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Flexibility in European starlings' use of social information: experiments with decoys in different populations

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Individuals confronted with novel environments, for instance recently modified environments such as towns or recently occupied habitats such as colonization fronts, have to cope with a lack of information about the location of resources. We hypothesized that, under these conditions, individuals of a social species such as European starlings, *Sturnus vulgaris*, would be more responsive to social cues indicating food presence than individuals belonging to populations already established in a well-known habitat. To test this hypothesis, we displayed starling decoys with various age, group size and interindividual distance characteristics in feeding postures to evaluate their attractiveness to starlings from towns and colonization fronts and noted whether attracted individuals joined particular decoy groups. Our results supported our hypothesis that sensitivity to social cues varied according to the population's history, and we suggest that these cues enhance the success of starlings in occupying new habitats.
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Before occupying and breeding in a new environment, animals must explore it and collect information. Individuals need to have at least partial knowledge of their environment's food, habitat resources (Beauchamp & Ruxton 2005) and suitable breeding sites (Doligez et al. 2002).

Information about habitat characteristics may have various origins: (1) 'preharvest information' gained before arriving on a site (Valone 1991); (2) 'private' or individually gained information collected by exploration and trial-and-error learning (Chesler 1969; Valone 1989); and (3) 'social information' obtained through social facilitation by watching other individuals foraging, testing new food or solving new problems (Clayton 1978; Coussi-Korbel & Fragaszy 1995; Galef & Laland 2005; Jackson & Ruxton 2006). The proportion of each kind of information and its characteristics depend on accessibility, individuals' experience and social context (Valone & Giraldeau 1993; Templeton & Giraldeau 1996; Valone & Templeton 2002). Social information is usually also divided into social cues and public information. Social cues are simple indicators of the presence of conspecifics in a potentially interesting site, whereas public information involves more precise information such as the feeding or breeding success (indicated by the number of prey captured by conspecifics in a patch or the number of surviving young in a breeding area; Danchin et al. 2004; Parejo et al. 2008). Public information thus gives more precise information about patch quality. In the study conducted here we focused on social cues.

Individuals that leave their population of origin and disperse into new habitats can be confronted with a lack of preharvest and private information. Nevertheless, it is crucial to get information about resource distribution efficiently to avoid starvation and ensure survival. In 'new' areas such as those individuals have colonized after an increase in resources or where they have been translocated, individuals have to cope with unpredictability and the potential dangers of novelty. Taking account of conspecific activities and experience can thus be a strategy to compensate for these difficulties. On the one hand, Ryer & Olla (1992) demonstrated that juvenile walleye pollocks, *Theragra chalcogramma*, exploit spatially variable, ephemeral food patches more successfully when foraging

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in groups by local enhancement. On the other hand, red crossbills, *Loxia curvirostra*, avoid exploring patches where other individuals have already foraged unsuccessfully and thus spend less time foraging on poor patches and longer on rich patches (Smith et al. 1999).

Joining successful foraging conspecifics on suitable sites and avoiding unsuccessful ones can thus be a good mechanism to cope with unpredictability in 'new' habitats. It can be especially useful to be able to recognize experienced individuals that could give reliable information about resource distribution. For example, young canaries, *Serinus canaria*, eat more seeds after seeing their fathers eating seeds than when they have no tutor, and they tend to eat the same kinds of seeds (Cadieu et al. 1995). Adret-Hausberger & Cumming (1987) and Wauters et al. (2002) demonstrated that young chickens, *Gallus gallus domesticus*, are attracted to older individuals at feeding places and that they choose the same type of food as their mothers or older peers. These observations suggest that information from adults or experienced peers can be important for naïve individuals. In the same way, Slaa et al. (2003), who studied social stingless bees, found that in the species *Trigona amalthea*, the decision to join other foragers was affected by the experience of individuals with a food source: newly recruited foragers showed local enhancement, whereas experienced foragers showed social avoidance conducive to local inhibition.

We hypothesized that social information is thus more important for populations in newly colonized areas than for well-established populations and that particular visible characteristics of animal groups may influence their attraction. Not only the age and activity of conspecifics but also the number and form of the group could be informative (Clergeau 1982; Burger 1988).

We chose the European starling, *Sturnus vulgaris*, as our biological model since it has colonized a variety of habitats successfully, becoming an invasive species in many regions (Feare 1984). We investigated the attraction to 'foraging' starling decoys of starlings from: (1) long-established populations in rural areas; (2) populations that have recently colonized new environments such as towns; and (3) populations that have invaded new areas at the edge of the species' European range in the colonization front. As the positions and the numbers of individuals on a feeding site may influence the landing decisions of birds flying over the area, we also tested the influence of social aspects such as groups' sizes and interindividual distances by modifying the presentation of the decoys. The birds' age and experience (naïve or informed, adult or young) may also influence the decisions to join different types of groups. We suggest that naïve individuals should more frequently rely on the information provided by experienced ones (as adults) and thus should tend more frequently to join these kinds of individuals. For this reason, we also tested the effect of the age of the birds on their reaction towards three groups of decoys representing different ages.

METHODS

Studied Populations

We compared the reactions of starlings from four areas where the populations had different colonization histories and that reflected different situations in which individuals have different access to information. We chose to test starlings on 10–15 sites in each area rather than to focus on only one group per population, thus accounting for the distribution and density of colonies.

Two populations and their respective geographical areas were selected in western France.

(1) Rural populations in Brittany (Rural Brittany) where starlings have been established for several centuries (Richard 1826). This population includes experienced adults which know the habitat well and are capable of transmitting information to younger individuals, reducing the proportion of naïve individuals. Sixteen sites in agricultural areas were selected in the country near Rennes and Saint-Brieuc (towns approximately 100 km apart; 175 birds were tested during the breeding period and 439 during the postbreeding period).

(2) Urban populations in Brittany (Urban Brittany). Starlings have been breeding in these urban areas for 30–100 years (Clergeau 1981). This population uses habitats frequently disturbed by anthropogenic activities and with scarce resources particularly difficult to get during the breeding period (Mennechez & Clergeau 2006). Twelve sites within Rennes and Saint-Brieuc were selected (153 birds were tested during the breeding period and 123 during the postbreeding period).

We also selected two Italian populations, located in the propagation front in the south where individuals exploited some cities and cliffs along the Adriatic Sea less than 30 years ago. Recent touristic activities and new irrigation practices have changed the landscape structure and availability of new food resources (G. La Gioia, personal communication). These populations can also receive individuals from the north, increasing the proportion of naïve individuals in them.

(3) Rural populations in the Apuglia region (Rural Italy) described as one of the most southern and recent colonization fronts in Europe (Castiglia & Tabarrini 1982). Eleven sites between San Cataldo and Otranto (70 km along the Adriatic coast) were selected (152 birds were tested during the breeding period and 91 during the postbreeding period).

(4) Urban populations of Apulia (Urban Italy), also on the colonization front (Pasquali 1984). Nine sites in Bari and Mola di Bari were selected (130 birds were tested during the breeding period and 66 during the postbreeding period).

In addition, we experimented in an area of buildings and gardens (Suburban Brittany) on the periphery of Rennes during the postbreeding period to evaluate the attraction gradient from urban to rural areas (224 birds tested).

All experimental sites were open short-grass fields measuring between 60 × 45 m and 120 × 90 m. We chose lawn parks, football grounds and grazed grass fields so that sites were as similar as possible.

Experimental Procedure

Decoys have proven to be good attractors facilitating aggregation (Williams & Schwab 1973; Jeffries & Brunton 2001) and useful tools to study patch selection and lek composition (Pius & Leberg 2002; Master et al. 2005; Jiguet & Bretagnolle 2006).

Most studies using decoys to test their visual attractiveness to birds have shown that stuffed decoys are better attractors than two- or three-dimensional plastic decoys (Fancher 1984; Kotliar & Burger 1984; Harvey et al. 1995; Crozier & Gawlik 2002). Decoys with their heads pointing down (as if they were eating) test attraction to foraging sites more effectively than upright decoys that represent vigilant individuals (Drent & Swierstra 1977; Inglis & Isaacson 1977; Clergeau 1981). For these reasons, we used stuffed starlings with their heads pointing down and beaks touching the ground. Dead birds were obtained from hunters, as this species is a game bird in France (construction details in Clergeau 1982).

To increase local enhancement (Guyomarc'h 1995), decoys in all experiments were placed in circular groups (Fig. 1), as this is the most attractive distribution of decoys (Clergeau 1981, 1982). To ensure that the attraction effect of the decoys was independent of the nutritive quality of the patch, we conducted a preliminary experiment testing the attraction of decoys to starlings flying over a football ground covered with artificial plastic turf. During this

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