



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.

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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

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