Behaviour

The social context of individual foraging behaviour in long-finned pilot whales (Globicephala melas)

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The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*)

Short title: Foraging behaviour of long-finned pilot whales

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Summary

Long-finned pilot whales (*Globicephala melas*) are highly social cetaceans that live in matrilineal groups and acquire their prey during deep foraging dives. We tagged individual pilot whales to record their diving behaviour. To describe the social context of this individual behaviour, the tag data were matched with surface observations at the group level using a novel protocol. The protocol comprised two key components: a dynamic definition of the group centred around the tagged individual, and a set of behavioural parameters quantifying visually observable characteristics of the group. Our results revealed that the diving behaviour of tagged individuals was associated with distinct group-level behaviour at the water's surface. During foraging, groups broke up into smaller and more widely spaced units with a higher degree of milling behaviour. These data formed the basis for a classification model, using random forest decision trees, which accurately distinguished between bouts of shallow diving and bouts of deep foraging dives based on group behaviour observed at the surface. The results also indicated that members of a group to a large degree synchronised the timing of their foraging periods. This was confirmed by pairs of tagged individuals that nearly always synchronized their diving bouts. Hence, our study illustrates that integration of individual-level and group-level observations can shed new light on the social context of the individual foraging behaviour of animals living in groups.

Keywords

diving behaviour, cetaceans, group-level sampling, long-finned pilot whale, foraging, *Globicephala melas*, digital archival tags, social animals

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Introduction

Animal behaviour is traditionally studied at the level of the individual (Williams, 1966). In social animals, however, the behaviour of an individual also influences, and is influenced by, the behaviour of other individuals with whom it interacts. In social insects, fish and birds, groups composed of individuals following simple decision rules can make complex decisions about where to forage or nest (Deneubourg & Goss, 1989; Couzin et al., 2005; Sumpter, 2006). Social mammals, such as primates and ungulates, often democratically reach group-decisions (Conradt & Roper, 2003), although despotism may also occur (Lusseau & Conradt, 2009). Social behaviour often requires a high degree of coordination among group members, as exemplified by several species of social cetaceans that to a large extent depend upon conspecifics for foraging (e.g., Pitman & Durban, 2012), group defence (e.g., Pitman et al., 2001), alloparental care (Whitehead, 1996) and access to females (Connor et al., 1992).

Long-finned pilot whales (*Globicephala melas*) are social cetaceans that live in long-term stable, matrilineal groups (Amos, 1993; Ottensmeyer & Whitehead, 2003; de Stephanis et al., 2008). Pilot whales forage mainly on deep-sea squid, during short but relatively deep dives up to 800 m depth (Shane, 1995; Baird et al., 2002; Heide-Jørgensen et al., 2002; Sivle et al., 2012). The function of the deep foraging dives becomes apparent from their distinct vocal signature. During deep dives, individuals produce echolocation signals to localise prey, consistent with bio-sonar based foraging (Soto et al., 2008; Miller et al., 2011; Madsen et al., 2013).

Pairs of long-finned pilot whales can perform highly synchronous surfacing behaviour, at less than one body length apart (Senigaglia & Whitehead, 2012). Their behavioural synchrony can be maintained during deep foraging dives, when they jointly swim to several hundred meters of depth in search for prey (Aoki et al., 2013). This suggests that long-finned pilot whales employ a social foraging strategy,

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whereby individuals coordinate their foraging behaviour (Marshall et al., 2012). Social foraging is found across a wide range of taxa, and is known to influence the foraging decisions and pay-offs of individuals living in social groups (Marshall et al., 2012). For social animals such as long-finned pilot whales, studies of their foraging behaviour will therefore benefit from detailed observations of both individual and collective behaviour (Deneubourg & Goss, 1989; Conradt & Roper, 2003).

The social foraging behaviour of deep-diving cetaceans has been difficult to study using traditional observation techniques. This partly stems from challenging observation conditions; deep-sea foraging cannot be directly observed visually. Moreover, fluid movement patterns, submerged individuals, lack of distinctive markings and limited sexual size dimorphism often prevent rapid identification of individuals at the next surfacing. Hence, many cetacean studies have focused on group-level behaviour at the surface (Mann, 1999; Whitehead, 2004). However, recent methodological breakthroughs make it more feasible to monitor the diving behaviour of individual cetaceans. Digital archival tags can record individual movements and vocalisations (Johnson & Tyack, 2003). These data can be used to identify foraging behaviour of the tagged individuals (e.g. Soto et al., 2008), and can be matched to surface observations of group behaviour.

Here, we investigate the social context of the individual foraging behaviour of long-finned pilot whales, by integrating tagging data of individuals displaying foraging and non-foraging dives with visual observations of group-level behaviour at the water's surface. We designed a novel sampling protocol that quantitatively records behavioural parameters of the group centred around the tagged individual. We then analysed the extent to which individuals synchronised their diving behaviour, and whether group-level behaviour visible at the surface varied between foraging and non-foraging states of the tagged individual.

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Materials and Methods

The behaviour of long-finned pilot whales was monitored from the research vessel M/S Strønstad (29 m, engine driven) in the Vestfjord basin off Lofoten, Norway (67°00'N, 11°50'E to 68°30'N, 17°00'E). The study was conducted from May 17 to June 5, 2009, and from May 23 to June 6, 2010. We collected two types of behavioural data: 1) dive parameters collected from individuals tagged with non-invasive suction-cup tags, and 2) focal follow observations of group behaviour at the surface, conducted using a novel sampling protocol described below.

Tag recordings of individual whales

Following initial sighting of a group of pilot whales, a small tagging vessel was directed to the group. It was not possible to select a predetermined individual for tagging. Instead, individuals were tagged at the first available opportunity, when they came sufficiently close to be tagged with a 6 m long pole holding the tag.

We deployed two different types of non-invasive suction cup tags (DTAG version 2, Woods Hole Oceanographic Institution, MA, USA, Johnson & Tyack, 2003; Little Leonardo W2000-PD3GT Type B tag, Atmosphere and Ocean Research Institute, University of Tokyo, Japan, Aoki et al., 2013). The tags contained a VHF beacon transmitting a radio signal when the tag surfaced. This radio signal was used to track the tagged whale during deployment using radio direction finding equipment, informing the observers when the whale was at the surface and giving its bearing from the research platform. Both tags recorded dive depth of the tagged individual, at 20 Hz (DTAG) and 32 Hz (Little Leonardo). The DTAGs also recorded sound at the whale, with 16 bit resolution and 192 kHz sampling rate (Johnson & Tyack, 2003).

Dive depth was obtained by calibrated conversion of the values from the pressure sensor on the tags. Long-finned pilot whales typically forage upon their prey

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during deep dives, while shallow dives are seldom associated with foraging (Miller et al., 2011). To distinguish between foraging and non-foraging periods, dives were assigned to either deep or shallow diving bouts using log-frequency analyses of dive depths and time intervals between consecutive deep dives (Sivle et al., 2012), and the presence of echolocation signals indicative of the localisation of prey.

To determine the presence of echolocation activity, we recorded the timing and length of the echolocation signals of the individuals tagged with a DTAG using Adobe Audition 2.0. Echolocation clicks were series of short broadband signals classified as click trains or buzzes. Consecutive but distinct broadband clicks recorded less than 2 s apart were classified as a click train. Buzzes were defined as rapid successions of clicks that fused together on the spectrogram, and are indicative of prey capture attempts (e.g. Madsen et al., 2013). All click trains or buzzes that were clearly audible and/or visible on the spectrograms (Blackman-Harris window, 4096 sample FFT, 75% overlap) were included in the analysis. We did not discriminate between clicks of the tagged whale and those of nearby individuals.

In total, we tagged 11 individuals during 8 focal follows. Hence, in 3 of the 8 focal follows, we recorded the diving behaviour of two simultaneously tagged individuals within the same group. The diving patterns of the two individuals were compared to investigate dive synchrony between group members.

Visual observations of group behaviour

Visual observations of group behaviour were made from the observation platform of the research vessel at 6 m above water level. The focal group consisted of the individuals associated with the tagged individual. During all observations, the research vessel aimed to maintain a distance of 100 – 400 m to the focal group. Behavioural data were collected by two dedicated observers, alternating in 6-hour shifts. The observer was assisted by a second person recording the observations

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onto a laptop-based data logger. The observers regularly calibrated their distance estimates using a laser range finder. In addition, the distance estimates of the two observers were calibrated by comparison of their estimates of the distance between the observation platform and a gps-equipped buoy from randomly chosen distances and angles. The first 30 minutes after tagging were excluded from the data set to allow the focal group to recover from any behavioural response it may have had to the tagging. Analyses conducted here ended at the release of the tag, or at the start of sound exposure experiments (reported in Miller et al., 2012, not discussed here). Sampling was conducted during all hours of the day, enabled by the 24-hour daylight conditions of the arctic summer.

Definition of the focal group

The composition of pilot whale groups was dynamic and could change during the focal follows. We therefore defined the focal group as the group of individuals in closer proximity to the tagged individual and each other than to other individuals in the area (Figure 1). For this purpose, we first defined different spacing categories based on the distance between individuals measured in body lengths (Table 1). Closely associated pairs (<1 body length), such as mother-calf pairs, were treated as a single unit in the assessment of distances between individuals. When the tagged whale surfaced, the first step in estimating group size was to determine the nearest neighbour of the tagged individual. The focal group included all individuals with similar proximity (according to the individual spacing categories; Table 1) to the tagged whale or other group members as the nearest neighbour. If the nearest neighbour was in closer proximity to other individuals than to the tagged whale, then the tagged whale was assigned as solitary. Thus, focal group membership was based on the relative distribution of individuals around the tagged whale (Figure 1). Our definition is comparable to the chain-rule, which identifies group members based

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upon maximum distance between nearest neighbours (e.g., 50 m; Smolker et al., 1992). However, instead of a predetermined absolute distance, we based group membership on the relative distances between individuals to capture the variation in individual spacing that we observed in our study animals.

More distant individuals, not included within the focal group, might still be in close enough proximity to have interactions with the focal group. For instance, cetaceans can communicate acoustically over large distances (Payne & Webb, 1971). The number of individuals in the wider area can thus provide an important social context, describing a second level of cohesion (Figure 1). Therefore, our sampling protocol also included the number of individuals and non-focal groups in the wider vicinity (focal area) of the tagged individual. For practical reasons, the focal area was here defined as the 200 m radius around the tagged individual, as delineated by a laser range finder, because this was the maximum area over which we could reliably monitor the number of whales present during the entire observation period. Non-focal groups were defined in the same way as the focal group, based on clusters of individuals with similar proximity to each other according to the individual spacing categories (Table 1).

Sampling strategy

The functionality of cetacean behaviour can be difficult to determine with certainty. Therefore, we argue that the behaviour of cetaceans should be sampled using directly observable parameters without an *a priori* interpretation of the function of their behaviour (Martin & Bateson, 2007). For example, parameters such as 'individual spacing' and behavioural events such as 'tailslaps' can be directly observed and lack the functional interpretation of composite activities such as 'foraging'. Furthermore, whenever possible, we recorded quantitative descriptors. For example, 'surfacing synchrony' can be defined as 'the proportion of individuals within

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the focal group that surfaced during the surfacing of the tagged whale'. This quantitative definition is less prone to observer bias than a more qualitative definition of, e.g., 'low, medium and high' synchrony, and avoids the implicit suggestion that the behaviour of all group members is synchronised.

We choose to monitor the behavioural parameters of groups based on the principles outlined above, distinguishing between group states and individual events (Table 1). Group states were defined as characteristics of relatively long duration of the focal group as a whole, such as group size and the spacing between individuals. Individual events were defined as behaviours of short duration, displayed by individuals in the focal group. The parameters were recorded using a combination of existing sampling methods. Group size and composition, group geometry (individual spacing, line swimming) and proximity to other groups (number of individuals and groups in the focal area, distance to nearest other group) were determined for each sampling interval by scanning the area around the tagged animal. Synchronicity parameters (surfacing synchrony, milling index) were quantified from the timing or orientation of surfacing of the associates relative to the tagged animal using traditional scan sampling (Altmann, 1974). The individual events in the focal group were recorded for each sampling interval using incident sampling (Mann, 1999). All parameters were recorded at 2-minute intervals, or at first surfacing of the tagged individual following dives of more than 2 minutes duration. This sampling interval was shorter than the time scale at which the state parameters were expected to change (Martin & Bateson, 2007), and ensured observation of the tagged individual.

Statistical analysis of behavioural differences

The data gathered in our study enabled a comparison between diving patterns of tagged individuals and the behaviour of the focal groups to which these tagged individuals belonged. Differences in group behaviour between bouts of deep

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and bouts of shallow diving of the tagged individuals were quantified using Generalised Estimating Equations (GEEs; Hardin & Hilbe, 2003). The input data comprised behavioural time series from 8 different focal groups, each group consisting of different whales. GEEs extend Generalized Linear Models (GLMs) in that they are designed to model correlated data, and return predicted values for the average response across the entire dataset. GEEs account for residual autocorrelation within individual time series (panels), while assuming independence between time series. Surface behaviour events (Table 1) and the presence of milling and line swimming were modelled as binary response types with diving state as explanatory variable, using GLMs with GEEs and a logit link function. The other behavioural parameters in our protocol (Table 1) contained multiple categories, and were modelled as ordinal categorical response types using GEEs with a cumulative logit link function. The GEEs were fitted using empirical standard errors to ensure that model results did not depend on a potentially incorrect correlation structure (Zeger et al., 1988; Kauermann & Carroll, 2001). The GEE models were fitted with the GENMOD procedure in SAS 9.3 (SAS, 2011), using the time series of the tagged animal as panel variable. We applied a Bonferroni correction to control for multiple hypothesis testing.

Classification of diving behaviour from surface behaviour

We used Random Forest (RF) analysis (Breiman, 2001) to test whether the diving behaviour of the tagged individual could be predicted from the behaviour of the focal group at the surface. RFs consist of a series of unpruned classification trees generated from one dataset. At each node of a tree, a fixed small number of predictor variables is randomly selected, and the predictor that yields the best split is chosen. The model can simultaneously handle a large number of input variables, and parameters can be used multiple times within one tree. For each tree, *N* records of

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the *m*-sized dataset are randomly selected, with replacement, and run down the tree. Each record is then classified based on the majority vote from all trees. The error estimate of the model is determined internally by using the out-of-bag (OOB) data (the data not used in the iteration, about one-third) as test data (Breiman, 2001).

RF models can be used to estimate the relative importance of the predictor variables (Breiman, 2001; Kehoe et al., 2012). However, estimates of parameter importance in RF models can be biased if the parameters vary in their scale of measurement, which was the case in our dataset (Table 1). This issue is solved by an adaptation to RF models, known as Conditional Inference Forests (CIF), using subsampling without replacement (Hothorn et al., 2006; Strobl et al., 2007).

The adapted RF model, based on CIF, was created using the group behavioural parameters at the surface as predictors and the deep versus shallow diving bouts as the response variable. The model was run with 1000 trees, randomly selecting 5 predictor variables at each node, using a subsample size of two-thirds of the dataset without replacement. The predictor variables with the lowest variable importance were then removed one by one from the model, until further removal did not improve the OOB error rate. Potential cross-correlation of the predictor variables was controlled for by using the conditional computation of variable importance in the RF model (Strobl et al., 2008). To account for the difference in occurrence of deep and shallow diving states, weights were assigned to both states, inversely proportional to their occurrence.

To test for potential effects of stratification on the results of the RF analysis, we investigated the classification accuracy of the RF model for each focal follow separately. This was done by running the model using seven (out of eight) of the focal follows as a training dataset. The resulting RF model was then used to classify the one focal follow not used in model training. This procedure was repeated eight times, to classify all eight focal follows one by one. Analyses were performed using the package ‘party’ in R version 2.14.1 (R development core team, 2011).

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Results

We collected 34.9 h of data containing simultaneous records of individual tag data and behavioural observations of pilot whale groups. The data comprised 8 focal follows with a total of 595 samples of group-level behaviour. Focal follow duration ranged from 0.8 – 8.9 h. In 3 of the 8 focal follows, the focal group contained two tagged individuals. The tagged individuals were 5 medium-sized individuals associated with a calf, 4 medium-sized individuals without a calf, and 2 large-sized adults without a calf. Photo-identification records confirmed that the tagged whales were different individuals for each focal follow.

Characteristics of group behaviour

All 8 focal groups were part of larger aggregations of 60-100 pilot whales, generally organised in subgroups and spread out over an area spanning several square kilometres. Focal group size ranged from 1 to 30 individuals, with a median of 11 individuals and interquartile range of 6 individuals. In 48% of the samples, at least one other group of pilot whales was present within the focal area. The number of individuals in the focal area ranged from 2 – 50, with a median of 15 individuals and interquartile range of 11 individuals. Calves were present in 7 of the 8 focal groups. Individuals in the focal group were often tightly spaced (56% of samples). Loosely spaced (18%) and very tightly spaced (16%) individuals were also commonly observed, while very loose spacings (9%) and solitary individuals (1%) were rare. Milling and line swimming were observed in 7.5% of the samples. Loggings (11%) and spyhops (5%) were the most frequent surface behaviour events. An example of a focal follow is shown in Figure 2a-f.

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Deep and shallow diving bouts

Log-frequency analysis of the tag data indicated a threshold depth of 34 m to separate shallow from deep dives. Echolocation signals indicative of the localisation of prey were recorded during all dives deeper than 34 m for the 7 whales equipped with a DTAG. In particular, clicking and buzzing were recorded 57% and 3.3% of the time, respectively, during deep dives. In contrast, clicking and buzzing were recorded only 25% and 1.1% of the time during shallow dives less than 34 m. Furthermore, log-frequency analysis of the tag data suggested a maximum time interval of 14.5 min between consecutive deep dives within the same diving bout. A deep diving bout thus started at the first dive deeper than 34 m and ended 14.5 min after the last deep dive. Bouts of deep diving consisted of alternating periods of deep and shallow dives, while shallow diving bouts solely held shallow dives (Figure 2g,h). In total, 20 shallow diving bouts and 18 deep diving bouts were recorded for the tagged pilot whales, where shallow diving bouts comprised 72% and deep diving bouts 28% of total recording time. The maximum depth per diving bout ranged from 4 – 34 m for shallow bouts. The deep diving bouts showed two clusters, with maximum dive depths ranging from 46 – 175 m (8 bouts) and from 291 – 617 m (10 bouts). All tagged whales performed both shallow and deep dives, except for one individual that performed shallow dives only.

In all three focal groups containing two tagged individuals, the pairs of tagged whales showed clear temporal synchrony in their diving behaviour (Figure 3). In total, the 3 pairs of tagged whales performed 5 shallow diving bouts and 3 deep diving bouts, and their diving state overlapped during 84% of the recording time (7.5 out of 8.9 h). In all cases, the tagged whale pairs initiated their deep diving bouts simultaneously. Differences in diving state resulted from one of the whales breaking off its deep diving bout earlier than the other whale.

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Group behaviour during deep and shallow bouts

Comparison of the focal follows with the tagging data revealed a striking difference in group behaviour between deep and shallow diving bouts (Figure 4), which was confirmed by the GEE-based statistical analysis (Table S1). During deep diving bouts, the surface behaviour of the pilot whales shifted to smaller groups (Figure 4a), with more loosely arranged individual spacing (Figure 4e). The number of groups in the focal area slightly increased during deep diving bouts (Figure 4c). However, observations of solitary individuals remained rare (1% of the samples). Concordantly, milling occurred more often during deep diving bouts (Figure 4g). Combined, this indicates that deep diving bouts were associated with a characteristic group behaviour at the surface in which the individuals of cohesive groups spread out and broke up in smaller units, while their extent of coordinated swimming decreased.

Random forest classification of foraging behaviour

The presence of specific surface group behaviour associated with deep diving bouts was confirmed by the RF model analysis. The RF model classified deep and shallow diving bouts from the group behaviour quite accurately, with an error rate of 15.8% (Table 2). The most important parameters distinguishing between deep and shallow diving bouts in the RF classification were individual spacing, distance between groups, and group size (Figure 5), which is in good agreement with the GEE results (Figure 4; Table S1). The relative importance of the variables active body contact, tailslap, breach, line swimming, calf presence and spyhops was marginal, and they were therefore removed from the final model.

We also investigated to what extent the deep and shallow diving bouts of each individual focal follow could be predicted from a RF model built from the 7 other focal follows. The error rate of the 7 focal follows used for model training was 15.9%,

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which is nearly identical to the error rate of the complete data set. The error rate of the individual focal follows used for model prediction was 22.4%. This indicates some degree of variation in social foraging behaviour between the different focal follows. Hence, the RF model is certainly not a perfect predictor, but it can predict the diving behaviour of new individuals with reasonable accuracy.

Identification of model misclassifications

In some cases, the RF model predicted a shallow dive while the tagged individual performed a deep dive, and vice versa. In total, such misclassifications occurred for 94 samples (Table 2). Almost a third of all misclassifications (27 samples) occurred at the transitions from deep to shallow and from shallow to deep diving bouts (Figure 2g). This may indicate that, during these transitions, individuals in the focal group varied in their behaviour. For instance, the tagged individual may have ended its deep diving bout, while other members of the group still performed deep dives and associated surface behaviour. This was confirmed by our observations of pairs of tagged whales, where one tagged individual sometimes broke off its deep diving bout earlier than the other.

A second important category of misclassifications (18 samples) was represented by deep diving bouts that were not recognised by the RF model (Figure 2g). This occurred for only 4 deep diving bouts, which were all relatively shallow and of short duration (maximum dive depth: 46 - 166 m; duration: 2 – 18 min). In contrast, the deeper deep diving bouts (max. dive depth: 291 – 617 m) were always correctly identified by the RF model. This might indicate that “shallow deep dives” represented different foraging behaviour or were associated with a different social context at the water’s surface. Removal of these two sources of misclassification reduced the error rate of the complete data set from 15.8 to 8.2%.

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Discussion

Our results illustrate that the combination of individual-level and group-level observations can provide new insights into the foraging behaviour of social animals. We showed that periods of active foraging, monitored by the diving behaviour of tagged whales, were reflected by a distinct group behaviour at the surface. During foraging bouts, focal groups broke up into smaller and more widely spaced groups. Concordantly, the degree of coordinated swimming decreased. These results formed the basis for a classification model that could accurately predict diving behaviour of a tagged whale from the surface behaviour of the group.

Foraging behaviour of long-finned pilot whales

Long-finned pilot whales are often observed in large aggregations, consisting of several pods. Pods are long-term stable associations of one or more matrilines (Ottensmeyer & Whitehead, 2003). Also in our study, focal groups were always part of larger aggregations dispersed over a wider area of several square kilometres. The focal group size ranged from 1 – 30 individuals, with a median of 11 individuals. This closely matches the pod sizes identified by photo-identification studies across the North Atlantic and in the Mediterranean Sea (mean: 11 – 14, median: 10 - 11 individuals; Fullard, 2000; Cañadas & Sagarminaga, 2000; Ottensmeyer & Whitehead, 2003; de Stephanis et al., 2008). During foraging, several focal groups disaggregated into smaller units of 1-5 individuals. This decrease in observed group size might be partly due to a larger number of submerged individuals that were not recorded by the observer. However, this is certainly not the only explanation for the smaller group size, because we clearly observed the breaking up of focal groups into smaller units (F. Visser, pers. obs.), consistent with the increase in the number of groups in the focal area during deep diving bouts (Figure 4c). These smaller units

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might consist of more closely related individuals within matrilines (Fullard, 2000; de Stephanis et al., 2008), although this could not be verified because we lacked information on the genetic relatedness of the individuals.

The group-level patterns at the surface indicated temporal synchrony in functional behaviour between individuals within the same focal group. This is supported by recent observations that pairs of pilot whales can be highly synchronous in their breathing and diving behavior (Senigaglia & Whitehead, 2012; Aoki et al., 2013). Our data show that pairs of tagged individuals synchronized the timing of their deep and shallow diving bouts during 84% of the total recording time, although the deep dives were not always performed simultaneously. Synchrony was temporarily lost when the tagged individuals broke off from their foraging bouts at different times. This temporary mismatch between the behaviour of different individuals also emerged in the misclassifications of the random forest model at the transition between deep and shallow diving bouts. In total, these results indicate a social foraging strategy with a high degree of temporal synchrony, although the exact timing of the foraging dives may differ between individuals.

Coordinated foraging by several individuals can have several advantages. For example, in social animals such as wolves (*Canis lupus*) group members often cooperate to catch their prey (Mech, 1999). Sperm whales (*Physeter macrocephalus*) are known to forage in rank formations, which could function to avoid mutual interference or to catch prey that eludes other members of the formation (Whitehead, 1989). Pilot whales forage mainly on deep-sea squid, which may flock in dense aggregations but may also be widely dispersed over several hundred meters depth (Shane, 1995; Baird et al., 2002). Simultaneous foraging by several individual whales may confuse or herd their prey, which may have fewer options to escape from predation. Synchronised timing of foraging bouts could also be motivated if individuals with more local knowledge (e.g., pilot whales at greater depth) signal good feeding opportunities, initiating the start of group foraging. This signalling could

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happen actively (Lusseau & Conradt, 2009) or passively (eavesdropping on cues; Dawson, 1991). As pilot whales forage at depth on patchy prey fields (Shane, 1995; Baird et al., 2002), signalling of good opportunities could improve foraging efficiency of each whale in the group.

Methodological development

Our results rely on the simultaneous collection of two data streams: (i) tagging data indicative of foraging activity of individual pilot whales, and (ii) group-level behaviour observed at the water's surface using a novel sampling protocol. Our protocol was specifically designed to overcome several methodological difficulties that may restrict studies of group-level behaviour. In particular, observations of group behaviour were structured around the tagged individual (Figure 1). This approach facilitates sampling of dynamic groups, because the sampling regime is consistently centred around one and the same individual, rather than a group of individuals that may vary in composition during the observations. Hence, it is straightforward to decide which group should be monitored when groups split up into smaller units.

Our definition of the focal group does not attempt to define the 'true' group as perceived by the tagged animal. An individual may perceive different kinds of relationships depending upon proximity and behavioural context. Cetaceans can communicate acoustically over distances spanning many kilometres (Payne & Webb, 1971), they can often see one another at ranges of up to about 10-20 m, but they must be within a body length to touch one another. Therefore, there is not a single spatio-temporal scale that constitutes a 'true' group. However, our characterization of the focal group does describe animals that certainly are close enough to interact, with the definition based on the relative proximity of the tagged animal to other individuals.

A common problem in behavioural studies is that the observer has to choose between two (or more) mutually exclusive behavioural states. For instance, is the

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animal resting or foraging? At the group level, this choice is further complicated if some animals are resting while others are foraging (Altmann, 1974; Mann, 1999). Our sampling protocol avoids this dilemma by the use of quantitative parameters to describe group behaviour without interpreting the functionality of this behaviour. For instance, rather than describing the aggregate functional behaviour of the group (e.g., resting, foraging), we quantified individual behaviour of the tagged animal in combination with directly observable parameters of the group (e.g., the spacing and directionality between group members).

Foraging strategies and diving capabilities can differ between animals of different age- and sex classes, potentially resulting in individual patterns of behaviour (Heide-Jørgensen et al., 2002; Ruckstuhl & Neuhaus, 2002). Our results indeed indicate some degree of individual variation, as illustrated by the diving patterns of pairs of tagged individuals within the same focal group (Figure 3). Furthermore, our results also indicate some degree of variation between the focal groups, because the accuracy of the classification of diving behaviour was slightly lower for separate focal groups than for the full dataset. However, controlling for context dependent variation, the analysis identified a distinct surface group behaviour during foraging that was present across all focal groups. This illustrates that the data obtained from our sampling protocol can be classified into different functional activities (e.g., foraging vs. non-foraging behaviour), even when animals participating in this group behaviour display some degree of individual variation.

Conclusions

Our study revealed that long-finned pilot whales coordinate the timing of their foraging behaviour. They employ a social foraging strategy, where group members synchronize their diving bouts although they do not always synchronize their individual dives. These results relied on the combination of group-level observations

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with data on the foraging dives of tagged individuals. A similar research strategy may also be applied to other cetaceans, and may create novel opportunities to understand the interplay between individual-level and group-level behaviour of social animals.

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Supplementary material

Supplementary material for this article is available, in the online version, at <to be completed upon acceptance>

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Tables

Table 1. The parameters recorded in our study.

Parameter	Definition (gs = group state; ie = individual event)	Quantification
Group size	Number of animals most closely associated with the tagged individual and with each other (gs)	Number of individuals
Individual spacing	Distance between individuals in the focal group (in body lengths (BL)) (gs)	Very tight: < 1 BL Tight: 1 – 3 BL Loose: 3 – 15 BL Very loose: >15 BL and within focal area Solitary: no other individual in focal area and/or distant from nearest neighbour
Number of individuals in focal area	Number of individuals within 200 m of the tagged individual (gs)	Number of individuals
Number of groups in focal area	Number of groups within 200 m of the tagged individual (gs)	Number of groups
Distance to nearest other group	Distance between the focal group and the nearest other group (gs)	Distance in meters
Calf presence	Presence of calves in the focal group (gs)	Presence / absence
Surfacing synchrony	The proportion of individuals in the focal group surfacing during the surfacing of the tagged individual (gs)	Proportion of individuals
Milling index	Presence of individuals in the focal group that surface with another orientation than the tagged individual (gs)	Presence / absence
Line swimming	Presence of lined-up geometry of ≥50% of individuals in the focal group (gs)	Presence / absence
Surface behaviour events	Number of events per type of surface behaviour in the focal group (ie)	Number of loggings, spyhops, tailslaps, breaches and active body-contacts*

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Comments	Additional comments on (rare) behavioural states or events not covered by the protocol (gs/ie)	E.g., tagged animal blows bubbles

**Logging: floating at or just below the water's surface. Spyhop: a vertical rise partially out of the water. Tailslap: slapping of tailflukes on the water's surface. Breach: leap during which >40% of the body clears the water. Active body contact: physical, non-synchronous interaction between 2 or more individuals, visible at the water's surface.*

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680 **Table 2.** Random Forest model classification results.

RF classification	Observed from tag	
	SHALLOW	DEEP
SHALLOW	**388**	53
DEEP	41	**113**

681 The table shows the number of samples with shallow and deep diving bouts of
682 tagged individuals versus the number predicted by the Random Forest classification.
683 Total number of samples = 595. Error rate: (41 +53) / 595 = 15.8%.

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Figure legends

Figure 1. Determination of the focal group. The focal group (grey area) is the group of individuals in closest proximity to the tagged individual (grey animal) and each other. The focal area (dashed circle, not to scale) encompasses the 200 m radius around the tagged whale. For example, a focal group of 7 individuals (left) changes its organisation. Top right: Two individuals become more distantly spaced (3-15 BL) from the tagged whale and other individuals in the focal group than the spacing within the focal group (<1 BL). The group splits up in two smaller groups, and the group with the tagged animal remains the focal group. Bottom right: The focal group becomes more widely spaced, but the relative spacing between individuals remains the same (3-15 BL). One animal leaves the focal group and the focal area.

Figure 2. Example of group behaviour and individual diving behaviour of long-finned pilot whales during 8 hours of observation. (a) Group size (filled circles) and number of individuals in the focal area (open circles), (b) individual spacing, (c) surfacing synchrony, (d) number of groups in the focal area, (e) distance of the focal group to the nearest other group (n.i.s. = none in sight), (f) surface behaviour events, (g) deep diving bouts (black) and shallow diving bouts (grey) recorded by the tagged individual (TAG), and classified by the Random Forest model (RF) based on surface behaviour of the group, (h) diving pattern of the tagged individual. The data were all recorded on May 23, 2010.

Figure 3. Diving patterns of two tagged individuals within the same focal group. Horizontal dotted line: boundary between deep and shallow dives at 34 m depth. Vertical dotted lines: transitions between deep and shallow diving bouts for one or both individuals. The whale icons indicate whether the individuals performed deep diving bouts (icon below 34 m) or shallow diving bouts (icon above 34 m). The data

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were recorded on May 17, 2009.

Figure 4. Comparison of group-level data observed at the surface during shallow versus deep diving bouts of the tagged individual. (a) Group size, (b) number of individuals in the focal area, (c) number of groups in the focal area, (d) distance of the focal group to the nearest other group (n.i.s. = none in sight), (e) individual spacing, (f) surfacing synchrony (g) presence of calves, line swimming and milling, and (h) surface behaviour events. Differences between deep and shallow diving bouts were tested with Generalised Estimating Equations: ** Significant after Bonferroni correction (P/number of hypotheses tested) at $p < 0.05/12 = 0.0042$; * Marginally significant after Bonferroni correction at $p < 0.10/12 = 0.0083$; n.s. = not significant.

Figure 5. Relative importance of the behavioural parameters included in the final Random Forest model.

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Figure 1.

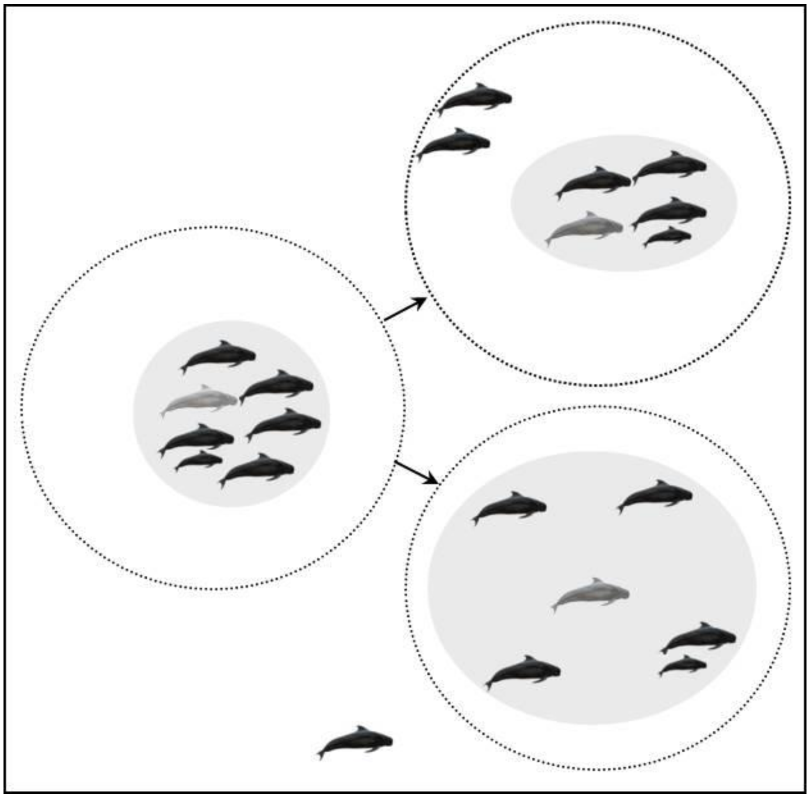

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Figure 2.

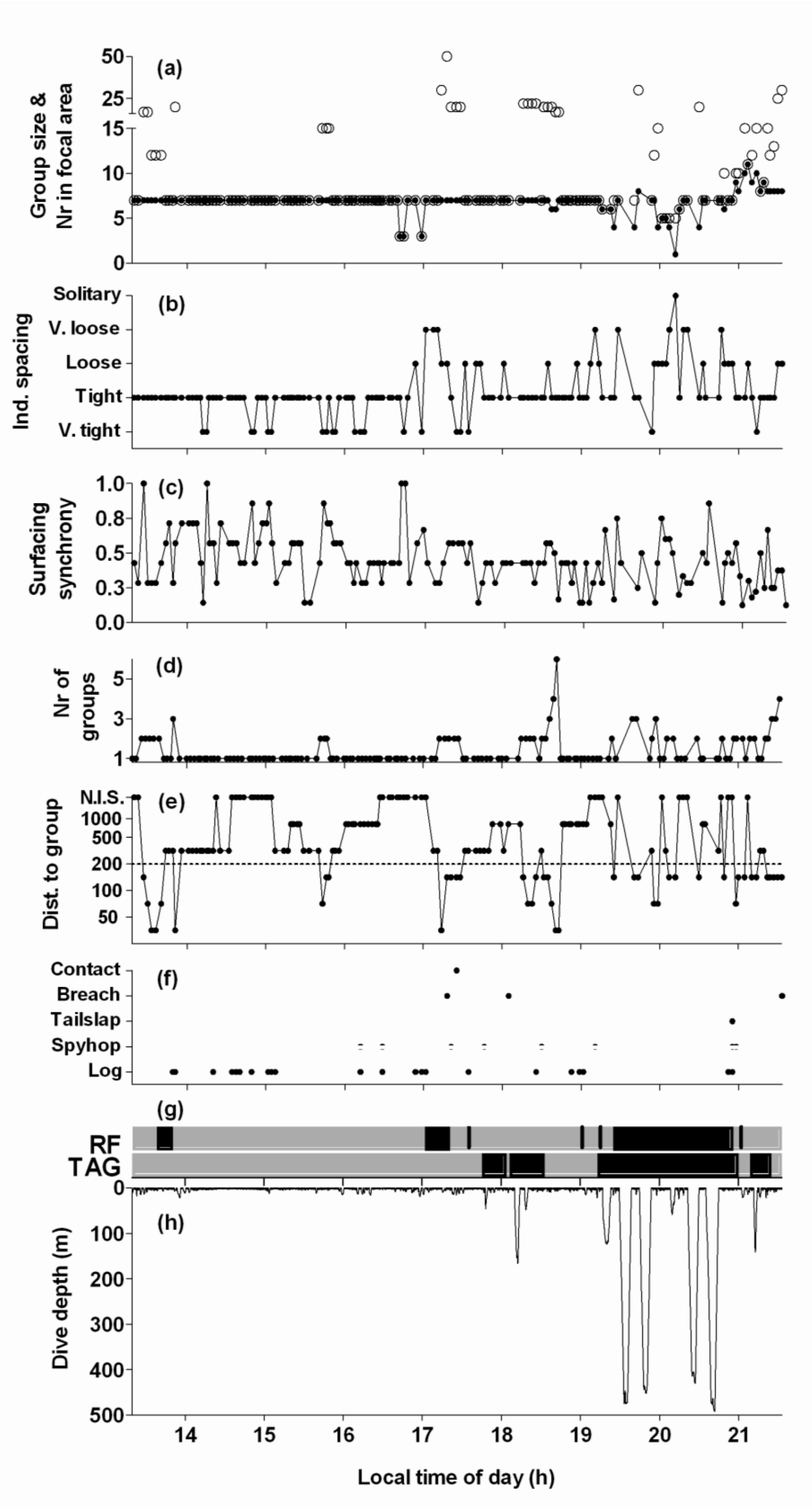

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Figure 3.

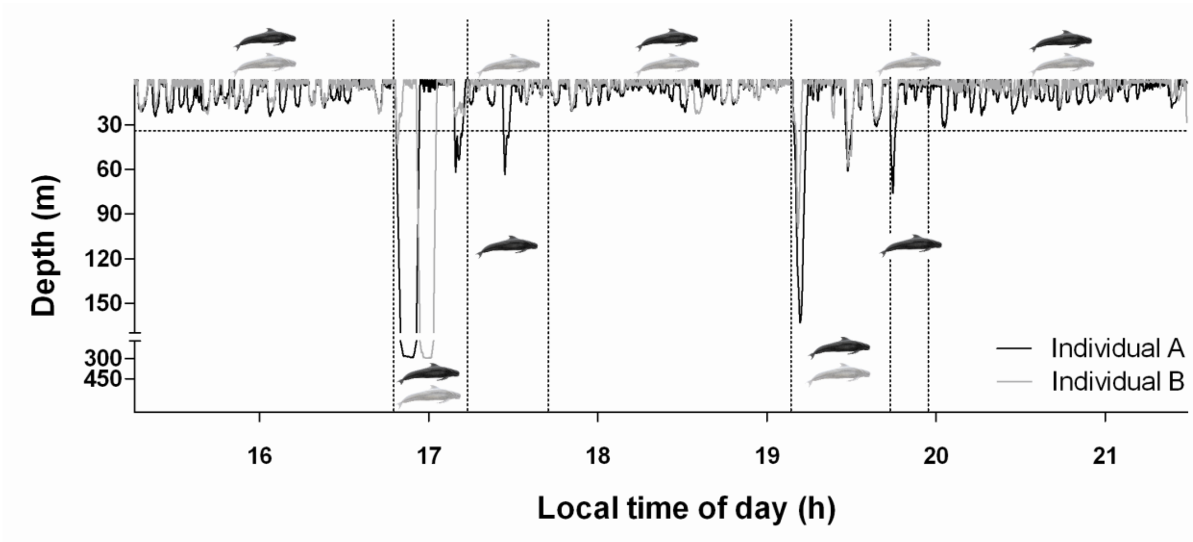

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Figure 4.

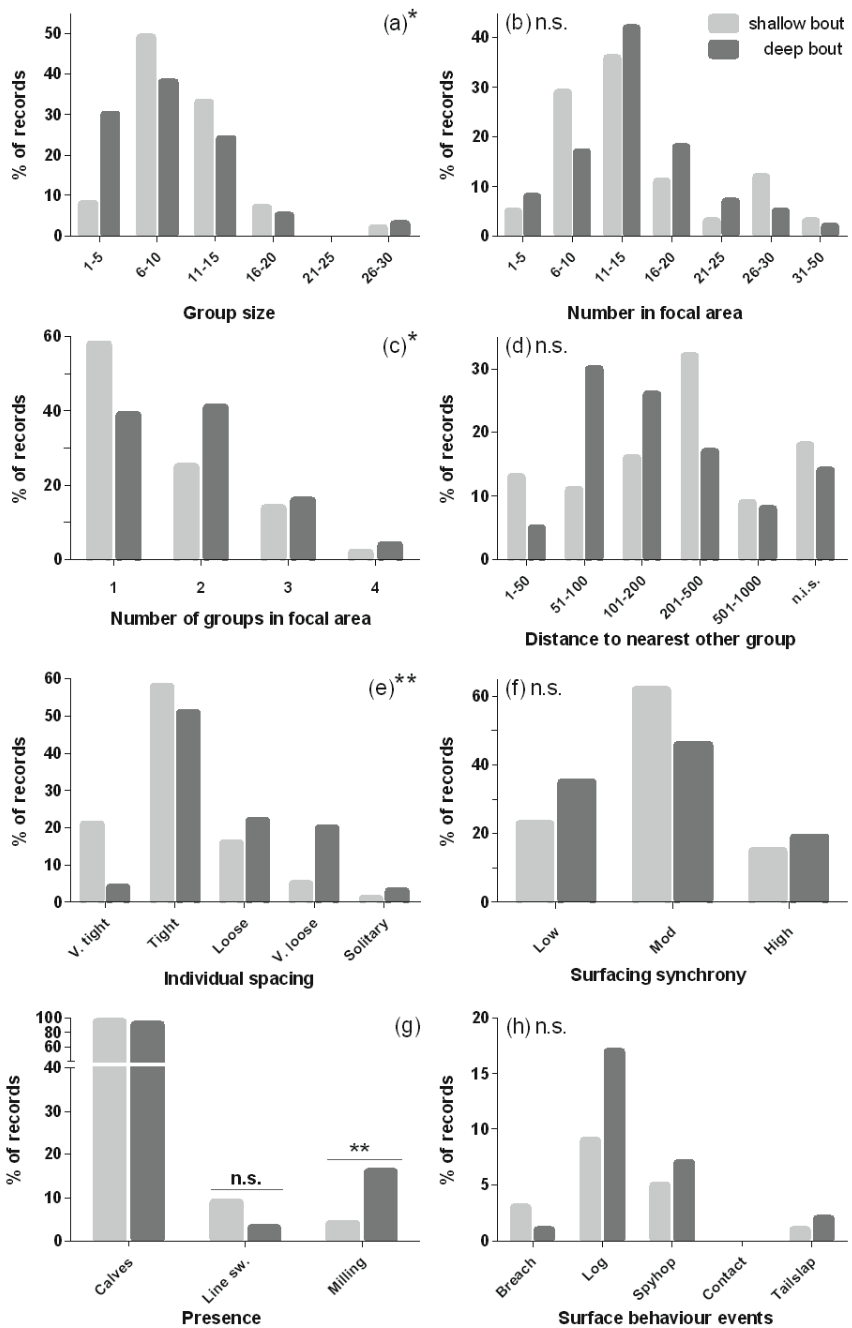

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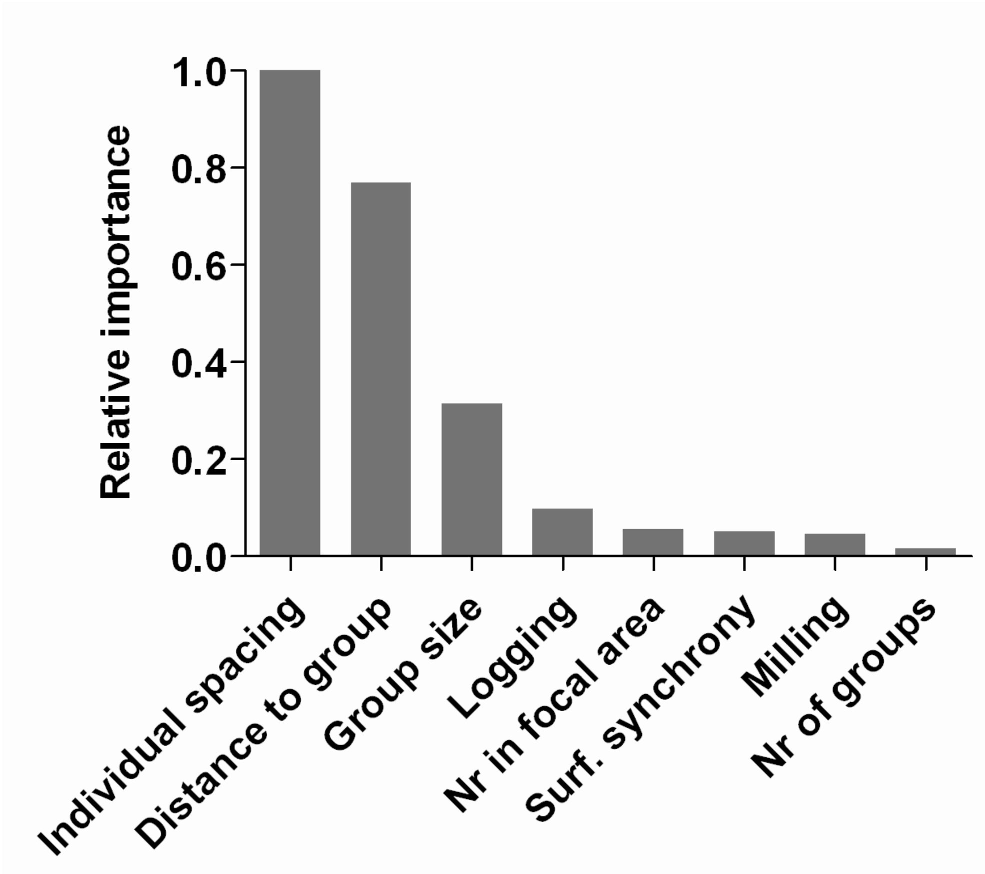
Figure 5.



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