Figures and figure supplements

Compound-V formations in shorebird flocks

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Figure 1. Shorebird flock recording. (a) Multi-camera videography was used to reconstruct 3D trajectories of shorebirds flying near high-tide roosts in Humboldt Bay, California. (b) Overhead and (c) profile views of an example flock. Symbol sizes reflect actual scales for birds with outstretched wings. Flock position data are available in Figure 1—source data 1.
DOI: https://doi.org/10.7554/eLife.45071.003
Figure 2. Within-flock positioning. (a, b) Histograms of nearest-neighbor alignment for birds flying within ±1 wingspan of elevation (godwit flock 0420–1) show a distinctive peak at a trailing distance and lateral distance of approximately one wingspan; focal birds are shown in light gray and nearest neighbors in black. Inset bird silhouettes show profile views of the birds’ relative flight elevations. (c, d) Histograms of nearest-neighbor alignment for birds flying outside ±1 wingspan of elevation for the same flock show a largely random distribution with a modal location of nearly straight above or below the focal bird. Data used for generating this figure are available in Figure 2—source data 1.

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Figure 3. Modal positioning among flocks and species. (a) Summary of modal neighbor position for nearest neighbors within ± 1 wingspan in single-species flocks of all four species, depicted in absolute metric distance and (b) the same data plotted in distances relative to the wingspan of each species. Open symbols indicate modal neighbor positions for individual flocks. Closed symbols and silhouettes show the average position for each species. Data used for generating this figure are available in Figure 3—source data 1.

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**Figure 3—figure supplement 1.** Distribution of nearest neighbors in the horizontal slice (±1 wingspan elevation) from a chimney swift roosting flock (Evangelista et al., 2017). The silhouettes show the position of the focal bird at the origin and the lateral and horizontal position modes. The dashed line box shows the ‘aerodynamic neighbor’ region for comparison with shorebird flocks Figure 3—figure supplement 2. Note that the lateral and horizontal modal positions are calculated separately, and the result is not necessarily congruent with the most populated 2D grid cell. Data used for generating this figure are available in Figure 3—source data 1.

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Figure 3—figure supplement 2. Distribution of nearest neighbors in the horizontal slice (±1 wingspan elevation) from all shorebird flock data described here, regardless of species. The dashed line box shows the ‘aerodynamic neighbor’ region for comparison with shorebird flocks, 29.3% of all nearest neighbors fall within this region. Data used for generating this figure are available in Figure 3—source data 1.
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Figure 4. Positioning in mixed-species flocks. Data from mixed species flocks show that birds adjust their lateral spacing depending on the species (and size) of their nearest leading neighbor. (a) Godwits following conspecifics adopt a larger lateral distance than (b) godwits following the smaller dowitchers. (c) Dowitchers following conspecifics use a shorter lateral distance than (d) dowitchers following the larger godwits. These results support the hypothesis that shorebirds adopt a lateral spacing rule that is dependent on the size of their leading neighbor. Dashed lines are provided to facilitate comparison of modal lateral positions between (a) and (b) and between (c) and (d). Data used to generate this figure are available in Figure 4—source data 1. DOI: https://doi.org/10.7554/eLife.45071.013
Figure 5. Godwit simple-V formation. Incidental to our cluster flock recordings, we also recorded several instances of godwits flying in a simple-V, echelon or line formation, and the largest of these examples is shown here. (a) Overhead view of the flock; average flight direction is along the positive Y axis; blue circles show bird positions and black lines are 2D velocity vectors. All birds are within a ±1 wingspan horizontal slice. (b) The relative location of nearest neighbors; the modal location (red circle) was at a displacement of 0.8 wingspans lateral and 0.5 wingspans trailing distance. Trailing position was more varied than lateral position. Wind speed was low (<2 m s⁻¹) according to weather station data and the wind speed estimated from the ground speed and flight direction of the birds. The data used to generate this figure are available in Figure 3—source data 1.

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Figure 6. Extended flock structure. (a) Polar plot showing mean neighbor angle for right-aligned and left-aligned flocks over a range of distances. Shaded regions show 95% confidence intervals. (b) Overhead and profile views of an example right-aligned flock (avocet flock 1220–2). Note the many echelon formations aligned from back left to front right and the overall shape of the flock. The inset shows scale in wingspans. The data used to generate this figure are available in Figure 6—source data 1.

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Figure 7. Effect of positioning for aerodynamic interaction. Here we show the effect of neighbor position on flight speed. (a) Flight speed residuals after accounting for species, flapping frequency, distance from flock edge, nearest neighbor distance in terms of wingspans and overall position along the length of the flock. (b) Flight speed residuals after accounting for just species and flapping frequency. White spaces in the heat map are bins with fewer than 20 samples, out of 2848 possible in (a) and 3306 possible in (b). Both analyses reveal a broadly similar pattern, where the positive effect of neighbor position on flight speed is strongest at a one wingspan lateral displacement and a trailing distance of 0 to 0.5 wingspans. This pattern cannot be generated by trailing birds passing leaders because the roles reverse after passing occurs, leaving Figure 7 continued on next page
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no net speed difference. The data used to generate this figure are available in Figure 7—source data 1. DOI: https://doi.org/10.7554/eLife.45071.023
Figure 8. Species identification in mixed flocks. (a) Histogram of scaled pixel area of birds within a mixed-species flock. The two peaks are modeled as normal distributions. The area value where the two distributions intersect (indicated by the arrow) is used as the threshold for species identification. (b) Example section of a mixed-species flock with species identifications labeled by color.

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Figure 9. Determining flock edge and maximum radius. An overhead view of an example flock of avocets (flock 1220–2). Because flocks were always spread out in the horizontal direction, a compact hull is fitted to the XY-coordinates to create a boundary. The minimum horizontal distance of each bird to the hull is the bird’s edge distance. The median edge distance is taken as the flock’s maximum radius for computing alignment metrics (Figure 6). Here, birds within the maximum edge distance (6.5 wingspans or 4.55 m) are labeled edge, and birds beyond the maximum edge distance are labeled core.

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