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Quorum decision making coordinates group departure decisions in Eurasian oystercatchers, *Haematopus ostralegus*

Leah Gray [a, b, *], Mike M. Webster [a]

[a] Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, U.K.
[b] School of Biological Sciences, University of Aberdeen, Aberdeen, U.K.

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Prey species that form groups gain a range of benefits from associating with conspecifics, including access to social information. Groups typically coordinate collective movement through local interactions, where individuals copy their nearest neighbours' behaviour to generate group level decisions. However, individuals in a group may not always make 'correct' decisions, and blind copying of behaviour can lead to the spread of poor information and maladaptive cascades. To impede the spread of poor information, many animals that form groups have developed information-dampening mechanisms such as consensus decision making through the quorum response. In this study we monitored flocks of roosting Eurasian oystercatchers with a view to understanding the mechanics of group departure decisions and to test for the presence of a quorum response. Nearing high tide, oystercatchers would leave the roosting site en masse, where the timing of departure of many individuals was coordinated. Coordinating the timing of mass departures was a complex task as single birds and small groups frequently joined and departed from the roosting site, meaning individuals had to decide which departures to copy and which to ignore. Individual oystercatchers were more likely to depart within 10 s of another bird if they were closer together in the group, suggesting that departure information may be transferred locally between neighbouring birds. While single departures were very common, most individuals departed in groups of 10 or more, showing that single departures were a relatively weak departure cue and were frequently ignored by the rest of the group. The probability of an individual joining a departure event was higher with increasing departure group size in a nonlinear (sigmoidal) relationship. This trend is consistent with a quorum response with the propensity to copy the departure of groupmates sharply increasing at a quorum threshold of about 10 birds.

Animals that form groups gain a range of benefits from associating with conspecifics, with one of the key advantages being access to social information (Ward & Webster, 2016, pp. 73–156), that is, information that is gained by interacting with other animals or their products (Heyes, 1994). Social information is used widely across animal species (Ward & Webster, 2016, pp. 73–156), from colonies of ants following conspecific pheromone trails to locate food (Sumpter & Beekman, 2003) to birds analysing the flight characteristics of their groupmates to infer the detection of predators (Beauchamp, 2010; Cresswell et al., 2000; Davis, 1975). Using social information allows animals to learn about both the presence of target resources (food, shelter, mates; Pitcher et al., 1982; Webster & Laland, 2015) and the presence of predators (Lima, 1995) without directly detecting them, allowing individuals to access a broader range of information than any one individual could gain from direct experience. When detecting predators, larger groups have been shown to respond both sooner and at greater distances to approaching predators (Boland, 2003; Lazarus, 1979; Siegfried & Underhill, 1975; Treherne & Foster, 1981; Ward et al., 2011). In larger groups, at any one time there will be more animals scanning for danger; therefore, it is more likely that any one individual will successfully detect an approaching predator ('the-many-eyes-effect'; Lima, 1995). Additionally, by responding to conspecifics as opposed to relying on the direct detection of predators, an individual does not incur the costs of vigilance; for example, a bird in a flock may not have to scan for danger as often as a single bird, and so can forage continuously for longer periods (Lima, 1995). However, despite its

* Corresponding author.
E-mail address: l.gray.22@abdn.ac.uk (L. Gray).

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advantages, social information is typically less reliable than direct personal sampling (Templeton & Giraldeau, 1996). For example, individuals rarely detect predators with 100% accuracy, and false alarms appear surprisingly common in prey animals (Beauchamp, 2010; Cresswell et al., 2000; Gray & Webster, 2023; Haftorn, 2000; Kahlert, 2006; Trail, 1987). In another example, due to the ambiguous quality of social information, European starlings, *Sturnus vulgaris*, only used social information about resource distribution if personal information gathering was difficult or costly (Templeton & Giraldeau, 1996). When copying unverified socially acquired information, animals in a group can become vulnerable to the propagation of poor information.

To gain the benefits of grouping, animals must make decisions collectively to maintain the cohesion of the group. However, regulating these collective decisions becomes difficult when social information is of ambiguous quality. Information typically flows through animal groups in a wave of local communication, where each individual responds to the behaviour of their close neighbours (Fig. 1; Reynolds, 1987; Sumpter, 2005; Ward & Webster, 2016, pp. 73–156). Group behaviour is an emergent property of this system,

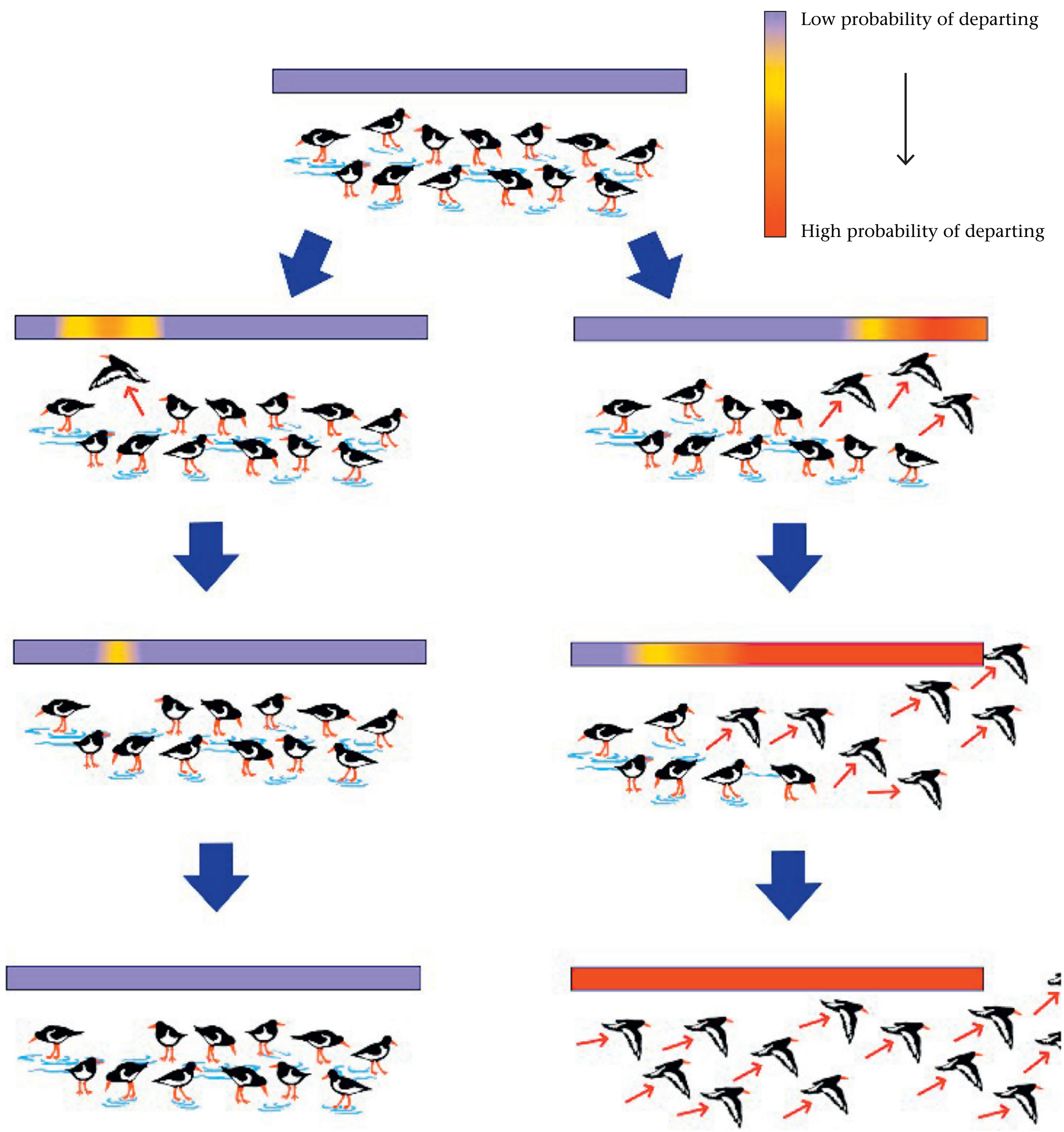

Figure 1. A theoretical cascade of departures in a group of Eurasian oystercatchers displaying local information transfer between neighbouring birds with two different outcomes. In the left-hand scenario a single bird departs, creating a slightly higher likelihood that neighbouring birds will also depart; however, in this case no other birds depart. In the right-hand scenario multiple birds depart creating a stronger cue and a higher likelihood that other birds will depart. This information cascades through the group leading to a full group departure. Here, the strength of the cue is dependent on the number of birds performing the behaviour, displaying a quorum response (Sumpter & Pratt, 2009).

with complex group information processing arising from simple interactions between neighbouring individuals (Reynolds, 1987; Rosenthal et al., 2015). For example, highly complex starling murmurations were found to arise from simple association rules where birds maintained a set distance from their nearest six neighbours while copying their flight direction (Giardina, 2008). In addition to transient decision-making processes such as travel direction, discrete decisions are also generated through local information transfer, for example the decision to remain in an area or to depart as a group. However, as information from individuals in the group can be unreliable, blindly copying neighbouring conspecifics can be maladaptive (Templeton & Giraldeau, 1996). Therefore, many species of group-forming animals have developed information-processing mechanisms which govern when a group should respond to social information from groupmates, and when it should be disregarded. One of the most widespread group processing mechanisms is the quorum response (Sumpter & Pratt, 2009). In a quorum response, the likelihood of copying a conspecific is higher the more individuals are performing the behaviour in a nonlinear function (Fig. 2). When a small number of individuals perform the behaviour, copying is unlikely, and the action is first supressed. This means that false responses from a small number of misinformed individuals are less likely to spread through the group. After a threshold number of individuals perform the behaviour and the information is verified by more conspecifics, the propensity for individuals to copy sharply increases. At this point a quorum is reached and a whole group response is made (Sumpter & Pratt, 2009). In jackdaws, *Corvus monedula*, the decision to leave the roost is decided through a quorum response, where a threshold number of birds must call before the group leaves en masse (Dibnah et al., 2022). Redshanks, *Tringa totanus*, were also found to implement a quorum response by self-verifying predator information from single conspecifics and only copying alarm behaviours if multiple groupmates made escape flights simultaneously (Cresswell et al., 2000).

This study aimed to analyse the dynamics of group departure decisions in Eurasian oystercatchers. The oystercatchers followed a tidal schedule where they began gradually arriving at the roosting site at mid-tide before leaving the site en masse at high tide as the area became gradually covered by the tide. These mass departures appeared to demonstrate an ability to coordinate departure decisions at appropriate times. This study monitored the formation and disbanding of these groups to test for both the presence of local information transfer and evidence for a quorum response in regulating mass departure decisions. Analysis focused on the timing of departure decisions, the flow of departure information, and the processing of departure information by the group, centering around three core questions: (1) does tide height influence departure events, (2) does departure information propagate through local interactions between birds and (3) are departure decisions decided by a quorum response?

METHODS

Study Site and Subjects

Data were collected from groups of wintering Eurasian oystercatchers that were feeding and roosting on the southern banks of the Eden estuary, eastern Scotland (56.358326, −2.826364; Fig. 3). Eden Estuary is a wide, shallow estuary with an average diurnal tide range of 5 m (Maynard et al., 2011). A main channel meanders through the centre of the estuary (approximately 9 km long) and the estuary's widest point is approximately 2 km (Wade, 2018). The Eden estuary is an important wintering site for many species of migratory waterbird and is a designated Site of Special Scientific Interest, Special Protected Area and Special Area of Conservation (Wade, 2018). At various times of year, the site supports large populations of wading bird species including Eurasian curlews, *Numenius arquata*, northern lapwings, *Vanellus vanellus*, grey plovers, *Pluvialis squatarola*, bar-tailed godwits, *Limosa lapponica*, black-tailed godwits, *Limosa limosa*, common redshanks, common shelduck, *Tadorna tadorna*, and ringed plovers, *Charadrius hiaticula* (Frost et al., 2021). In winter, oystercatchers aggregate on coastal estuaries and feed on shellfish and other small marine invertebrates found on the intertidal mudflats. They also exploit soil invertebrates on nearby pastures when the tide is high or when food resources from the estuary are insufficient (Durell et al., 1993; Buchanan et al., 2006). During the observations, at low tide oystercatchers tended to feed close to the water's edge in diverse, mixed-species flocks; however, at mid−high tide they typically came together to roost, forming (primarily) single-species groups close to the estuary's edge.

Oystercatchers at this location are under predatory threat from birds of prey such as Eurasian sparrowhawks, *Accipiter nisus*, and peregrine falcons, *Falco peregrinus*, and land predators such as foxes, *Vulpes vulpes*, and domestic dogs, *Canis lupus familiaris*. However, oystercatchers are relatively less vulnerable to attack

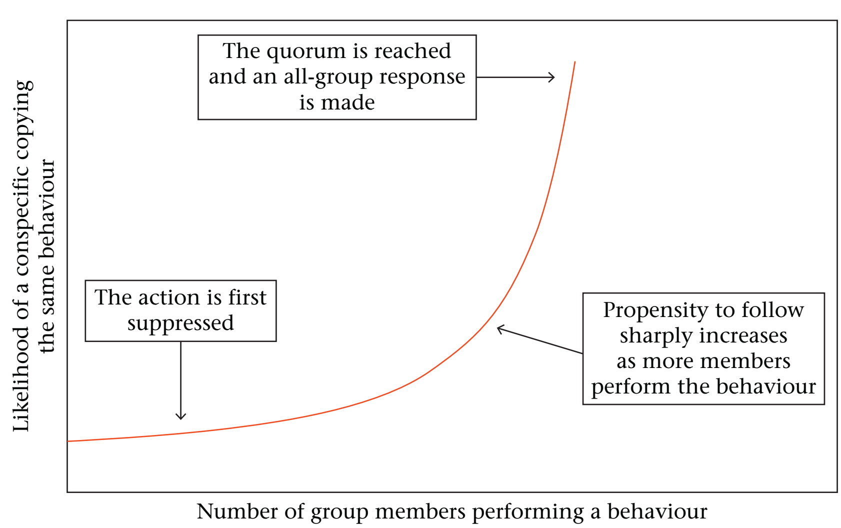

Figure 2. Diagram showing the nonlinear relationship of a quorum response. Adapted from Sumpter and Pratt (2009).

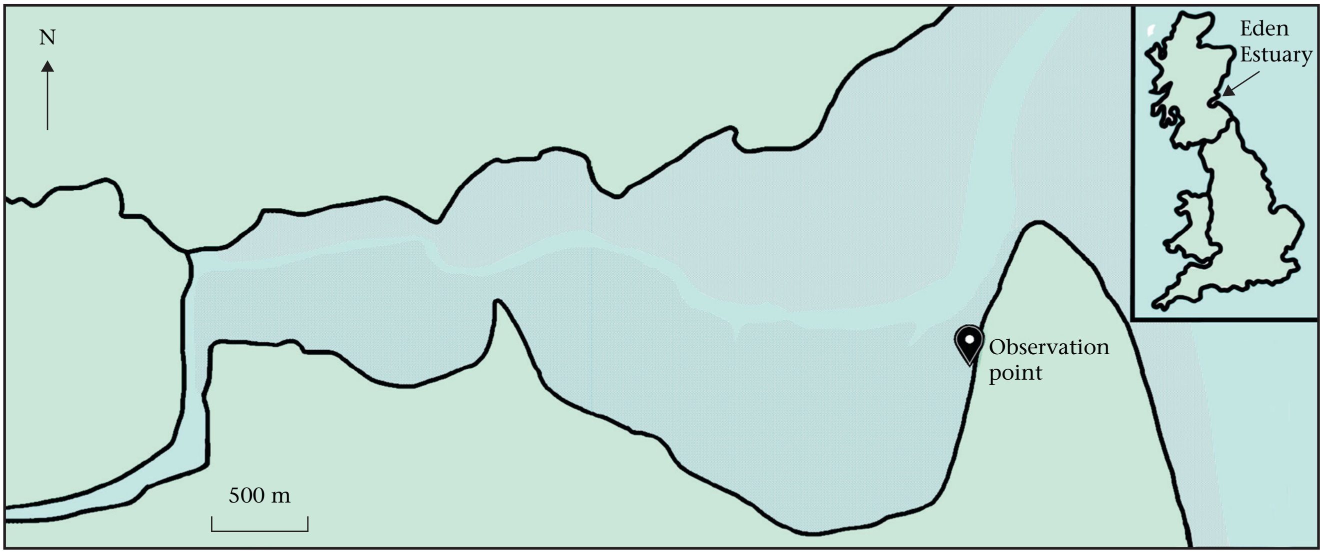

Figure 3. A map of Eden Estuary displaying the location of the observation point. Grey areas show the furthest extent of the mudflats at low tide, blue areas show water and green areas show land. This map was created using data from Open Street Maps (OpenStreetMap, 2021).

compared to other smaller waders on the estuary such as redshanks (Whitfield, 1985), especially by smaller birds of prey. In the colder winter months, when observations were made, thermoregulatory costs account for a large proportion of energy expenditure in wading birds (Kersten & Piersma, 1986; Duriez et al., 2012; Schwemmer et al., 2014). This leads to an increased risk of starvation, which in turn leads to a higher pressure to acquire sufficient food resources (Whitfield, 1985). Therefore, the loss of feeding opportunities caused by alarms and subsequent abandonment of feeding patches are more impactful during the winter months.

Field Methods

A single observer watched quietly at the estuary's edge while recording video of groups of oystercatchers from 50 to 300 m away. Observations were taken from 11 November 2021 until 23 December 2021 in a total of 15 h of footage over 17 different sampling days. Recordings were taken at mid–high tide when single-species groups formed, and the flocks were close enough to the estuary's edge to film. During each sampling occasion, video of a single group of oystercatchers was collected using a digital camcorder (Panasonic HC-V180). The camera was periodically panned and adjusted to follow the group, ensuring all individuals were always in the frame of the video. On each sampling occasion, the group was recorded for 1 h unless the flock departed from the area, the majority of the group moved to an area that was out of view (for example, behind a tall grass verge) or it began to rain. During filming, the observer scanned the estuary from the vantage point (Fig. 1) and noted information about the arrival of predators including the species of the predator, time of arrival, time of departure, the occurrence of attack attempts, the target of any attacks and the outcome of attacks. Audio of bird vocalizations from the group were collected using a condenser microphone (Sennheiser K6-ME6) attached to a parabolic reflector aiming to detect the occurrence of alarm calls. However, during high winds the audio quality was limited, and consistent assessment of call data was not possible. Data on tide levels were obtained from Met Office (2022) predictions for the River Eden mouth entrance.

Video Analysis

The video footage was reviewed and analysed using the BORIS video coder (version 8.0.13; Friard & Gamba, 2016). The video was watched continuously and the timing of every arrival and departure from the group was recorded. An arrival was defined as a bird joining the group by flying or walking from outside the frame of the video and a departure was defined as a bird taking flight and leaving the frame of the video. Counting arrivals as well as departures allowed a very accurate tally of group size to be taken. The relative placement of each departing bird was also recorded by dividing the group into four equally distanced sections, left to right, and assigning each bird to a quadrant (Fig. 4). Groups tended to arrange themselves semilinearly in line with the tide edge, typically being longer in length than width if viewed from above. The density of each zone and the position of each bird fluctuated as birds moved around within the group. Each departure was categorized to the zone the bird was a member of immediately before it departed. Video from 2 days of sampling (four groups) was discarded due to poor image quality.

Limitations

The STRANGE framework (Webster & Rutz, 2020) encourages researchers to declare and discuss potential sources of sampling bias and limits on generalizability in their studies. We observed one population of wild, free-living oystercatchers at one location in this study. The estuary borders a golf course, and resident birds were likely to be frequently exposed to the presence of humans. Observations were taken from the same point overlooking the estuary, meaning that birds that frequented that roosting site were more likely to be sampled, and the same birds may have been observed over multiple days. Observations were also conducted over one field season, meaning that the results could be impacted by factors that were specific to this season, and that could change between years, including weather, density of predators, oystercatcher population, etc. Observations were taken during winter when wading birds expend more energy through temperature regulation and are at a higher risk of starvation. Therefore, maximizing feeding

Figure 4. A screenshot from a video of roosting Eurasian oystercatchers on the mudflats of Eden Estuary, Scotland, displaying the defined group limits and the division of the group into four equal quadrants.

efficiently and minimizing energetic costs is of greater importance compared to warmer seasons, which may have affected the cost of departing compared to summer months.

Statistical Methods

All statistical analyses were completed using R (version 4.0.4; R Core Team, 2021) and aimed to answer three core questions. (1) Does tide height influence departure events, (2) does departure information propagate through local interactions between birds and (3) are departure decisions decided by a quorum response? Each question was assessed using mixed models (standard treatment contrasts; for factor variables, the intercept was set to the first level of that factor).

A departure event was defined as a single or string of departures where birds took flight and departed from the group within 2 s of the previous departing bird. Two seconds between departing birds was a semiarbitrary selection, as a cutoff time for when one departure string began and where one ended had to be set. As this study focused on group departures, a value needed to be selected where the actions of one individual were plausibly influenced by the actions of the previous individual. Two seconds was chosen as a trade-off value that was not too short to allow the birds time to respond and not too long to make the action of one bird likely to be related to that of the previous bird.

Does tide height influence departure decisions?

During the observations we noted that birds commonly departed en masse when the tide was higher, and the mudflats were reduced in space. To test this observation, the number of large departures (departure events involving over 10 departing birds) occurring at different tide points was counted: 3.25–3.49 m, 3.5–3.74 m, 3.75–3.99 m, 4.0–4.24 m, 4.25–4.5 m. Departures of under 10 individuals were not considered in this analysis as we aimed to understand whether large departures were more common later in the tide; therefore, single/small departures were not relevant. Observations were taken during the rising tide, approximately 2 h before high tide, with the lowest tide point during the observations being 3.25 m and the largest being 4.5 m. A Gaussian mixed model was fitted where the tide height was set as a predictor of the number of large departure events. Gaussian models were chosen as they evaluate unbounded, continuous data and compare between categories (tide height categories). Since multiple observations were made on the same groups, to account for potential variation in the behaviour of different flocks and varying flock sizes (smaller flocks will have smaller departure sizes), group ID was added to the model as a random factor:

$$\text{Number of large departure events} \sim \text{tide height} + (1|\text{group})$$

Does departure information propagate through local interactions between birds?

These analyses aimed to determine whether birds were more likely to depart if another nearby bird also departed. For every departing bird, the time between that bird departing, the next bird departing and a further +1 bird departing was calculated (time difference from bird A to B and A to C; B to C and B to D; C to D and C to E, etc.; Fig. 5). The design of these comparisons ensured no two birds were compared more than once. The distance between the zones of each bird was also calculated (e.g. two birds leaving from the same zone would be a distance of zero zones, and a bird leaving from zone 1 and a bird leaving from zone 2 would be a distance of 1 zone). These departure strings were then categorized depending on the timeframe between departures: within 0–10 s, within 10–20 s, within 10–20 s, within 20–30 s, within 30–40 s or within 40–50 s. They were then further categorized depending on the distance between the departing birds: 0 zones, 1 zone, 2 zones or 3 zones. The number of instances where birds departed within each time–distance category was then analysed using a Gaussian mixed model, where the number of instances where a bird also departed was dependent upon the distance from the first departing bird in an interaction with the timeframe. Since multiple observations were made on the same groups, to account for potential variation in the behaviour of different flocks and different environmental conditions across days, group ID was added to the model as a random factor:

$$\text{Number of instances where a bird also departed} \sim \text{distance from the first departing bird} * \text{timeframe} + (1|\text{group})$$

Are departure decisions decided by a quorum response?

For each departure event, the probability of a bird departing from the group was calculated by dividing the number of birds that departed in the event by the total group size. The number of birds in a departure event was then set as a predictor of the probability of a bird departing from the group in a three-parameter Gompertz sigmoidal model:

$$\text{Probability of a bird departing} \sim \text{number of birds in a departure event}$$

Two outliers were removed from the data as both had departure group sizes of over 150 birds. These outliers were removed as they were substantially higher in number than every other observed departure group size, and more data would be required to extend conclusions to departure group sizes of over 150 birds.

Ethical Note

The procedures described here were reviewed and approved by the Animal Welfare and Ethics Committee (AWEC) of the School of

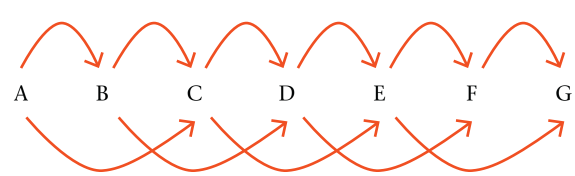

Figure 5. An example sequence of departures where each letter displays a departing bird with A being the first departure and G being the last. The red arrows display the comparisons conducted in analysis (2), showing that each bird is compared to the previous departing bird, plus the second closest (in time) departing bird. The design of these comparisons ensured no two birds were compared more than once.

Biology, University of St Andrews. This study was purely observational and no birds were intentionally disturbed at any point.

RESULTS

The oystercatchers gathered to roost in the study site in small arrival groups (ca. one to five birds) from their feeding grounds. The birds would then begin to depart en masse as the tide cumulatively covered more area of the mudflats (Fig. 6). Group size varied greatly within and between observations, with the lowest starting group size observed at three birds (at the beginning of recruitment to the roosting area) and the highest observed group size being 565. Observations ranged from 15 min to 1 h with the average observation length being 40.8 min.

Over the 17 days of observations, one bird of prey attack was observed from a peregrine falcon; however, it was unsuccessful. During this attack there was a mass hopping behaviour where the majority of the group reoriented and hopped along the ground away from the direction of the diving predator. In addition, one sparrowhawk was seen flying over a group but did not attack, and one domestic dog ran within ca. 10 m of the flock but did not attack. The group made a mass hopping response away from the approaching dog; however, there was no apparent response from the oystercatchers to the presence of the sparrowhawk. No oystercatchers were observed making an escape departure in response to any of these predator encounters. No other predators/apparent fright stimuli were observed outside these instances.

Does Tide Height Influence Departure Decisions?

Larger departure events (involving 10 or more birds) were more common later in the tide with the highest numbers occurring when the tide height was 4.25–4.5 m high (Fig. 7, Table 1). When added as a random factor, group ID accounted for a negligible amount of residual variance in the model (0.0%), demonstrating that tide height was likely to be the most important factor in determining the likelihood of large departures and was likely to be unaffected by general group size.

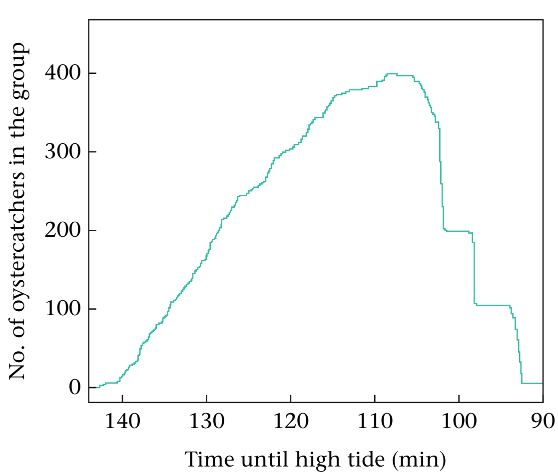

Figure 6. Group size and the time until high tide for one example group of Eurasian oystercatchers to demonstrate the typical forming and disbanding of roosting groups. This group was chosen as the best illustrative example as it demonstrates a full sequence of recruitment to the group and disbanding (starting at zero individuals and ending with zero individuals). Birds would typically join the group in small arrival groups over time (one to five individuals), before departing en masse in large departing groups as shown by the sequential step-downs in the descending line gradient. The data were collected from a single group.

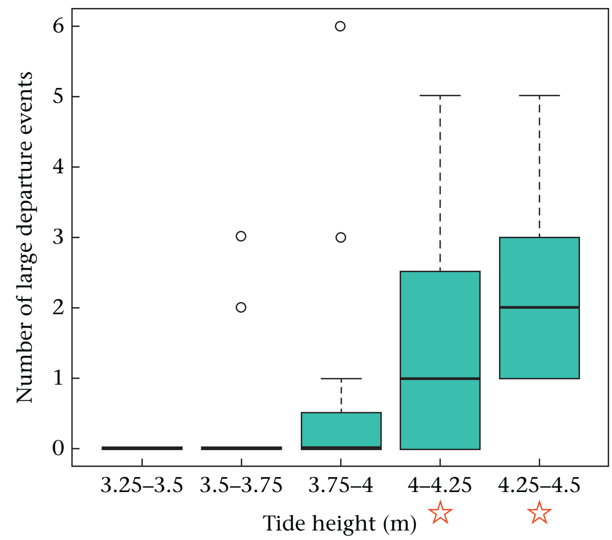

Figure 7. The tide height and the number of departure events involving more than 10 birds. A departure event was categorized by a string of departures where each bird took flight and departed from the group within 2 s of the previous departing bird. The data were collected across 14 sampling days from 18 different groups of wintering oystercatchers and 46 large departures were observed. Red stars signify a significant increase in large departures in a mixed linear model where tide height was set as a predictor of the number of departure events compared to tide height of 3.25–3.5 m. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Does Departure Information Propagate Through Local Interactions Between Birds?

Birds were more likely to depart within 10 s of another departing bird the closer they were to them in the group (Fig. 8, Table 2). Strings of departures where birds took flight within 10 s of each other occurred most commonly between birds in the same zone.

Are Departure Decisions Decided by a Quorum Response?

The large majority of departure events were single departures with 413/601 departures involving only one bird (Fig. 9). Only 46/601 departure events involved over 10 birds.

The probability of a bird joining a departure event was significantly higher the larger the group size of the departing group in a sigmoidal relationship (Fig. 10; b (slope): estimate $= -0.062$, $t = -12.97$, $P < 0.001$; d (upper-limit): estimate $= 0.64$, $t = 21.09$, $P < 0.001$; e (mid-point): estimate $= 22.04$, $t = 14.40$, $P < 0.001$; $df = 590$).

DISCUSSION

This observational study aimed to assess the dynamics of group departure decisions in roosting Eurasian oystercatchers including an analysis of local information transfer between neighbouring birds and consensus decision making through the quorum response. Large departure events (involving over 10 birds) were more common later in the tide, with the highest number of departure events occurring at 4.25–4.5 m. This suggests that most large departure events were a coordinated response to the rising tide and a decrease in available mudflat area. When departing, birds were more likely to depart from the group within 10 s of another departing bird if they were closer to them in the group. This may suggest departure information is transferred between

Table 1
The model output of a linear mixed-effect model where the tide height was set as a predictor of the number of large departure events (involving over 10 birds)

Fixed effect	Estimate (no. of large departure events)	95% confidence intervals (lower–upper)	SE	*t*	*P*
3.25–3.49 m (intercept)	0.00	−0.62 0.62	0.33	0	1.00
3.5–3.74 m	0.33	−0.55 1.22	0.46	0.72	0.47
3.75–3.99 m	0.73	−0.15 1.61	0.46	1.59	0.12
4.0–4.24 m	1.42	0.48 2.35	0.49	2.89	**0.005**
4.25–4.5 m	2.28	1.18 3.39	0.58	3.94	**<0.001**

Data were collected from groups of Eurasian oystercatchers. The model included a random effect for group ID. Bold lettering indicates a significant impact of the fixed effect. Group ID, included as a random effect, accounted for 0.0% of variance.

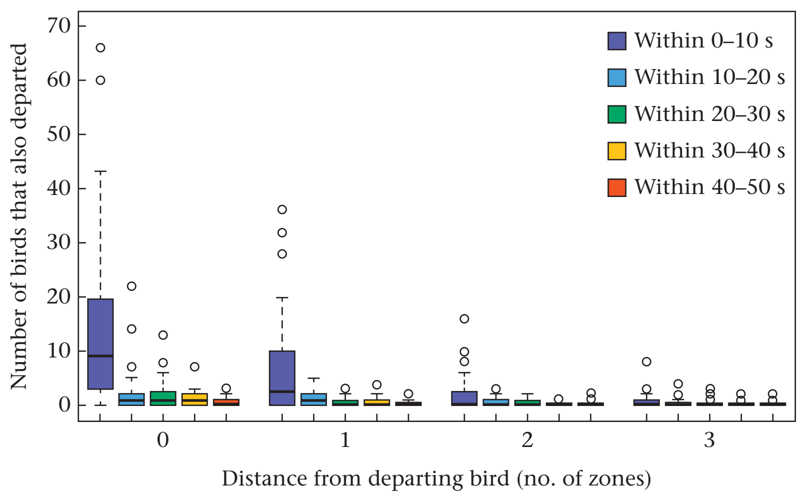

Figure 8. The number of instances where a Eurasian oystercatcher departed from the group within different timeframes of the previous departing bird, and +1 previous departing bird, and the distance between those birds. The group of roosting oystercatchers was divided horizontally into four equal zones and distance was measured as the number of zones away. The data were collected from 18 different groups of wintering oystercatchers and 601 departures were observed. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 2
The model output of a linear mixed-effect model which tested the number of instances where a bird departed within different timeframes and distances of another bird

Fixed effect	Estimate (no. of instances where a bird also departed)	95% confidence intervals (lower–upper)	SE	*t*	*P*
Within 0–10 s	12.84	11.46 14.22	0.71	18.19	**<0.001**
Within 10–20 s	−10.75	−12.42 −9.10	0.85	−12.61	**<0.001**
Within 20–30 s	−11.32	−12.99 −9.08	0.85	−13.28	**<0.001**
Within 30–40 s	−11.87	−13.53 −10.20	0.85	−13.91	**<0.001**
Within 40–50 s	−12.47	−14.15 −10.82	0.85	−14.54	**<0.001**
Distance	−4.59	−5.22 −3.96	0.32	−14.24	**<0.001**
Distance * 10–20 s	3.96	3.07 4.84	0.46	8.68	**<0.001**
Distance * 20–30 s	4.08	3.20 4.98	0.46	8.97	**<0.001**
Distance * 30–40 s	4.29	3.40 5.18	0.46	9.40	**<0.001**
Distance * 40–50 s	4.51	3.62 5.40	0.46	9.90	**<0.001**

Data were collected from groups of Eurasian oystercatchers. The model included a random effect for group ID. Bold lettering indicates a significant impact of the fixed effect. Group ID, included as a random effect, accounted for 11.5% of variance.

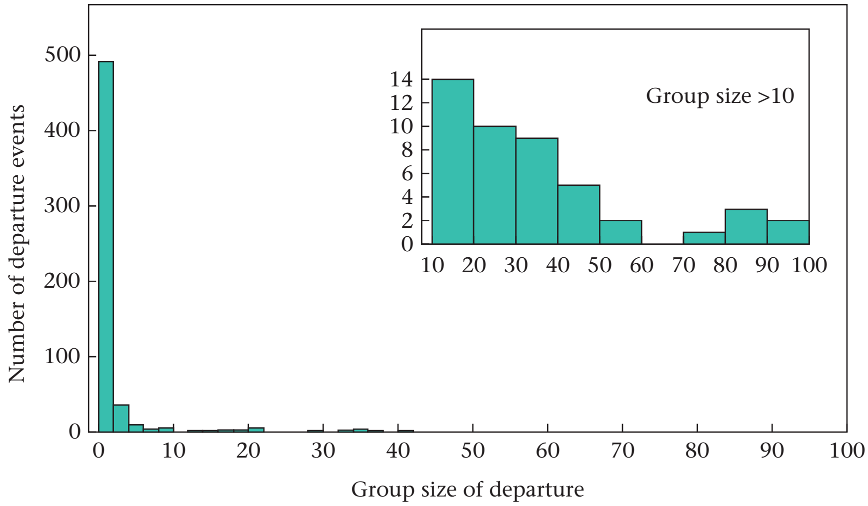

Figure 9. A histogram displaying the frequency of different group sizes of departure events in groups of Eurasian oystercatchers. A departure event was categorized as a string of departures where birds take flight and depart from the group within 2 s of the previous departing bird. The data were collected from 18 different groups of wintering oystercatchers and 601 departures were observed. The inset shows the same data where group size is constrained to departure events with greater than 10 birds ($N = 14$ groups and 46 departure events).

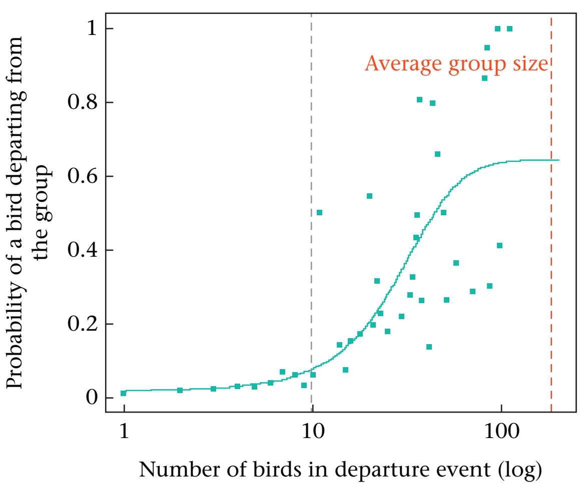

Figure 10. The number of birds in a departure event and the probability of a bird departing from the group in groups of Eurasian oystercatchers. A departure event was defined as a single or string of departures where birds take flight and depart from the group within 2 s of the previous departing bird. The data were collected across 14 sampling days from 18 different groups of wintering oystercatchers and 601 departures were observed. The solid blue trendline displays a significant three-parameter Gompertz sigmoidal model. The dashed grey line shows the threshold where the trend begins to increase. The dashed red line is the average size of the group during each departure event. The probability of a bird departing the group was calculated by dividing the size of the departing group by the total group size.

birds locally, where the departure of a groupmate sets off a chain reaction of departures locally within the group (Fig. 1). However, since the tide is more likely to reach birds that are in proximity more closely in time, there is a possibility these results could arise by multiple birds reacting to the tide, as opposed to each other. The flocks typically arranged themselves approximately parallel to the tide (longer in width than depth if viewed from above); therefore, birds across zones would be similarly close to the water's edge. In this case, it would be expected that many birds would leave at once and that these departures would be spread across the zones, not concentrated within them. Additionally, there were many instances where a bird on the shore departed concurrently with a bird standing in the water. These observations are most consistent with local information transfer between neighbouring birds. The large majority of departure events involved just a single individual. Since single departures were very common, and birds did not respond to most single departures, this demonstrates that single conspecific departures were a weak departure cue for other groupmates and typically did not trigger additional departures. The probability of a bird departing from the group increased with the number of birds also departing in a sigmoidal relationship, with the probability of departure sharply increasing at ca. 10 birds. This relationship is consistent with the presence of a quorum response.

The more oystercatchers that departed from the group, the more likely other conspecifics would join the departure event. This relationship was nonlinear, sharing close resemblance to quorum systems where group decisions are made through consensus between group members (Sumpter & Pratt, 2009). In a quorum response, the likelihood of a conspecific copying a behaviour is higher the more group members there are performing that behaviour in a nonlinear relationship. When there are a small number of group members performing a behaviour, the action is first supressed and groupmates are unlikely to copy the behaviour. This is exemplified in the oystercatchers, as single departures from the group were common but not often copied or transferred through the group. As the number of group members performing the behaviour increases, the propensity for conspecifics to copy increases, and after a certain threshold, the likelihood of copying a response rises sharply, with a quorum being reached and a majority group decision being made. This theoretical threshold value in the oystercatchers would be ca. 10 individuals, where the sigmoidal model rises sharply (Fig. 10). The observed relationship in oystercatchers is consistent with the presence of a quorum-based decision mechanism regulating group departure decisions. There is always an expected positive relationship between departure group size and the likelihood of a bird being part of that departure (since the factors are linked); however, the exact shape of the sigmoidal curve observed in the oystercatchers does not fit what would be expected if no quorum response was present. If oystercatchers did not follow a quorum response, the likelihood of departing would be expected to increase linearly until the average group size, before levelling off at the maximum observed group size. As seen in Fig. 10, the sharp rise in the likelihood of copying a departure was at ca. 10 birds, whereas the average group size was 148 birds. With the threshold of joining a departure event occurring far before the average group size, these results are more consistent with the presence of a quorum response.

Following a quorum response allows groups to coordinate decisions through consensus while dampening the influence of a small number of potentially misinformed individuals. In oystercatchers, this could allow the group to coordinate mass departures from an area at appropriate times, saving energy by minimizing unnecessary departure events. Quorum responses are a common mechanism for regulating departure decisions across the animal kingdom, for example, collective antipredator movement in three-spined sticklebacks, *Gasterosteus aculeatus*, was found to be regulated by a quorum response (Ward et al., 2008). Ward et al. (2008) argued that consensus decision making reduced the transfer and amplification of false antipredator behaviour, with larger groups ignoring incorrect responses produced by a single replica conspecific. Similarly to oystercatchers, groups of jackdaws, *C. monedula*, were found to regulate mass departures from their roosts using a quorum response (Dibnah et al., 2022).

Conclusion

Our results suggest that in flocks of oystercatchers, departure information is transferred locally between close neighbours. However, the threshold for responding to conspecific departure cues appears relatively high. Across the observations, most departure events involved just one bird; however, single departures were typically ignored by the group and most individual birds departed as a member of a larger group (over 10 birds). The majority of larger departure events occurred later in the tide (4.25–4.5 m) when rising water began to reduce the available area on the mudflats, suggesting most large departures appeared to be a coordinated group response to the rising tide. The probability of an individual joining a departure event was greater the larger the group size of the departure event in a nonlinear (sigmoidal) relationship. This trend is consistent with a quorum response with the propensity to copy the departure of conspecifics sharply increasing at a quorum threshold of ca. 10 birds. The implementation of a quorum response could allow oystercatchers to dampen the spread of departure information and to coordinate the initiation of mass departures at appropriate times, saving energy by minimizing unnecessary departure events.

Author Contributions

Leah Gray: Conceptualization, Methodology, Formal analysis, Investigation, Writing–Original Draft, Writing–Review & Editing, Visualization. **Mike Webster:** Conceptualization, Methodology, Validation, Writing–Review & Editing, Supervision.

Data Availability

Data and code are available in the Supplementary material.

Declaration of Interest

None.

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Supplementary Material

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