller 2008)). The FID was the horizontal distance at which the individual took flight. The starting distance (i.e., the distance from where the observer started walking up to the bird) was in most cases (> 98% of all observations) fixed at ca. 30 m to avoid confounding FID with starting distance. If the bird was located in the vegetation, the height above ground was also recorded to the nearest meter using the observer as a yardstick. This method is reliable when cross-validated using a laser Bushnell® Elite 1500. FID was then estimated as the Euclidian distance, which equals the square-root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein 2006). When possible, sex ($n = 4958$ observations), age ($n = 10{,}887$), and flock size ($n = 1387$) were also recorded to be included as confounds in the models. Although the FID of some individuals was measured twice, we only used the first measure in the analyses. All FID data are available as supplementary material.

Measuring POL

To estimate the fast-slow continuum, we searched for published information on six life history traits: (1) clutch size, (2) number of broods per year, (3) maximum lifespan (years), (4) incubation period (days), (5) nestling period (days), and (6) age at first reproduction (years). We found information of all six traits for 765 avian species (see Sol et al. 2016). As originally defined, the fast-slow continuum results from the existence of a fecundity-survival trade-off (Stearns 1992). Consequently, we empirically defined the fast-slow continuum as the combination of life history traits that better predicts the relative sensitivity (i.e., elasticity) of population growth to changes in adult survival (Caswell 2000; Oli and Dobson 2003; Oli 2004). To this purpose, we used the COMADRE Matrix database (Salguero Gomez et al. 2016) to obtain age-structured population matrices that incorporate accurate information on the rates of survival, growth, and reproduction from natural populations. We removed four matrices for which elasticities did not sum up to 1, which could reflect mistakes in the data, and for the remaining matrices ($n = 53$ from 49 species), we estimated the elasticity for adult survival. To combine the life history traits, we conducted phylogenetic principal component analyses (PPCA) (Revell 2009) based on the 765 species, including a minimum of three traits in each analysis (i.e., 42 PPCAs). The species scores of each PPCA was then used as predictor of elasticities in a phylogenetic least square models (PGLS) (Orme et al. 2013), and the best models were classified according to AICc. The combination of life history traits that best predicted variation in elasticity for adult survival included lifespan, clutch size, and fledging period. We therefore defined the position of each species in the fast-slow continuum by extracting the scores of this PPCA. In our best PPCA, species with high scores (i.e., high adult survival elasticities) were slow-lived and those with low scores (i.e., high fecundity elasticities) were fast-lived. We note that the results of our approach based on adult survival elasticities are similar to those based on estimates of elasticities for fecundity or on generation time extracted from the demographic matrices (JM and DS, unpublished).

Modeling FID

To model variation in FID, we used Bayesian phylogenetic mixed models (BPMM) with Gaussian error structure, as implemented in the R package "MCMCglmm" (Hadfield 2010; Hadfield and Nakagawa 2010). FID was log transformed before analyses to improve model convergence. As our units of analysis were the FID observations, species identity was included as a random factor together with phylogeny. The phylogeny was a maximum clade credibility phylogeny (CCP) consensus tree based on a sample of 1000 phylogenies from the pseudo-posterior distribution in Jetz et al. (2012), built with the TREEANNOTATOR software (Drummond et al. 2012). When appropriate, country was also included as a random factor to better account for data heterogeneity (see results for details). We first ran models without predictors to estimate FID consistency within species and phylogenetic heritability by means of a variance components analysis (Housworth et al. 2004). Then, we added predictors as fixed effects to explain variation in FID. To demonstrate the existence of POLS, we modeled FID as a function of the fast-slow continuum, including habitat (i.e., rural or urban), sex, age, flock size, and height at which the bird was observed as possible confounding effects. Using non-informative priors, the MCMC chains were run for 330,000 iterations with a burn-in interval of 30,000 and sampling each 300 iterations to ensure satisfactory convergence.

As we found evidence for a link between FID and FS, we tested whether this was caused by their common association with body size. To this purpose, we used phylogenetic path analyses on species' trait averages (von Hardenberg and Gonzalez-Voyer 2013; Gonzalez-Voyer and von Hardenberg 2014). The minimal set of conditional independencies for each path model (von Hardenberg and Gonzalez-Voyer 2013) was tested using PGLSs models as implemented in the package *ape* (Paradis et al. 2004) in R. Models were run estimating an evolutionary parameter (λ) simultaneously with model fit that adjusts the variance–covariance matrix to adequately fit the model of evolution, in our case a Brownian motion model (Freckleton et al. 2002). The fit of a given path model to the data was estimated via the C statistic. The C statistic tests whether the minimum set of conditional independencies of a model is fulfilled by the observational data, thus it provides an estimate of the goodness of fit of the model to the data (Shipley 2013). A significant C statistic indicates that the model is a poor fit to the data. We employed an information theoretical approach and compared the different path models using the C statistic information criterion (CICc; analogous to the Akaike information criterion; von Hardenberg and Gonzalez-Voyer 2013).

We finally investigated whether changes in FID between urban and rural habitat were larger in slow-lived species than in fast-lived species, using the same BPMM approach described above. To do so, we averaged the FID values of each species per habitat and then estimated FID difference as $\log(\text{mean FID}_{\text{rural}}) - \log(\text{mean FID}_{\text{urban}})$. We therefore only used species present in both habitats for the analyses. FID differences were then used as response variable in a BPMM with the fast-slow continuum as fixed effect and the phylogeny as a random factor. Unlike previous models, the level of analysis here was the species instead of FID observations. Thus, the conclusions could be sensitive to the sample size used to estimate FID differences. We tackled this limitation in two ways. First, in the BPMM we weighted FID differences by $1/(n{-}3)$, being n the number of individuals sampled per species. Second, we re-ran the model for the subset of species with at least 15 FID observations in each habitat. To test whether differences in FID across habitats were related to differences in brain size, we used information published in Sayol et al. (2016) on the residuals of a log-log PGLS of brain volume against body mass. Positive residuals mean that the brain of the species is larger than expected by body size and negative residuals that is smaller than expected by body size.

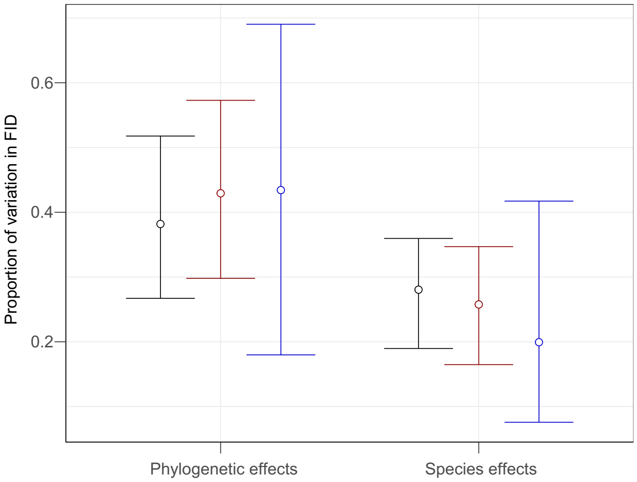

Fig. 1 Proportion of variance in FID accounted for the phylogeny and within species variation when considering all observations (black), rural observations only (red) and urban observations only (blue). Values are the intra-class coefficients estimated by means of a BPMM with the constant as fixed effect and the phylogeny and species identity as random factors. Error bars are 95% credible intervals

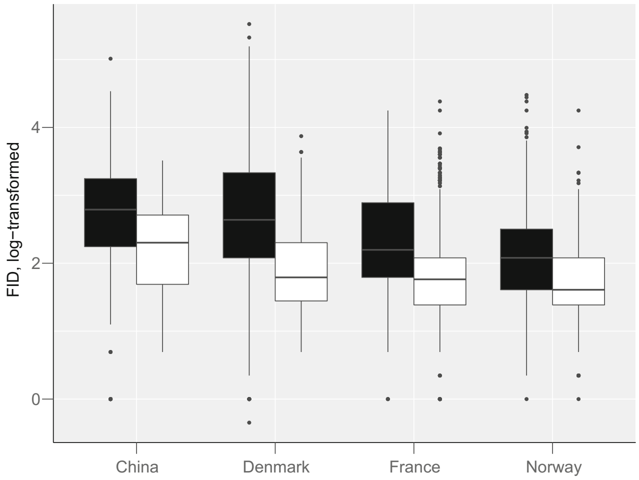

Fig. 2 Differences in FID between urban (white) and rural (black) habitats across countries. The plot shows the median, interquantile range and 1st and 3rd quartiles

Results

A Bayesian phylogenetic mixed model (BPMM) based on 11,852 observations of 317 bird species confirmed the existence of consistent among-species variation in FID (mode = 0.65, CI = 0.57–0.77), much of which was shared among close relatives (Fig. 1, Table S1). FID did not vary with sex (pMCMC = 0.920), age (pMCMC = 0.518), and flock size (pMCMC = 0.696). However, birds did tend to exhibit longer FID when located at certain height above the ground (mode = 0.026, CI = 0.013–0.038). Of the remaining residual variation, a significant fraction was accounted for differences among habitats. As shown in previous studies (reviewed in Møller 2014), FID was consistently shorter in urban than in rural habitats across all study regions (pMCMC < 0.0001, Fig. 2, Table S2). Variation in FID across species was also more consistent in rural than in urban habitats (Fig. 1).

The studied species exhibited substantial variation in their position along the fast-slow continuum, reflecting the existence of a fecundity-survival trade-off (Fig. 3). As expected, species at the slow extreme of the continuum tended to exhibit longer FID than those at the fast extreme (pMCMC < 0.0001, Table S3), consistent with the existence of a POLS. However, there was a negative interaction with habitat (Table 1), reflecting that FID and life history variation became decoupled in urban environments (Fig. 4). This pattern was largely due to changes in FID across habitats by slow-lived species (Table 2, Fig. 4). In rural environments, where the POLS was detected, the best phylogenetic path models suggest that the FID-FS association was primarily caused by their common association with body size (Figs. 5, S2). In urban environments, there is no direct effect of body size on FID, which might explain why the FID-FS association is no longer present (Figs. 5, S3).

Because slow-lived species tend to have disproportionally larger brains than fast-lived species (Fig. 3), the reduction in FID observed in slow-lived species could reflect enhanced learning capacities. Species with larger brain residual exhibited longer FID in rural habitats than those with smaller brain residual (pMCMC = 0.008, Table S4), but they did not experience a more substantial change in FID between rural and urban habitats (Table S5).

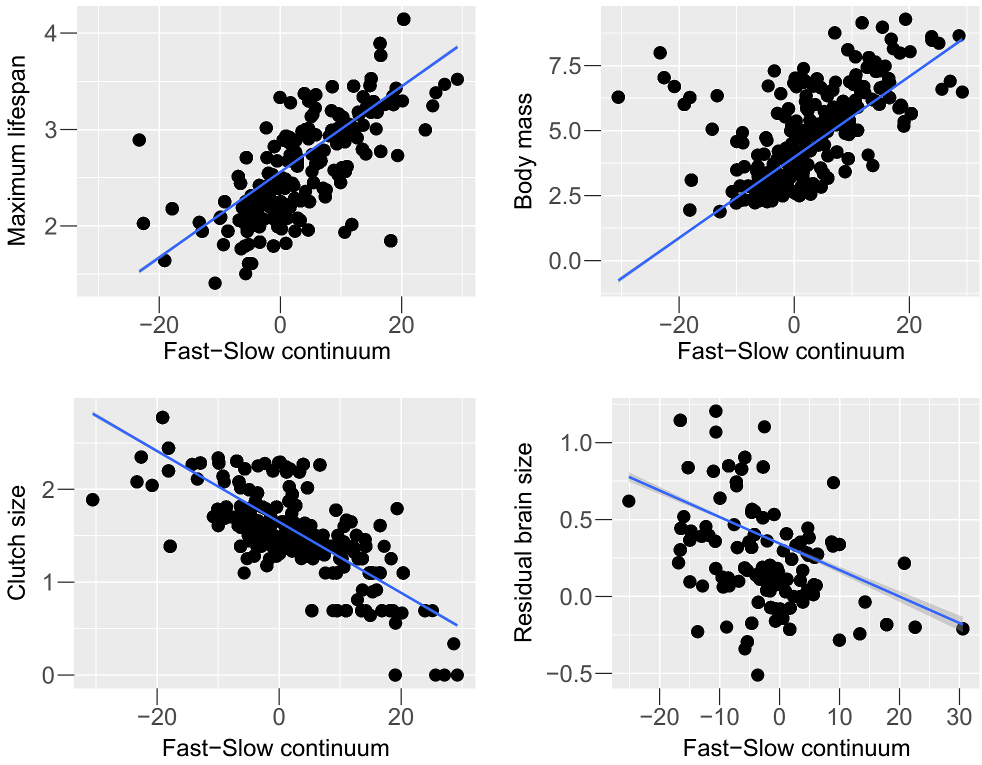

Fig. 3 Relationship of the fast-slow continuum (FS) across species with maximum lifespan, clutch size, body mass, and residual brain size. The three first traits have been log transformed. Residual brain size represent the residuals of a log-log PGLS of brain volume against body mass (i.e., positive residuals mean that the brain of the species is larger than expected by body size and negative residuals that is smaller than expected by body size)

Table 1 BPMM accounting for variation in FID (response variable, log transformed) as a function of the interaction between habitat and the fast-slow continuum, based on information from all regions for which both urban and rural FID observations were available (Denmark, France, Norway, and China). The model was run with a Gaussian structure of the errors and a non-informative prior, the number of iterations being defined by nitt = 330,000, burnin = 30,000 and thin = 300

	Post mean	L-95% CI	U-95%	Effect sampling	pMCMC
Random effects					
Phylogeny					
Species	0.143	0.095	0.199	1000	
Country	0.168	0.011	0.477	1000	
Residual	0.196	0.190	0.201	1000	
Fixed effects					
Intercept	3.123	2.567	3.669	1000	< 0.001
FS	0.024	0.0114	0.035	1000	< 0.001
Habitat:urban	− 0.321	− 0.3444	− 0.299	1000	< 0.001
Height	0.014	0.0114	0.017	1000	< 0.001
FS*Habitat:urban	− 0.032	− 0.035	− 0.028	1000	< 0.001

Discussion

Life history theory has mostly been developed under the view that organisms are passive subjects of selection, ignoring that behavior largely mediates how animals interact with their environment (Sol and Maspons 2016). However, recent years have witnessed an increased appreciation that behavior can co-vary with the life history, an idea crystalized in the POLS concept (Ricklefs and Wikelski 2002; Réale et al. 2010). Our results are in line with this new paradigm, confirming previous suggestions and evidence that FID can be part of a POLS.

Our finding that slow-lived species tend to be more risk-averse than fast-lived species in natural conditions fits well with life history theory. The fitness of slow-lived animals largely depends on ensuring a long reproductive life (Stearns 2000); hence, individuals should favor risk-avoidance strategies when the perception of risk is high (Martin et al. 2000; Wolf et al. 2007; Hau et al. 2010; Møller and Garanszegi 2012; Møller and Liang 2013). Under this view, behavior would be a consequence of life history. However, our analyses suggest that the relationship between FID and the fast-slow continuum is largely mediated by differences in body size among species. As body size is a major determinant of the fast-slow continuum, this does not deny the existence of a POLS. However, larger species may also decide to flee before than smaller species for reasons not directly induced by their life history, including a higher likelihood to be detected by predators, lower maneuverability to escape when attacked and higher energetic costs associated with flight (Blumstein 2006).

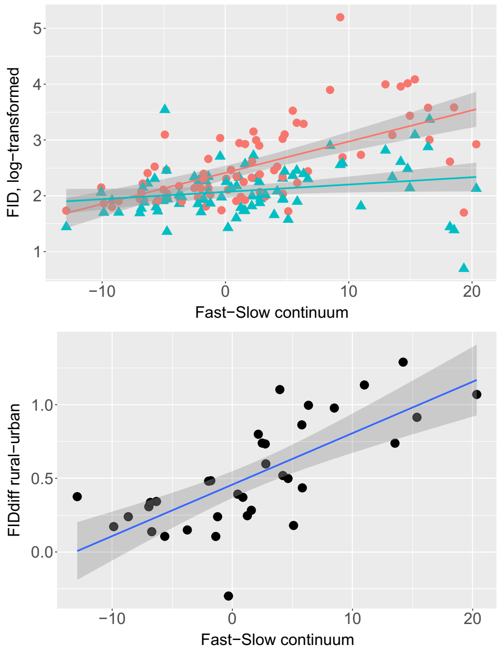

Fig. 4 Above, relationship between FID and the fast-slow continuum for urban (blue triangles) and rural (red circles) habitats. Below, difference in FID between rural and urban habitats as a function of the fast-slow continuum

An animal that is unable to tolerate human presence is likely to have problems to feed, communicate, or mate in densely populated urban environments. This may explain why FID is shorter in urban than in rural environments (Møller 2010; Møller et al. 2015). While slow-lived species showed shorter or larger FID according to the perception of risk, fast-lived species did not accommodate their FID to the degree of human frequentation. The changes in FID observed in slow-lived species may reflect plastic adjustments, selection, and/or a non-random sorting of individuals by behaviors that affect invasion success. Our analyses do not allow us to distinguish between these alternatives, although plasticity is an obvious possibility. After detecting an approaching human, animals may decide to ignore the threat or to flee, and cognition may be involved in allowing informed decisions (Møller and Erritzøe 2014). Some animals are, for instance, able to discriminate between people that pose a threat from people that do not (Levey et al. 2009; Lee et al. 2011). There is also evidence that fear of humans can diminish when individuals are exposed to human presence for long periods (e.g., Perals et al. 2017). However, current evidence that FID may be modified by habituation in the wild remains inconclusive (Møller 2015). Indeed, we did not find

Table 2 BPMM accounting for the decline in FID per species from rural and urban habitats (response variable) a function of the fast-slow continuum, based on information from species for which both urban and rural FID observations were available. The decline of each species was estimated as the log(mean FID_{rural}) − log(mean FID_{urban}). The model was repeated again restricting the species to those with at least 15 FID observations in each habitat. The models were run with a Gaussian structure of the errors and non-informative priors. We weighted the observations by $1/(n{-}3)$, being "n" the number of FID observations of the species. The model was run with a Gaussian structure of the errors and a non-informative prior, the number of iterations being defined by nitt = 440,000, burni = 40,000 and thin = 400

Model with all species					
	Post mean	L-95% CI	U-95%	Effect sampling	pMCMC
Random effects					
Phylogeny	0.074	0.000	0.197	539	
Residual	0.086	0.035	0.152	637	
Fixed effects					
Intercepts	0.560	0.283	0.857	889.5	<0.001
FS	0.031	0.015	0.048	718.4	0.002
Model with species with at least 15 FID observations per habitat					
	Post mean	L-95% CI	U-95%	Eff. samp	pMCMC
Random effects					
Phylogeny	0.095	0.019	0.192	794	
Residual	0.018	0.000	0.043	703.6	
Fixed effects					
Intercepts	0.711	0.358	1.010	1000	<0.001
FS	0.021	0.006	0.036	878.2	0.006

evidence that enlarged brains facilitate accommodating FID to the perception of risk, although this may simply indicate that habituation to humans does not require the type of advanced cognition associated with enlarged brains (Overington et al. 2009). Our insufficient understanding of how cognition and neural structures affect FID is also highlighted in the fact that we found that species with relatively larger brains exhibited longer FID, while a previous study found the opposite pattern (Møller and Erritzøe 2014). As big-brained species tend to be at the slow extreme of the fast-slow continuum, the weak effect we found may be a mere by-product of the association between the FID and life history. Another possibility is that sense organs like eyes play a role in determining flight distance, with brain size only secondarily accounting for the response (Møller and Erritzøe 2014).

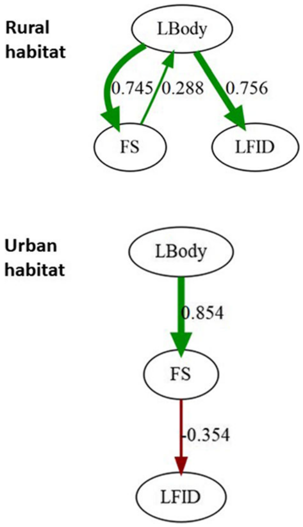

Fig. 5 Phylogenetic path model averaged over all tested models (see Figs. S2 and S3, in the supplementary material) for rural and urban habitats, depicting the relationship between flight initiation distance (log transformed, LFID) and the fast-slow continuum (FS) according to differences in body mass (LBody) across species

The reasons why fast-lived species did not see their FID altered according to the perception of risk are also unclear. While it may be argued that these species already possess the appropriate behavior to persist in cities, it remains intriguing why they do not increase their FID in places where interactions with humans are rare enough to allow habituation. Elucidating whether this reflects constrains, perhaps associated with life history trade-offs, will represent an important avenue for future research. The existence of substantial phylogenetic heritability in FID, particularly when recorded in rural habitats, is consistent with the existence of such constrains (Blomberg et al. 2003). Further examples of possible constrains can be found in Møller et al. (2013), who reported that while FID of several species of birds became shorter after a cold winter, this was only true in resident urban populations (frequently exposed to humans) but not in migratory or rural populations of the same species.

Much past theoretical and empirical work on life history has attempted to understand why organisms have diversified in a plethora of life history strategies (Stearns 1992). The possibility that certain life histories offer advantages over others when it comes to adjustment to environmental changes has also been acknowledged (e.g., Sæther and Engen 2003), but empirical support has been more difficult to assemble (but see Sol et al. 2012b, 2014). Similarly, little effort has focused on considering behavior as a component of life history (e.g., Blumstein 2006; Møller and Garamszegi 2012), despite recent calls for the need to integrate behavior into life history theory to better understand how animals cope with environmental changes (reviewed in Sol and Maspons 2016; see also Estrada et al. 2016). Our discovery of a POLS associated with risk-taking behavior contributes to fill these gaps, suggesting new ways by which behavior and life history interact to influence the response of animals to sudden changes in their environment.

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Compliance with ethical standards

Ethical approval The study was conducted in accordance with the current laws in all visited countries. We recorded FID by approaching birds in the field until they flew away. However, this activity is similar to what birds experience when people walk around in urban environments, and there are no known negative effects of such activities on the behavior of birds.

Conflict of interest The authors declare that they have no conflicts of interest.

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