



Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk

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To test the hypothesis that variation in aerial flocking behaviour is adaptively related to predation risk, we described and quantified the flocking patterns of starlings, approaching two urban roosts, which differed in predation pressure (by peregrine falcons, *Falco peregrinus*). We predicted that the higher predation pressure in one of the roosts would be reflected in larger and more compact flocks, thought to be less vulnerable to predation than small flocks. Incoming flocks, not under direct attack, were observed during winter for 53 days. We identified 12 flocking shapes. Significantly higher frequencies of compact and large flocks were observed in the roost with high predation pressure, while small flocks and singletons were more frequent at the roost with low predation pressure. Similar patterns were observed in both roosts when other flocks displayed antipredator behaviour, even when far away and in the absence of the predator at the focal roost. This may indicate that social information passed between flocks affects flocking decisions. Predation success was higher at the roost with low predation. These results suggest that aerial flocking patterns are affected by predation risk and possibly by the behaviour of other flocks in response to direct attacks.

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Group formation is widespread in the animal kingdom: more than 50% of fish and avian species form schools and flocks (Lack 1968; Shaw 1978; Beauchamp 2002). Avian flocking is a striking example of collective behaviour in animal aggregations (Emlen 1952). Many features of bird flocking are also present in other instances of collective behaviour, such as fish schools, mammal herds and insect swarms (e.g. Krause & Ruxton 2002; Couzin & Krause 2003).

A major factor in the evolution of avian flocking behaviour is predation (many eyes theory, selfish-herd theory, dilution effect, confusion effect, e.g. Siegfried & Underhill 1975; Cresswell 1994; reviewed in Krause & Ruxton 2002; Beauchamp 2004). Most empirical and theoretical studies on avian sociality and flocking in relation to predation have been carried out in the context of foraging, focusing on vigilance and departure or escape responses (e.g. Caraco et al. 1980; Hilton et al. 1999; Carbone et al. 2003; Quinn & Cresswell 2005; Sirot 2006). In foraging contexts, animals joining groups face a trade-off between the antipredator

advantages and the costs of increased competition (Krause & Ruxton 2002; Carbone et al. 2003; Devereaux et al. 2006). However, birds also spend a considerable time flying, for migration and on local movements between foraging areas and from foraging areas to roosting sites, and aerial predation during these movements is very common (Feare 1984). Aerial flocking behaviour has received little attention, with the exception of flight energetics in which studies have focused on large species such as geese or pelicans (e.g. Weimerskirch et al. 2001; Videler 2005).

The factors influencing the trade-off between foraging and vigilance should vary with the context. If birds move for long distances from foraging areas to the roost, they might not incur competition foraging costs and therefore they may display full flocking behaviour and be affected mainly by external factors such as weather conditions, predation and the behaviour of other flocks. In this study we focused on such factors. In particular, the perception of predation risk could affect flocking decisions in the short term, being based on direct individual perception, on the predictability of predator presence and on the observation of other birds in the flock or in other flocks (signalling hypothesis, Ward & Zahavi 1973; Richner & Heeb 1995; public information, Danchin et al. 2004). We are not aware of any empirical support for information about predation risk being passed between flocks, but similar mechanisms are probably at play as in within-flock information transfer. The efficiency of information

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transfer is thought to decrease with distance so at first sight one would expect little information transfer between flocks that are found orders of magnitude further than companions within a flock. However, flight manoeuvres during predation attempts are very obvious and, given the size of the flocks involved in starlings, these displays may be very conspicuous and unambiguous. Another major advantage of flocking is therefore the use of social information (Krause & Ruxton 2002), which in the context of sharing information about predators is referred to as collective detection (e.g. Lima & Zollner 1996; Roberts 1997; Cresswell et al. 2000).

It is likely that different flocking patterns may serve this latter function with different efficacy. In recent models, although in a foraging context, Sirot (2006) has shown that vigilance and flight are not independent behaviours, because when social information about predators is taken into account, synchronization is a possible outcome of antipredator behaviour even in the absence of a real predator attack, while Beauchamp & Ruxton (2007) reported that individuals should ignore information provided by companions to some extent, as this may lead to too many false alarms taking time away from foraging. In addition, disturbed flocks of foraging sanderlings, *Calidris alba*, were more cohesive when taking off (Roberts 1997). It is therefore possible that certain cohesive and compact flocking patterns, requiring a high degree of synchronization, can be actively adopted even in the absence of a predator, in preparation for coping with predation. This may be especially true in areas such as roost locations that are stable over weeks or months, where the same sites are used in successive years (Cacamise & Lyon 1983) and predator presence is regular and thereby predictable. We studied flocking patterns at two stable roost sites where predator presence and predictability differed.

On their wintering grounds, European starlings, *Sturnus vulgaris*, form aggregations of thousands of individuals especially in the proximity of the nocturnal roosts, which are usually located in urban areas (Brodie 1976; Feare 1984; Beauchamp 1999). Every day before sunset, the flocks return to their roost from the foraging areas situated up to 40 km away (Feare 1984; Peach & Fowler 1989). Flocks have strong spatial coherence (Ballerini et al. 2008a, b; Cavagna et al. 2008) and are capable of very fast, highly synchronized manoeuvres, either spontaneously, or as a response to predator attacks. Avian predators such as sparrowhawks, *Accipiter nisus*, and peregrine falcons, *Falco peregrinus*, are typically attracted to the roost sites because of the large aggregations of prey (Krause & Ruxton 2002; Botham et al. 2005). To our knowledge, no systematic study has ever documented variation in aerial flocking behaviour of birds, except for a study of responses to raptor attacks in mixed flocks of dunlin, *Calidris alpina*, and ringed plovers, *Charadrius hiaticula*, where an antipredator flight display was reported in response to direct attack (Michaelsen & Byrkjedal 2002). In fish, some studies have classified shapes and manoeuvres in schools under the direct threat of predation, identifying well-defined and consistent patterns (Partridge et al. 1983; Parrish 1992; Nøttestad & Axelsen 1999).

We carried out a qualitative and quantitative study of flocking patterns of starlings approaching two urban winter roosts in the city of Rome, Italy, which were exposed to different predation pressure (by peregrine falcons). We also recorded predation behaviour and predation success at both roosts, as well as the presence of antipredator aerial displays of other flocks near or far from the roosts. In this town these two main roosts of many thousands of birds have been known since more than 70 years (Termini) and 20 years (Eur) while several other satellite roosts, unstable in time and location and hosting fewer birds, are also present. Up to 70 000 birds attend each roost per day from around mid-October to mid-March (personal observations in the same study seasons). During the day they disperse to feeding areas outside the town.

We carried out systematic observations from fixed locations at the roosts on flocks arriving from the countryside and directed to

the roosts, in the very last part of their daily trip. Our goals were (1) to classify flocking patterns, building a 'flocking ethogram' and (2) to explain the variation of such patterns in relation to predation risk. The 'confusion' effect, that is, disorientation of a predator by a large group of prey (Neil & Cullen 1974), and the 'selfish herd' theory (Hamilton 1971), according to which individuals use their flockmates as a shield, led us to predict that higher predation pressure would be reflected in more compact and larger flocks, thought to be less vulnerable to predation than less cohesive and small flocks. Similar effects should be observed in the presence of conspicuous antipredator aerial displays of conspecifics under direct attack, even without a predator near the roost.

METHODS

Study Areas

We observed flocks from 14 January to 17 March 2006 for 53 sessions. Observations were made in two roosts in Rome (41°44'N, 12°24'E) 10 km from each other, one in the city centre (Termini) and the other in the south of the city (Eur). The roosts have different structures: Termini consists of a large square completely surrounded by high (15–20 m) buildings and with rows of trees, mainly *Quercus ilex* and *Pinus pinea*, whereas Eur is a park area (*Cupressus cupressus*, *Cedrus libani*, *P. pinea*, *Q. ilex*, *Eucalyptus* sp.) surrounding an artificial pond and few high buildings around it. In the study period Termini hosted on average about 20 000 birds and Eur about 50 000 per day.

Data Collection

Data were collected by three persons (C.C., S.M., F.M., who trained together for a week to identify flock shapes) during 53 daily sessions (26 sessions at one roost and 27 at the other) on alternate days (on 4 days observations were made simultaneously at both roosts). At the end of the week an almost perfect agreement among raters was achieved (inter-rater reliability: Fleiss's kappa = 0.870). The observations began about 1 h before sunset, when no starlings were present, and went on until darkness. We used binoculars (8 × 42) to detect flocks on the horizon, and a compass to determine their direction of arrival. Observations were directly registered on a digital tape recorder. Opportunistic video recording was done with a video camera (JY-HD10, JVC). Flocks and singletons were followed for about 40–60 s and characterized from the moment of their appearance until their disappearance as a discrete unit when they merged with other flocks above the roost or landed in the trees. We assigned each flock to one of the 12 flocking patterns identified during the training period (Fig. 1). Flock shapes were mainly maintained during the recording period (minor deformations might occur with negligible differences in the flock shape). Moreover, flocks neither merged with other flocks nor landed in the trees during the recording time. We also recorded the presence/absence of peregrine falcons during each session (excluding episodic passages without any evident hunting behaviour) and the daily number of individual falcons observed simultaneously.

We noted any flight displays of other flocks in direct response to the hunting predator when the flocks under observation were arriving. Two types of displays were often observed. (1) 'Splitting displays' occurred when the flock under attack split into two or more parts (of the same or of different dimensions), often immediately merging again; this succession of splitting and merging could occur repeatedly during the same hunting sequence. (2) 'Agitation waves' consisted of changes in density, which propagated in about 1 s from one side to the other of flocks of thousands of birds. The latter display has been systematically studied in one fish species (Gerlotto et al. 2006), and described in starlings and

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