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Assessing Foraging Tradition in Wild Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

We analysed the association patterns of 22 bottlenose dolphins (*Tursiops truncatus*) identified as resident in the waters of the Archipelago de La Maddalena (Italy) to verify the existence of defined groups with a particular foraging strategy: to feed from fishing trammel nets. Two relatively well-defined communities were identified. Bottlenose dolphins that were observed feeding from trammel nets constitute one of these communities, and the other is mainly made up by individuals who have never been seen foraging from nets. The influence of sex, habitat, school size, location, and the presence of calves over the bottlenose dolphins' feeding behavior was also analyzed. Only the presence of calves shows a significant effect. It alone explains 23% of the variability in the foraging behavior. This percentage is not high enough to conclude that the presence of calves in a community of bottlenose dolphins is what determines their foraging behavior, but it seems that their presence does incite the net-foraging behavior by the adults. This study provides evidence for socially learned tradition in foraging tactics within a community of wild bottlenose dolphins, and it demonstrates the advantage of using the Ward's minimum variance method of hierarchical clustering to assess the existence of association patterns among individuals.

Key Words: association patterns, bottlenose dolphin, *Tursiops truncatus,* cetacean culture, foraging specializations, social learning

Introduction

Considerable attention has recently been focused on the role of social learning in explaining variation in foraging strategies for different species (e.g., Fragaszy & Perry, 2003; Laland & Hoppitt, 2003; Sargeant et al., 2007; Sargeant & Mann, 2009). Laboratory experiments have established numerous ways that animals can socially learn foraging behaviors, and several studies have documented social learning on species in captivity (e.g., Laland & Williams, 1997; Galef & Whiskin, 2008) and in the field (Terkel, 1996; Reader & Laland, 2002). Social learning is a result of complex cognition, individual differences, and behavioral flexibility that allows animals to adapt quickly to changes in their environment (Estes et al., 2003; Laland, 2004; Whiten & van Schaik, 2007; Sargeant & Mann, 2009). Moreover, social learning is regarded as the most essential requisite to define a "culture" in animals (Laland & Hoppitt, 2003), and it is defined as a process that involves the social transmission of a novel behavior, both among peers and between generations (De Waal, 2001). This behavior is shared by a group of animals but not necessarily between separate groups of the same species.

Bottlenose dolphins (*Tursiops truncatus*) are particularly well-known, among all marine mammals, as one of the species with the most powerful imitation skills (Herman et al., 1993), as well as complex cognitive and sophisticated learning abilities (Marino et al., 2007), both in the wild and in captivity (Xitco & Roitblat, 1996; Kuczaj et al*.*, 1998; Boran & Heimlich, 1999; Mann & Sargeant, 2003; Krützen et al*.*, 2005). Additionally, bottlenose dolphins possess features thought to support social transmission (Coussi-Korbel & Fragaszy, 1995) such as social tolerance (Scott et al., 2005), coordination in time and space (Mann et al*.*, 2000), complex cognition (Marino et al., 2007), and motor imitation (Herman, 2002). Furthermore, vertical transmission between mothers and calves probably contributes to the transfer of behaviors that are usually tested, stable, conservative, and experience-based (Herzing, 2005). Behavior of this kind is also slow to change and is particularly likely to be transmitted given that calves spend between 3 to 8 y of their life with the mother (Mann et al., 2000; Mann & Sargeant, 2003; Sargeant et al., 2005).

Different innovative foraging techniques have been documented for bottlenose dolphins, including mud plume feeding (Lewis & Schroeder, 2003), kerplunking (Connor et al., 2000), crater feeding (Rossbach & Herzing, 1997), and sponge-feeding (Smolker et al., 1997; Sargeant & Mann, 2009). Bottlenose dolphins have also adapted to human activity by following fishing boats to obtain discarded fish (Corkeron et al., 1990; Chilvers & Corkeron, 2001), visiting fish farms (Mann & Kemps, 2003; Diaz-López, 2006), and fishing directly from nets (Bearzi, 2002; Lauriano et al., 2004).

In particular, several studies have recognized that bottlenose dolphins have learned that catches from fishing gear comprise a new, easily accessible food resource (Reeves et al., 2001). The removal of fish from nets results in a loss to fishermen of time, money, or gear (Bearzi, 2002; Lauriano et al., 2004), and it increases the potential to seriously injure or kill the animals through entanglement (Wells & Scott, 1994; Wells et al., 1998). However, sometimes bottlenose dolphins' interaction increases the chances of a fishery's success (Silva et al., 2002), and such events can be described as cooperative in nature (Pryor et al., 1990; Neil, 2002).

Social learning probably contributes to the development of this kind of foraging strategy from nets, which results in an increase in the rate of feeding and a decrease in the energy expenditure required (Fertl & Leatherwood, 1997; Díaz López, 2006). Differences in foraging behavior may also be explained by other factors independent of social learning such as sex, school size, and habitat use (Mann & Sargeant, 2003; Sargeant et al., 2005; Mann et al., 2008).

Although several studies have evaluated and quantified the interactions between bottlenose dolphins and fishing activities, few studies have been undertaken to understand whether this type of foraging technique is due to social learning. To test the existence of social learning, researchers typically attempt to rule out ecological and genetic factors as possible explanations for differences between groups, leaving social learning as the remaining candidate (Whiten et al., 1999; van Schaik et al., 2003).

In the waters of the Archipelago de La Maddalena (Sardinia, Italy), a net-foraging behavior has been documented and quantified (Rotta, 2009), but only in regard to the interactions with the fishing activities. In this study, we used hierarchical cluster analysis to verify the existence of different communities among the bottlenose dolphins observed in this Archipelago in order to test if there is a correlation between the foraging strategy of the bottlenose dolphins and community membership. A significant correlation would indicate social learning and foraging tradition if other factors, such as location, habitat, season, school size, or presence of calves, do not explain the occurrence of this specific foraging tactic. We use a logistic regression to assess other plausible hypotheses for the observed pattern.

Methods

Study Area

This study was carried out in the waters within 4.8 km of the coasts of the Archipelago de La Maddalena, located in northeastern Sardinia, Italy (41° 13' 0" N, 9° 24' 0" E). The entire area is included in a National Park (established May 1996) located on the strait of Bonifacio, between the islands of Sardinia and Corsica, and is part of the Pelagos Cetacean Sanctuary, recognized by Italy, France, and Monaco in 1999.

Only 18 authorized fishing boats from La Maddalena National Park can practice artisanal fishing activities. These activities are conducted in accordance with park regulations throughout the year, except for 45 d every winter when the fishery is closed. Bottom-set fishing gear, such as trammel nets, is the main fishing gear; while other gear, such as traps, is sporadically used. The net mesh size is chosen based on the main target species and on the season (see Table 1).

Field and Study Methods

From January to September 2006, a preliminary study was conducted in Archipelago de La Maddalena waters. During this first pilot year, almost all bottlenose dolphins were identified, photographed, and classified with an alphanumeric identification code. Photo-identification was based on the pattern of nicks, lesions, scars, and variation in dorsal fin shape (Wilson et al., 1999). Each individual was categorized as *trammel feeders* (TFs) or *non-trammel feeders* (NTFs) based on whether it had been observed foraging on trammel nets at least five times (Chilvers & Corkeron, 2001).

This first-year pilot study was essential to design an appropriate research survey protocol. Following this protocol, research data were obtained from October 2006 to September 2008. The study area was divided into five subareas of equal dimension and each was monitored for 40 h in a boat travelling at a speed of 8 to 10 kts. The courses followed during the monitoring were random transects as was appropriate for the geological characteristics of the area. Data collected included sighting date, location, school size, sex, and behavior. To ensure that all behaviors were visible across the study area,

Table 1. Seasonality of the use of trammel nets and the primary targeted species

Net mesh size	Target species	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
20-25 mm	*Mullus surmuletus*							X	X	X	X	X	X
28-36 mm	Molluscs			X	X	X	X						
20-36 mm	Other fish	X	X	X	X	X	X	X	X	X	X	X	X
50-62 mm	Spiny lobster			X	X	X	X	X	X				

surveys were only performed when the sea state was less than Douglas sea force 3 and in clear conditions with no precipitation. A *school* was defined as a group of bottlenose dolphins sighted within an approximate 100 m radius (Wells et al., 1987). Individuals were identified as belonging to three arbitrary age classes based on visual assessment using the average adult size: (1) adult (a bottlenose dolphin approximately 2.5 to 3.0 m long), (2) juvenile (about two thirds of an adult), and (3) calf (newborn with evident fetal folds or individual about one-half of an adult in constant association with its mother) (Bearzi et al., 1997). The gender was determined when possible by the presence of a dependent calf or direct views of the genital area (Connor & Smolker, 1985; Smolker et al., 1992).

Behavioral data were collected using the predominant group activity sampling method (Altmann, 1974; Mann, 1999) with the group activity being scored every 5 min. To standardize data collection, behavioral activity was sampled for at least 45 min unless contact with the group was lost before that time.

In order to avoid harassment of bottlenose dolphins, we observed them from a safe and respectful distance, avoiding approaching them closer than 30 m, using binoculars or telephoto lenses to get a good view of the animals. If bottlenose dolphins approached the boat, we maintained its course, avoiding abrupt changes in direction or speed to prevent running over or injuring the animals.

The behavior of dolphins was classified either in the field or *a posteriori* (based on detailed descriptions) into one of five exclusionary categories, according to Smolker et al. (1992), Mann & Smuts (1999), and Chilvers & Corkeron (2001):

1. *Foraging/Feeding* – Rapid surfaces, frequent direction changes, fast swims, fish chases, and observations of fish catches. Feeding as defined by long dives in the vicinity of trammel nets was considered "trammel foraging."
2. *Resting* – Very slow travel or hanging at the surface.
3. *Socializing* – Physical contact, splashing, chases, pokes, and plays with little consistent directional progress.
4. *Travelling* – Swimming in a constant direction with regular surfacing intervals.
5. *Unknown* – Not classifiable in the previous categories.

In addition, in order to assess more precisely the evidence for *trammel foraging* behavior, an observer aboard commercial boats collected data on bottlenose dolphin attacks and depredation. Evidence of trammel foraging behavior was estimated by the presence of at least one damaged fish on nets and/or new holes (Lauriano et al., 2004). Based on the nature of the damage, the depredation was identified as due to bottlenose dolphins or other species, such as sea turtles.

Bottlenose dolphins that were identified in all seasons (regardless of year), and at least five times, were considered to be residents. Individuals sighted only during a single season were defined as seasonal residents. Those seasonal residents that were seen less than five times were considered to be transients. Although 71 individuals were photo-identified, we included in the analysis only the 22 of these classified as resident; and only those encounters in which at least 50% of all adult bottlenose dolphins were photo-identified were used for the analyses (Lusseau et al., 2006).

Statistical Analysis

Hierarchical cluster analysis was performed to estimate the degree of association between the individuals of the study in order to test the existence of different communities, or groups of individuals, showing a significant degree of association. Cluster analysis can be used to find structure in the data, most often by identifying groups of similar objects or, as in this study, objects that occur more frequently together. Unlike classification and regression trees, cluster analysis falls into the category of unsupervised learning methods since it does not require a set of observations for which group membership is known. It is possible to assess the uncertainty obtaining approximately unbiased *p*-values (AU *p*-values) for all clusters contained in the clustering of original data.

Each sighting was considered a sample unit, and the presence/absence of the 22 individuals were considered dichotomous variables. Thus, the higher the number of times that two individuals were viewed together, the closer they will be in the resulting dendrogram.

There were 93 sightings available for the analyses. However, it would be partially tautological to include in the analyses sightings of net-foraging behavior to test if those bottlenose dolphins that practice net-foraging are more associated. In order to avoid this problem, 24 sightings in which this net-foraging behavior was recorded were excluded for the cluster analyses.

Distances between individuals were computed using the Ward's (1963) minimum variance method. This method uses an analysis of variance approach to evaluate the distances between clusters, attempting to minimize the total within-cluster variance. This makes it especially useful for finding compact clusters, essential for the identification of "communities," or groups of individuals showing a significant degree of association. We used the *pvclust R* package to both perform the cluster analysis and assess the AU *p*-values (R Development Core Team, 2012).

Additionally, a logistic regression was used to analyze the extent to which other factors, such as location, depth of seabed, season, school size, or presence of calves, explained the occurrence of this specific foraging tactic.

The 93 sightings available for the analyses were modeled as a binary process, $Z_i \sim \text{Binomial}(\pi_i)$. In particular, 1 indicates sightings in which the trammel foraging behavior was recorded, and 0 indicates the opposite. The probability of recording the trammel foraging behavior is indicated by π_i. The model can be expressed as

$$Z_i \sim \text{Ber}(\pi_i)$$
$$\text{logit}(\pi_i) = X\beta$$

where β represents the vector of the regression coefficients, X is the matrix of covariates, and the logit transformation is defined as $\text{logit}(\pi_i) = \log(\pi_i/1 - \pi_i)$.

As covariates, we used location, depth of the seabed, season, school size, and presence of calves for each sighting.

Logistic regression analysis was also performed using *R* software. Different models were run, and the goodness-of-fit of each one was assessed using both the Akaike Information Criterion (AIC) (Akaike, 1974) and the adjusted coefficient of multiple determination R^2_K (Neter et al., 1990).

Results

Sixteen out of 22 resident dolphins (72.7%) were identified as females, 11 of which (68.8%) were identified as mothers as determined by the presence of a dependent calf.

In 54 out of 93 sightings (58.1%), feeding behavior was recorded, 24 of which (44.4%) was net feeding. Travelling was recorded in 21 encounters (22.6%), socializing in seven (7.5%), resting in another three (3.2%), leaving the remaining eight encounters (8.6%) to be classified as unknown.

Among the 22 resident dolphins, 13 (59.1%) were identified as TFs and nine (40.9%) as NTFs. Figure 1 shows the dendrogram resulting from cluster analysis together with the AU *p*-value of each cluster. Two main clusters, significant at least at the 95% CI ($p < 0.04$), are observed, together with two independent individuals associated with each other. One of these clusters is clearly related to the TFs (capital letters) and the other cluster to the NTFs (lower case letters). The two independent individuals are also TFs. All the individuals of each main group share the same feeding habits, with the sole exception of one individual in each group.

In the cluster of TF, seven out of 11 are females (64%), while seven out of nine are females in the NTF cluster (77%). No significant sex influence was found with respect to the two main groups (Fisher's exact test $p = 0.06$). Five out of seven females in both clusters, TF and NTF, are recognized as mothers by the presence of a dependent calf. Obviously, no significant differences were found between the groups (Fisher's exact test $p = 0.08$).

The logistic regression showed that only the presence of calves is a driving factor in the trammel-feeding behavior ($p < 0.0012$). Throughout the process of selection of the significant variables using the backward method, the AIC value improved from 99.45 with the initial six variables to 85.94 with only the variable of presence of calves. Location, season, depth of the seabed, and school size were not selected in the final model. On its own, the presence of calves explains 23% of the variation of the trammel-feeding behavior.

Discussion

Our results show that two relatively well-defined communities of resident bottlenose dolphins share the same area in the Archipelago de La Maddalena waters. In addition, there exists a high correlation between the foraging strategy of bottlenose dolphins and the community membership. With the exception of two independent individuals, bottlenose dolphins that were observed feeding from trammel nets constitute one of these communities, while the other is mainly made up by individuals who have

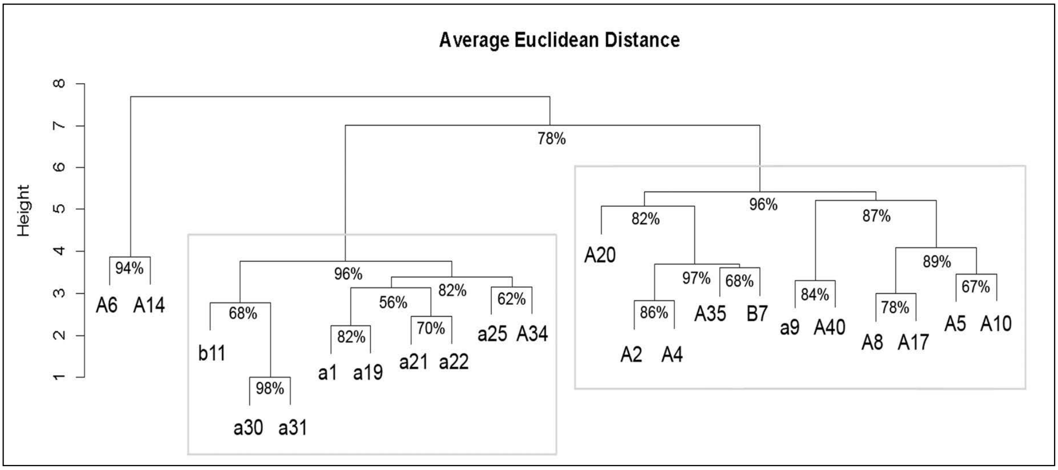

Figure 1. Cluster dendrogram with AU *p*-values (%); each bottlenose dolphin is classified with an alphanumeric code. The trammel feeders (TFs) are identified with capital letters, while the non-trammel feeders (NTFs) are identified with lower case letters.

never been seen foraging from nets. The correlation between the foraging strategy of bottlenose dolphins and the community membership was found using only sightings in which net-foraging behavior was not recorded, so it cannot be a simple artifact of our data collection technique.

Several species of cetaceans exhibit similar colocality with foraging specializations; of these, the best known is the killer whale (*Orcinus orca*), particularly those that live around Vancouver Island, Canada. In this area, two different stable groups with specific foraging patterns have been well-described: (1) a fish-eating group and (2) a marine mammal-eating group (Ford et al., 1998). In addition to these group-specific patterns of killer whales, there are some local behavioral patterns of cetaceans that do not live in such stable groups (Rendell & Whitehead, 2001).

Bottlenose dolphins at Laguna off the coast of Brazil have an unusual group-specific feeding technique which seems to date from 1847 and has been transmitted within a matrilineal community for at least three generations (Pryor et al., 1990). These bottlenose dolphins collaborate with local fishermen driving fish into the nets. Only young adults whose mothers took part in the fishing later adopted it themselves, although not all the offspring of fishing mothers did so (Pryor et al., 1990).

Another example is the bottlenose dolphin population of Moreton Bay, Australia, that was described to form two separate communities of trawler and non-trawler individuals (Chilvers & Corkeron, 2001). This study showed that members of the two communities almost never associated, despite overlapping home ranges. Nevertheless, a recent study (Ansmann et al., 2012) has shown that, since changes to fisheries legislation have substantially reduced trawling, the individuals of these two communities have shown more social connections between them. In our study, the presence of a dolphin identified as TF in the NTF cluster, and of a NTF dolphin in the TF cluster, probably also demonstrates that members of the two studied communities can interact.

We have no data on the bottlenose dolphin community's social structure prior to the current fishing legislation. However, taking into account the generally dynamic nature of bottlenose dolphin communities (Cox et al., 2003; Mann & Sargeant, 2003), it is plausible that the two studied groups interacted with each other. Usually, the basic nursery group includes mothers and their most recent offspring. After 3 to 6 y, individuals usually leave the nursery group and get involved in groups of juveniles (both males and females). Adult males generally live alone or in pairs, while females may return to their mother or female relatives to raise their own calves, thus comprising a multigenerational group. Most likely, the cultural learning occurs within these nursery groups. Our results are fully compatible with the existence of two culturally independent nursery groups and other individuals related to them.

The presence of two relatively well-defined communities with different foraging strategies could be the result of having different foraging traditions. However, this could also be a consequence of differences in other features between the groups such as sex, habitat, group size, feeding area, or presence of calves. In such a case, these features, alone or in combination with others, should explain a significant percentage of the variability in the foraging strategy. Our results show that the presence of calves has the only significant effect, which explains 23% of the variability in the foraging behavior. This percentage is not high enough to conclude that the presence of calves in a community of bottlenose dolphins is what determines their foraging behavior, but it does seem that their presence incites the net-foraging behavior by the adults. Another explanation could be that vertical transmission in this population appears to be a case of "directed" social learning (Coussi-Korbel & Fragaszy, 1995). Directed social learning is likely to create within-group differences in behavior (Coussi-Korbel & Fragaszy, 1995) such as those observed in Shark Bay. Learning from mothers is more likely simply because of the substantial amount of time that mothers and dependent calves spend together, but it also could be most adaptive. Indeed, to summarize findings by Kuczaj et al. (2005), calves are more likely to watch and imitate behaviors of other calves than they are to imitate behaviors of adult bottlenose dolphins (including their mothers). Calves are more likely to observe and reproduce novel behaviors than behaviors they already know. Innovation by an individual is necessary in order to add new behaviors to a group's behavioral repertoire, even though it is not the case that all innovations are adopted by all group members (Kuczaj et al., 2012). This could be a possible explanation for the reduced number of calf sightings when the NTFs are feeding. Most likely, NTF calves are driven to imitate the innovative foraging strategy from the TF calves and, consequently, calf numbers in the TF group seem greater. Another possibility could be that NTFs are foraging deeper/longer, so the number of calves observed is reduced because both adults and calves are spending less time on the surface.

Considering these results, if the high concentration of fish in the trammel nets is available to all the bottlenose dolphins in the area, and only the individuals of one of the two communities access this source of food, the most probable explanation is that the net-foraging behavior is a tradition socially learned within the community.

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