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ORIGINAL PAPER

Highly dynamic fission–fusion species can exhibit leadership when traveling

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Abstract Leadership by specific individuals is thought to enhance the fitness of followers by allowing them to take advantage of the knowledge or skills of key individuals. In general, consistent leadership is expected to occur primarily in stable groups of related individuals where the benefits enhance the inclusive fitness of a leader. Societies with less stability in group composition (i.e., fission–fusion groups) are less likely to feature unshared decision making. However, in situations where frequent interactions among individuals occur (e.g., small population size and small range of movement) and/or the complexity of the environment requires substantial experience and knowledge, consistent leadership might be expected. We tested if a highly dynamic fission–fusion population of bottlenose dolphins (*Tursiops truncatus*), inhabiting a complex environment, exhibited leadership when traveling. A small number of specific individuals led group travel more often than expected by chance, and were more likely to initiate successful direction changes of groups than following individuals. The number of leaders in a group remained relatively constant across a wide range of group sizes and was not affected by the number of potential leaders (i.e., those that had led previously) present in the group. Together, these results suggest that leadership can occur in species with high rates of group fission and fusion. Therefore, the loss of key individuals could have disproportionate effects on population dynamics.

Keywords Bottlenose dolphin · Decision making · Fission–fusion · Group movement · Group size · Leadership

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Introduction

Unraveling the costs and benefits of group formation has been a primary goal of behavioral biologists, resulting in studies across a wide range of taxa and ecological conditions (see Krause and Ruxton 2002). Less work has focused on the relative contributions of specific individuals to the success of groups and to individuals in them. This perspective is important because individual contributions to foraging, reproductive success, and survival of group members can be divided unequally, either through proportion of time engaged, or through variation in tactics used (e.g., producer/scrounger dynamics, Caraco and Giraldeau 1991; "keystone individuals", Sih and Watters 2005).

Leadership, "where one or a few individuals steer the behavior of many" (King et al. 2009), also results in variation in group member contribution. For some species, direction of travel is guided primarily by a small number of individuals (e.g., Erhart and Overdorff 1999; Reebs 2000; Peterson et al. 2002; Stueckle and Zinner 2008). As a result, these "leaders" contribute disproportionately to the relative success of other group members because they guide them to or away from profitable resources (e.g., Conradt and Roper 2005; Fischhoff et al. 2007). For example, in African elephants (*Loxodonata* sp.) matriarchs appear to provide leadership for group travel (Payne 2003). Memory of water sources (sometimes in locations not visited in over a year's time) by matriarchs appears to be responsible for the relative success of this species compared to others during severe droughts (Viljoen 1990; Payne 2003). In species where group membership is relatively unchanging over time (e.g., gray wolves, *Canis lupus*, Peterson et al. 2002), followers must abide by the leader's decisions in order to maintain group stability (i.e., "unshared consensus decision making" Conradt and Roper 2005). However, in species exhibiting high levels of fission–fusion dynamics, where group composition and size changes frequently, individuals can select the group size, and potentially, the specific group that will maximize their fitness. Although fission–fusion societies exhibit considerable variation in the organization level and rate at which groups change in size and composition, in highly dynamic fission–fusion societies (i.e., high rates of change), interactions with the same individuals will be less frequent than in societies with stable groups. Therefore, consistent leadership by a restricted set of individuals should be less likely (Fischhoff et al. 2007). Such consistent leadership by specific individuals has been described primarily in species with relatively stable groups characterized by a dominance hierarchy (e.g., capuchins, *Cebus* sp., Di Bitetti and Janson 2001; gray wolves, Peterson et al. 2002). However, there may be situations where species with dynamic fission–fusion grouping might also demonstrate consistent leadership. For example, in complex habitats where resources are not easy to locate or navigation among habitats could be dangerous without adequate experience and understanding (e.g., risk of predation or starvation), knowledgeable individuals may consistently lead groups even if group composition is unstable. Additionally, individuals in some fission–fusion populations (i.e., those with small population size, restricted individual ranges, and small group sizes) interact frequently with other individuals providing an opportunity for individuals to identify effective leaders. Anecdotal evidence suggests that leadership, when traveling, does occur in some fission–fusion species (e.g., African elephants, Payne 2003, and spider monkeys, *Ateles* sp., Milton 2000). However, formal testing has yet to provide conclusive evidence for specific individual leadership, particularly in highly dynamic fission–fusion species.

Bottlenose dolphins (*Tursiops* sp.) are an example of a dynamic fission–fusion species in which individual recognition has been demonstrated (e.g., Connor et al. 2001). Recent work in Doubtful Sound, New Zealand on bottlenose dolphins has indicated that specific individual bottlenose dolphins may influence activity shifts through slapping the water surface ("side flops" and "lobtailing") (Lusseau and Conradt 2009). This finding suggests that in bottlenose dolphins, specific individuals have the capacity to influence movement of group members. However, it remains unclear whether this finding extends to other bottlenose dolphin populations and whether specific individuals influence group movement during travel.

The population of bottlenose dolphins inhabiting the heterogeneous coastal habitats of the Lower Florida Keys (LFK), USA offers a model system for examining these questions. First, the complexity of the area provides an impetus to follow knowledgeable individuals (i.e., multiple shallow basins divided by islands and deeper channels with accessibility affected by daily tides). Second, study of individuals within groups is possible in the LFK because the population is small (~150–200) and residential, and features small group sizes (mean = 4.4 ± 3.3 SD, Lewis 2002) and easily recognized individuals. LFK dolphins are characterized by a high rate of fission–fusion (mean = 54 ± 23 min SD between changes in group composition; unpublished data), such that the composition of all groups in this study was different.

We used the LFK population to test: 1) if certain individuals led by position (i.e., front of the group) more often than expected by chance; 2) if positional leaders controlled direction change more often than positional followers (to determine if control was correlated with position); and 3) whether factors including group size and number of potential leaders contributed to the number of individuals that led a group.

Methods

Data collection

Dolphins were located during surveys (n=238) from a 5-m fiberglass boat with an 110-hp outboard between Oct 2001 and Sept 2007 in the LFK (Fig. 1). Surveys followed predetermined routes along smaller zones within the study area (Fig. 1), traveling at approximately 22 km/hr. One to four zones were covered each survey day (depending on weather conditions). The habitat within these zones is mostly shallow (average depth ~2 m, range 0.5–10 m) with both vegetated (seagrass) and unvegetated regions (sand or hard bottom), bifurcated by deeper channels (range 4–10 m). Surveys occurred primarily (>95%) in zones 1, 2, 4, and 5 for the current study because dolphin sightings are more frequent in those areas. Survey routes allowed complete observation of all navigable waters within these zones. Surveys were only conducted under Beaufort wind conditions of three or less. When dolphins were located, we initiated continuous data collection of group members (Altmann 1974). We defined different groups (varying in composition from one another) to be our sampling units, and refer to these as "group samples". During our study, we

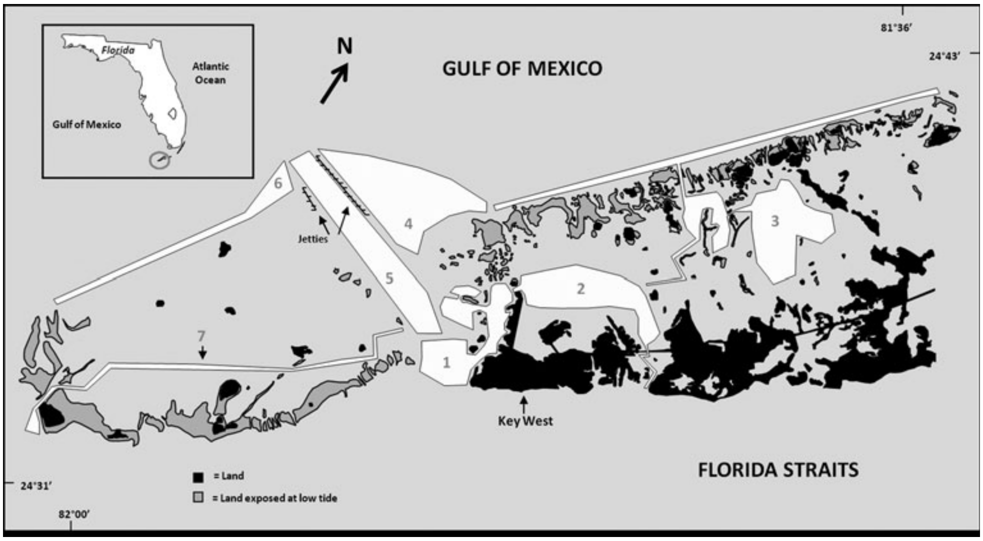

Fig. 1 Lower Florida Keys research area. Numbered zones within the study area include all navigable waters

collected 171 group samples (>1 individual). For data analysis, we used only group samples ≥30 min (n=161). Time spent sampling per group (for those used in analysis) averaged 87 min (SD=50 min, range 30–231 min). Individual dolphins were identified using unique patterns of nicks and cuts on their dorsal fins (Würsig and Würsig 1977). We recorded the relative positions of all individuals when animals surfaced, direction change attempts by all animals (change in heading estimated at >35º) and success of the attempts (i.e., other group members followed the new heading). It was possible to collect data on individual dolphins in LKF groups, especially the identity of individuals in the front position of groups, because group sizes are small and fins are easily identifiable. Group size and composition were continuously monitored during sampling. Groups were defined as all animals within approximately 100 m that likely were interacting, (i.e., traveling in the same direction, socializing, and maintaining proximity when foraging) (Shane 1990). Group fission was considered a physical separation (generally considered when over 100 m apart) of previously grouped individuals who were no longer interacting (i.e., no longer traveling, socializing, or foraging together). This definition was useful for our particular study because dolphins in the LFK tend to travel in different directions when fission occurs (personal observation). Also the multiple islands and shallows (<0.3 m) that divide areas where the LFK dolphins live hinder vocal communication as dolphins move apart. When fissions occurred, we maintained sampling with the portion of the group that contained the individual that had previously been in the front position during group travel.

Because our data included relative positions of individuals during surfacing events, it was important to verify whether surfacing positions corresponded to subsurface travel. This was done using an overhead video camera (Sony® CD52W) mounted below a tethered airship (Floatograph®) (Fig. 2). Pan, tilt, and zoom of the lens, mounted below the airship, were controlled on board the vessel where video was displayed on a monitor and recorded to DVD. Because waters of the Florida Keys are relatively clear (visibility averages ca. 6 m), the overhead camera allowed continuous viewing of dolphins across most of our study area. We collected positional data for 41 individuals in 17 groups (15 h of footage) using the airship. Footage was reviewed using The Observer® (Noldus Information Technology).

Data analysis

We used two methods to define a threshold level for the time spent in the front position that could be considered as "leading" for each group sampled. These methods were used not to test explicitly for consistent leadership by specific individuals, but to identify a threshold for classifying individuals during a particular group sample as assuming a greater proportion of time in the lead position than is typical (i.e., calling a dolphin a "leader" during a particular group sampling). Using this threshold for leadership during a group sampling, we could then investigate if particular individuals led during more group samples than would be expected by chance (i.e., displayed "consistent leadership" across group samples). Methods for determining this within-group sample threshold for leadership included 1) comparing the number of individuals that "fit" into each bin for proportion of leadership through surfacing during the first 30 min of each group sample (Bins used included 0%, >0% to 10%, >10% to 20%, etc.), and 2) comparing the average leadership values between individuals that had been sampled at least five times (n=47 individuals). Using individuals who had been sampled at least five times

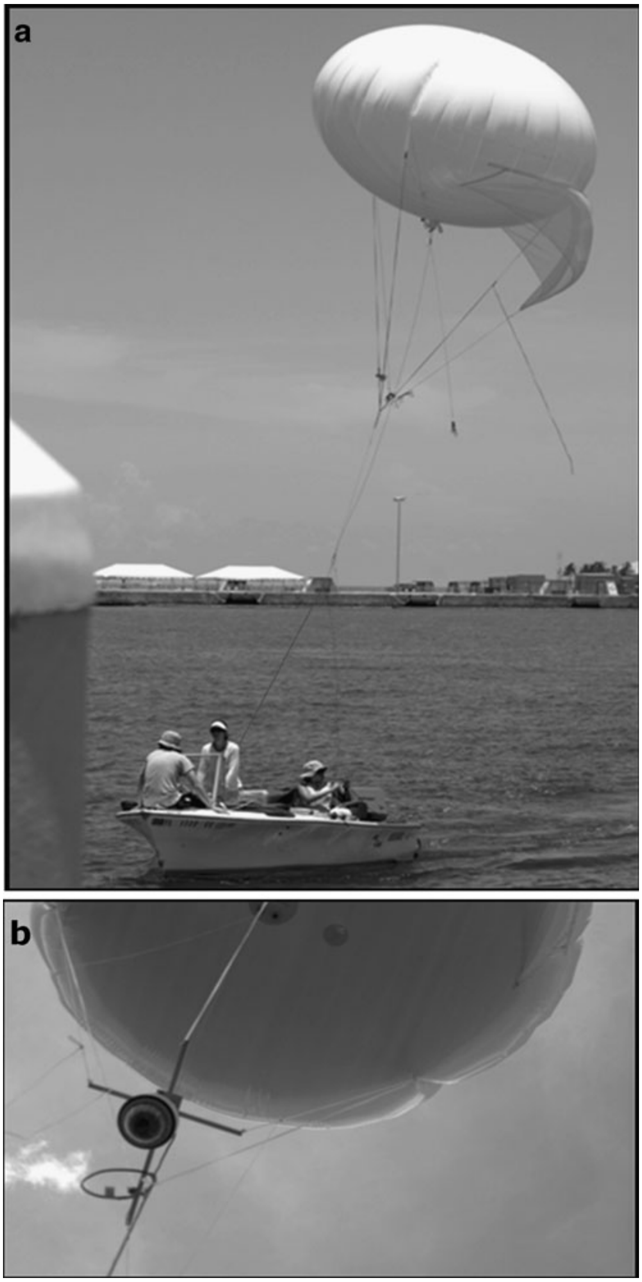

Fig. 2 A Floatograph® airship (**a**), was used to mount a video camera, (**b**), for continuous monitoring of dolphin behavior. The airship was tethered to the research vessel and towed during surveys and group sampling

provided us with a representative group that included 47% of the 100 individuals sampled for leadership.

Using the within-group sample leadership threshold (20% of group sample duration in lead position; see Results), we examined if specific individuals exhibited leadership during more group samples than would be expected by chance. Data used included only the part of a group sample prior to any fission or fusion event (if one occurred during that group sample). We employed a randomization protocol (Manly 2006) using data from 20 individuals. These individuals were chosen based on sample size requirements per individual (power analysis, $\beta \geq 80$). We compared the number of times each individual led ≥20% of a group sample to the number expected based on 1,000 randomization iterations for each individual (i.e., a test was performed for each individual). For each iteration, we randomly reallocated the observed proportions of time individuals spent in the lead among all group samples of the 20 individuals tested. We then determined the number of times the focal individual was in the lead position of a group sample ≥20% of the time based on the randomizations. We compared our field observations to the distribution of expected number of group samples that individuals were leaders and considered an individual to consistently be a leader if the field observation was greater than 97.5% of the randomizations ($P<0.05$ for a two-tailed test).

To determine if positional leaders controlled group movement, we examined factors affecting the probability of successfully changing the direction of a group's travel (defined as having other group members follow the new heading). Using logistic regression (Tabachnick and Fidell 1996), we tested whether position within a group (i.e., lead position or following), group size, or number of participating leaders influenced the probability of successfully changing the direction of a group's travel. No individuals were used more than once in this test.

To examine how the number of leaders in a group (leading defined using threshold) was affected by group size, we used Theil's regression (Daniel 1990). We included only adults, because calves could not be potential leaders and did not move ahead of group members when traveling. Number of leaders was also compared pre- and post-fission and fusion (using Wilcoxon tests). To determine whether the number of leaders per group differed from the number available, we used a Wilcoxon sign rank test. Available leaders used were those that had led (according to our threshold of leadership) during the year of the group sample tested. Finally, we examined the number of leaders per group sample to the length of the group sample to determine if sample length affected the number of leaders noted (Spearman's rank correlation).

Results

Dolphin groups used in the analyses reported below ranged between two and 27 individuals when calves were included in counts (mean = 6.3 ± 4.1 SD, median=5). When calves were excluded from group size calculations, groups ranged between two and 22 (mean = 5.1 ± 3.3 SD, median=4). Note that these group sizes are larger than those reported for this area (mean = 4.4 ± 3.3 SD; Lewis 2002) because our current analysis excludes lone individuals.

Using video collected from the airship, we found a strong positive correlation between the proportion of time individuals spent in the lead position of a group (both surface and subsurface observations) and the proportion of time in lead position by those individuals based only on surfacing events (Spearman's rank test r_s=0.94, P<0.0001). Thus, relative positions of individuals during surfacing bouts reflect total time spent in lead positions.

The majority of individuals (69%) spent <20% of the time leading during the first 30 min of all group samples (Fig. 3). Seventy percent of all individuals also had average leadership values that were <20% (Fig. 3). Because both methods indicated that the majority of individuals spend <20% of their time leading, we established 20% as the threshold for an individual to be classified as a leader for a specific group sample.

The Monte Carlo simulation showed that three of the 20 individuals tested led during more group samples than expected based on chance (Fig. 4; see Fig. 5 for an example). These individuals led ≥20% during the majority of all group samples where they were present (proportion of group samples where individuals led ranged from 77% to 84%).

The probability of initiating a successful direction change was influenced by the position of the individual (leader vs. follower) (χ^2=22.52, df=1, P=0.0001) but not by group size (χ^2=0.52, df=1, P=0.47) or the number of leaders in the group (χ^2=0.49, df=1, P=0.49). Leaders made more attempts at changing direction and were more successful than followers (88% of 26 leader attempts, compared to 38% of 13 follower attempts) (Pearson Chi-square χ^2=18.59, df=1, P<0.0001) (Fig. 6).

The number of individuals in a group that led during a group sample remained constant over all group sizes (slope= 0, τ=0.13, P=0.06). Total number of leaders per group sample never exceeded three, and most group samples had only one (46% of group samples) or two (44% of group samples) leaders. The number of leaders did not change significantly after fission (Wilcoxon test P>0.999) or fusion (Wilcoxon test z=−0.78, P=0.44).

The number of participating leaders (mean = 1.61 ± 0.61 SD) was significantly lower than the number of potential leaders in a group (mean = 3.75 ± 2.39 SD), (Wilcoxon test z=−8.474, P<0.0001, n=122), and the number of leaders did not vary with the length of time that a dolphin group was sampled (Spearman's rank test r_s=0.12, t=1.37, n=131, P=0.17).

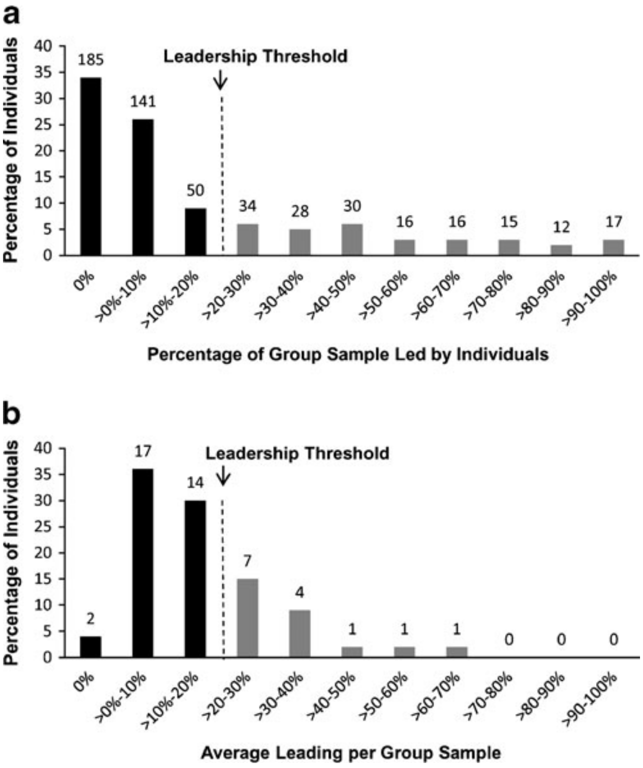

Fig. 3 Measures for time spent leading by individuals. These preliminary analyses allowed determination of leadership threshold to be used in each group sampling. (**a**) The proportion of individuals that led groups for different percentages of time during the first 30 min of 104 group samples [e.g., 34% (185 of 544 individuals), never led] and (**b**) the proportion of individuals with various average time spent leading across group samples (individuals used had >5 group samples, n=47 individuals) [e.g., 4% (2 of 47 individuals) never led]. Bars representing the number of individuals that were <20% of all observations are colored black for each graph. Black bars in both graphs represent greater than the majority of observations for each comparison (69% and 70%, respectively). Numbers above bars are the number of individuals

Discussion

Our findings indicate that most individual bottlenose dolphins in the Lower Florida Keys spend little time leading group movement, but a small number of individuals consistently spend a significant amount of time in the lead position. This small subset of leading individuals was disproportionately responsible for the direction of group travel (through position and success at direction change).

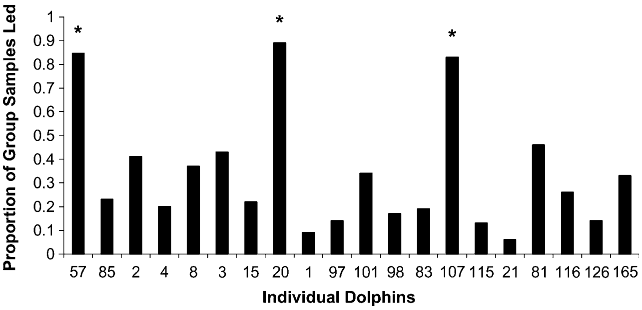

Fig. 4 The proportion of group samples where individual dolphins spent more than 20% of the sample in the lead position. Individuals that led significantly more than expected based on chance are labeled (*). All animals leading more than expected had P<0.002

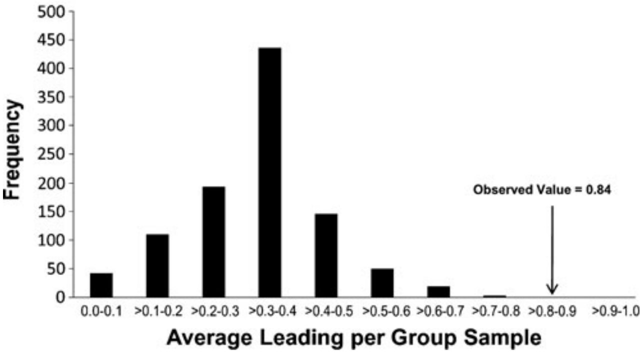

Fig. 5 Example of a frequency histogram generated by randomizations (n=1,000 iterations) to test for greater than expected leadership by dolphin 057. The observed value is indicated with an arrow

Together, these results provide the first evidence for leadership by specific individuals when traveling in a species using highly dynamic fission–fusion grouping.

To date, consistent leadership when traveling has been documented primarily in societies with stable group composition (e.g., Rasa 1987; Peterson et al. 2002). Such leadership roles tend to coincide with dominance hierarchies (Peterson et al. 2002; Fischhoff et al. 2007; King et al. 2008; Jacobs 2008). In non-hierarchical groups, leaders tend to be those in need of a specific resource (i.e., "diversified leadership", Levin 1996; or "leading according to need", Conradt et al. 2009). Hungrier animals will start traveling first, and because others within the group tend to follow these movements, they will travel in the direction established by the leader (Šárová et al. 2007; Barelli et al. 2008). Under "diversified leadership", the animal in the lead can vary from travel point to travel point and the individual in front changes frequently with no consistency in leader identity over time. Because the composition of groups changes frequently, and is often based on the particular needs and behavioral state of individuals, animals using fission–fusion grouping would be expected to follow a particular individual for relatively short periods of time, but specific individuals should not consistently be found in the lead position (Fischhoff et al. 2007).

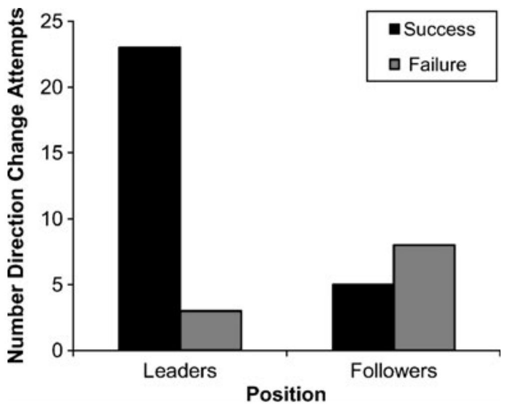

Fig. 6 Number of successful and unsuccessful direction change attempts by leading and following bottlenose dolphins

Certain conditions are likely necessary for consistent leadership by specific individuals in highly dynamic fission–fusion populations. These may include a complex environment or spatiotemporal variation in resource abundance and/or predictability that requires significant learning for efficient movement. Leadership may be important for LFK dolphins because of the heterogeneous and complex nature of the marine habitat in this region. Seagrass flats and unvegetated shallow water basins are surrounded by many large stretches (ranging from ~1 to 20 km^2) of extremely shallow water (<0.5 m) that are not accessible at low tides. Many expanses of productive shallow habitats are accessible only via a handful of deeper channels. Because some areas can only be accessed or traversed during high tides, and others are only accessible via few deeper channels, mistakes regarding movement paths could lead to stranding or a loss of foraging opportunities. Therefore, dolphins without sufficient experience would benefit by following others with greater knowledge.

There is some evidence for using experienced individuals as leaders in stable groups. For example, within a controlled setting, naive fish will follow experienced individuals when foraging (Reebs 2000). Anecdotal accounts of traveling gorillas also report that group members look to older, more experienced males for leadership when encountering complex environments (Milton 2000). Within fission–fusion type species, accounts related to leadership hint at knowledge (bottlenose dolphins in New Zealand, Lusseau and Conradt 2009; African elephants, McComb et al. 2001) of leaders as a useful source for group members.

Leadership may also be related to physiological state of individuals (i.e., hungrier individuals may be more likely to lead, Krause et al. 1998; Fischhoff et al. 2007). Although energetic demands may contribute to leadership behavior within particular groups, our results suggest that it is not the primary driver of leadership in the LFK population. Indeed, if energetic demands were the primary motivation for leadership in LFK dolphins, we would not have expected to find particular individuals consistently leading group movements. Furthermore, we might expect that individuals with greater energetic demand (e.g., larger individuals or lactating females) might be more consistent leaders. This also does not appear to be the case. There is little sexual size dimorphism in bottlenose dolphins in Florida waters, and it is difficult to distinguish adult animals based on size. Therefore, it is not surprising that we did not note any obvious differences in the sizes of individuals leading relative to those that followed. Two of the consistent leaders were mothers (indicated by presence of calf next to the individual on >5 occasions), but seven of the ten female followers that were tested for consistent leadership were also mothers. Further studies are necessary for elucidating factors that determine leadership by specific individuals in the LFK.

Particular features of a fission–fusion population may also help to determine if specific individuals will consistently lead group movements. Leadership by specific individuals on a repeated basis requires frequent and regular interaction among the same individuals so that followers can identify effective leaders. Therefore, populations would need to be small, form small groups, with individuals inhabiting small and stable home ranges. The LFK population exhibits all of these features. Some bottlenose dolphin populations with fission–fusion dynamics, may be less likely to exhibit consistent leadership because of large population sizes (e.g., Mississippi Sound, Hubard 1998), long-distance migrations (e.g., Atlantic Coast, United States, Barco et al. 1999; Wood 1998) large group sizes (e.g., Pacific Coast, United States, Defran and Weller 1998), or relatively predictable resources and easily navigable habitats (e.g., Shark Bay, Australia, Heithaus and Dill 2002).

Interestingly, in the LFK, the number of individual dolphins that led during a group sample remained low (never greater than three and usually only one or two) regardless of group size or length of group sample, even when multiple potential leaders were present. Because it only takes a few informed individuals to move a group accurately from one point to another (Couzin et al. 2005; Dyer et al. 2008), it is likely that having a low number of leaders per group provides a mechanism for more efficient travel (Conradt and Roper 2005). A low number of leaders may reduce chaos in decision making, wasting less time and energy. For example, social insects use a small fraction of colony members as scouts to aid in group movement decision making, such as location of food or hive relocation (Hölldobler and Wilson 1990).

The mechanisms for control of group movement vary within and among species (Overdorff et al. 2005; Fischhoff et al. 2007) and can be context dependent (King et al. 2008). In another closely related bottlenose dolphin species, *Tursiops aduncus*, in Shark Bay, Australia, male pairs and trios control movement of individual reproductively cycling females through aggressive herding (Connor et al. 1992). We have not observed herding in LFK bottlenose dolphins. Instead, males usually interact reproductively with females in larger mixed-sex groups. Sexual activity in LFK groups usually occurs towards the rear of a group because the involved individuals are slower to progress. These individuals follow movement choices but do not initiate them. Because foraging behavior usually occurs at the end of prolonged travel bouts in LFK groups, finding prey is likely a primary goal for movement and movement decisions of dolphins in this area. In Doubtful Sound, surface slapping (side flops and upside down lob tails) by bottlenose dolphins (*Tursiops truncatus*) initiates activity changes in groups (Lusseau and Conradt 2009). In the LFK, surface slapping occurs rarely, and only in a social context. Although these factors (herding or control of movement through surface impact behavior) did not contribute to control of movement in the LFK population, they need to be considered in studies of leadership for other dolphin populations. Indeed, results from Shark Bay, Doubtful Sound, and LFK suggest that specific individuals may disproportionately influence group activities and/or movements in multiple bottlenose populations.

The presence of leadership in the LFK population has important implications for conservation and management. LFK animals guiding movement may be “keystone individuals” and potentially play an important role in the viability of the LFK population by shaping habitat use patterns, and enhancing foraging opportunities for other individuals. When matriarchs in groups of African elephants (*Loxodonta africana*) are lost from the population, significant disruption can occur to remaining group members, because these “leaders” (Payne 2003) act as storehouses of critical social information that enable groups to manage time efficiently (McComb et al. 2001). Coastal dolphins are under pressure from many sources (e.g., contaminants, Litz et al. 2007, habitat alteration, Watson-Capps and Mann 2005, and vessel traffic, Nowacek et al. 2001), and although these stressors may not disproportionately affect leaders, our results suggest that the loss of specific individual dolphins (leaders) from the LFK population may have a greater proportional impact on the population than would be expected otherwise. Further investigations of the specific roles of leaders and the characteristics of individuals that are consistent leaders, therefore, should be a priority.

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