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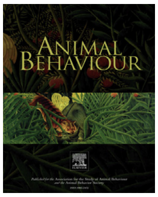

Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment

Virginie Demeyrier*, Marcel M. Lambrechts, Philippe Perret, Arnaud Grégoire

Centre d'Ecologie Fonctionnelle et Evolutive, CEFE UMR 5175, Campus CNRS, Université de Montpellier, Montpellier, France

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An ecological trap occurs when animals prefer to settle in poor-quality habitats even though alternative high-quality habitats are available. Thus, to find evidence of a trap one must show (1) a habitat preference and (2) a mismatch between the settlement decision and reproduction or survival. However, demonstrations of traps in the wild are currently limited because the misleading cues have to be identified and are usually difficult to manipulate experimentally. Places where humans transform habitats, such as urbanized areas, are particularly prone to this ecological phenomenon. Here we tested whether the size of a human-made structure (artificial cavities) can induce maladaptive breeding responses via an ecological trap mechanism in an urban secondary-cavity nesting bird, the great tit, *Parus major*. Previous studies showed that great tits prefer to breed in large cavities; cavity size is thus used as a cue in nest site selection. Reproductive investment in great tits has also been shown to be influenced by the breeding cavity size. However, this behaviour can only be adaptive if cavity size matches the quality of the breeding habitat. This is not necessarily the case in urbanized environments where natural habitat has been removed or breeding habitat modified. We performed a cavity choice experiment, providing an opportunity for great tits to choose between three cavity size options, and monitored their subsequent breeding attempts. We found that urban great tits preferred the largest artificial cavities for breeding when they could choose between small, medium-sized and large cavities. Individuals from the largest cavities also invested more in egg production, yet had a lower fledging success than those from medium-sized cavities, experimentally showing a trap mechanism in free-living animals. With this study, we shed light on maladaptation associated with human-transformed habitat.

Adaptation-based theory predicts that organisms use environmental cues to estimate habitat quality to improve their choice of where to live and breed (Hickford & Schield, 2010; Kristan, 2003; Schlaepfer, Runge, & Sherman, 2002). In a natural system, where cues match the real quality of the environment, the associated choice is expected to lead demographically to a source–sink dynamic (e.g. Dias, 1996). In these conditions, rich source habitats are preferred to poor sink ones, and individuals will settle in poorer sink habitat only when a better option is not available (i.e. default choice B in Fig. 1). However, in systems facing human-induced rapid environmental change (HIREC, e.g. Hale & Swearer, 2016; Sih, 2013), cues exploited for habitat selection could be decoupled from the true quality of the habitat, potentially causing maladaptive responses. Because of HIREC, poor quality habitat may become attractive but in fact reduce survival or reproduction. These kinds of habitat have been defined as ecological or evolutionary traps (Gilroy & Sutherland, 2007; Hale, Treml, & Swearer, 2015; Robertson & Hutto, 2006; Robertson, Rehage, & Sih, 2013; Schlaepfer et al., 2002) and can, in extreme cases, become attractive sinks (option A in Fig. 1; Delibes, Ferreras, & Gaona, 2001). Ecological traps are predicted to occur especially in human-transformed habitat representing one aspect of HIREC (Hale & Swearer, 2016; Robertson et al., 2013). For instance, in natural conditions, sea turtle hatchlings use the moon light reflecting on the oceanic horizon to find the ocean essential for survival, but the attractive artificial light from the human-made beach front might guide the hatchlings inland, therefore preventing survival. The artificial beach environment would thus represent an ecological trap for the turtle hatchlings (Witherington, 1997).

In the ecological framework, Robertson and Hutto (2006) defined three proximate causes for ecological traps where habitat attractiveness is decoupled from habitat quality. First, the cues used in habitat selection might change in expression (e.g. intensity, type,

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* Correspondence: V. Demeyrier, CEFE-CNRS, UMR 5175, 1919, route de Mende, F34293 Montpellier Cedex 5, France.

E-mail address: virginie.demeyrier@cefe.cnrs.fr (V. Demeyrier).

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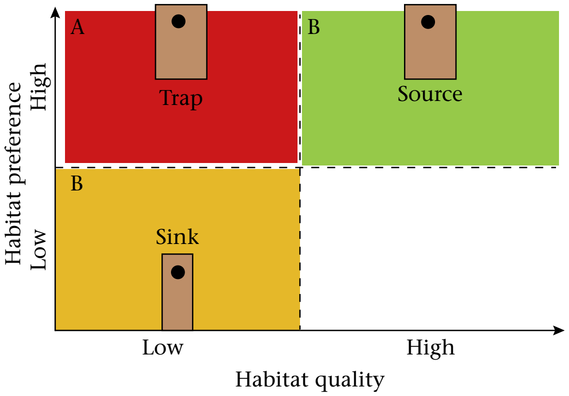

Figure 1. Preference for habitat in relation to its quality. (A: perturbed environment; B: natural environment, adapted from Gilroy & Sutherland, 2007).

number) making a habitat more attractive without changing habitat quality. Second, the cues used in habitat selection might not be altered in a rich habitat that is transformed into a poor habitat. Third, integrating the two previous causes, habitat attractiveness might increase whereas at the same time habitat quality declines. However, demonstrating an ecological trap in the wild is usually difficult because the cues involved in the preference and selection of the habitat have to be identified with precision. In addition, these cues are extremely difficult to manipulate experimentally following robust experimental designs (e.g. Johnson, 1980; Robertson & Hutto, 2006). Experimental demonstration of an ecological trap in the wild is therefore limited despite the extensive efforts of empirical research to assess behavioural effects of traps (e.g. Hale & Swearer, 2016; Robertson & Hutto, 2006).

At least one of the three main causes of ecological traps is expected to occur in urbanized environments, considered to be among the extreme examples of HIREC. Urbanization is a fast-developing process worldwide, currently involving more than 50% of the human population (Gaston, Visser, & Hölker, 2015; Marzluff, 2001) and more than 3% of the global terrestrial area (Aronson et al., 2014). This urban expansion induces degradation of the natural environments and will especially promote species able to successfully adapt to cities (Adams & Lindsey, 2011; Clergeau, Croci, Jokimäki, Kaisanlahti-Jokimäki, & Dinetti, 2006). Urban areas have recently been described as potential ecological traps for wildlife, especially when animals are attracted to the massive presence of artificial human-fabricated cues, cues that reflected true habitat quality in rich natural environments, but that are misleading in a transformed, poor, urbanized environment (MacGowan, 2001; Marzluff, 2001; Robertson et al., 2013). Among the human-fabricated cues that might be used in habitat selection are artificial cavities exploited as breeding sites, such as human-made nestboxes. Preference for a certain box design as reflected in its shape or size is species-specific and perhaps population-specific or even a matter of individual choice (e.g. Lambrechts et al., 2010). For instance, previous studies in secondary-cavity nesting great tits, *Parus major*, have shown that females prefer to breed in large nestboxes (Löhrl, 1986; Maziarz, Wesolowski, Hebda, & Cholewa, 2015; Møller et al., 2014). In addition, clutch size has been shown to increase with the size of the nesting cavity, either through individual plastic adjustment or nonrandom distribution of individuals varying in reproductive capacity (Karlsson & Nilsson, 1977; Löhrl, 1980; Slagsvold, 1987; Van Balen, 1984). Breeding in a large cavity might limit hyperthermia risks, reduce nestling competition for space or decrease predation risks inside the cavity, therefore not penalizing larger broods (Löhrl, 1986; Van Balen, 1984). However, these behavioural responses to nestbox size would be adaptive only if cavity size were closely associated with the quality of the breeding environment. For instance, cavity size associated with brood size also has to be linked to some extent to food availability in the habitat at the time the nestlings are reared, to increase fledging success. In natural conditions, the cavity size used for nesting is expected to be positively associated with the tree trunk diameter and therefore with a larger volume of the tree canopy providing more niches for arthropods, such as caterpillars, required to rear the nestlings (Lambrechts et al., 2010, 2012; Robles, Ciudad, & Matthysen, 2011). It has therefore been hypothesized that cavity size could be used as a cue to estimate the quality of the selected breeding habitat and at the same time be used to adjust clutch size, and thus brood size, to the future arthropod availability required to rear the nestlings (Mänd, Tilgar, Lohmus, & Leivits, 2005). However, the more attractive larger boxes, when present in poorer urbanized environments, might disassociate cavity size and the associated clutch size from the future prey availability required to rear the nestlings, whatever the potential benefits of breeding in larger cavities listed above, and therefore might proximately cause an ecological trap because of one of the three main reasons outlined in Robertson and Hutto (2006). To our knowledge, this scenario has never been experimentally studied (Mainwaring, 2015; Robertson et al., 2013).

To test formally whether artificial cavities may become potential ecological traps in urbanized environments, three conditions have to be verified (Gilroy & Sutherland, 2007; Robertson et al., 2013; Schlaepfer et al., 2002). First, urban breeders should have a stronger preference for larger boxes when they have the option to choose between larger, medium-sized and smaller nestboxes. Second, clutch size should be positively associated with box size; the birds are expected to lay more eggs in the more attractive larger boxes. Finally, if the size of the box becomes disconnected from habitat richness in the more urbanized environments, and if these environments are globally restrictive for food resources and/or experience higher anthropogenic disturbance, fledging success is predicted to be lower in the larger more attractive boxes. To examine these three conditions, we performed a 2-year choice experiment in which wild urban great tits could breed in one of three box sizes within the range of the cavity sizes accepted by this species (Lambrechts et al., 2010). The cue for nest site selection provided (i.e. cavity size) therefore did not differ from the natural, nonurbanized, conditions. We also quantified the level of urbanization around each of the nestboxes following procedures applied in previous studies in urban areas to account for the potential heterogeneity of urban areas and their potential consequences for the avifauna (e.g. Dauwe, Janssens, Bervoets, Blust, & Eens, 2004; Titulaer, Spoelstra, Lange, & Visser, 2012).

METHODS

Study Species, Area and Data Collection

The field experiment was conducted in 2011 and 2012 in the city of Montpellier, south of France (43°36′43″N, 3°52′38″E) on wild urban great tits from March to July. The area was equipped in autumn 2010 with 243 nestboxes placed along an urbanization gradient. Because of vandalism, at the beginning of the 2011 breeding season, only 168 nestboxes were still there and in the 2012 breeding season, 163. We chose three box designs encompassing the size range of breeding cavity accepted by great tits throughout Europe (Johnson, 1980; Lambrechts et al., 2010). Small, medium-sized and large boxes differed only by internal base area (small = 6 × 6 cm, 36 cm^2, 43–48 boxes versus medium = 11 × 11 cm, 121 cm^2, 45–47 boxes, versus large = 14.5 × 14.5 cm, 210 cm^2, 43–44 boxes), and hence