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Propagating waves in starling, *Sturnus vulgaris*, flocks under predation

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The formation of waves is a vivid example of collective behaviour occurring in insects, birds, fish and mammals, which has been interpreted as an antipredator response. In birds a quantitative characterization of this phenomenon, involving thousands of individuals, is missing and its link with predation remains elusive. We studied waves in flocks of starlings, a highly gregarious species, by both direct observation and quantitative computer vision analysis of HD video recordings, under predation by peregrine falcons, *Falco peregrinus*. We found that waves originated from the position of the attacking predator and always propagated away from it. We measured their frequency and velocities, the latter often being larger than the velocity of the flock. A high positive correlation was found between the formation of waves and reduced predation success. We suggest that the tendency of a prey to escape, when initiated even by a few individuals in a cohesive group, elicits self-organized density waves. Such evident fluctuations in the local structure of the flocks are efficient in confusing predators.

The formation of waves is a vivid example of self-organized collective behaviour occurring in insect swarms, bird flocks, fish schools and mammalian herds (Krause & Ruxton 2002; Couzin & Krause 2003; Gerlotto et al. 2006; Kastberger et al. 2008). Several authors have described such waves as (1) a collective response possibly facilitating cohesion in the presence of a predator, (2) rapid reorganization of a group upon predator attacks and (3) rapid information transfer within a large group (Radakov 1973; Webb 1980; Treherne & Foster 1981; Gerlotto et al. 2006).

Where a predator approaches a group of prey, those nearest the predator become aware of it first and react, for example by alarm call or acceleration, thereby alerting other members of the group otherwise unaware of the threat. If the rate of transmission of this information is faster than the predator's speed of approach, individuals on the far side of the group will be alerted earlier than if they were alone. In water insects and fish this phenomenon has been labelled the 'Trafalgar effect' because of the signals that were sent between ships to Admiral Nelson before the battle of Trafalgar informing him that the French and Spanish combined fleet was leaving Cadiz, even though it was below the horizon of his flagship, HMS Victory (Caro 2005). Treherne & Foster (1981), who coined this term, showed that marine isopods, *Halobates robustus*, increased velocity in response to a model predator and this change of motion spread across the group faster than the speed of approach of the predator. The same hypothesis has been suggested for flocking birds under predation risk (Heppner 1997; Michaelsen & Byrkjedal 2002; Caro 2005). In particular, in flocking dunlins, *Calidris alpina*, an accelerating wave has been described, reaching a speed three times higher than would be possible if birds were reacting only to the nearest neighbours, in an organization similar to a human chorus line in which individuals observe the approaching wave and time their own performance to coincide with its arrival (Potts 1984).

It could be that waves represent a peculiar form of 'mobbing', which occurs when individuals of certain species mob a predator by

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cooperatively harassing it, in order to scare it (Krause & Ruxton 2002). If this were the case, waves would be expected to move towards the predator. Another hypothesis is that wave activity, by means of a local breaking of the spatial order of the group, can confuse the attacking predator, thereby reducing its chance of success (Treherne & Foster 1981; Buchanan et al. 1988; Kastberger et al. 2008).

Few systematic observations, or quantitative and qualitative descriptions, of waves in bird flocks have been made. It is therefore relevant to carry out detailed characterization studies to understand their mechanism(s) of formation and ultimate functions as well as to provide empirical data for individual-based models of collective behaviours. The European starling is an extremely gregarious bird species that forms flocks of thousands of individuals during autumn and winter (Feare 1984). In starlings, a commonly observed aerial collective behaviour results from waves that can be detected from a great distance. Although this phenomenon has been described anecdotally and is thought to occur in relation to aerial predation by falcons (Tinbergen 1951; Feare 1984), its mechanism and function remain largely unknown. In this study, we quantified the occurrence of propagating waves and their relation to predation.

In the following, we refer to a wave event (WE), which we define as a train of several observable pulses of optical intensity that propagates along a given direction across the flock, not preceded and not followed by any other train for at least 10 s. Our aim in this study was to investigate (1) the circumstances under which a WE occurs; (2) the correlation between waves and the success of the predator; (3) the wave's direction of propagation; (4) the correlation between predator position and origin of the wave; and (5) the frequency and speed of propagation of the waves. We first focus on the whole WE and on its links to predation, and then on the propagation of single pulses.

METHODS

Field Video Recording

Data were collected from flying flocks of European starlings in proximity to two winter urban roosts in Rome, Italy (41°44′N–12°24′E), situated 10 km from each other. Between 14 January 2006 and 17 March 2006 we carried out 53 video-recording sessions, and between 12 December 2006 and 2 March 2007 57 video-recording sessions, in parallel with behavioural observations. One roost is located in the city centre (Termini), it comprises approximately 20 000 birds and has been used for at least 50 years; the other roost is located in the southern part of the city (EUR), with about 60 000 birds roosting daily, and it has been in use for about 20 years.

Flocks were videotaped from a fixed location (roof of a building for roost Termini; open field for roost EUR; the distance from the birds ranged from 200 m to 500–1000 m) with the operators being in place about 90 min before sunset (when the first flocks arrive), until darkness. Opportunistic video recording was carried out with a High Definition video camera (JY-HD10, JVC, 30 fps) on miniDV digital tapes. These video recordings were specifically aimed at the aerial displays of the flocks above the roost before and during landing when a predator was actively hunting, eliciting visible collective responses. Peregrine falcons, *Falco peregrinus*, frequently attack the incoming flocks in both roosts (Carere et al. 2009: Zoratto et al. 2010). During the first winter sessions they were observed in 31 of 53 observation sessions at the roosts, whereas during the second winter sessions they were observed in 50 of 57. In both winters, attacks came from two individuals in Termini and up to five individuals in EUR. We successfully videotaped more than 100 wave events, from which we selected those that matched the requirements for frame processing (see below and the video clips in the Supplementary Material) and that were recorded on days with stable atmospheric conditions, especially wind speed [wind intensity was limited to a range of 0–4 (Beaufort scale)], and with high visibility.

Field Observations

From 12 December 2006 to 2 March 2007 we performed behavioural observations at the roosts for a total of 16 days in Termini and 41 days in EUR. Hunting falcons were observed during 10 days in Termini and 40 days in EUR. On these days we recorded the number of all hunting sequences (HSs) occurring at the roosts, where a single HS is defined as the whole set of manoeuvres adopted by one or more attacking predators against the same flock. A sequence started when at least one falcon approached a flock and stopped when the falcon caught a starling (successful sequence) or when it withdrew from one flock, either disappearing or moving to another flock (unsuccessful sequence). This definition is equivalent to the term 'hunt' used for the first time by Rudebeck (1951) and more recently by Dekker (2003) and to the term 'attack' used by Cresswell (1996). For each HS we also recorded its duration and the number of attacks. Within each HS we recorded the number of WEs; each observed WE (occurring in the presence of the predator in close proximity to the flock) was characterized by the direction of propagation of the wave front with respect to the position of the falcon.

We note that, as mentioned by other authors, any rigid rotation of a flock can result in a fast wave that is just an optical illusion because of a sort of interference resembling 'moiré patterns' (Davis 1980; Heppner 1997). In such a scenario, the WEs that we filmed would be just signals without any information transfer, that is, without biological meaning. Technically, identifying and quantifying such an effect is a very demanding task. Even so, in the WEs that we analysed we can reasonably exclude the presence of similar illusions by direct observations from the field: we firmly believe that such experience leaves no doubt to the density nature of starlings' waves and their causal interaction with the predator.

Statistical Analyses of the Observations

For all the quantitative variables from the field observations we used both parametric and nonparametric tests. For variables with three or more levels, we used analysis of variance (parametric ANOVA) with a completely randomized design (one between-subjects factor) and a Kruskal–Wallis test. For variables with two levels we used Student *t* tests for independent groups (both homogeneous and nonhomogeneous variances) and a Mann–Whitney test. A Levene test for variance homogeneity was conducted in all cases prior to the analysis. For categorical (or categorized) variables we used a chi-square test for variables with three or more levels and a Fisher's exact test for variables with two levels.

Video Processing and Measurements of Frequency and Velocity

Each movie, in mpeg2 format, was converted into frames, JPEG format (1280×720), with the software HiMovie HD (package HiLife, Apple). We computed the frequencies of 21 WEs: these were selected because of their particularly clear optical flow, which allowed us to follow the waves along their propagation. To measure frequency, two of us (A.P. and C.C.) independently counted the waves composing a WE, in a given temporal boundary, in both normal and slow motion. The measurements agreed perfectly between observers (Appendix Table A1).

To retrieve information on velocity, the images were processed with an in-house-built program using LTI libraries (http://ltilib.sourceforge.net/doc/homepage/index.shtml), which transforms