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Consensus movements by groups of sperm whales

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Abstract

When animals live in cohesive groups they need to make consensus decisions about movements. As a very large-scale example of communal movement, nomadic female sperm whales (*Physeter macrocephalus*) travel about 50 km per day as coherent groups of 10–50 animals spread over several km of ocean. From 543 h of data during which 3,873 headings of small clusters of whales or individual whales were recorded, I quantified the heading behavior of groups foraging off the Galápagos Islands. The groups made both sudden and gradual turns. Using piecewise regression models, I estimate that sudden and gradual turns in heading both occurred at rates of 0.10/h. The mean change in heading was 69° for sudden turns and 84° for gradual turns. The mean duration of gradual turns was 1.3 h, so turns were often slow. Using the recorded headings within 30 min of each of 1,798 focal headings, a regression of heading on time gave a mean rate of turn of the group and error of each focal heading about the mean heading. Absolute heading errors increased with absolute turn rate ($r_S = 0.241$; $P = 0.0000$), so turns were often messy. Thus sperm whales often make slow and messy—likely democratic—consensus decisions when groups change heading.

Key words: consensus decisions, democratic decisions, heading changes, movement, *Physeter*, sperm whale, turns.

Group living has many potential benefits (Krause and Ruxton 2002), but to live effectively in a group, an individual needs to calibrate its behavior in relation to its group mates. In particular, when animals live in behaviorally cohesive groups, they will need to make consensus decisions about behavior, especially movements, because without consensus about movement the group breaks apart (Conradt and Roper 2010). Consensus decisions can be autocratic in which just one or a small minority of animals dictate the behavior of the group (*e.g.*, Brent *et al.* 2015), or democratic when decision making is shared more broadly (*e.g.*, Strandburg-Peshkin *et al.* 2015). Unless knowledge is highly biased towards one or a few leading individuals, democratic decision making is theoretically more accurate (Conradt and Roper 2003). But democracy has costs (Conradt and Roper 2005), tending to be “slow and messy” (Doherty and Carroll 2002).

I look at a particularly large-scale instance of consensus decision making in animals. Female and immature sperm whales (*Physeter macrocephalus*) travel as coherent groups of 10–50, with group members spread over several kilometers, displacing an average of about 50 km per 24 h day (Whitehead 2003, Whitehead *et al.* 2008).

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Their tracks vary in shape (*e.g.,* Fig. 1), generally being straighter in poor feeding conditions and more tortuous when food is plentiful (Whitehead 2003). To perform these group movements through a boundary-free ocean, the members of each group must make consensus decisions (Conradt and Roper 2005): when to turn, how much to turn? Except when socializing, speeds are fairly constant (Whitehead 2003), so decisions about speed of movement are likely less important. How do groups of sperm whales change direction?

The groups of female and immature sperm whales are partially matrilineal in that a female is likely to be in the same group as her mother while they are both alive, but in the eastern Pacific groups typically contain several matrilines (Whitehead 2003). In some matrilineal societies, such as African elephants (*Loxodonta africana*) and "southern resident" killer whales (*Orcinus orca*), older females have a large role in consensus decisions (McComb *et al.* 2011, Brent *et al.* 2015). So these societies fit the connotation of "matriarchal." In contrast, in groups of olive baboons (*Papio anubis*), which also have a matrilineally based social structure, decisions about movements are widely shared (Strandburg-Peshkin *et al.* 2015).

Here I use heading data (records of the compass heading of whales observed at the surface) to describe the group movements of the sperm whales, and in particular how they turn. I look for two characteristics of democratic decisions: slowness and messiness. I predict that if changes in group heading are democratic, then the changes will be gradual rather than sudden, and that individual variation about the group mean heading will increase during turns. I also tried to investigate whether there are

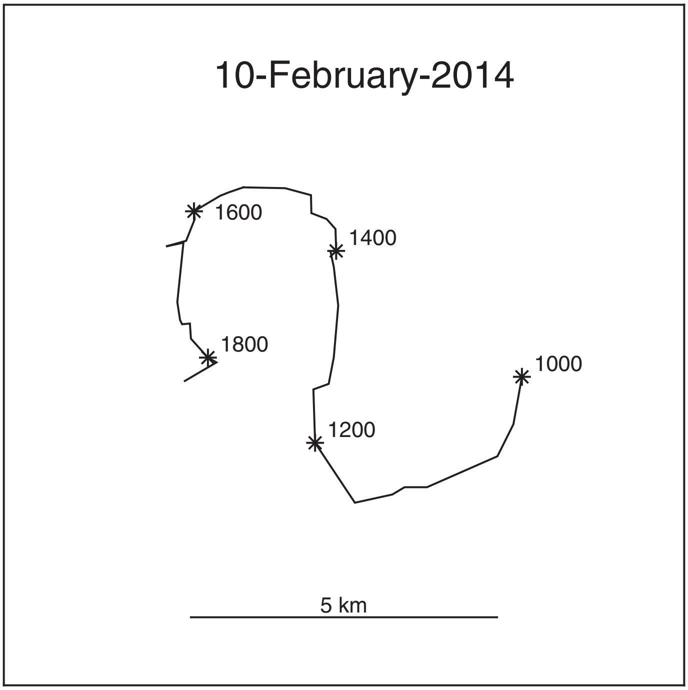

Figure 1. Track of research vessel when following a group of foraging sperm whales off the Galápagos Islands, 10 February 2014.

particular individuals who initiate changes in group heading, or whether group turn characteristics differ between sympatric cultural clans of sperm whales (Rendell and Whitehead 2003), but the power of the data was limited for these objectives.

METHODS

Sperm Whale Movements

This subsection describes elements of the biology and behavior of sperm whales (from Whitehead 2003), setting the background for the study.

The analysis refers to groups of female and immature sperm whales. Mature and maturing males accompany these groups for periods of hours or less, but are more normally solitary or form small "bachelor" groups apart from the females. I do not use data on mature and maturing males, either when they are alone or accompanying the females.

The females and immatures form groups of about 10–50 animals, which are comprised of one or more stable, matrilineally based, social units, each containing about 11 animals. A group typically retains its membership of social units, and thus individuals, for periods of one to several days. The whales spend approximately 75% of their time foraging. While foraging, each adult makes dives lasting about 40 min, with dives separated by periods of about 8 min breathing at the surface. While at the surface between dives, the whales typically form clusters of one to about three individuals, a few meters apart and heading the same direction. Although the members of a group may be spread over a few kilometers of ocean, they move in a cohesive fashion at roughly 3.5 km/h when foraging (Fig. 1).

About 25% of the time the whales socialize, staying at or near the surface, and typically forming larger, more slow-moving, clusters. I do not use data on socializing whales in this analysis.

Field Methods

Data came from studies of sperm whales off the Galápagos Islands in 1985, 1987, 2013, and 2014. Sperm whale groups move into and out of the study area from a much larger region containing many thousand animals, of which we have photo-identified about 4,000 (Whitehead *et al.* 2008). Groups of whales were tracked acoustically and visually for periods of 6 h to 13 d from a 10 m auxiliary sloop (1985 and 1987) or 12 m auxiliary cutter (2013 and 2014) (Whitehead and Gordon 1986). Whales were individually identified by natural markings on their flukes (tails) through photographs taken at the start of their dives (Arnbom 1987) using Canon SLR cameras with 300 mm lenses (Ilford HP5 black and white film in 1985 and 1987; digital color in 2013 and 2014).

In 1985 and 1987, scan samples were recorded every 5 min during daylight (approximately 0600–1800 local time; UTC -6) (Whitehead and Weilgart 1991). For these scan samples, we recorded data on each visible cluster of whales including the composition (number of mature males, calves and other individuals, mostly adult females) of the cluster and the heading of the cluster (in degrees magnetic from compasses) when this could be determined with reasonable accuracy (limits ±~15°). The scan sample data were used to allocate the hours spent studying sperm whale groups into hours when the whales were foraging or socializing (Whitehead and Weilgart

1991). The location of the research vessel, and thus approximate location of the group of whales, was determined approximately every 90 min using a Tracor Transtar satellite navigator (±~500 m).

In 2013 and 2014, cluster heading was recorded with each photo-identification photograph taken during dives, when this could be determined with reasonable accuracy (limits ±~15°). Following the results from the earlier scan sample analysis, hours spent tracking sperm whales were allocated to either "socializing" (clearly socializing), "foraging" (clearly foraging), "foraging/socializing" (some elements of both behavioral states), or unknown, in real time at sea. The location of the research vessel, and thus approximate location of the cluster of whales, was recorded continuously using a Garmin GPS system (±~10 m).

Analytical Methods

For each day with recorded headings I isolated movement segments that satisfied three conditions. First, the whales were observed foraging for at least two consecutive hours. For the 1985 and 1987 data, I distinguished foraging for each daylight hour using the metric of Whitehead and Weilgart (1991): "*Sociality* (visual) <0.5." *Sociality* (visual) is a metric derived using multivariate analysis of several measures, such as group size and speed of movement, with high values indicating socializing whales, and low values foraging whales. For the 2013 and 2014 data, I analyzed segments with hours recorded as either "foraging" or "foraging/socializing." Second, at least one individual animal was photo-identified earlier on that day, as well as later. Thus essentially I removed the infrequent situations when we inadvertently switched the group being tracked during the day. Third, I did not include the very infrequent occasions when turns were precipitated by the whales heading into waters <1,000 m deep that are not usually sperm whale habitat (Whitehead 2003).

For each of these segments I made a plot of the recorded headings of the observed clusters against time of day (*e.g.,* Fig. 2). Then, in order to describe quantitatively the movements of the whales, I fit two types of regression line to the data. The first modeled the headings of the group through time, and the second focused on characteristics of individual cluster headings. In both types of regression, I used the chordal distance measure of the difference between two angles: $2 \cdot \sin(|O - E|/2)$, where, for instance, O and E are the observed and expected (from a model) values of each heading angle, respectively. This gives a measure of the distance apart after one time unit of two animals starting together and moving at the same speed but with headings of O and E, respectively.

Tracks of the research vessel while following the groups (*e.g.*, Fig. 1) as well as plots of recorded heading against time (*e.g.*, Fig. 2) show periods when the grouped whales maintained a mean heading for hours, sudden changes of group heading, and gradual changes in group heading, but with variation in recorded headings of clusters about these means. I fit piecewise regression models to the data incorporating these features to describe group headings. The models divided the segments into sections during which the whales maintained a constant mean heading. The sections were separated by either sudden turns, in which the mean heading of the group changed suddenly, or gradual turns, in which the mean heading changed linearly with passing time from that in the previous straight section to that in the following straight section. The models were constructed iteratively. Given a representation containing one or more straight sections, then, at each splitting iteration, the straight section with the greatest mean sum of squares of recorded headings about the regression line was

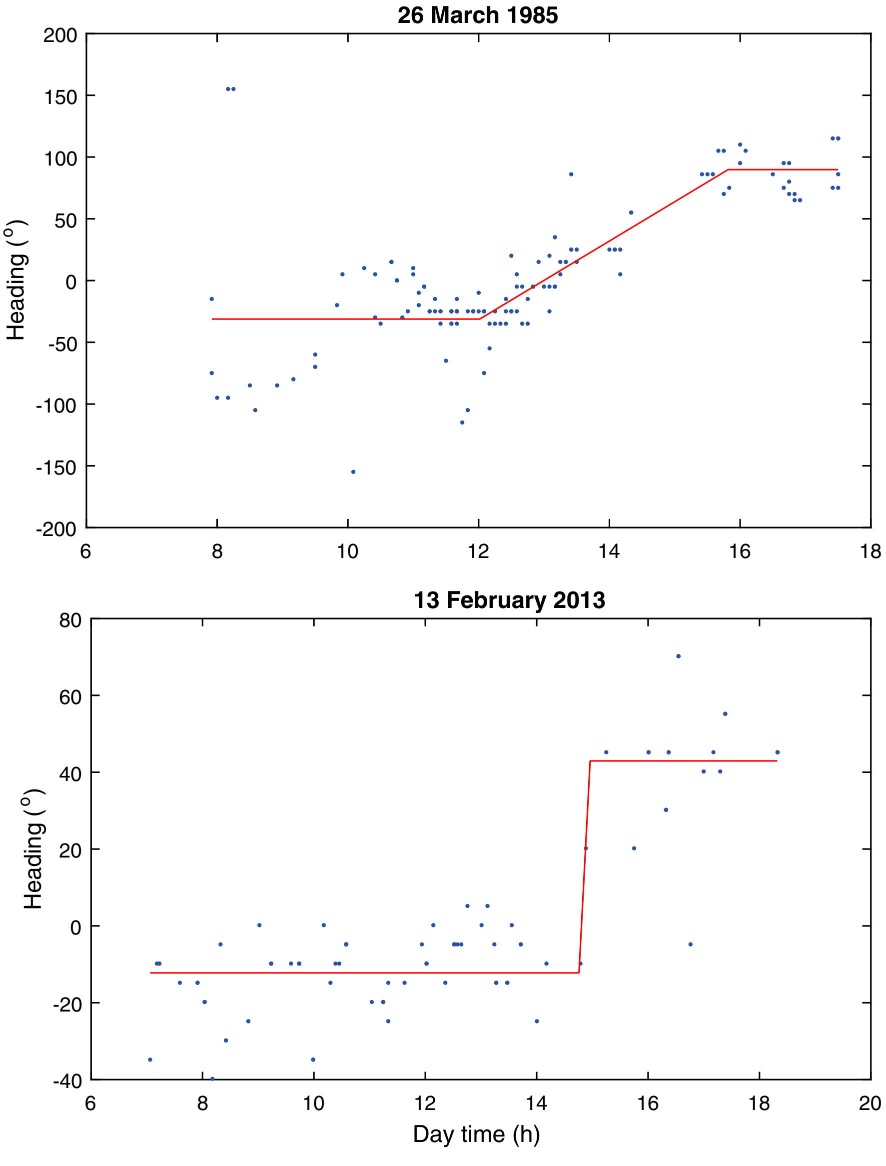

Figure 2. Recorded headings of clusters of sperm whales (relative to mean daily heading, 0°) with time of day (blue), showing fitted piecewise regression (red) indicating a gradual turn (26 March 1985) and sudden turn (13 February 2013). Full data Figures S1–S13.

chosen; this section was split at 6 min intervals, either with a sudden or gradual turn, so that each of the two new sections (including half the turn time in the case of gradual turns) would be at least 1 h long. In the case of gradual turns start times at 6 min intervals before the turn time were tried (with end times the same duration after the turn time). Thus for a chosen section from 1000 to 1230, turn times of 1100, 1106, 1112, 1118, 1124, and 1130 were tried, and for the 1106 turn time the potential gradual turns were from 1006 to 1206, 1012 to 1200, 1018 to 1154, 1024 to 1148, 1030 to 1142, 1036 to 1136, 1042 to 1130, 1048 to 1124, 1054 to 1118, and 1100 to 1112. The model for either sudden or gradual turn with lowest AIC was chosen (note gradual turns introduce one more degree of freedom than sudden turns). If this AIC was lower than that of the model without the new turn, then the new representation was chosen, and a new splitting iteration commenced. If the model without the new turn had lower AIC than any of those with the new turns, it was considered the best fit for the data of that segment.

I also made regressions of heading against time focusing on each heading record (*e.g.*, Fig. 3). I considered each focal heading record with at least three headings recorded in the previous 30 min, and at least three in the subsequent 30 min. (I also made analyses with the minimum number of headings in the 30 min before and after the observation reduced to two or increased to five, but results were similar). I then made a linear regression through these surrounding headings (excluding the focal observation itself). This gave estimates of the rate of change of heading of the group at the time of the focal cluster heading record (slope of regression line) as well as the

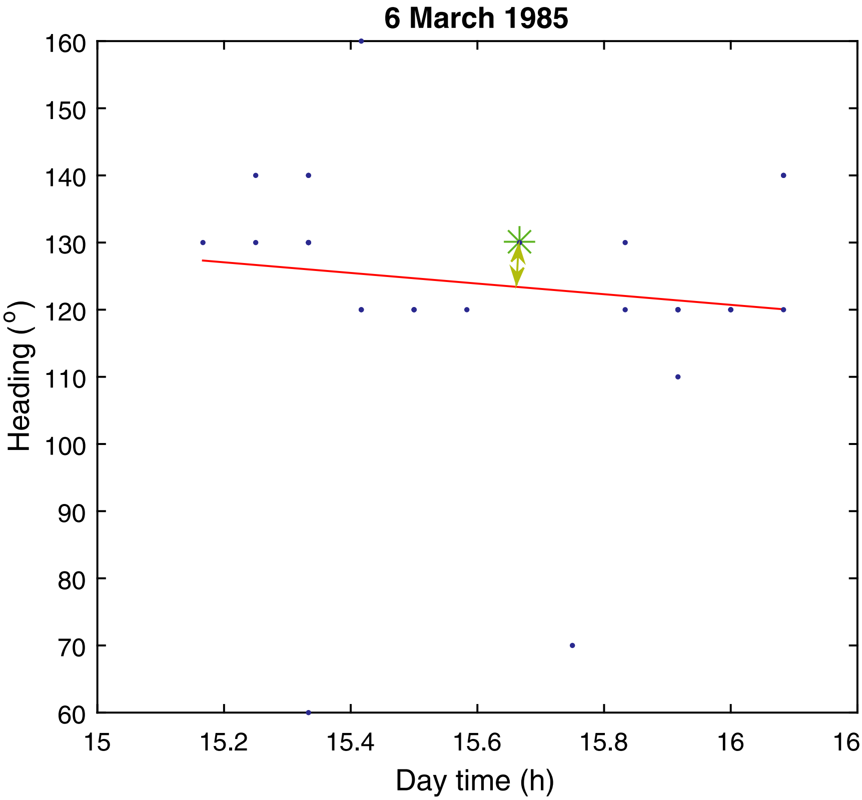

Figure 3. Regression (red) of heading against time for a focal cluster (green asterix), using all other recorded headings within 30 min (blue), giving rate of change of heading (slope), and difference between recorded focal heading and group heading (olive).

displacement of the focal heading above or below the regression line. I call these individual regression data.

Results

There were 543.1 h of foraging data, divided into 96 segments each at least 2 h long, and including 3,873 observations of the headings of clusters of whales (*i.e.*, a mean of 7.1 clusters/h). The cluster-focused individual regression analysis included 1,798 focal clusters with sufficient surrounding data. Results are generally similar from the 1985/1987 and 2013/2014 data, although variation in heading around the piecewise and individual regression lines is generally less in 2013/2014 (Table 1), probably because headings were recorded more precisely in the later studies.

Using the piecewise regression models, shown together with the heading data in Figures S1–S13 (also Fig. 2), I estimate that sudden turns occurred at a rate of 0.10/h of straight movement, and gradual turns at a rate of 0.10/h of straight movement. The mean change in heading was 69.4° (median 56.4°) for sudden turns and 84.0° (median 74.9°) for gradual turns. The mean duration of gradual turns was 1.3 h (median 0.8 h), and the mean turn rate was 63.4°/h (median 91.8°/h). These models are only quite crude representations of the behavior of the whales, and the observations on which they are based are sometimes sparse (see Fig. 2, S1–S13). However they do indicate that sperm whale groups sometimes make substantial sudden turns, but also turn gradually over protracted periods.

Variation in heading about the piecewise regression lines averaged 19.7° (median 12.5°, n = 3,873), and about the individual regression lines 17.7° (median 10.7°,

Table 1. Summary of results from piecewise and individual regression analyses.

	1985 and 1987	2013 and 2014	All
Hours of data	363.8	179.3	543.1
Segments (>2 h)	66	30	96
Observations of headings	3,037	836	3,873
Observations /h	8.3	4.7	7.1
Piecewise regression			
Sudden turns			
n	34	15	49
Rate /h	0.11	0.09	0.10
Mean magnitude (°)	71.5	64.6	69.4
Gradual turns			
n	40	10	50
Rate /h	0.13	0.06	0.10
Mean magnitude (°)	82.4	90.4	84.0
Variation (°)	22.6	14.6	19.7
When moving straight (°)	19.9	14.2	18.7
During gradual turns (°)	28.9	17.6	26.9
Individual regression			
n	1,600	198	1,798
Variation (°)	18.6	10.9	17.7
Correlation: slope *vs.* error (r_S)	0.24	0.17	0.24
P	0.000	0.020	0.000

n = 1,798). This variation was larger during gradual turns (mean 26.9°, median 14.0°, n = 493), than when the whales were moving straight (mean 18.7°, median 12.3°, n = 3,380). The null hypothesis that variation in heading about the regression line was equal when engaged in gradual turns and when moving straight was rejected (Kruskal-Wallis test; two-sided $P = 0.0005$). However there is a potential confounding factor in this comparison as in the piecewise regression procedure turns were preferentially placed in sections with high variation in heading. The individual regression analysis is free from this issue, but also supported more variable headings during turns (Spearman correlation among clusters between absolute displacement from expected heading and absolute rate of turning of $r_S = 0.241$; two-sided $P = 0.0000$; Fig. 4): median heading errors about the regression line were 7° when turn rates were 10°/h or less, rising to 11° with turn rates of 30°/h.

Discussion

Why and How Do Sperm Whales Turn?

Sperm whale movements are a striking phenomenon. Their vertical movements constitute some of the deepest mammalian dives, and the resultant transfer of

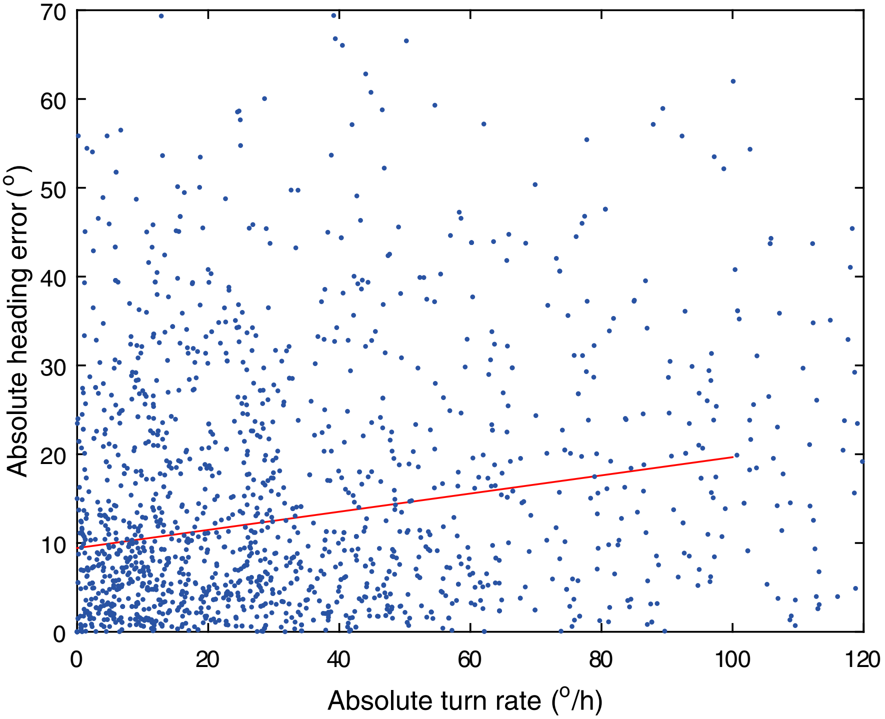

Figure 4. Absolute difference between focal cluster heading and group heading estimated from a heading-time regression, against estimated absolute rate of turn (as in Fig. 3). The red line shows a robust regression line through these data.

nutrients from the depths, where they feed, to the surface, where they defecate, may have important consequences for oceanic productivity (Watkins *et al.* 2002, Lavery *et al.* 2010). In the horizontal movements of the groups of females and immatures, 500 or so tonnes of mammalian biomass spread over 1 km or more travel large distances, sometimes using convoluted paths, as a coordinated whole.

First, why do they turn? A group of sperm whales travelling in a fairly straight line will sometimes reach the boundary of their habitat, land or shallow waters, and have to turn. Such situations were not considered in this analysis. It is likely that the turns that are documented were usually about foraging: the group received information that a change in direction might improve expected foraging success. This information could have been from the group itself. Perhaps the animals on the left of the dispersed formation were having greater success, so then the group turned that way. Alternatively, a group with recent good foraging but experiencing a reduction in rate might double back, producing the tortuous tracks that are typical of sperm whale groups when foraging is generally good (Whitehead 2003). While diving to forage, sperm whales make extremely loud, directional clicks about once per second, audible over at least several km (Whitehead 2003). Food finding is indicated by audible "creaks" (Miller *et al.* 2004), and most individuals can be distinguished using the interpulse intervals of their clicks (Schulz *et al.* 2010). Thus members of a foraging group should be aware of each other's presence, approximate locations (or maybe precise locations, I do not know), and feeding success for much of the time. This information almost certainly affects movement.

Turns could also be triggered by information external to the group. Foraging animals often turn as they pursue moving prey. However, the primary food of sperm whales off the Galápagos, histioteuthid squid (Smith and Whitehead 2000), have very limited mobility, so the turns of sperm whale groups are unlikely to be responses to movements of individual or groups of prey. The bottom away from the continental shelf in our Galápagos study area is moderately flat and about 3,000 m deep (and thus several times the typical depth of dive of these whales, Whitehead 2003), so it seems unlikely that many of the turns in our data set are driven by whales following contours, or otherwise reacting to bathymetry. However, the Galápagos oceanography is dynamic, and there are typically strong and variable upwelling zones, oceanic fronts and currents (Houvenaghel 1978) which might well be used as signals by sperm whales to change direction. Sounds from other groups of foraging sperm whales or other species might initiate turns, towards the source if the sounds are perceived as indicators of food, or away if they indicate competition or predation. Anthropogenic sounds are known to affect sperm whale behavior (Watkins *et al.* 1993), but there is little evidence for avoidance (Miller *et al.* 2009) and our study area off the Galápagos Islands is relatively little affected by anthropogenic noise. Other senses have either too limited ranges underwater (touch, vision) or are insufficiently developed in sperm whales (chemoreception, Oelschläger and Kemp 1998) to be likely drivers of the turns. The turns could also be driven by learned foraging strategies, either general or specific to the particular area or oceanographic conditions.

Thus I can presume that sperm whales have quite good information about the movements of their group members at the individual level, whether spatially close (a few meters) or separated (a few kilometers), and relevant environmental information, either acoustic or oceanographic, will usually be available to all members of the group at about the same time. This means that sperm whales' consensus decisions about movements could be local or global within the group (Conradt and Roper 2005).

Democracy or Autocracy?

In Conradt and Roper's (2005) conceptual framework for analyzing consensus decisions in nonhumans, an important consideration is whether there is conflict of interest among group members in decisions. In the case of changes in heading by sperm whale groups there is likely little conflict of interest as the primary goal of all members will generally be to increase feeding success, and there is likely little competition for food among group members (Whitehead 2003). But are the decisions democratic or autocratic?

Sperm whales are unusual animals, with no close phylogenetic relatives or ecological counterparts (Whitehead 2003). However, two species with which they share the general attributes of a multilevel, matrilineally based social structure, as well as general life-histories and ecologies, are the elephant and killer whale (Weilgart *et al.* 1996, Whitehead 2003). While comparable direction-change analyses have not been published for either species, for both elephants and killer whales consensus decision-making about at least some issues is clearly autocratic, being made largely by older females (McComb *et al.* 2011, Brent *et al.* 2015).

Some of the turns by the grouped sperm whales were sudden and clear, characteristics of autocratic decisions, perhaps by a matriarch. However, they could also be largely autonomous reactions by group members to a commonly perceived acoustic or oceanographic signal, such as a current, the creaks of group members indicating feeding success or the sounds of potential predators (perhaps especially killer whales) or competitors (maybe other sperm whales).

An important question that I have been unable to address with any power is whether particular individuals were leading the changes in group movement. In some clusters in 1985 and 1987, and virtually all in 2013 and 2014, we were able to photo-identify individuals whose headings we recorded, and thus characterize whether they anticipated or lagged the communal changes in group heading. I wanted to see whether particular individuals tended to consistently anticipate such changes. I used the product of the slope and error from the individual regression analysis as a measure of leadership: leaders were "ahead of the game" when the group was turning, having a positive error about the mean regression line when the group heading was increasing with time, and a negative error when it was decreasing with time. (The focal individual in Fig. 3 lags the group change in movement as its error is positive while the rate of change of group heading is negative.) In the data, there was no indication of "leader" whales who generally anticipated turns. However a power analysis in which some individuals were randomly designated "leaders", and then given high values of the leadership measure when the group was turning, failed to produce consistently statistically significant individual effects with the study's sample size and data structure. Thus the question of consistent individual leadership in sperm whale movement remains open.

The long, messy turns seem more directly indicative of group decision-making. The data seem to suggest that individuals gradually respond, imperfectly, to different degrees and in different ways, to the behavior of their group mates. However, it is possible that the slow turns are generated by gradual changes in external stimuli that the animals largely respond to individually. But there must be some social awareness for the groups to stay cohesive, and it is hard envisage external stimuli that would gradually change the preferred movement direction at the requisite temporal scale of an hour or so. It is also perhaps feasible that the slow turns are generated by consensus among a smaller group of "leaders."

This study of movement in sperm whales is unique in its methodology, as well as in its study species. The results, which fully support neither autocratic nor democratic decision-making, are consistent with a mixed picture emerging from research on other social mammals. Experiments with wild chacma baboons (*Papio ursinus*) found dominant males consistently led group foraging decisions, while detailed GPS tag-based studies of the movements of olive baboons showed that decisions were shared in complex ways (Strandburg-Peshkin *et al.* 2015). While older females tended to lead groups of foraging "southern resident" killer whales, this was far from universal (Brent *et al.* 2015). Thus both between and within species, there is considerable variation in how social mammals make consensus decisions about movements.

Culture?

Does culture affect collective decisions by sperm whales? This is another tantalizing question for which the power of the data was insufficient to give more than a hint. In the eastern tropical Pacific the population of female and immature sperm whales is divided into separate cultural clans. Social units of females and immatures belonging to different clans use the same waters, but do not associate (*i.e.*, form groups) with each other, and have distinctive dialects, movement patterns and other behavior (Rendell and Whitehead 2003, Whitehead and Rendell 2004). Do they differ also in their collective decisions about heading? In 1987 (but not 1985, 2013, or 2014) we collected a fair quantity of heading data on two clans using the waters off the Galápagos, the "Regular" clan (709 recorded headings) and "Plus-one" clan (354 recorded headings). Most of the measures taken from the heading analysis (as described for the full data set in the Results section) were similar for the Regular and Plus-one clan data in 1987. For instance the mean absolute error about the piecewise regression line when the whales were moving straight was 24.7° for the Regular clan, and 19.8° for the Plus-one clan. However, during the gradual turns the Plus-one clan appeared much more erratic (mean error 48.2°) than the Regular clan (mean error 26.3°), perhaps indicating differences between the clans in procedures or abilities for consensus decision making. However, I view this result as tentative for several reasons: the data are from only one study year; the data were collected in January–March 1987 for the Regular clan and April–June 1987 for the Plus-one clan, so no temporal overlap; and using the individual regression data, the regression lines of absolute error against turn rate (*cf.* Fig. 4) were almost identical for the two clans.

The Study of Movement

Studying the behavior of marine mammals at sea is challenging for the obvious reason that most of what they do is unavailable to human sensing in any direct way. Recordings of vocalizations have generally provided our most comprehensive and accurate behavioral measures. But movements are also amenable to study over a range of scales, with changes in individual location recorded using observations, tags, photo-identifications and other methods. These data are generally used to describe how individuals use their oceanic habitat. But the movements of marine mammals, and especially cetaceans, are typically communal, and likely often socially learned. Thus, through records of movement, we can study culture (Whitehead *et al.* 2008) and decision making (this study). The statistical methodology used in this study is, to my knowledge, novel in its application to consensus decisions. Such methods may prove useful in studies of consensus movement in other marine mammal populations.

They could be used for species with no previous studies of consensus movements, such as pilot whales (*Globicephala* spp.), as well as adding breadth to our understanding of consensus movement in species, such as killer whales, which have been examined using other techniques addressing rather different questions (Brent *et al.* 2015). The concept of using movement data to study the makeup of cetacean societies is not new, but is underused. I hope this paper will encourage further studies of animal societies using movement data.

Conclusion

The consensus decisions of sperm whales about movement headings may involve 30 or more animals, are likely largely free of conflict of interest, and are probably organized through global communication among group members. In the intersection of these attributes they seem unusual among the consensus decisions of animals (Conradt and Roper 2005). My study using incidentally collected data could only address a few of the relevant issues. Detailed records of individual locations and movements (*e.g.*, Strandburg-Peshkin *et al.* 2015) of group members would be revealing. The powerful acoustic signatures of echolocating foraging sperm whales, which are likely used by the whales themselves to monitor their group's layout and movement, can similarly be monitored by scientists (Thode *et al.* 2002) and may provide a way for us to understand how they make decisions. Time delays and phase shifts of recordings of clicks from a fixed or mobile array of hydrophones could be used to provide nearly continuous records of the three-dimensional locations of each member of a foraging group, while the interpulse intervals of the clicks allow individual identity to be quite consistently ascribed to each set of movement records (Schulz *et al.* 2010). Then, with detailed individual movement records, the relationships between the movements of each pair of animals can be analyzed, looking for dependencies and lags in changes of direction, building up a picture of how movements of one animal affect those of another, and thus how consensus decisions about changes in direction are reached (Strandburg-Peshkin *et al.* 2015).

As they move through the ocean, groups of sperm whales make consensus decisions about where to go. Sometimes they turn suddenly, perhaps responding largely independently to external stimuli, or signals from "leaders." However, often they change direction gradually, taking an hour or more to complete a turn, and messily, with individual variations about the mean heading markedly increasing compared with straight movement. Although there are other potential explanations, these results suggest some shared decision making.

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Cientifica 002-12) (permit numbers only available for 2013 and 2014 field seasons). The manuscript was improved with comments from D. Boness, M. Cantor, R. Wells, and three anonymous reviewers.

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SUPPORTING INFORMATION

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Figures S1–S13. Recorded headings of clusters of foraging sperm whales (relative to mean daily heading, shown by black line) with time of day (blue dots), showing fitted piecewise regressions (red lines) with each plot representing a different segment. There are sometimes two segments for a day.