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Escape behaviour of birds provides evidence of predation being involved in urbanization

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Altered predation risk in urban environments may contribute to animals becoming successfully urbanized by individuals from rural habitats. Escape behaviour has evolved to allow an individual to escape once captured by a predator. We tested whether altered predation risk in urban environments is associated with colonization of such habitats by comparing escape behaviour of 1132 individual birds belonging to 15 species from nearby rural and urban populations when captured by a human. Raptors (of which the Eurasian sparrowhawk, *Accipiter nisus*, was one of the most common species) were more common in rural than in urban habitats, whereas cats, *Felis catus*, showed the opposite pattern. There were consistent differences in escape behaviour between habitats, showing divergence in behaviour from the ancestral rural state. Urban birds wriggled less, showed higher tonic immobility, more often lost feathers, were less aggressive by biting less often, and emitted fear screams and alarm calls more often than rural birds. Furthermore, differences in escape behaviour between habitats were related to susceptibility to predation by sparrowhawks, as expected if differences in behaviour were due to differences in predation risk. Finally, an analysis of differences in escape behaviour between rural and urban birds revealed a significant relationship with time since urbanization, suggesting that escape behaviour has changed in urban environments over time. These findings suggest that release from predation and change in predator community associated with urbanization has altered the antipredator behaviour of birds colonizing towns and cities.

Urbanization is defined as the process by which animals and plants adapt to urban environments, with the change from ancestral rural to recent urban environments being the relevant transition. This urbanization process is affected by several factors. For example, urban habitats provide significant advantages in terms of benign microclimate (e.g. Lowry 1998), longer growing seasons (White et al. 2002) and higher food abundance (e.g. Fuller et al. 2008). However, urban habitats also generally have higher levels of pollution (e.g. Sharp 2002) and a higher abundance of exotic species (e.g. Devictor et al. 2007), which may be the cause of reduced fitness.

Predation is an additional potentially important factor accounting for colonization of urban areas. Urban landscapes show considerable variation in communities of predators (Haskell et al. 2001; Sorace 2002), and urban densities of predators are higher than rural densities for corvids (Richner 1989; Jerzak 2001; Antonov & Atanasova 2003), cats, *Felis catus* (Lepczyk et al. 2003; Gaston et al. 2005; Sims et al. 2008) and generalist avian predators (Sorace & Gustin 2009). Predation by cats is much more common in urban than in rural habitats (Baker et al. 2008; Sims et al. 2008; Stracey 2011), whereas predation by avian predators appears to be less common in urban than in rural areas (Stracey 2011). However, even if there is a higher density of potential predators in urban environments, this may not necessarily translate into a higher predation rate because many predators such as corvids and cats mainly rely on food provided by humans (van Heezik et al. 2010; Stracey 2011; Tschanz et al. 2011). The change in predator community from avian to mammalian predators across the gradient from rural to urban areas could have important consequences for antipredator behaviour.

Antipredator behaviour of urban compared to rural birds may also have implications for the relative importance of predation as a selective agent affecting urbanized birds. Flight distances of birds when approached by a human differ consistently between rural and urban populations, with distances twice as long in rural compared with urban habitats (Cooke 1980; Møller 2008a; Carrete & Tella 2011). Furthermore, invasion of urban habitats was mainly by species with short and less variable flight distances in their ancestral rural habitat, resulting in a subset of individuals with

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uniformly short flight distances becoming established in urban areas (Møller 2010). This was followed by an increase in variation in flight distance during subsequent establishment and expansion in urban areas (Møller 2010). These differences in flight distance between urban and rural habitats have important implications, because they are related to susceptibility to predation (Møller 2008a). Moreover, species with long flight distances have negative population trends, as expected if there are costs associated with frequent disturbance by humans, dogs and other potential predators (Møller 2008b). Bird species that have successfully managed to invade urban habitats have a history of weak predation, reflected by the evolution of a strong force being required for loss of feathers from the rump by urban compared with related rural species (Møller 2009), suggesting that urbanized species initially were less subject to predation than nonurbanized species.

The objective of this study was to test whether there were consistent differences in escape behaviour between rural and urban birds, under the assumption that mammalian predation due to cats was more common in urban than in rural habitats, whereas the opposite applied to avian predators. To do so we captured birds in urban and rural habitats while studying escape behaviour of birds when handled. First, we predicted that urban birds would have higher frequency of alarm calls and fear screams because low levels of dispersal and a high degree of small-scale genetic differentiation (e.g. Rutkowski et al. 2005; Baratti et al. 2009; Evans et al. 2009; Björklund et al. 2010) would result in many relatives living in the same neighbourhood and thus benefiting from such calls (see Møller & Nielsen 2010). Second, if urban birds have low levels of predation, we expected them to have lower intensity of wriggle behaviour and lower level of tonic immobility when captured than birds from rural populations (Møller et al. 2011). Third, we predicted that an analysis of difference in escape behaviour between rural and urban birds should reveal a significant relationship with time since urbanization, if escape behaviour has changed in response to altered selection pressures due to change in predator community between rural and urban environments. Fourth, we predicted that difference in escape behaviour between rural and urban areas should be related to susceptibility to predation by Eurasian sparrowhawks, *Accipiter nisus*, and cats, if differences in behaviour were caused by differences in the relative importance of predation risk by raptors and cats in the two habitats. Fifth, we predicted that feather loss would be more common in urban populations because urban birds are exposed to higher levels of cat predation, and cat predation has selected for feather loss (Møller et al. 2010). Finally, biting may allow a potential prey individual to escape from a predator. However, that might similarly be the case for predation attempts by cats and raptors, preventing us from making a clear prediction.

METHODS

Study Sites

We studied the behaviour of birds during capture in Brønderslev, Denmark and Granada, Spain during 2008–2011. Breeding birds were censused in Brønderslev, Denmark and Granada, Spain. Birds were either captured in mist nets (closed habitats) or in spring traps (open habitats) for bird ringing, were measured and weighed, and were scored for escape behaviour, as explained in detail below. In total we investigated the behaviour of 1132 individuals belonging to 15 species that were recorded in both rural and urban habitats.

Raptor Censuses with Point Counts

We censused raptors by using standard point counts of breeding birds with unlimited distance (e.g. Voříšek et al. 2010), twice with an interval of 3–4 weeks, during the spring of 2009–2010 in both urban and rural habitats in Brønderslev, Denmark and Granada, Spain. Point counts provide highly reliable estimates of relative population density that is comparable among habitats (Voříšek et al. 2010). First, we placed 25–50 points (depending on the size of the particular urban area) in each urban and rural study plot at a distance of at least 100 m between two consecutive points, using a stratified random sampling design. The exact location of each point was determined with a global positioning system (GPS), allowing us to make the second census in exactly the same sites as the first census. Second, we made a first census in early spring, starting early April in Southern Spain, delaying the census in Denmark so that it was completed in late May. The census started at sunrise, with the observer remaining for 5 min at each point recording all birds seen or heard (Voříšek et al. 2010). Censuses started on separate days in urban and rural study plots, ensuring that there was no difference in the timing of censuses between habitats. The same observer made all the surveys in each city and their surrounding rural areas.

Vegetation cover (trees, shrubs, herbs and grass) and cover with buildings and other man-made structures such as roads were evaluated in the field within 50 m of each survey point. These habitat variables were used to test whether the estimates of population density were similar when controlling for differences in coverage for the three vegetation layers and cover with buildings.

Behavioural Variables

When we captured a bird, we assessed the following six components of escape behaviour, some of which are significantly correlated with susceptibility to predation by hawks and cats (Møller et al. 2011).

(1) Wriggle score: the extent to which the bird struggles while held in a hand (a score of 0 = no movement, 1 = moves rarely, 2 = moves regularly, but not always, 3 = moves continuously).

(2) Biting: whether the bird bit (a score of 1) when the right hand index finger was held in front of the beak, or did not bite (0).

(3) Feather loss, whether the bird lost feathers (a score of 1) or not (a score of 0) during handling.

(4) Distress call: whether the bird gave a fear scream (Högstedt 1983) (a score of 1) or not (a score of 0) while handled.

(5) Alarm call: whether the bird gave an alarm call, when departing from our hand (a score of 1), or not (a score of 0).

(6) Tonic immobility: we placed the bird with our right hand on its back on our flat left hand. When the bird was lying still, we removed the right hand and recorded the time until the bird righted itself and flew away, allowing up to 30 s. This is a standard measure of fear in poultry research with both environmental and genetic components (Hoagland 1928; Jones 1986; Boissy 1995; Forkman et al. 2007). The longer time a bird stays, the higher the level of fear. In chickens and barn swallows, *Hirundo rustica*, measurements have a strongly bimodal distribution, with most individuals having tonic immobility for 0–5 s, but some 10–20% for 25–30+ s (Hoagland 1928; Jones 1986; Boissy 1995; Forkman et al. 2007; Møller et al. 2011).

Difference in escape behaviour between rural and urban habitats was estimated as the mean behaviour in the ancestral rural habitat minus the mean behaviour in the recent urban habitat.

Time Since Urbanization

We estimated the approximate year of urbanization as described in detail by Møller (2008a, 2009, 2010). Timing of urbanization will result from colonization followed by establishment or extinction and recolonization. Obviously, there is no information on such

processes, nor is there empirical information about the development of urban population sizes since colonization. In the following we assume that colonization of urban environments can be approximated from observations by keen ornithologists that habitually follow changes in composition and distribution of birds closely. Any heterogeneity in colonization processes or increase in population size will cause noise in the data and ultimately make it more difficult to discern any clear patterns. We estimated the year when different species became urbanized using two different approaches. First, we asked keen amateur ornithologists living in our study areas to state when different species of birds were first recorded as breeding in urban areas. An approximate year of urbanization was recorded, with a conservative value of 1950 assigned to species that were known to breed in urban habitats before the observers started watching birds. Second, we recorded timing of invasion of urban environments from old published records. If the year of urbanization was before records reported in these sources, we assigned 1850 as the year of urbanization. Although urbanization is likely to have occurred much earlier for some species, these estimates are conservative. See Møller (2008a, 2009, 2010) for a detailed description of this approach and for cross-validation among observers and methods.

Susceptibility to Cat and Eurasian Sparrowhawk Predation

Predators can be assumed to encounter prey relative to the abundance of prey in the environment. Any deviation from such a random process will result in an over- or under-representation of prey in the diet relative to abundance. We estimated susceptibility to predation by cats and Eurasian sparrowhawks on a logarithmic scale expressed as log-transformed observed number of prey minus log-transformed expected number of prey according to estimates of breeding density assessed using standardized point counts during the breeding season 1992–1996 in Northern Denmark (see Grell (1998) for description of this national census; see Møller et al. (2006) for a previous study using the estimates of susceptibility to cat and Eurasian sparrowhawk predation), that includes the Danish study area of the present study. Thus, a value of 0 for the susceptibility index implies that prey are consumed according to expectation from their abundance; an index of +1 implies that a given prey species is consumed 10 times more often than expected from its abundance; and an index of −1 implies that a given prey species is consumed 10 times less often than expected from its abundance. We have previously described these estimates and their reliability in detail elsewhere (e.g. Møller & Nielsen 2007; Møller et al. 2010). We were unable to collect similar data on susceptibility to cat and Eurasian sparrowhawk predation from Spain. However, we note that the susceptibility index for Eurasian sparrowhawk predation in Denmark is positively correlated with the index based on data from Finland (Huhta et al. 2003), showing consistency in susceptibility across large spatial scales ($F_{1,27} = 4.18$, $r^2 = 0.16$, $P = 0.049$, slope (SE) = 0.30 (0.14)).

Body Mass

We recorded body mass using Pesola spring balances.

Statistical Analyses

Summary statistics for all variables are reported in Appendix Table A1. We developed best-fit statistical models by reducing full models until the final model only contained factors with an associated $P < 0.10$. To assess possible problems of collinearity, we calculated variance inflation factors that in all cases were less than 3, which is much less than the commonly accepted levels for significant collinearity of 5–10 (McClave & Sincich 2003).

Closely related species may have more similar behaviour than species that are more distantly related, owing to closely related species sharing foraging habits, predators and habitat preferences. We controlled for similarity in phenotype among species due to common phylogenetic descent by calculating standardized independent linear contrasts (Felsenstein 1985), using the program CAIC (Purvis & Rambaut 1995). We tested the statistical and evolutionary assumptions of the continuous comparative procedure (Garland et al. 1992) by regressing absolute standardized contrasts against their standard deviations. In order to reduce the consequent problem of heterogeneity of variance: (1) outliers (contrasts with Studentized residuals > 3) were excluded from subsequent analyses (Jones & Purvis 1997); and (2) analyses were repeated with the independent variable expressed in ranks. In neither case did these new analyses change any of the conclusions.

The composite phylogeny used in the analyses was based on Davies (2008) (Appendix Fig. A1). Because information for the composite phylogeny came from different sources using different methods, consistent estimates of branch lengths were unavailable. Therefore, branch lengths were transformed assuming a gradual model of evolution with branch lengths being proportional to the number of species contained within a clade. Results based on these branch lengths were compared to those obtained using constant branch lengths (a punctuated model of evolution). Finally, we used a standard bird taxonomy (Howard & Moore 1991) to test for consistency in findings independent of phylogenetic hypothesis. Nowhere were results qualitatively different (results not shown).

Regressions based on contrasts were forced through the origin because the comparative analyses assume that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis & Rambaut 1995).

A common underlying assumption of most statistical analyses is that each data point provides equally precise information about the deterministic part of total process variation (i.e. the standard deviation of the error term is constant over all values of the predictor variable(s); Sokal & Rohlf 1995). The standard solution to violations of this assumption is to weight each observation by sampling effort in order to use all data, by giving each datum a weight that reflects its degree of precision due to sampling effort (Draper & Smith 1981; Neter et al. 1996; Garamszegi & Møller 2010). Comparative analyses (just as any other analysis) may be confounded by sample size if sampling effort is important, and if sample size varies considerably among taxa (Garamszegi & Møller 2010). Therefore, we weighted statistical models by sample size. In order to weight models by sample size in the analysis of contrasts, we calculated weights for each contrast by calculating the mean sample size for the taxa immediately subtended by that node (Møller & Nielsen 2007).

We evaluated the magnitude of associations between escape behaviour and predictor variables based on effect sizes according to Cohen's (1988) criteria for small (Pearson $r = 0.10$, explaining 1% of the variance), intermediate (Pearson $r = 0.30$, 9% of the variance) and large effects (Pearson $r = 0.50$, 25% of the variance).

Ethical Note

All captures were made under licence from The National Ringing Center, University of Copenhagen (Denmark) and the Ministerio de Medio Ambiente, Rural y Marino (Spain). Licence numbers: CMA-62012; MMA-620023. We used mist nets (12 m long) and spring traps (40 cm diameter) to capture birds; these were used from 30 min before daybreak until noon and only under good weather conditions. All nets and traps were constantly watched in the

distance (>20 m away) from a hidden location by at least two people who immediately removed any bird captured. Traps were installed carefully following standardized protocols recommended by the Spanish Ornithological Society and baited with mealworms. All experimental tests were done very carefully not to harm the birds and within the least time possible. We immediately released the individual once we had tested it for the six components of escape behaviour. All birds flew away from us in their usual way, without apparent consequences of our experiments. We are confident that our manipulation did not provoke any additional stress to birds because this escape behaviour is always produced when a bird is captured, and we only systematically noted it following a standardized and quick protocol. Furthermore, we took advantage of birds captured originally for other purposes (i.e. long-term bird monitoring programmes).

RESULTS

Summary Statistics

Mean ±SE abundance of all raptors combined was 0.093 ± 0.026 raptors per 5 min observation, $N = 291$, in rural habitats and 0.043 ± 0.016, $N = 300$, in urban habitats ($\chi^2_1 = 11.20$, $P = 0.008$). The raptors recorded during these censuses were: common kestrel, *Falco tinnunculus*, 19; Eurasian sparrowhawk 12; common buzzard, *Buteo buteo*, five; booted eagle, *Hieraaetus pennatus*, three; and peregrine falcon, *Falco peregrinus*, one. The sparrowhawk was the second most abundant species. Because the main diet of common kestrel in cities is passerine birds, it was more meaningful to include all raptors in the analyses. Mean abundance of cats in rural habitats was 0.027 ± 0.011 cats per 5 min observations, $N = 291$, but 0.097 ± 0.020, $N = 300$ in urban habitats ($\chi^2_1 = 9.99$, $P = 0.002$). In fact, the interaction between habitat and type of predator was significant ($\chi^2_1 = 10.40$, $P = 0.001$). These analyses provided similar conclusions if they included habitat cover and cover with buildings as covariates (all raptors combined: $\chi^2_1 = 12.93$, $P = 0.0003$; cat: $\chi^2_1 = 8.51$, $P = 0.004$; interaction: $\chi^2_1 = 8.46$, $P = 0.004$).

Summary statistics for escape behaviour are reported in Table 1. The six aspects of escape behaviour were only weakly correlated with each other, with the maximum correlation being between wriggle and feather loss (Pearson $r = 0.16$, $t_{1121} = 5.35$, $P < 0.001$). These effects are so small that problems of collinearity are no cause for concern.

Escape Behaviour in Rural and Urban Habitats

Escape behaviour was significantly different between rural and urban habitats in nested analyses that accounted for variation within species among populations (Table 2). Alarm calls and fear screams were much more common in urban than in rural birds (Table 1). Biting was less common and wriggle behaviour less intense in urban birds (Table 1). Feather loss was more common in urban birds, and urban birds had tonic immobility that lasted longer than in rural birds (Table 1).

Table 1
Summary statistics for escape behaviour of birds in rural and urban habitats

Variable	Rural mean	Rural SE	Urban mean	Urban SE
Alarm call	0.277	0.072	0.359	0.066
Biting	0.587	0.091	0.554	0.088
Fear scream	0.139	0.020	0.348	0.088
Feather loss	0.235	0.080	0.335	0.089
Tonic immobility	0.774	0.059	0.878	0.112
Wriggle	1.226	0.073	1.113	0.065

Sample size was 15 species in all comparisons.

Table 2
Nested analysis of variance of the relationship between escape behaviour and habitat nested within species and species

Variable	Predictor	Sum of squares	*df*	*F*	*P*
Alarm call	Habitat [Species]	10.361	16	4.291	<0.0001
	Species	24.729	15	19.925	<0.0001
	Error	164.480	1090		
Biting	Habitat [Species]	9.161	16	4.070	<0.0001
	Species	33.552	15	15.900	<0.0001
	Error	153.203	1090		
Fear scream	Habitat [Species]	8.593	16	4.421	<0.0001
	Species	14.003	15	7.686	<0.0001
	Error	132.517	1090		
Feather loss	Habitat [Species]	5.475	16	3.207	<0.0001
	Species	59.657	15	37.275	<0.0001
	Error	117.367	1090		
Tonic immobility	Habitat [Species]	14.513	16	2.421	0.001
	Species	27.581	15	4.908	<0.0001
	Error	407.613	1090		
Wriggle	Habitat [Species]	23.603	16	3.314	<0.0001
	Species	25.901	15	3.879	<0.0001
	Error	485.717	1090		

The *F* statistic reported for the error term is that for the full model.

Change in Escape Behaviour and Susceptibility to Predation

Susceptibility to cat predation was on average −0.249 ± 0.204, $N = 14$, and to sparrowhawk predation 0.017 ± 0.090. Susceptibility to sparrowhawk predation was significantly negatively correlated with susceptibility to cat predation ($F_{1,12} = 5.88$, $r^2 = 0.33$, $P = 0.03$, slope (SE) = −0.253 (0.104)). The difference in biting between rural and urban populations was negatively related to susceptibility to cat predation (Table 3). However, that was not the case for an analysis of contrasts (Table 3), implying that this result was a phylogenetic effect. The difference in feather loss between rural and urban populations was positively related to susceptibility to sparrowhawk predation (Table 3), even in a phylogenetic analysis (Table 3), implying that species least susceptible to predation had higher rate of feather loss in urban than in rural populations (Fig. 1). Finally, the difference in intensity of wriggle behaviour between rural and urban populations was negatively related to susceptibility to cat predation (Table 3), although that was not the case in a phylogenetic analysis (Table 3).

Table 3
Difference in escape behaviour between rural and urban habitats (rural minus urban behaviour) in relation to susceptibility to cat and sparrowhawk predation

Variable	Sum of squares	*df*	*F*	*P*	Estimate (SE)
Biting					
Species:					
Cat predation	41.484	1	8.764	0.012	−0.303 (0.102)
Error	56.803	12			
Contrasts:					
Cat predation	4.373	1	3.451	0.09	−0.183 (0.098)
Error	15.208	12			
Feather loss					
Species:					
Sparrowhawk predation	10.953	1	9.855	0.009	0.670 (0.213)
Error	13.337	12			
Contrasts:					
Sparrowhawk predation	11.821	1	9.530	0.005	0.722 (0.210)
Error	9.675	12			

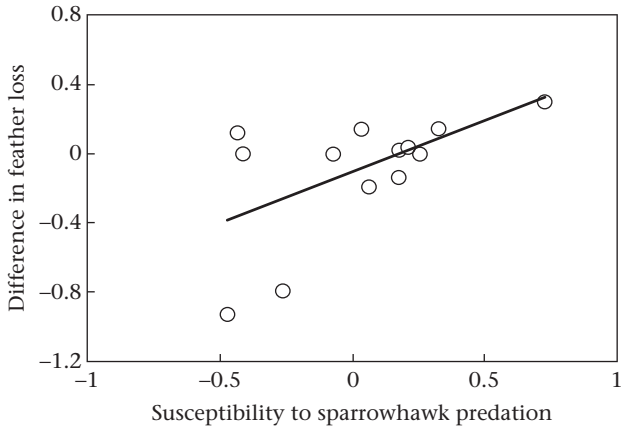

Figure 1. Difference in feather loss between rural and urban populations (rural minus urban behaviour) in relation to susceptibility to sparrowhawk predation. The line is the linear regression line.

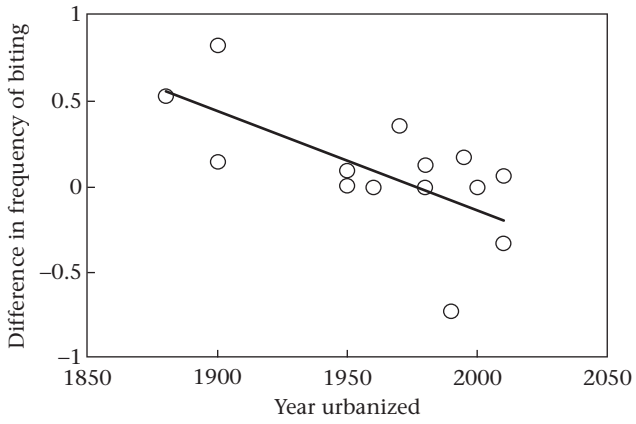

Figure 2. Difference in frequency of individuals biting between rural and urban populations (rural minus urban behaviour) in relation to time of urbanization. The line is the linear regression line.

Change in Escape Behaviour and Time Since Urbanization

Two aspects of escape behaviour were significantly related to time since urbanization (Table 4). First, species that have been urbanized for a longer time had a higher frequency of biting individuals in rural compared with urban populations (Fig. 2). Thus, there has been a decline in biting frequency from relatively high levels in recently urbanized populations to relatively low levels in populations that have been urbanized for a long time (Fig. 2). This was also the case in a phylogenetic analysis (Table 4). Second, the intensity of wriggle behaviour declined from relatively high in recently urbanized populations to relatively low levels in populations that were urbanized early (Table 4), and this effect was maintained in a phylogenetic analysis (Table 4). There was no significant effect for the other four behavioural variables (alarm call: $F_{1,13} = 0.41$, $P = 0.53$; fear scream: $F_{1,13} = 0.001$, $P = 0.98$; feather loss: $F_{1,13} = 1.22$, $P = 0.29$; tonic immobility: $F_{1,13} = 0.001$, $P = 0.98$).

DISCUSSION

We found consistent differences in antipredator behaviour in this study of escape behaviour of nearby rural and urban populations of birds belonging to the same species. Raptors (that included sparrowhawk as one of the most abundant species) were significantly more common in rural than in urban habitats, whereas the opposite was the case for cats (see also a similar result reported by Møller (2011) for three cities in Norway, Denmark and France). As predicted, urban birds showed a higher frequency of alarm calls and fear screams. These results could be explained as a behavioural adaptation to warn relatives given the low level of genetic differentiation among urban birds (e.g. Rutkowski et al. 2005; Baratti et al. 2009; Evans et al. 2009; Björklund et al. 2010). Furthermore, individuals living in urban landscapes bite less frequently and wriggle less often than those inhabiting rural habitats. These differences fit with the prediction of relaxed antipredator behaviour in cities (Cooke 1980; Møller 2008a; Carrete & Tella 2011). Hence, our results seem to support the general observation that urban habitats pose low risk of predation (Richner 1989; Jokimäki & Huhta 2000; Haskell et al. 2001; Jerzak 2001; Antonov & Atanasova 2003; Lepczyk et al. 2003; Gaston et al. 2005; Sims et al. 2008; Sorace & Gustin 2009; Ibáñez-Álamo & Soler 2010). However, tonic immobility was higher and feather loss more common in urban than in rural populations. These differences in behaviour during capture between rural and urban populations were related to susceptibility to predation by sparrowhawks. Because adaptation is a gradual process of change in phenotype with time, we predicted that escape behaviour would diverge over time between rural and urban populations, as observed for biting behaviour.

Table 4
Difference in escape behaviour between rural and urban habitats (rural minus urban behaviour) in relation to year of urbanization

Variable	Sum of squares	*df*	*F*	*P*	Estimate (SE)
Biting					
Species:					
Year	32.388	1	6.380	0.025	−0.004 (0.002)
Error	65.993	13			
Contrasts:					
Year	6.982	1	6.269	0.026	−0.004 (0.001)
Error	14.478	13			
Wriggle					
Species:					
Year	26.977	1	4.360	0.057	−0.004 (0.002)
Error	80.434	13			
Contrasts:					
Year	8.926	1	6.891	0.021	−0.004 (0.002)
Error	16.840	13			

Escape behaviour was related to urbanization, suggesting that antipredator behaviour has diverged between ancestral rural populations and recently established urban populations. We hypothesized that the behaviour of birds captured by humans would differ between rural and urban populations as a consequence of adaptation to urban environments, where the predator community differs from that of their ancestral rural habitats. Urban habitats have many more cats than nearby rural areas, although more cats do not necessarily reflect higher predation rates (Sorace 2002; Baker et al. 2008; Sims et al. 2008; Sorace & Gustin 2009; van Heezik et al. 2010; Stracey 2011; Tschanz et al. 2011). In contrast, rural areas generally have many more raptors than urban habitats (Sorace 2002; Sorace & Gustin 2009). These differences in relative abundance of different categories of predators have implications for the evolution of antipredator behaviour in urban environments because behaviour that is efficient as a route of escape from cats may differ from behaviour facilitating escape from raptors. Here we have shown that the difference in escape behaviour between rural and urban habitats was related to susceptibility to cat predation (frequency of individuals biting and wriggle behaviour), whereas feather loss was related to susceptibility to sparrowhawk predation. These findings provide evidence of recent divergence in escape behaviour between neighbouring rural and urban populations of birds.

We studied escape behaviour by birds when captured by a human under the assumption that such behaviour reflected

antipredator behaviour of birds when attacked by a real predator. Historically, any individual bird that was captured by humans was almost certain to be dead. Hence, the functional interpretation of escape behaviour is that it reflects a last-minute attempt to evade capture and certain death. We tested and found evidence for this important assumption by relating differences in escape behaviour to susceptibility to two different kinds of predators. Previous studies have shown that bird species with more intense wriggle behaviour and tonic immobility are more susceptible to predation by hawks and cats (Møller et al. 2011). Here we have shown that species that were most susceptible to predation had a higher frequency of feather loss in urban than in rural populations. The fact that only the difference between rural and urban habitats for one of the six kinds of escape behaviour tested was significantly related to susceptibility to predation does not mean that the remaining behaviours have not evolved and are not maintained by predation. Many other predators affect rural and urban populations of birds; predation in rural habitats may be a more powerful selective force than in urban habitats, and we cannot exclude the possibility that escape behaviour may relate to susceptibility to these predators. Indeed, additional studies of feather loss (Møller et al. 2006), fear screams (Møller & Nielsen 2010), tonic immobility (Boissy 1995; Forkman et al. 2007) and alarm calls (Marler 1955) suggest that they have evolved in the context of predation. Finally, we only had information on 15 species and 1132 individuals, suggesting that conclusions may change when more data have been collected.

Why did escape behaviour differ between rural and urban populations of birds? Differences in escape behaviour between rural and urban areas may arise as a consequence of differential urbanization of individuals with particular characteristics of escape behaviours, phenotypic plasticity in antipredator behaviour that differs between habitats owing to differences in exposure to predators, or micro-evolutionary adaptation of ancestrally rural populations to urban environments. It seems unlikely that differential urbanization accounted for our findings because we investigated difference in escape behaviour between populations of the same species in the two habitats. If phenotypic plasticity accounted for the difference in behaviour, we would expect relatively rapid changes, whereas micro-evolutionary change would imply gradual change over long periods of time. The difference in frequency of biting and intensity of wriggle between urban and rural habitats was significantly related to time since urbanization. Thus, as more time elapsed since urbanization, the difference in behaviour between rural and urban habitats changed. Such gradual change is consistent with a scenario of micro-evolution, and previous studies of urbanization of birds have shown similar divergence in behaviour being linked to time since urbanization (Møller 2008a, 2010). Given genetic differentiation between rural and urban habitats or among urban areas (Rutkowski et al. 2005; Baratti et al. 2009; Evans et al. 2009; Björklund et al. 2010), this implies a reduction in dispersal distance and a lack of interbreeding between individuals from rural and urban habitats. Indeed, urbanization characteristically results in loss of migration in birds (Klausnitzer 1989; Luniak et al. 1990; Stephan 1999), and resident bird species have much shorter dispersal distances than migratory species (Paradis et al. 1998; Belliure et al. 2000). Species that have been urbanized for a long time had a higher frequency of biting individuals in rural compared with urban populations and higher intensity of wriggle behaviour in rural compared with urban populations. Thus, there has been a decline in biting frequency from relatively high levels in recently urbanized populations to relatively low levels in populations that have been urbanized for a long time. For wriggle behaviour urban populations wriggled more than rural populations in recently urbanized species, whereas rural populations wriggled more in species that have been urbanized for a long time.

In conclusion, we have shown that urban populations of birds have diverged from ancestral rural populations in terms of behaviour when captured by a human being, reflecting escape behaviour, with urban birds being less aggressive, more often giving alarm calls and fear screams, showing higher tonic immobility and more often losing their feathers. Divergence in escape behaviour between rural and urban populations was related to susceptibility to predation by sparrowhawks, and degree of divergence was related to time since urbanization. These findings are consistent with the hypothesis that differences in predation and predator communities between rural and urban habitats have affected the way in which birds respond to capture as a last resort of escape and suggest that predation is an important selection force driving adaptation to urban habitats in birds.

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Appendix

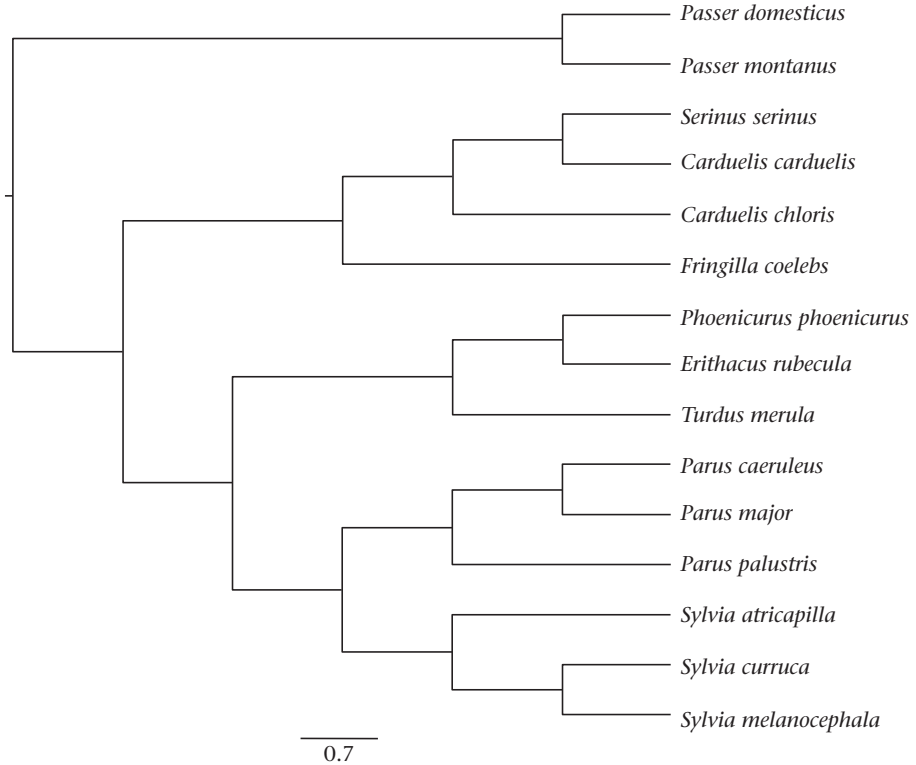

Figure A1. Phylogenetic relationships between the 15 species included in the study on urbanization and capture behavior.

Table A1. Summary statistics for behavioural variables, body mass (g), sample size, and susceptibility to cat and sparrowhawk predation (see text for details)

Species	Wriggle rural	Wriggle urban	Tonic immobility rural	Tonic immobility rural	Feather loss rural	Feather loss urban	Fear scream rural	Fear scream urban	Biting rural	Biting urban	Alarm call rural	Alarm call urban	Body mass (g)	Sample size for rural birds	Sample size for urban birds	Susceptibility to cat predation	Susceptibility to sparrowhawk predation
Carduelis carduelis	0.52	0.80	0.84	1.49	0.06	0.80	0.03	0.20	0.39	0.20	0.99	1.00	15.60	33	5	0.30	−0.26
Carduelis chloris	1.00	0.93	0.95	0.97	0.21	0.26	0.10	0.09	0.71	0.37	0.92	0.49	27.65	38	43	−0.60	0.18
Erithacus rubecula	0.97	1.40	0.80	1.24	0.06	0.20	0.07	0.20	0.08	0.40	0.05	0.40	16.35	105	5	0.37	0.18
Fringilla coelebs	1.22	0.86	0.66	0.74	0.11	0.29	0.16	0.10	0.89	0.76	0.20	0.33	24.20	146	21	−0.60	0.06
Parus caeruleus	1.28	1.06	0.42	0.51	0.09	0.00	0.33	0.77	1.00	1.00	0.40	0.65	11.75	43	17	0.60	0.04
Parus major	1.35	1.06	0.53	0.92	0.11	0.07	0.23	0.26	0.93	0.94	0.14	0.35	18.50	80	31	−0.88	0.33
Parus palustris	1.10	1.00	0.20	1.39	0.00	0.00	0.20	0.00	0.80	1.00	0.00	0.00	11.90	10	2	−0.70	−0.42
Passer domesticus	1.36	0.53	0.27	0.51	0.00	0.00	0.00	0.07	1.00	0.47	0.36	0.40	30.35	19	15	−1.82	0.26
Passer montanus	1.69	0.86	0.51	0.97	0.08	0.00	0.00	0.00	0.54	0.17	0.08	0.11	21.70	13	36	−0.87	0.73
Phoenicurus phoenicurus	1.46	1.40	0.98	0.00	0.06	1.00	0.15	0.00	0.20	0.00	0.46	0.41	15.90	66	1	0.70	−0.47
Serinus serinus	0.88	1.00	1.08	1.20	0.62	0.00	0.00	0.00	0.12	0.00	0.25	0.33	11.95	8	3		
Sylvia atricapilla	1.38	1.00	0.82	1.49	0.12	0.00	0.10	1.00	0.25	1.00	0.01	0.00	18.85	87	2	1.00	−0.44
Sylvia curruca	0.68	1.00	0.89	0.00	0.00	0.00	0.09	1.00	0.00	0.00	0.03	0.00	12.40	66	1	−0.40	−0.07
Sylvia melanocephala	2.00	2.00	1.49	0.48	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	13.45	1	1	−0.40	−0.07
Turdus merula	1.44	1.42	1.03	1.03	0.84	0.79	0.18	0.47	0.74	0.55	0.31	0.58	95.85	147	53	−0.19	0.21