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Original article

Effect of urbanisation on habitat generalists: starlings not so flexible?

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ABSTRACT

The small variability of habitat generalist abundances in relation to landscape changes has been related to their behavioural flexibility. We hypothesise that successful generalists, such as the starling, compensate for feeding resource difficulties (poor quality of food, accessibility) in habitats such as urban ecosystems and that its behavioural flexibility allows for similar breeding performance in rural and urban areas. Along an urbanisation gradient we compared simultaneously (1) success factors such as the abundance of breeding starlings, their breeding performance and the fitness of nestlings, and (2) possible flexibility quantified through the rate of parental food-provisioning, and the composition and the amount of food delivered to nestlings. Abundance of breeding starlings are similar throughout the urbanisation gradient, but urbanisation profoundly and negatively affects reproductive parameters of starlings. Differences in the amount of food delivered to nestlings by parents (less food in town centre), and the small masses of nestlings reared in the urban sectors support the idea that urban nestlings received insufficient food loads. Despite modifications to their diurnal food-provisioning rhythm and the incorporation of some human food refuse into their diet, starling parents have a significantly reduced production of young in the urban centre sector. We rebut the idea that the "generalist" starling is able to breed successfully anywhere: other more "specialist" species succeed in producing their young by innovating more in terms of diet resources. We suggest defining successful birds with respect to colonisation or invasion process through behavioural innovation rather than an ambiguous habitat generalist definition.

1. Introduction

Modifications in land use expose species to completely new conditions to which they might not be able to adapt (e.g. for birds see review in Cody, 1985; Marzluff et al., 2001). It is generally agreed upon that different species do not react to landscape changes in a similar way, because of differences in life history traits and degree of specialisation (Urban et al., 1987; Andrén et al., 1997). Habitat specialist species (*sensu* Andrén et al., 1997) often decline or disappear whereas habitat generalist species (*sensu* Andrén et al., 1997) do not seem to be affected and can even be favoured by existing human-caused modifications to the landscape (Andrén, 1992; Lidicker, 1995; Coppedge et al., 2001).

The small variability of habitat generalist abundances with landscape changes has been related to their high behavioural flexibility, as described by Henein et al. (1998). Unlike inflexible habitat specialist species which are restricted to one habitat type and are reluctant to cross the matrix surrounding their habitat patch, habitat-generalist species can

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adjust their movement behaviours and their resource uses to the pattern of the landscape they are living in. Thus, generalist species are able to access the resources they need, such as food or shelter, by making use of novel man-made patches and can thereby mitigate the consequences of landscape changes (Gascon et al., 1999). It is exactly the same process as in biological invasion, where behavioural flexibility allows animals to respond more rapidly to changes in the environment and can consequently be an advantage when invading novel habitats. Among rapid adjustments to new conditions, the feeding innovation frequency, i.e. changes in foraging techniques or diet items, in animal generalists and successful invaders has recently been highlighted (Sol and Lefebvre, 2000; Sol et al., 2002; Prinzing, 2003; O'Brien et al., 2005).

In this paper, we investigated how a "generalist" bird reacts to new challenges that landscape changes impose both in terms of its classically-quantified success, i.e. abundance in the locality, breeding performance or nestling fitness, and in its behavioural flexibility that can be quantified as adjustments in nestling care. To do this, we took advantage of urbanisation to model severe human-caused landscape changes. According to McDonnell and Pickett (1990), urbanisation can be viewed as an unprecedented quasi-experimental manipulation to study ecological processes. It offers a gradient of landscape modifications over a small area from a rural/semi-natural landscape to the highest level of human-caused modification: an urban landscape (Forman and Godron, 1986). We selected the European Starling (*Sturnus vulgaris* L.) as a model species as its biology is well known and corresponds to that of a generalist species (Feare, 1984). This bird can notably inhabit deserts, saltmarshes and cities where it can present high abundance (Cramp and Perrins, 1994). This habitat tolerance indicates that the species is a priori able to mitigate the effects of huge landscape changes that urbanisation involves (Clergeau et al., 1998, 2004).

For some generalist birds breeding in towns, the behavioural flexibility is clearly through diet plasticity, for example the Herring Gull (Brousseau et al., 1996), while for other generalists, such as the starling, it is less clear. Starlings can modify some behaviour, such as roost site selection (Lyon and Caccamise, 1981) and diet composition in winter (Feare, 1984), but its diet variability in towns during the breeding period seems to be limited (Mennechez and Clergeau, 2001). However, we hypothesise that successful generalists, such as the starling, compensate for feeding resource difficulties (poor quality of food, accessibility) linked to urbanisation and that its behavioural flexibility allows it to achieve similar breeding performances in rural and urban areas. So, in order to examine the behavioural flexibility of breeding starlings, we made a simultaneous comparison along an urbanisation gradient between (1) success factors such as the abundance of breeding starlings, their breeding performance and the fitness of nestlings, and (2) possible flexibility quantified through the rate of parental food-provisioning, and the composition and amount of food delivered to nestlings. Since feeding behaviour changes with brood size (Neuenschwander et al., 2003), we forced adults to raise the same number of nestlings by manipulating broods in our nest boxes.

2. Material and methods

2.1. Study area and urban–rural gradient

Our study was carried out in the eastern part of the Rennes District, Brittany, Western France (48°7′N; 1°41′W) from 1994 to 1997. European starlings are a very common bird in this region. The approximately 500 km^2 study area supports an urban–rural gradient which can be subdivided into three contrasting landscape types from the surrounding countryside to a highly urbanised core (Clergeau et al., 1998): the periurban sector (outside the city), and the suburban and the urban centre sectors (within the city, pop. 270,000). The periurban sector is dominated by a more or less intensive agricultural matrix with either grasslands supplying grazing and silage for dairy cows or open fields. A hedgerow network, some scattered farms and individual houses also characterised this sector. The suburban sector is a recent peripheral sector surrounding the historical centre of Rennes. It is characterised by a wide diversity of types of urbanisation. This landscape type is dominated by large apartment building complexes and industrial areas with large lawn plots and residential sectors. The urban centre is characterised by an old continuous building matrix. Three parks (from 5 to 10 ha) and small private gardens (from 10 to 500 m^2) are the only vegetated areas. The precise spatial definition of these three sectors was based on aerial photograph interpretation (1990, IGN). We measured the area extent of five land cover types on several 5 ha-sites in each sector using IDRISI Geographic Information System software (Clark University, Worcester, MA): Building, Paved Area, Cultivated Area (cropland and vegetable gardens), Grassland (pastures and lawns), and Woody Area (with trees and/or shrubs) (Table 1). Except for Woody Area, there are significant differences between percentages of composition elements between sectors (Fisher test, all $F > 4.4$, $P < 0.05$).

2.2. Relative abundances of breeding starlings

In 1994 and 1995, the abundances of breeding starlings within the three sectors were studied at 26 sites chosen along the urban–rural gradient to be representative of each of the landscapes: eight in the periurban sector, nine in the suburban sector and nine in the urban centre sector.

Table 1 – Characteristics of the three sectors studied along the urbanisation gradient at Rennes, western France. *n* = number of 5 ha-sites analysed. Mean ± S.E. are given

	Landscape type		
	Periurban sector (N = 21)	Suburban sector (N = 15)	Urban centre (N = 22)
% Cover			
Buildings	5.5 ± 3.1	17.3 ± 3.6	30.7 ± 3.0
Paved Area	14.1 ± 3.2	36.2 ± 3.7	44.0 ± 3.1
Cultivated	22.3 ± 3.4	0.5 ± 3.9	1.0 ± 3.2
Grassland	41.3 ± 4.9	38.2 ± 5.8	20.4 ± 4.8
Woody Area	16.8 ± 4.5	7.8 ± 5.3	3.9 ± 4.4
Type of buildings			
Number of stories	1	1–2 or 4–12	2–5
Distribution	Scattered	Neighbouring	Continuous