Supplementary Information

Title: Costs and Benefits of Social Relationships in the Collective Motion of Bird Flocks

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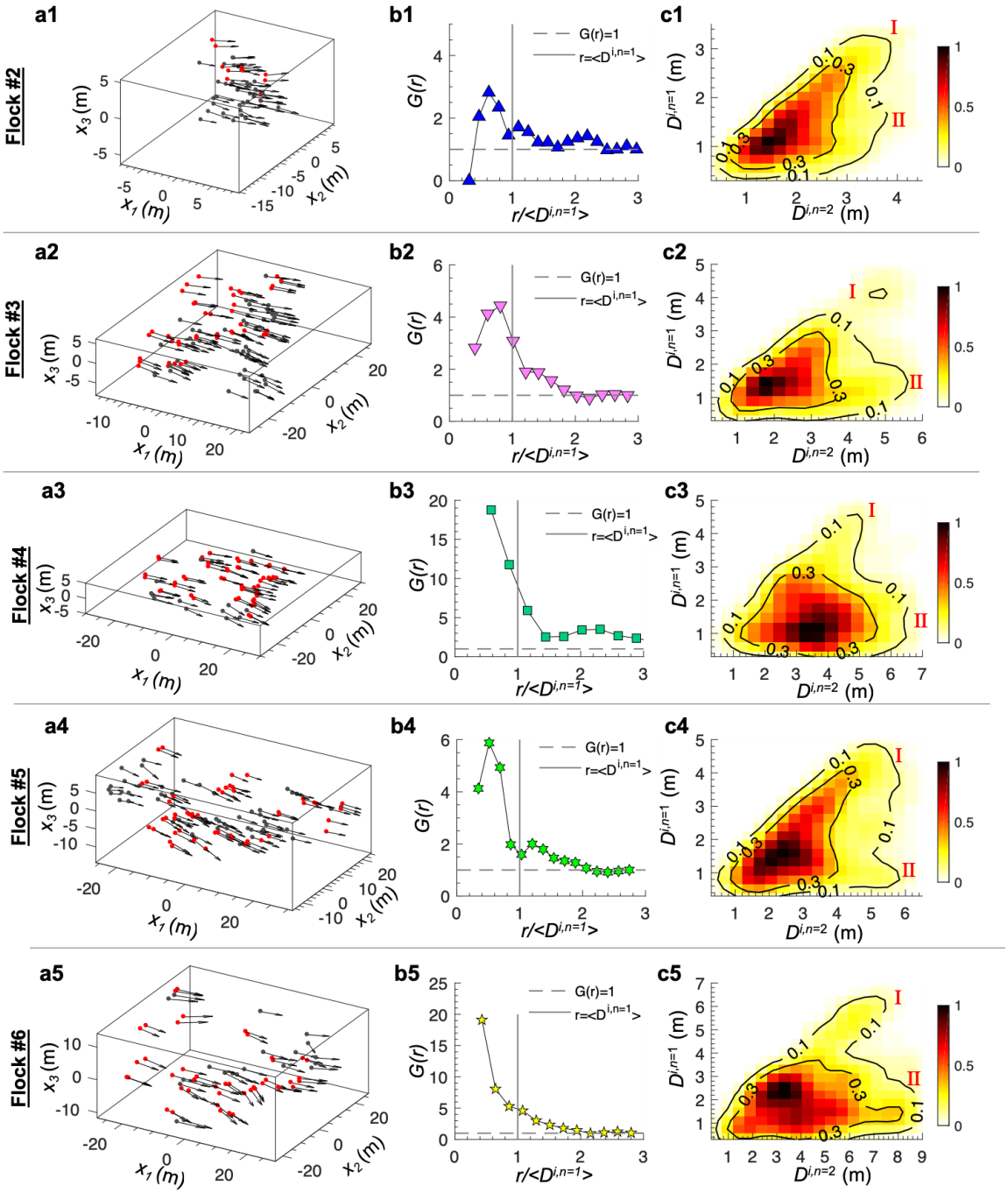
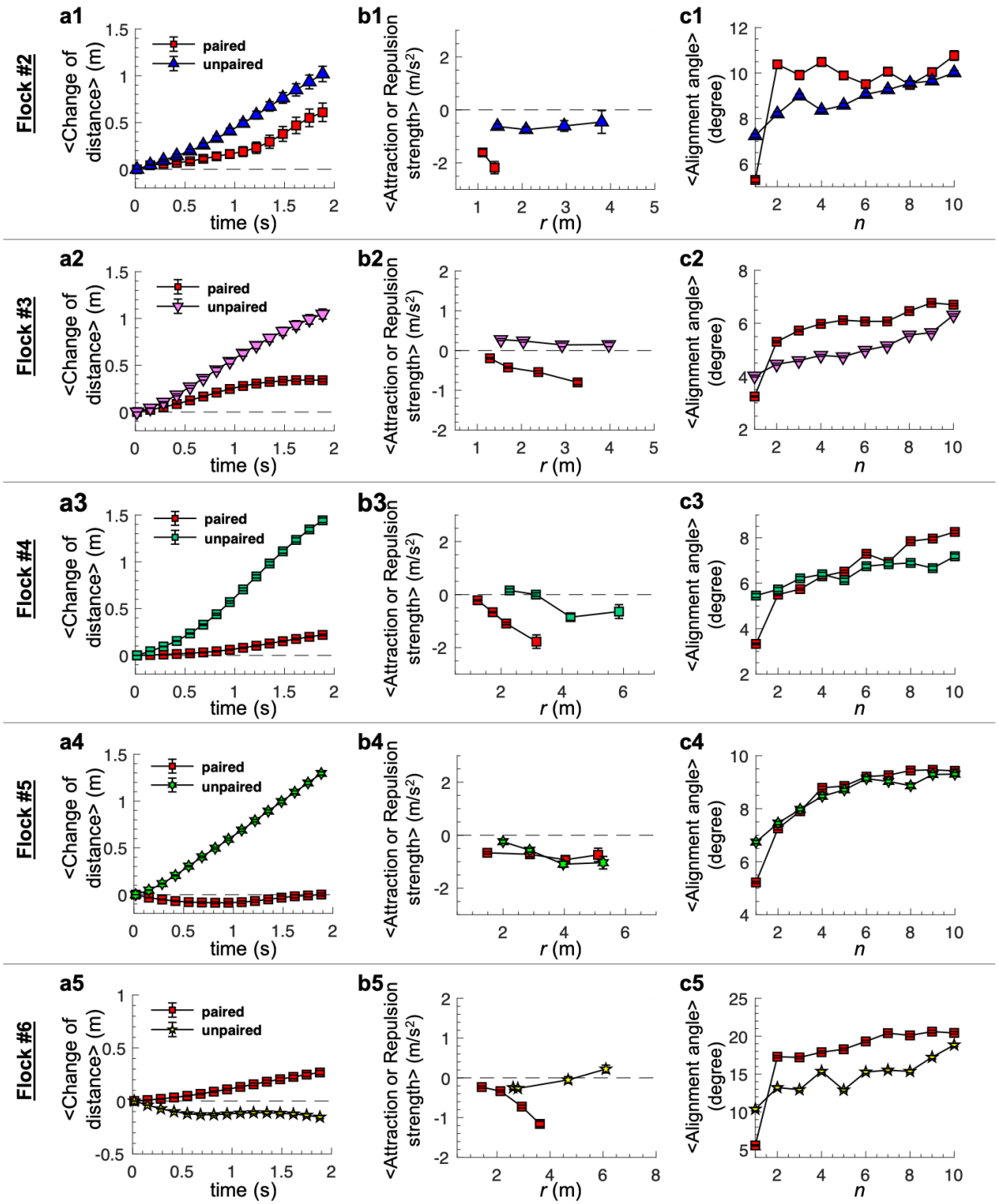
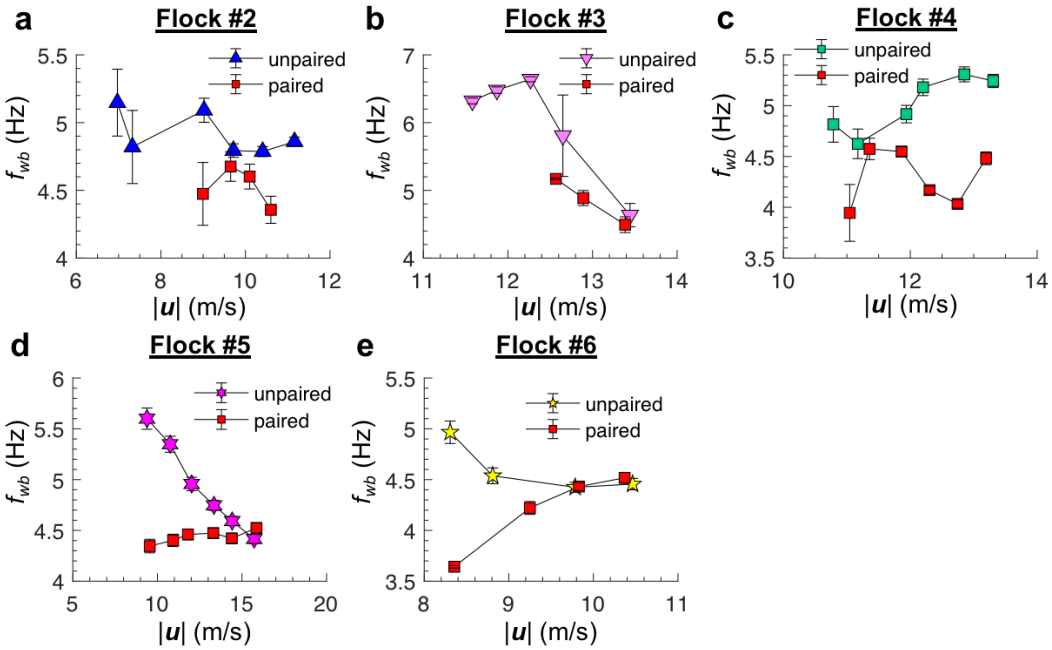


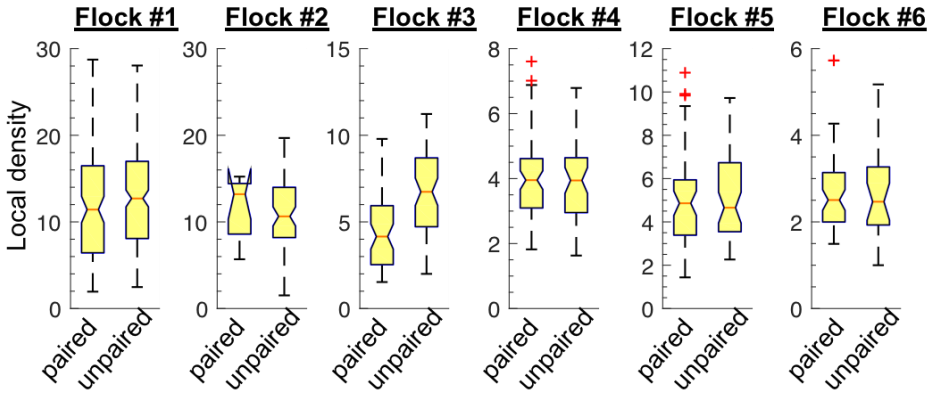
Supplementary Fig. 1 | Flock morphology and evidence of pairing for flocks #2 to #6. a1-a5, Spatial distributions and velocities of birds in three-dimensional space. Paired birds are colored in red. **b1-b5**, Radial distribution functions $G(r)$. **c1-c5,** Joint PDFs of $D^{i,\,n=1}$ and $D^{i,\,n=2}$.



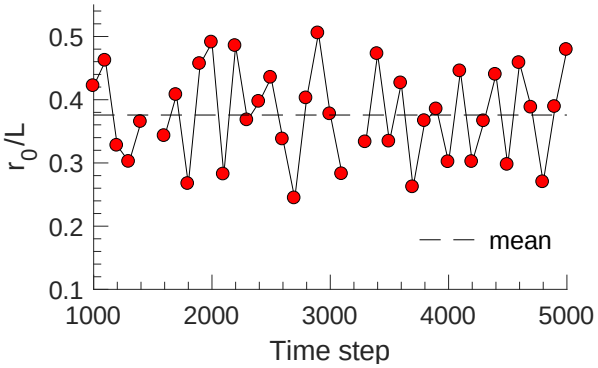
Supplementary Fig. 2 | Pairing causes variations in local interaction for flocks #2 to #6. a1-a5, Change of distance between a bird and its nearest neighbour at time 0. Flock #6 shows a somewhat different trend from the other flocks for unpaired birds, which may be due to the relatively large value of $\langle D^{i,n=2} \rangle$ in this flock. **b1-b5**, Acceleration in the direction away from the nearest neighbour; positive values are repulsive and negative values are attractive. Flock #5 shows a somewhat different trend from the other flocks for paired birds, which may be due to a tendency in this flock for paired birds to be located in front of or in back of each other. **c1-c5**, Alignment angle between a focal bird and its n^{th} neighbour. Error bars show the standard error and are smaller than the symbols in most figures.



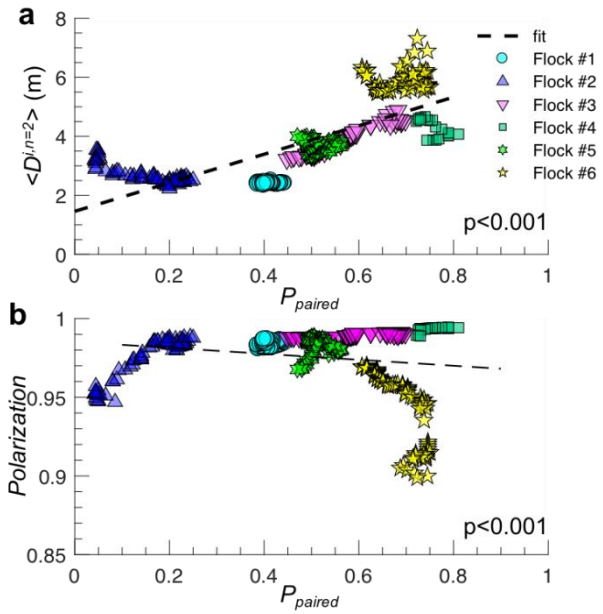
Supplementary Fig. 3 | Wingbeat frequency as a function of flight speed during cruising flight for flocks #2 to #6. Paired birds typically have lower wingbeat frequency than unpaired birds at same flight speed. Error bars show the standard error. The magnitudes of |***u***| represent ground speeds.



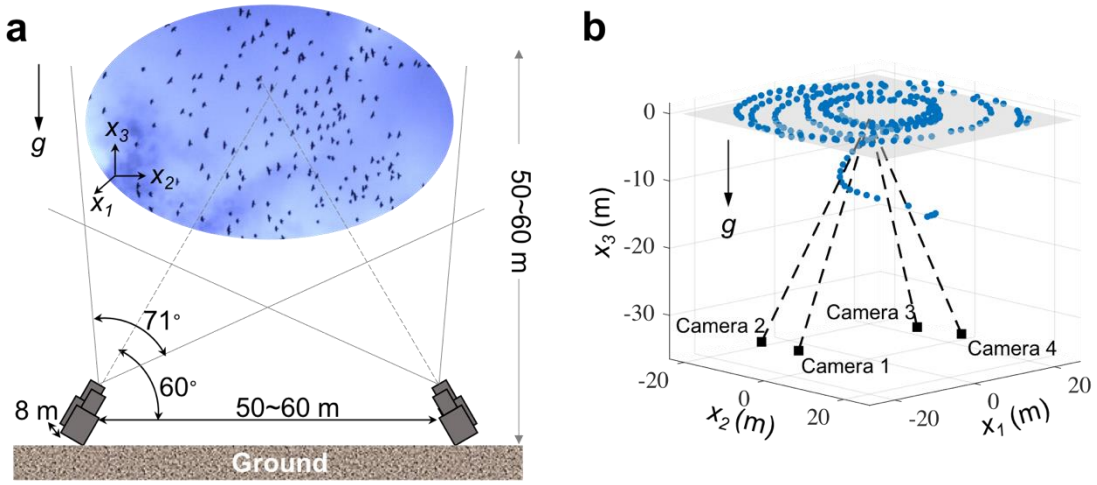
Supplementary Fig. 4 | Local density measured by total number of birds within a distance of 5 m from the focal bird. For different flocks, paired birds can fly either in denser or sparser regions of the groups.



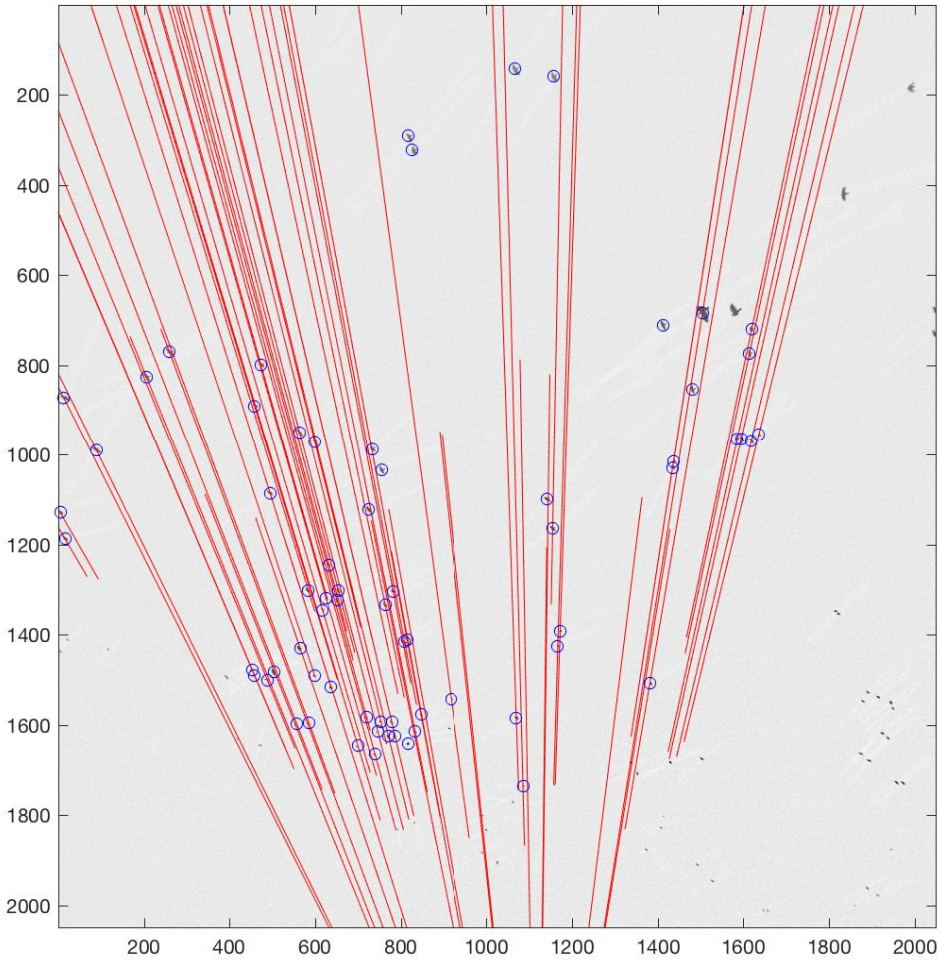
Supplementary Fig. 5 | Variation of r_0/L as a function time step in the numerical models. Each point shows r_0/L calculated from one time frame at that time step. Here, P_{paired}=0.50. The figure shows that even with the same value of P_{paired}, r_0 can vary between different time frames.



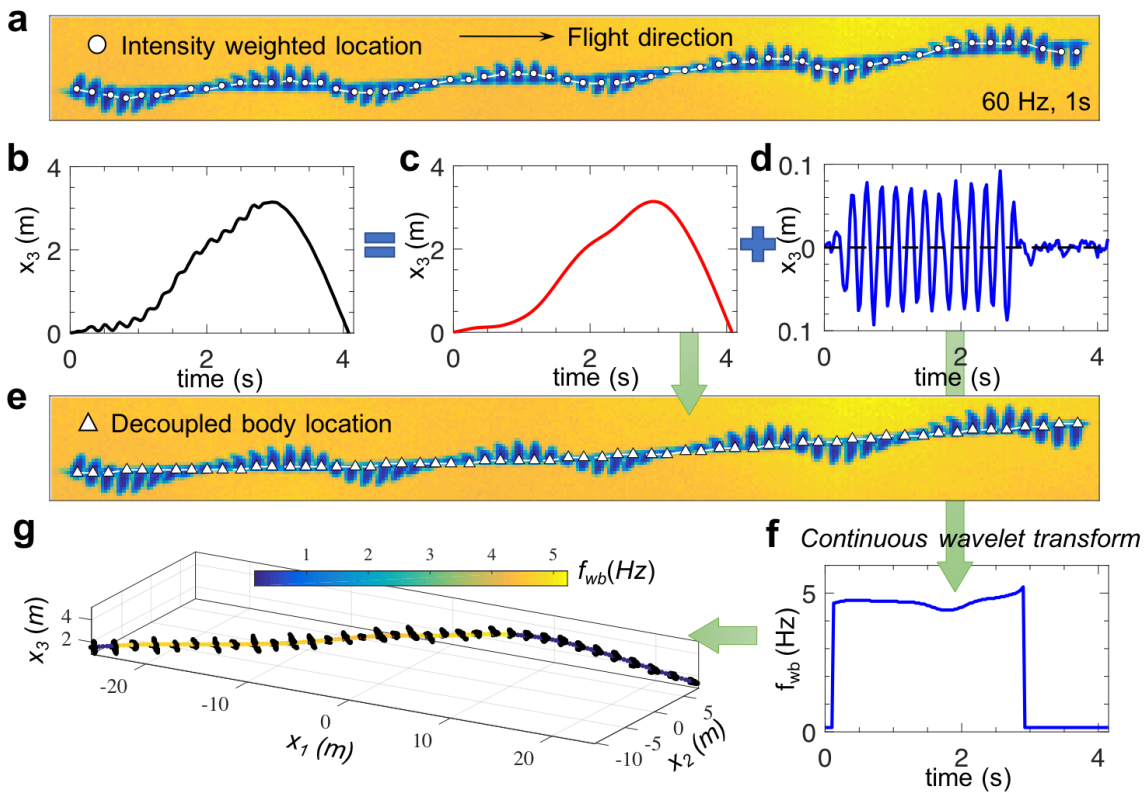
Supplementary Fig. 6 | Pairing reduces group density and polarization. a, Average distance to the second nearest neighbour (a proxy for the inverse of the group density) as a function of P_{paired}. **b**, Group polarization as a function of P_{paired}. Each data point is for one time frame for a given flock.



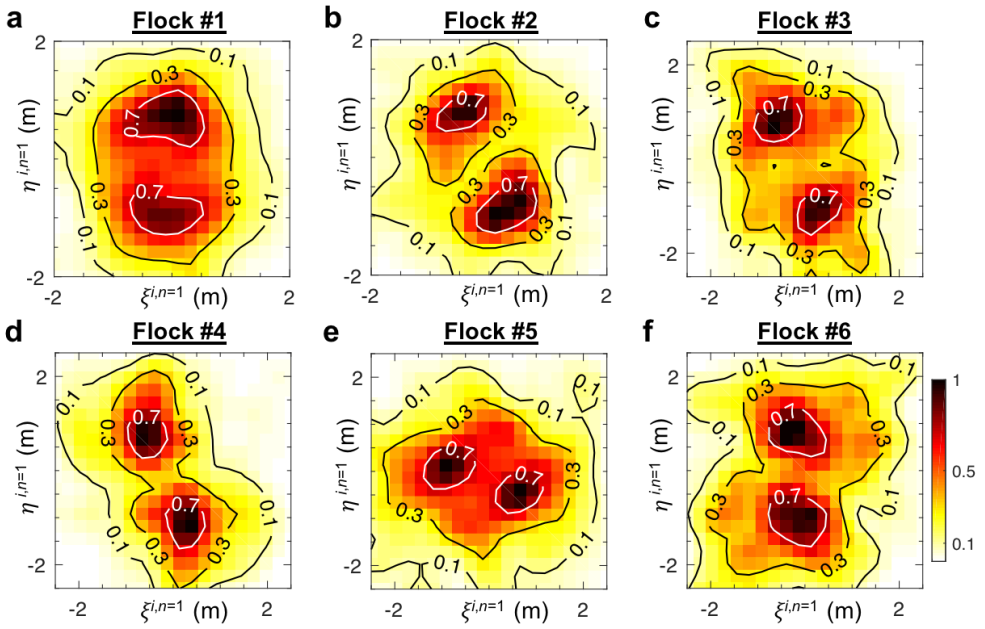
Supplementary Fig. 7 | **Camera setup and calibration. a**, The typical arrangement of the four cameras. **b**, Reconstructed calibration points and camera positions in three-dimensional space.



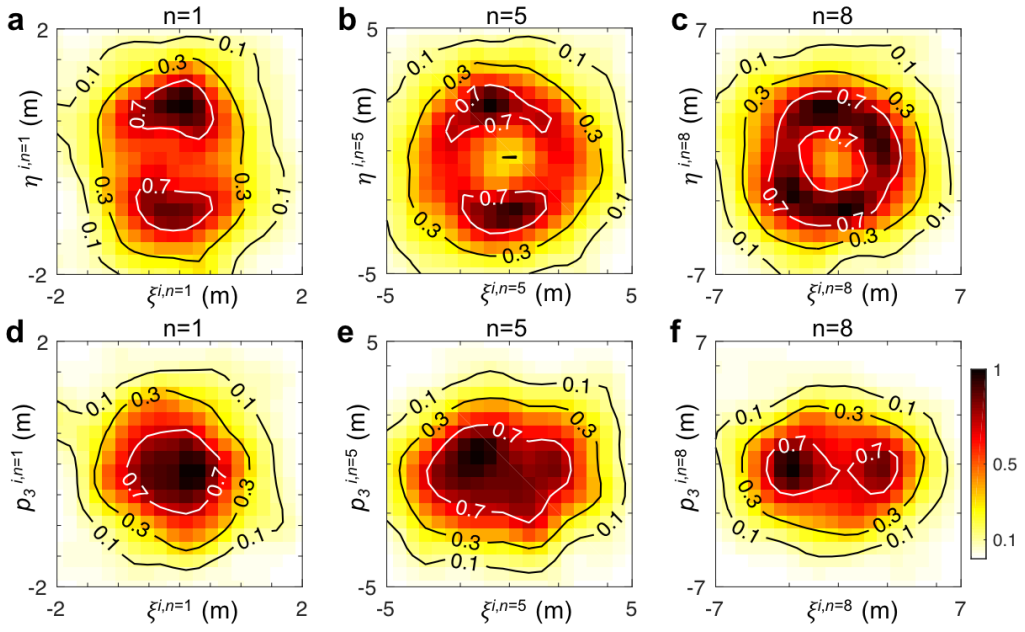
Supplementary Fig. 8 | An image captured by camera 3. Red lines are sample epipolar lines projected on camera 3. Blue circles are reconstructed birds' 3D positions re-projected on the image.



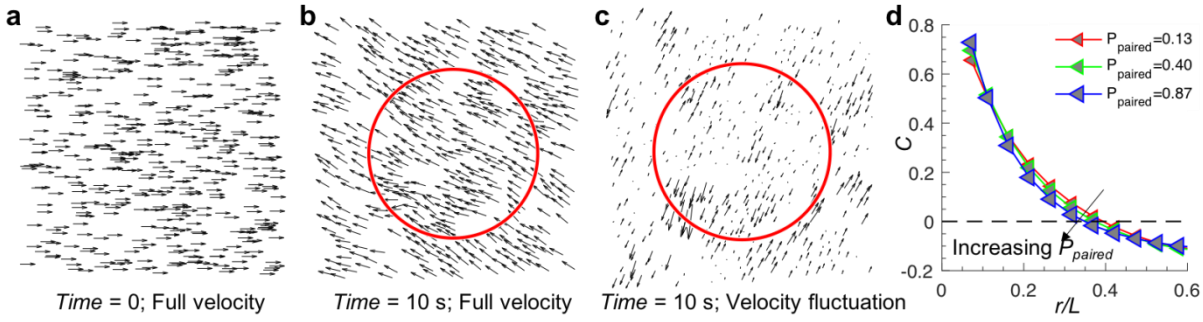
Supplementary Fig. 9 | Measurement of wing motion and wingbeat frequency. a, Time series of bird images on one camera along with the intensity-weighted centres. **b**, The measured trajectory in the gravity direction (x_3) showing the coupled body and wing motion. **c**, The decoupled body motion. **d**, The decoupled wing motion. **e**, The same time series of bird images on one camera along with the 2D positions obtained by re-projecting the measured body motion onto images. **f**, The wingbeat frequency. **g**, A sample 3D trajectory coloured by wingbeat frequency, and overlapped with sample 2D bird images.



Supplementary Fig. 10 | Statistics of the spatial position of the *nearest* neighbour in the horizontal plane (ξ, η) for all six flocks. The focal bird is placed at the origin, and $+\xi$ is the flight direction of the focal bird. In all flocks (except #5), the nearest neighbours were located on the side of the focal bird. The color bar in **f** applies to all panels.



Supplementary Fig. 11 | Statistics of the spatial position of the n^{th} neighbour in flock #1. a-c, Distribution in the horizontal plane (ξ, η). **d-f**, Distribution in the vertical plane (ξ, p_3). The focal bird is placed at the origin, $+\xi$ is the flight direction of the focal bird, and $-p_3$ is the gravity direction. The color bar in **f** applies to all panels.



Supplementary Fig. 12 | Two-dimensional self-propelled particle model. a, Initial positions and velocities of particles. **b**, Positions and velocities of particles after 100 time steps. **c**, Velocity fluctuations of the same particles shown in **b**. Only particles within the plotted circle are used for analysis. **d**, Correlation functions for three values of P_{paired} with each curve obtained by averaging 600 samples.

Supplementary Table 1 | Summary of dataset of six jackdaw flocks.

Flock #	Total number of birds	Total number of paired birds	Average group polarization	$\langle D^{i,n=1} \rangle$ (m)	$\langle D^{i,n=2} \rangle$ (m)	Range of P_{paired}
1	316	108	0.984	1.55	2.40	38 to 42%
2	78	12	0.973	1.77	2.53	5 to 25%
3	117	56	0.989	2.04	3.62	45 to 70%
4	113	68	0.992	1.92	4.41	72 to 81%
5	100	50	0.984	2.31	3.62	47 to 56%
6	81	56	0.946	2.67	5.88	60 to 75%

The average group polarization was calculated by averaging the instantaneous group polarization over an ensemble of different time instants for a given flock. A polarization value of 1 means that all birds are moving in the same direction. $\langle D^{i,n=1} \rangle$ and $\langle D^{i,n=2} \rangle$ denote the average nearest and second nearest neighbor distances. P_{paired} denotes the instantaneous percentage of paired birds in the group at any single time frame. Note that even in a single flock, P_{paired} may appear to vary somewhat over time due to birds leaving or entering the measurement domain.

Supplementary statistical analyses

a) *Wingbeat frequency of birds flying in flocks and in isolation*

Supplementary Table 2 | Mean wingbeat frequency of birds flying in isolation and within flocks.

	N (individuals)	Mean wingbeat frequency ± SE (Hz)
Isolation	64	4.27 ± 0.07
Paired within flock	348	4.49 ± 0.028
Unpaired within flock	457	4.61 ± 0.025

ANOVA analysis showed that grouping type (paired within a flock, unpaired within a flock or flying in isolation) had a significant effect on wingbeat frequency (ANOVA: $F_{2,886} = 14.07$, $r = 0.17$, $p < 0.001$). Bonferroni post-hoc tests confirm that isolated birds had lower wingbeat frequency than both unpaired birds within flocks ($d = 0.64$, $p < 0.001$) and paired birds within flocks ($d = 0.42$, $p = 0.006$). Analyses were conducted in R version 3.4.1.

b) *Wingbeat frequency of paired and unpaired birds within flocks*

We used a Linear Mixed Model (LMM) to examine the factors influencing wingbeat frequency of jackdaws within flocks. Analyses were conducted in R version 3.4.1 using the lme4 package[1], with p-values obtained using the lmerTest package. Full model results are shown in Supplementary Table 3 below.

Supplementary Table 3 | LMM Analysis of factors influencing wingbeat frequency of jackdaws within six different flocks.

Variables		Estimate	S.E.	t-value	p-value
Intercept		4.367	0.144	30.34	<0.001
Pairing:	Paired	0			
	Unpaired	0.105	0.039	2.70	0.01
Density		0.009	0.004	2.30	0.03
Flight Speed		0.006	0.011	0.50	0.62

The response term was the mean wingbeat frequency (Hz) of each individual (N = 805 individuals across six flocks). Pair status (paired or unpaired), mean density (number of birds within 5m of the focal bird) and mean flight speed (m/s) were fitted as explanatory terms, with flock identity (1-6) fitted as a random term to account for repeated measures within flocks. The variance (SD) attributed to the random term flock identity (1 to 6) was 0.003 (0.057).

Reference

1. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67,** 1–48 (2015).