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Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure

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Spinner dolphins (*Stenella longirostris*) commonly use inshore island and atoll habitats for daytime rest and social interactions and forage over deep waters at night. In Hawaii, they occur throughout the archipelago. We applied photoidentification mark-recapture techniques to study the population structure of spinner dolphins associated with remote Midway Atoll, far-western Hawaii. At Midway, spinner dolphins live in stable bisexually bonded societies of long-term associates, with strong geographic fidelity, no obvious fission-fusion, and limited contacts with other populations. Their large cohesive groups change little over time and are behaviorally/socially discrete from other spinner dolphin groups. This social pattern differs considerably from the fluid fission-fusion model proposed previously for spinner dolphins associated with a large island habitat in the main Hawaiian Archipelago. These differences correspond to geographic separation and habitat variation. While in the main islands there are several daytime resting places available at each island habitat; in far-western Hawaii, areas of suitable habitat are limited and separated by large stretches of open pelagic waters with potentially high risk of shark predation. We hypothesize that with deepwater food resources in close proximity and other atolls relatively far away for easy (day-to-day) access, it is energetically more beneficial in the remote Hawaiian atolls to remain "at home" than to travel to other atolls, so there is stability instead of variability; there is no fission-fusion effect. Thus, the geographic isolation and small size of remote atolls trigger a process in which the fluidity of the fission-fusion spinner dolphin society is replaced with long-term group fidelity and social stability.
Key words: geographic insularity/connectivity, group dynamics, Hawaii, Midway Atoll, social evolution, social structure, Spinner dolphin *Stenella longirostris.* *[Behav Ecol 16:675–685 (2005)]*

The recent proliferation of long-term mammalian studies over broad geographic areas and taxa as diverse as carnivores, ungulates, and primates (e.g., Gittleman, 1989; Lee, 1999; McGrew et al., 1996; Robbins et al., 2001; Rubenstein and Wrangham, 1986) provided considerable insights into the socioecology of mammalian groups. The general pattern is one of considerable behavioral flexibility and indicates that social variability is a common response to environmental variability. One such example, giraffes (*Giraffa camelopardalis*) show varying degrees of group stability, population density, ranges, and home-range size across different habitats in the Masai ecosystem, Tanzania (van der Jeugd and Prins, 2000). African wild dogs (*Lycaon pictus*) in the Serengeti have large overlapping home ranges, with males recruited into the pack and females dispersing as juveniles. However, in a different habitat of Kruger National Park, South Africa, the pack range is much smaller, and the density is higher; females in Kruger generally remain with their natal packs, and when packs become overcrowded, pack fission occurs (Moehlman, 1989; Reich, 1981). Among great apes, the two closely related species of *Pan*, the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) have long been viewed as behaviorally quite different, with bonobos living in cohesive female-bonded social groupings and chimpanzees forming generally less cohesive and smaller male-bonded groups (e.g., Kano, 1992; Nishida and Hiraiwa-Hasegawa, 1987; Wrangham, 1986). Recent studies, however, suggest that intraspecific variability caused by living under different ecological conditions is far greater than initially thought and that the apparent differences between the two species reflect the specific ecological conditions more than the species-specific characteristics (e.g., Boesch, 1996; Boesch et al., 2002; White, 1996).

Most cetacean studies lack the detail of studies on terrestrial species. Nevertheless, there are several indications of intraspecific behavioral variability. For example, bottlenose dolphins (*Tursiops truncatus*) form resident and socially stable populations in sheltered and seasonally stable environments, such as Sarasota Bay, western Florida (Wells, 1991, 2003; Wells et al., 1987). In contrast, along the open coastline of southern California, they roam over several hundred kilometers and show weak levels of social stability (Defran and Weller, 1999; Defran et al., 1999; Weller, 1991). Similarly, humpback dolphins (*Sousa chinensis*) off the exposed Eastern Cape coastline, South Africa, display fluid social patterns characterized by lack of consistency in group size and membership and generally short-lasting affiliations (Karczmarski, 1999; Karczmarski et al., 1999a,b). However, less than 1300 km north along the southern African coast, in relatively sheltered Maputo Bay, Mozambique, the same species occurs in more stable units of association and shows considerably stronger geographic fidelity (Guissamulo and Cockcroft, 2004).

Spinner dolphin (*Stenella longirostris*) behavioral ecology has been studied off the Kona coast of the Big Island of Hawaii (Norris and Dohl, 1980; Norris et al., 1994; Östman, 1994), off Moorea in French Polynesia (Poole, 1995), and—most recently—at Midway Atoll (reported here). In all cases, the Gray's (or long-beaked) spinner dolphin (*Stenella longirostris longirostris*), a subspecies that associates with tropical island

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systems, hence often termed "semipelagic," was studied. Two other subspecies, the Central American spinner (*Stenella longirostris centroamericana*) and eastern spinner (*Stenella longirostris orientalis*), are known from the Pacific coast of meso-America and pelagic eastern tropical Pacific, respectively (Perrin, 1990, 1998). Another pelagic form, an apparent hybrid between *S. l. orientalis* and *S. l. longirostris*, the so-called "white-belly spinner dolphin" occurs throughout most of the offshore eastern tropical Pacific (Perrin, 1998; Perrin and Gilpatrick, 1994). The group dynamics and social patterns of these forms of spinner dolphins remain largely unknown, although considerable geographic variation in the mating system has been suggested based on testis size (Perrin and Mesnick, 2003).

In all areas studied, Gray's spinner dolphins (hereafter referred to as spinner dolphins) use the inshore island habitat for daytime rest and social interactions, probably to reduce the chances of deepwater shark predation (Norris and Dohl, 1980). During the night, they feed on mesopelagic fishes, shrimp, and squid, as prey rise out of the abyss in association with the diel migration of the mesopelagic-boundary community (Benoit-Bird and Au, 2003; Clark and Young, 1998; Würsig et al. 1994a). Spinner dolphins that take advantage of large-island habitats off the main Hawaiian Archipelago live in a fission-fusion society: they band together into groups of hundreds to feed in deep waters at night and separate to "fit into" bays and behind reefs in groups of dozens during the day (Norris and Dohl, 1980; Würsig et al., 1994b). There is great day-to-day lability in group sizes and interindividual associations; however, larger bays tend to harbor more dolphins than smaller ones, suggesting that they may have different carrying capacities (Wells and Norris, 1994; Würsig et al., 1994b). The daytime social system is dynamic, with only some members of the population (community) seen together at a time. The nighttime pattern of associations remains unknown (Norris and Johnson, 1994; Würsig et al., 1994c).

Spinner dolphins occur throughout the Hawaiian Archipelago, a 2500-km-long island chain that stretches from the Big Island in the southeast (19° 35′ N, 155° 30′ W) to Kure Atoll in the northwest (28° 25′ N, 178° 20′ W). The archipelago represents a diverse ecological system, ranging from a large-island habitat of the closely located main islands to small isolated atolls at the western end of the archipelago. For spinner dolphins, each of the main islands provide a mosaic of closely located nearshore environments that represent a diverse choice for daily resting and socializing needs, where neighboring locations (and dolphin groups) are in close reach. The northwestern atolls, on the other hand, represent small, insular locations where the availability of suitable resting habitats is limited and where the distance to neighboring dolphin groups/populations is considerable. The study described here investigates the pattern of group living and social dynamics of a population of spinner dolphins associated with remote Midway Atoll, northwestern Hawaii. We present quantitative analyses of the population structure and compare our findings with previous research conducted at the main Hawaiian Islands (Norris et al., 1994). Based on a comparison with several other known mammalian systems, we interpret our findings relative to environmental variations, especially resource availability and the degree of geographic insularity.

STUDY AREA

Midway Atoll (28° 05–25′ N, 177° 10–30′ W), situated 280 km east of the International Dateline, is the second to last in the western Hawaiian Archipelago (Figure 1). The atoll is 10 km in maximum diameter, fringed by continuous emergent reef, and has two distinct openings, a 300-m-wide dredged channel to the south, and a 5-km-wide natural opening to the west. There are three islands in the southern portion of the lagoon. The waters within the lagoon range in depth from less than 1 m to almost 30 m, with >50% of the lagoon being <7 m deep. Sandy flats with occasional coralline outcrops dominate the bottom topography. Outside the atoll, depths of more than 2000 m are generally within <7 km from the reef.

Midway is neighbored by Kure Atoll (96 km to the west) and Pearl & Hermes Reef (168 km to the east). These three atolls represent insular small "oases" of habitat suitable for the daily resting needs of spinner dolphins in what is otherwise an open pelagic zone. The next closest area that can provide comparable sheltered conditions for spinner dolphins, French Frigate Shoals, is approximately 1000 km southeast of Pearl & Hermes Reef (Figure 1).

METHODS

Field approach

Photoidentification (photo-ID) surveys at Midway Atoll were conducted with a 9-m tri-hulled boat powered by two 115 HP outboard engines during 22 months between February 1998 and November 1999. These surveys were carried out at a sea state of Beaufort scale ≤3 and always covered the entire inner lagoon, unless deteriorating weather conditions truncated a survey. After location of a dolphin group and a binocular scan approximately 1–1.5 km radius for all other potential dolphins, the group was approached at speeds <2 knots. While the boat remained alongside the dolphin group, the group membership (ID-photographs), size, relative cohesion/dispersion, and general behavioral states were recorded. Movement pattern was monitored with a portable geographic positioning system and recorded in 10-min intervals, as were water clarity, temperature, depth, and the general features of the bottom topography. The animals were photographed with a motorized camera equipped with a variable length (zoom 100–300 mm) lens and 100 ISO color positive film. All dolphins were photographed at a distance at which the dorsal fin filled at least one quarter of the frame in the camera's viewfinder, irrespective of obvious marks (notches, coloration, etc.) and whether or not an individual was already photographed. A conscious attempt was made to distribute the photographic effort equally across the dolphin group.

In mid-1999, underwater observations (free-diving) were introduced to identify the sex of individually recognizable dolphins. Data were recorded in an underwater notebook and by means of underwater photography. Exceptional water clarity, which is a norm for the northwest Hawaiian region, facilitated effectiveness of the underwater observations.

For 2 days in mid-October 1998, ID-photographs were collected at Kure Atoll.

Definitions

Each time the research boat traveled within the study area in search of dolphins is referred to as a "photo-ID (identification) survey." Each time a dolphin group was located and photo-ID data were collected is referred to as a "dolphin encounter." When the research boat remained alongside the dolphins and moved with them it is referred to as a "dolphin follow." The term "sighting" of an individual refers to a case when at least one ID-picture of an individual met the minimum quality criteria for the full suite of photo-ID analyses described below.

A "group" is understood here as a spatial aggregation of animals that are involved in similar (often the same) activities

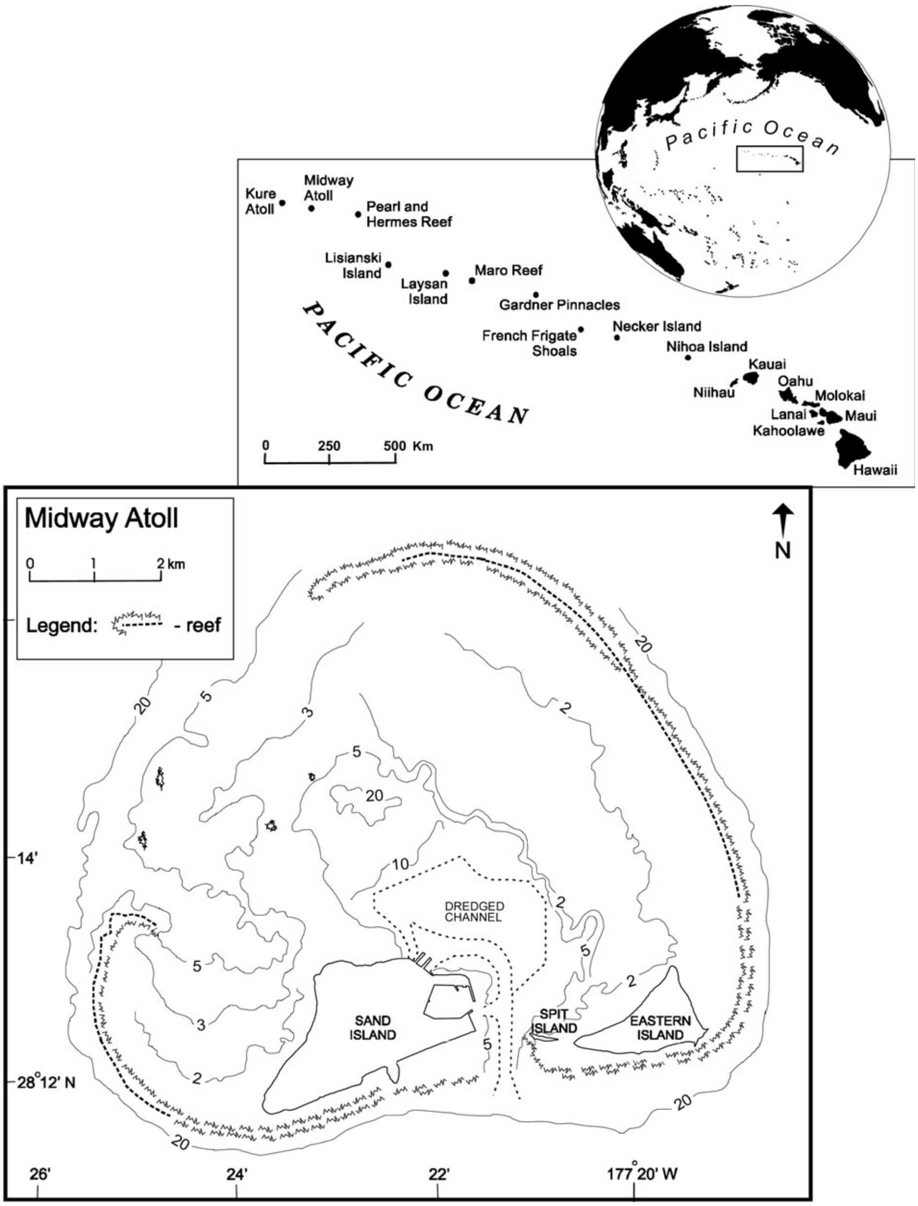

Figure 1
The Hawaiian Archipelago consists of 8 main islands and 10 northwestern islands, often referred to as the northwestern Hawaiian chain, extending over 2000 km northwest of the island of Kauai. A former U.S. naval base, Midway Atoll is the second to last at the western end of the archipelago.

and interact with one another over timescales sufficiently short that there are few (or no) changes in group membership. This is consistent with other studies on group-living mammals (reviewed in Whitehead and Dufault, 1999) and represents a similar meaning to the primatologists' "party." "Community" refers to regional assemblage (society) of animals that share ranges, interact socially, but do not represent closed reproductive units (sensu Wells et al., 1999), similar as in many primate studies (e.g., Boesch, 1996).

Three age classes were distinguished: calf, juvenile, and adult (see Perrin and Gilpatrick, 1994, for details on growth and reproduction). Calves are defined as animals 2/3 or less the length of an adult, regularly accompanying a larger animal presumed to be the mother. Newborn calves ($\leq$4 weeks old) were identified by the presence of features such as size ($<$1/2 the length of an adult), visible fetal folds, and behavior (mainly "overshooting" the water and head-slapping when breathing). When possible, the age of calf and month of birth were estimated. Juveniles were approximately 1.5–1.6 m in length, visibly less robust than adults, with the height of the dorsal fin approximately 2/3 that of its length, and they often swam independently. Individuals of approximately 2 m length, with the height of the dorsal fin generally equal to their length, were classified as adults.

Laboratory procedure

All photographic material was processed by a professional photolaboratory. Each photographic image (color transparency) was projected onto a screen, and its quality was assessed independent of the markings on the individual and assigned a quality grade between 1 and 100 (for comparison see Friday et al., 2000; Gailey, 2001; Gowans and Whitehead, 2001). Only photographs ranked $\geq$80 were classified as suitable for further analyses, which ensured that all images included into the data set were well exposed, in focus, the entire dorsal fin was visible above the water, and the fin filled generally not less than one-quarter of the frame with no or only moderate cases of parallax.

For this set of ID-photographs, a ratio that relates the number of dorsal fins that could be reliably identified to the total number of photographed fins was calculated. This calculation was performed for each dolphin encounter and represents the ratio of individuals that were reliably marked. Subsequently, the overall mean (referred to further as the "ID ratio") and standard error (SE) were calculated.

Next, each image was assessed on the bases of the distinctiveness of the photographed individual (for comparison see Friday et al., 2000; Gailey, 2001). Only dolphins with individually identifiable mark(s) that were sufficiently distinctive to permit future reidentification on another photograph of a similar quality were included in the photo-ID data set. Identification of individuals was based primarily on the pattern of notches on the dorsal fin. Although various other mark types (e.g., scratches, scars; Karczmarski and Cockcroft, 1998) were always assessed, they were infrequent on spinner dolphins, and only the notches on the dorsal fin in conjunction with the overall shape of the fin were sufficiently reliable for long-term reidentification.

The photo-ID catalogue was organized according to position and number of notches on the dorsal fin. The highest quality photographs (mounted slides) of each individual from each encounter were included into an individual sighting history catalogue. The highest quality ID-picture from each individual sighting history was projected and traced onto an A4-size sheet of paper. This set of tracings formed a "quick reference catalogue" that was periodically reassessed and used to assist in matching among the slides collected during all subsequent encounters.

Analytical treatment

General measure of associations

Quantitative analyses adopted the assumption that animals that are clustered spatially are interacting with one another, and, consequently, the membership of the same cluster (here called the group) defines associations. This is consistent with other studies of vertebrate social structure reviewed by Whitehead and Dufault (1999). The use of photo-ID techniques implies that individuals were considered to be associated if they were photographed within the same group during an encounter. The rate of association of any two individuals (the proportion of co-occurrence) was measured with the half-weight association index (Cairns and Schwager, 1987; Ginsberg and Young, 1992). The half-weight index was chosen because it introduces less bias compared to other association indices when two individuals are more likely to be recorded separate than when together (a common case for large delphinid groups where the number of photographed individuals is often <50% of the identifiable group members). However, in a case of considerable differences in group sizes and photographic coverage of a group (and consequently the probability of photographing two individuals in the same group), a comparison between half-weight and simple ratio indices has also been exercised to assess the bias caused by different sampling regimes (Cairns and Schwager, 1987). In both cases, the index values range between zero, for two individuals never seen in the same group, and one, for individuals always seen in the same group (Cairns and Schwager, 1987; Ginsberg and Young, 1992).

For all analyses, the sampling period was 1 day to avoid replicate associations within the same day and to ensure independence of data. Laboratory analyses made use of the social analysis software program SOCPROG 1.2 (Whitehead, 1999a,b) that statistically tests the fit of models to the observed data set.

A Mantel test was used on adults to test the null hypothesis that association rates (probability of being seen in the same group) were similar between and within sexes (Hemelrijk, 1990; Schnell et al., 1985). The mean and maximum association indices (and standard deviations [SDs]) were also calculated. The mean association index is an estimate of the probability that a randomly chosen member of one sex class was associated with another randomly chosen individual of the same sex or with a randomly chosen member of the opposite sex during any sampling period (Whitehead, 1997, 1999a), and the estimates are insensitive to different numbers of males and females. The maximum association index represents the mean of the association indices between maximum associates (individuals that shared the highest association rate) within and between sexes.

Preferred companionship

To determine whether the patterns of associations between individuals were significantly different from random and to test associations between individual dyads against random, the observed association matrix was permuted following the Manly/Bejder et al. procedure (Bejder et al., 1998; Manly, 1995). This procedure inverts the intersection of two rows and two columns randomly chosen from the association matrix while keeping constant the number of identified individuals in each group and the number of groups in which each individual was observed. As successive association matrices are not independent, the number of required permutations needs to be determined by increasing the number of permutations until the p value stabilizes, as too few permutations would produce an inaccurate p value (Bejder et al., 1998). In this study, 200,000 random permutations of the association matrix were performed.

Short-term preferred associations (within sampling periods) were tested by randomly permuting the group to which individuals were assigned while keeping constant the number of groups in which animals were observed. Computer simulations (Whitehead, 1999a) indicate that short-term preferred associations reduce the number of pairs of associated individuals, which significantly decreases the mean of the observed association indices versus the randomly permuted data. To test for long-term companionship, the associations of each individual within a sampling period were permuted while keeping constant the total number of associations of each individual. Simulations using half-weight and simple ratio indices (Whitehead, 1999a) indicate that if some pairs of animals preferentially associate with one another at different sampling periods more often than by chance, this significantly increases the SD of the observed association indices versus the randomly permuted data.

Temporal pattern and community structure

To quantify temporal stability of associations, lagged association rates between individuals were calculated (sensu Whitehead, 1995). The lagged association rate for any time lag t represents an estimate of the probability that two individuals associated at a particular time are still associated t time units later. The null association rate indicates the expected value of the lagged association rate if there are no preferred associations; in other words, if the associations are random. In this study, lagged and null association rates were standardized (divided by the number of recorded associates, Whitehead, 1999a) because it was logistically difficult to photograph all individuals in a group. A jackknife procedure, where data from each date were sequentially eliminated from the data set, was used to assess the precision of estimated lagged association rates (Sokal and Rohlf, 1995, Whitehead, 1999a). Models of the temporal permanence of associations were fitted to the data using maximum likelihood and Akaike information criterion (AIC) methods to determine best fit (Sakamoto et al., 1986). Jackknifing was used to calculate the SE for each model parameter, which indicates the precision of the estimates.

The residence rate of individuals was measured by calculating lagged identification rates, which represent the probability that an individual identified at any particular time will be identified again in the study area t time units later (sensu Whitehead, 2001). If the population is closed and identifications are independent, then this probability is the inverse of the population size. If there is emigration or mortality, then lagged identification rates typically fall with time lag (Whitehead, 1999a, 2001). Models of residency were fitted to the observed data with maximum likelihood and AIC methods used to determine the best model. Jackknife techniques were used to calculate 95% confidence intervals and SEs for each model parameter. Lagged identification rates were calculated and models fitted for all adults and for each sex separately.

RESULTS

Database

One hundred and thirty-five photo-ID surveys were completed (76 in 1998 and 59 in 1999), on average one survey every 5 days, with a total of 586 effort hours. Only during four surveys (three in 1998, and one in 1999) were spinner dolphins not seen within the Midway lagoon. Dolphin groups were approached and followed by the research boat 142 times (74 and 68 times in 1998 and 1999, respectively) for a total of 258 h. Almost 20,000 ID-photographs were taken during 127 surveys, 138 encounters (74 in 1998 and 64 in 1999), and 250 h of dolphin follows, which resulted in more than 6000 individual sighting records.

Group structure

In 1998, on 72 of the 73 surveys when dolphin encounters occurred, only one coherent group of some 200+ spinner dolphins was seen at Midway. Field estimates of the group size varied between 180 and 260 individuals, with a mean of 211 ($n = 119$, SD = 22.8). Generally, the more unfavorable the sea conditions, the lower the estimates. Although the overall group geometry and cohesion varied, the average distance between the group members was seldom greater than three body lengths. Unisexual groups were never seen, while calves and juveniles were seen in each encounter.

The cumulative number of photographically identified individuals (discovery curve) stabilized within the first 6 months of the study (Figure 2, continuous line). By the end of 1998, 132 dolphins (116 adults and 16 juveniles) were photoidentified and catalogued, of which three-quarters were identified during the first 15 surveys. In 1999, only six more individuals (one calf and five juveniles) were added to this discovery curve (Figure 2). All individuals seen (photographed) in 1998 were resighted in 1999, and 61 of them (46%) were seen at least once every fourth encounter during the 2-year study. The ID ratio was 53% ($n = 95$, SE = 1.9). One hundred and eleven of the identified and catalogued individuals (80.4%) are of known sex (42 females and 69 males).

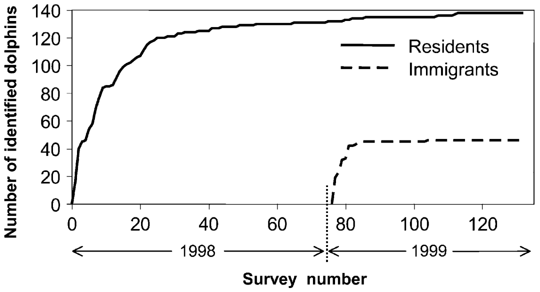

Figure 2
Rate of discovery of spinner dolphins identified as residents and immigrants at Midway Atoll between February 1998 and November 1999. Fifty-three percent of residents and 75.5% of immigrants are well marked and individually identifiable through photographic techniques. See text for details.

Based on the pattern of the discovery curve and sighting frequencies, this group of dolphins was assumed to be resident at Midway, and it is referred to further as "resident."

The only exception to this general sighting pattern occurred in July 1998 (encounter 39), when in addition to the frequently sighted large group, another group of approximately 35 spinner dolphins was seen at a distance of 7–8 km from the first group. Due to a late hour of the day, this group could only be followed for <15 min, with only three ID-pictures taken. Two individuals were photoidentified, neither of which were previously seen at Midway (these two individuals were not included in the resident discovery curve in Figure 2).

In February 1999, a "new" group of approximately 60 spinner dolphins was encountered, and two members of this group were identified to be the same two individuals seen during encounter 39. No other member of the new group had previously been seen in Midway lagoon, but 15 of them were photographed at Kure Atoll during opportunistic surveys in October 1998. During the following 57 surveys at Midway when dolphin encounters occurred, the new group was seen 34 times (59.6%) and despite occasional interactions with the resident dolphins (see further) remained a separate coherent unit for the entire time. The estimates of group size ranged between 54 and 65 (mean = 60, $n = 34$, SD = 3.2), with calves and juveniles seen at each encounter. The discovery curve for this group, referred to hereafter as "immigrants," reached a plateau after the first eight encounters and did not change thereafter, with 46 dolphins (39 adults and seven juveniles) individually identified by the end of 1999 (Figure 2, broken line). All but three individually identifiable immigrants were seen (photographed) on average once every fourth encounter, and 26 of them (56.6%) were seen every other encounter. Thirty-four (74%) are of known sex (11 females and 23 males). The immigrants' ID ratio (75.5%, $n = 29$, SE = 2.2) was significantly higher than that for residents (Mann-Whitney $U = 2.0$, $n = 124$, $p < .0001$).

The larger number of identified males reflects the greater distinctiveness of individual marks (larger notches and more severe scars and wounds) among males than females and not a greater number of males in the community.

Social stability

The large group sizes of spinner dolphins made it difficult to photograph each member of a group, causing a downward bias of association indices. This was especially true for the considerably larger group of residents, where on average 47 individuals (34% of all photocatalogued residents) were

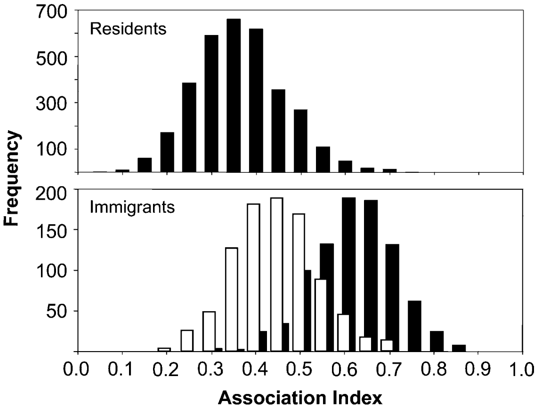

Figure 3
Distribution of values of the half-weight association indices (black bars) calculated for resident and immigrant spinner dolphins seen at Midway Atoll in 1998 through 1999. For immigrants, values of simple ratio indices (white bars) are also shown.

photographically "captured" per encounter (range: 25–88 individuals, 18–64%) versus a mean of 31 immigrants per encounter, 67% of all photocatalogued immigrants (range: 17–42 individuals, 37–91%). Nevertheless, values of half-weight association indices turned out to be high for both immigrants as well as residents (Figure 3), although for intergroup comparisons it may be useful to view the distribution of immigrant association indices as a simple ratio index (Figure 3), reducing to a degree the bias caused by dissimilar sampling regimes (dissimilar photographic coverage, Cairns and Schwager, 1987). For consistency, however, all further analyses are displayed using half-weight indices, which differed from the simple ratio indices only in the relative values and not in the overall patterns.

Association rates did not differ significantly between and within sex classes (Mantel test: $t = 7.22$, $n = 124$, $p > .95$ and $t = 3.75$, $n = 35$, $p > .95$ for residents and immigrants, respectively), indicating that both sexes had similar probability of being seen in the same group. Maximum association indices showed little variability, suggesting a high level of group stability (Table 1).

Permutation tests for preferential companionship were run on the 1999 data set when two dolphin groups were present.

Table 1

Mean and maximum half-weight association indices (and SDs) within and between sexes, calculated for resident and immigrant spinner dolphins seen at Midway Atoll between February 1998 and November 1999

	Mean associate (and SD)	Maximum associate (and SD)
Residents		
All	0.37 (0.09)	0.61 (0.14)
♀-♀	0.32 (0.05)	0.49 (0.07)
♀-♂	0.36 (0.07)	0.53 (0.08)
♂-♀	0.36 (0.06)	0.55 (0.08)
♂-♂	0.44 (0.07)	0.67 (0.10)
Immigrants		
All	0.63 (0.06)	0.78 (0.07)
♀-♀	0.59 (0.05)	0.70 (0.05)
♀-♂	0.63 (0.06)	0.75 (0.05)
♂-♀	0.63 (0.04)	0.74 (0.05)
♂-♂	0.69 (0.05)	0.81 (0.05)

Table 2

Results of permutation tests for preferential companionship run according to the Manly/Bejder et al. procedure (Bejder et al., 1998; Manly, 1995) on the 1999 data set

	Mean association index	SD of mean association index
Observed data	0.4441	0.2341
Random data	0.4557	0.2041
p Value	<.001	<.001

The mean association index for the observed data was significantly lower than the randomly permuted data, and the SD of the mean association index of the observed data was significantly higher than the randomly permuted data (Table 2). Consequently, the permutation tests indicated that individuals were associating within the resident and immigrant group significantly more often (by grouping together or avoiding one another) than expected by chance alone. In both groups, there were significant preferential associations that persisted over short sampling periods as well as significant preferred long-term companionships that span across sampling periods.

All dyads with association indices significantly greater than random (two-sided significance level < .05) were formed between two residents or between two immigrants, while the majority of dyads involving residents with immigrants had association indices significantly lower than random values.

The standardized lagged association rates, calculated for all adults (116 residents and 39 immigrants), were stable over time, higher than expected by chance alone, and never approached the random association rate (Figure 4), providing further evidence for preferential companionship. The error

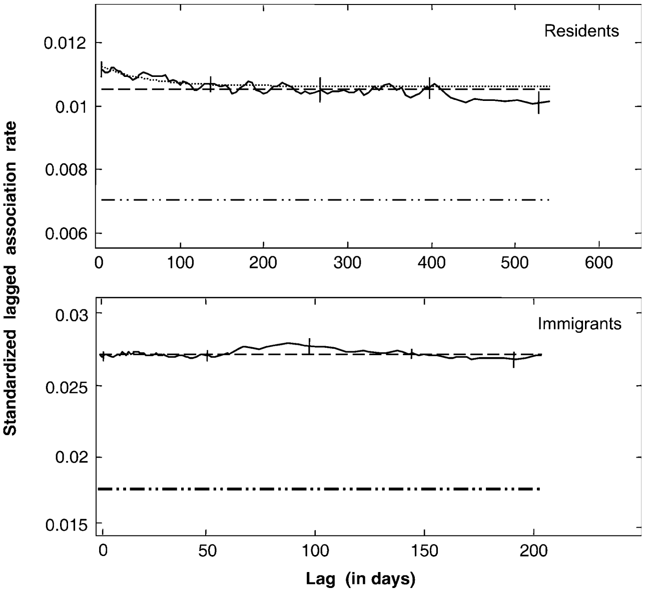

Figure 4
Standardized lagged association rates of all reliably marked adult resident and immigrant individuals, with jackknifed estimates of precision. The best-fitting models of the temporal permanence of association, constant companions (broken line), constant companions + casual acquaintances + rapid disassociation (dotted line), and the null (random) association (straight broken/dotted line) are also shown.

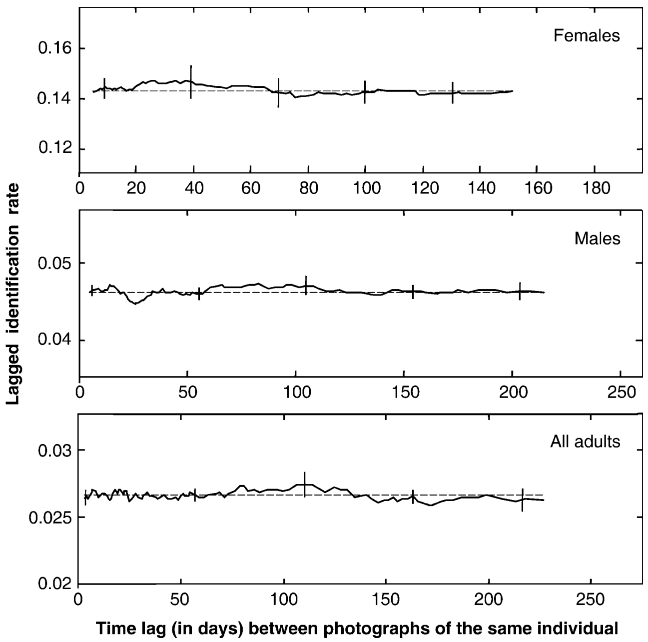

Figure 5
Lagged identification rates of immigrant spinner dolphins at Midway Atoll, with vertical lines indicating jackknifed error bars. The best-fitting model, closed population (straight broken line), is also shown.

bars were small, indicating considerable precision of the estimates. For immigrants, the model best describing the observed pattern of associations was "constant companions" (sensu Whitehead, 1995), which indicates stable associations over time, changed only by birth or death. For residents, the model that best described the observed pattern (dotted line in Figure 4) was "constant companions + casual acquaintances + rapid disassociation" (sensu Whitehead, 1995), suggesting that although there are long-term stable social affiliations, some associations are only brief. However, the decrease in lagged association rates projected over 550 days was very low, and the graphic display (and accuracy, measured with AIC) of this model differed only slightly from the next best-fit model, which was constant companions (broken line in Figure 4).

Community structure

Although the "daytime home ranges" of residents and immigrants overlapped extensively at Midway and both groups often resided in areas only 2–3 km distant, they interacted little, often remaining separate for the entire time within the lagoon. During the first 3 months of their recorded presence at Midway, the immigrants rested in the northern section of the lagoon in very shallow waters where residents were never observed resting. Apparent aggression (or aversion) was also seen, with the residents chasing the immigrant group into the shallow areas at the atoll's rim. It was only in mid-1999 that the immigrants began using the resting sites frequented by the residents, although seldom at the same time as residents. Through the end of the study period reported here, affiliative interactions between the two groups were infrequent, and when observed, the original group membership was retained when the groups separated again.

The lagged identification rates for immigrants were stable over time and best described by a "closed population" model with no influx and outflux (Figure 5; Table 3). SEs of these estimates were low, and the pattern was similar for "males," "females," and "all adults." For residents, lagged identification rates were also stable, with only a slight decrease over a lag of 550 days and small SEs. The observed pattern for all adults and males was best described by the "closed population with emigration and reimmigration" model (broken line in

Table 3
Estimated residency parameters (with SEs) for resident and immigrant spinner dolphins at Midway Atoll

Group/sex	Model	Number of marked individuals at given time	Mean residence time (days)	Mean emigration time (days)	AIC
Residents					
All adults	Closed	94 ± 1	—	—	926,206.87
	Closed with emigration + reimmigration	***89 ± 2***	***1413 ± 805***	***127 ± 74***	***926,157.89***
	Emigration/mortality	92 ± 2	6926 ± 2107	—	926,166.88
Males	Closed	57 ± 1	—	—	629,450.64
	Closed with emigration + reimmigration	***53 ± 1***	***1217 ± 764***	***101 ± 61***	***629,421.55***
	Emigration/mortality	55 ± 1	8058 ± 3286	—	629,429.41
Females	Closed	28 ± 1	—	—	117,375.97
	Closed with emigration + reimmigration	27 ± 7	46 ± 20,294	1 ± 738	117,379.96
	Emigration/mortality	***27 ± 1***	***8516 ± 5587***	—	***117,373.17***
Immigrants					
All adults	***Closed***	***38 ± 0.5***	—	—	***63,252.30***
	Closed with emigration + reimmigration	38 ± 0.5	24 ± 4	0.05 ± 0.01	63,256.30
	Emigration/mortality	38 ± 0.5	26,161 ± [a]	—	63,254.25
Males	***Closed***	***22 ± 0.2***	—	—	***38,315.47***
	Closed with emigration + reimmigration	22 ± 0.2	42 ± 7	0.05 ± 0.01	38,319.47
	Emigration/mortality	22 ± 0.2	128,360 ± [a]	—	38,317.47
Females	***Closed***	***7 ± 0.1***	—	—	***5582.55***
	Closed with emigration + reimmigration	7 ± 0.1	44 ± 7	0.04 ± 0.005	5586.55
	Emigration/mortality	7 ± 0.1	[b] ± [a]	—	5584.55

[a] SE more than 10 billion.

[b] Estimated mean residence time more than 10 billion days.

Best-fit models based on AIC are given in bold italics.

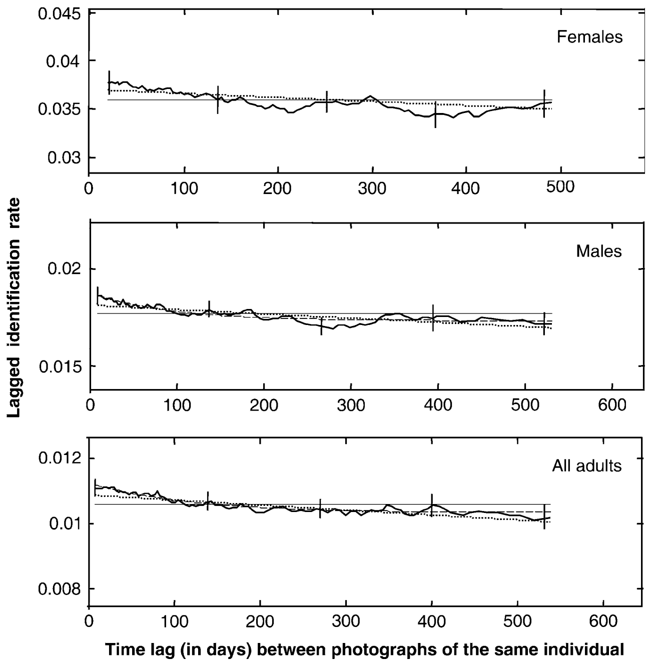

Figure 6
Lagged identification rates of resident spinner dolphins at Midway Atoll, with vertical lines indicating jackknifed error bars. The best-fitting models, closed population with emigration and reimmigration (broken line), emigration/mortality (dotted line), and closed population (straight continuous line), are also shown (see text for details).

Figure 6; Table 3). The next best-fit model was emigration/mortality (dotted line in Figure 6). In both cases, however, estimates of the residence time were considerably longer than the total duration of this study while estimates of emigration time were short, and both had large SEs (Table 3). The graphic display of these models differed relatively little from the next best fit, the closed population model with no influx and outflux (straight continuous line in Figure 6). The lagged identification rates for resident females were best matched by the emigration/mortality model (again with very long residence time and large SE), although the accuracy of this model's fit differed little from closed population followed by closed population with emigration and reimmigration, the latter two producing the same graphic display (straight line, Figure 6).

DISCUSSION

Effects of insularity on spinner dolphin population structure

At Midway Atoll, spinner dolphins live in stable societies of long-term associates, with strong geographic fidelity, no obvious fission-fusion, and no interindividual changes in group structure and fidelities from day to day. Both males and females associate together in the same group and form preferential companionships, suggesting a bisexually bonded society (although the persistence of nearest neighbor associations may differ between sexes, with males forming stronger pairs than females; Karczmarski, unpublished data). The "Midway population" is closed (or nearly so) and consists of two discrete social groups, one of which is likely long-term resident. Both groups are highly coherent, change little over time, and display the same sexual bonding pattern. Modeling of their social dynamics indicates that long-term group fidelity and social stability represent the norm for spinner dolphins in the insular atoll habitats of far-western Hawaii.

This social pattern of atoll-dwelling spinner dolphins is considerably different from the pattern described previously for spinner dolphins associated with a large island habitat in the main Hawaiian Archipelago (Norris et al., 1994). There appears to be openness of the society for all but mother-calf pairs in the large island case (Würsig et al., 1994c), with high fluidity that resembles that of some neotropical spider monkeys (*Ateles* sp.) and several populations of chimpanzees (Chapman et al., 1995; Kinzey and Cunningham, 1994; Robbins et al., 1991; Sussman, 2000; Symington, 1990). On the other hand, the stable units of associations and long-term relationships at Midway Atoll seem akin to such systems as killer whales (*Orcinus orca*; Baird, 2000; Bigg et al., 1990; Matkin et al., 1999) and long-finned pilot whales (*Globicephala melas*; reviewed in Connor, 2000) or to those of some primates such as bonobos (Hohmann et al., 1999; White and Burgman, 1990; Wrangham, 1986). We hypothesize that it is the variable influence of the nearshore environments that affects this difference in overall society structure. In particular, the availability of sheltered shallow-water habitats needed by spinner dolphins for their daytime resting likely represents a serious limiting factor in the midst of an open ocean. In the main Hawaiian Islands, each island provides a mosaic of closely located nearshore environments with several suitable resting habitats in close reach, each with the capability to hold a certain percentage of the nighttime feeding group. In far-western Hawaii, suitable resting habitats are restricted to atoll lagoons, limited in size, and separated by large stretches of open pelagic waters with potentially high risk of shark predation. With deepwater food resources in close proximity and other atolls relatively far away for easy (day-to-day) access, it is energetically more beneficial in the remote Hawaiian atolls to remain at home than travel to other atolls, so there is stability instead of variability; there is no fission-fusion effect.

This pattern, however, is likely to prevent interbreeding between spinner dolphin groups associated with different atolls and islands across the Hawaiian island chain. Consequently, variation in rates of gene flow between the different groups (or populations) may be expected, affecting the genetic structure of Hawaiian spinner dolphins across the archipelago. Current genetic evidence (Andrews et al., in press) supports this hypothesis, indicating that the Midway spinner dolphins differ genetically from dolphins at the main Hawaiian Islands and show low haplotype and nucleotide diversity compared to the dolphins off the main islands. This reduction in genetic diversity is considerable, despite the already low genetic diversity of the main islands spinner dolphins (Galver, 2002), ranking it among the lowest genetic diversities currently known for small cetaceans—seemingly a result of the small and isolated populations of the northwestern Hawaiian Islands as compared to the main islands.

With the current genetic evidence closely matching the findings of the analyses presented here, it seems reasonable to conclude that stability instead of variability and social cohesion instead of fission-fusion represent the norm for spinner dolphins inhabiting the remote atolls of the northwestern Hawaiian archipelago. The occasional "rapid disassociations" and "casual acquaintances" suggested for the Midway residents by the pattern of lagged association rates and the "emigration/mortality" suggested by lagged identification rates are likely to be sampling artifacts, where several individuals, although present at the time, could not be photographed due to the large group size. Alternatively, they may indicate a true pattern, suggesting that although infrequent, interactions with spinner dolphins inhabiting the neighboring atolls (Kure to the west and Pearl & Hermes to the east) occasionally take place. Considering the geographic distances between the atolls, it is unlikely that the Midway spinner dolphin population is totally isolated and closed, and it is the degree of insularity and "closeness" that is at the heart of the matter here. At least one of the females photographed frequently during the first 5 months of 1998 was not resighted for the next 11 months, after which she was again frequently seen within the resident group at Midway. This individual sighting history, representing a case of emigration and reimmigration, as suggested by the model best fitting the residents' lagged identification rates, is very likely an example of such occasional interactions between the neighboring populations. It seems likely that such interactions, including a change in group membership, may facilitate gene flow between populations. It is unlikely, however, that they take place often, as the individuals known to use the geographically closest atolls (Midway residents and the immigrants seen previously at Kure) showed little interaction and remained socially discrete for many months when exposed to each others' presence at one location.

Direct causes of the influx of the immigrant group at Midway remain unknown, although their first sighting in 1999 followed shortly after a massive atmospheric front that moved southeast, passing over Kure Atoll before reaching Midway. It is possible that if trapped by the severe sea conditions while feeding outside the atoll, at least some of the Kure spinner dolphins might have been forced by the heavy seas eastwards, ending up at Midway. At least for some of the immigrants, however, it was not their first time at Midway, providing another indication that occasional movement between atolls takes place. Demographic causes of the emigration from Kure and immigration to Midway also cannot be excluded, although this will remain speculative due to the lack of sufficient evidence (there were only two opportunistic photo-ID surveys in Kure Atoll in 1998). However, if isolation and social discreteness indeed represent the dominant pattern for spinner dolphins in the remote Hawaiian atolls, the demographic consequences of such an event (increased population density at Midway, competition for space at resting sites, etc.) may be considerable. Further monitoring of the Midway population and interactions between the two groups (currently underway) is likely to reveal further insights into group dynamics and social stability.

From a management-applicable standpoint, there appears to be a well-pronounced differentiation in the population structure and social dynamics of spinner dolphins across the Hawaiian island chain. The remoteness, isolation, and limited resting habitats (or carrying capacities) of the northwestern atolls promote strong geographic and social fidelity, a notable contrast to the spinner dolphins off the main Hawaiian Islands. The atoll populations are discrete and apparently "closed" (or almost so) behaviorally and genetically, and each atoll population may need to be considered a separate management unit.

Broader comparative perspective

Although the differences in the society structure of atoll-dwelling spinner dolphins at Midway and those off the Kona coast of the Big Island of Hawaii are considerable, they are not totally unexpected. Several studies of terrestrial mammalian systems show considerable intraspecific variability, a result of individual attempts to maximize fitness under local ecological conditions (Bekoff et al., 1984; Boesch, 2002; Boinski, 1999; Wrangham, 1987). For instance, there are striking cases of convergence in the social systems of distantly related primate species that have at least superficial similarities in their ecological adaptations, such as chimpanzees and spider monkeys, or talapoins (*Miopithecus telapoin*) and squirrel monkeys (Chapman et al., 1995; Kappeler, 1999; Robinson and Janson, 1987; Wrangham, 1987). On the other hand, there is also considerable intraspecific variability in primate social organization, sometimes seemingly caused by only subtle changes in ecology, as reviewed for squirrel monkeys, *Saimiri* sp., in Boinski (1999). In western lowland gorillas (*Gorilla gorilla gorilla*), the social pattern may vary between stable cohesive groups (similar to the grouping pattern of mountain gorillas, *Gorilla gorilla beringei*) and a more "chimpanzee-like" fission-fusion pattern, depending on the habitat type and amount of food resource it provides (Doran and McNeilage, 1998, 2001; Yamagiwa, 1999). Even greater intraspecific variability has been described for chimpanzees (Boesch, 1996; Boesch et al., 2002), and it is of particular interest in the context of the spinner dolphin research presented here. Chimpanzee grouping pattern differs greatly in the sexual bonding tendency: chimpanzees in the Taï forest (Ivory Coast) are characterized by strong bisexual bonding, those in Gombe (Tanzania) are male oriented in their bonding, while those in the Mahale mountains (Tanzania) show an intermediate tendency (Boesch, 1996). Grouping pattern and cohesion differ relative to habitat, demography, and geographic isolation (Boesch, 1996, 2002; Sugiyama, 1988, 1999), with a tendency towards smaller populations (communities) having larger parties (groups). In other words, the smaller the population, the higher the cohesion between society members.

There are some striking parallels between what we have learned recently about Hawaiian spinner dolphins and the variability in chimpanzee social systems described by Boesch (1996, 2002). The Midway spinner dolphin population of some 260 individuals (SE = 8.6; Karczmarski, unpublished data) is small in comparison to the previously studied population off the Kona coast (some 2000+ animals, Würsig et al., 1994c), and like the Taï (Boesch, 1996) and Bossou (Sugiyama, 1988, 1999) chimpanzees, the Midway spinner dolphins are relatively isolated from neighboring populations. The group size at Midway is an order of magnitude larger than the general group sizes off the Kona coast reported by Würsig et al. (1994c) and Östman (1994). For the Kona coast spinner dolphins, male-oriented bonding was suggested (although based on preliminary data, Johnson and Norris, 1994; Würsig et al., 1994c). This is not so for the Midway population, where bisexual bonding is evident, with no obvious fission-fusion. A similar case of increased social stability, although within the underlying fission-fusion social system, with long-lasting companionships within and between sexes and increased group sizes has been recently described for a small, geographically isolated population of bottlenose dolphins in southwest New Zealand (Lusseau et al., 2003).

Comparative analyses of chimpanzee and bonobo social grouping patterns across various research sites in Africa (Boesch, 1996; Boesch et al., 2002) indicate that for small and isolated communities, the fission-fusion social structure loses much of its fluidity in favor of a considerably more stable, bisexually bonded society. Based on the empirical evidence presented here, we suggest that for Hawaiian spinner dolphins, geographic isolation and limited accessibility of suitable habitats promote a process that remarkably parallels that proposed by Boesch (1996) for the Taï chimpanzees. In this process, geographic isolation of socially stable, bisexually bonded dolphin societies facilitates social discreteness and differential social structures, which in turn add another barrier—a social barrier—to the gene flow and affect population genetic structure. As the end result—in the remote insular atoll habitats—the fluidity of the fission-fusion society is replaced with long-term group fidelity and social stability. An intriguing parallel becomes apparent: that social dynamics of complex mammalian societies, even evolutionarily as distant as delphinids and primates, vary in a remarkably similar way if exposed to comparable ecological and social selective pressures. In this respect, a comparison between primate and dolphin societies provides useful insights into ecological pressures influencing sociality.

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REFERENCES

Andrews KR, Karczmarski L, Au WWL, Rickards SH, Vanderlip CA, Toonen RJ, in press. Patterns of genetic diversity of the Hawaiian spinner dolphin (*Stenella longirostris*). Atoll Res Bull.

Baird RW, 2000. The killer whale: foraging specializations and group hunting. In: Cetacean societies: field studies of dolphins and whales, 1st ed (Mann J, Connor RC, Tyack PL, Whitehead H, eds). Chicago: University of Chicago Press; 127–153.

Bejder L, Fletcher D, Bräger S, 1998. A method for testing association patterns of social animals. Anim Behav 56:719–725.

Bekoff M, Daniels T, Gittleman J, 1984. Life history patterns and the comparative social ecology of carnivores. Annu Rev Ecol Syst 15: 191–232.

Benoit-Bird KJ, Au WWL, 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav Ecol Sociobiol 53:364–373.

Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC III, 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep Int Whal Commn (Special Issue 12):383–405.

Boesch C, 1996. Social grouping in Taï chimpanzees. In: Great ape societies, 1st ed (McGrew WC, Marchant LF, Nishida T, eds). Cambridge: Cambridge University Press; 101–113.

Boesch C, 2002. Behavioural diversity in *Pan*. In: Behavioural diversity in chimpanzees and bonobos, 1st ed (Boesch C, Hohmann G, Marchant LF, eds). Cambridge: Cambridge University Press; 1–8.

Boesch C, Hohmann G, Marchant LF (eds), 2002. Behavioural diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press.

Boinski S, 1999. The social organisations of squirrel monkeys: implications for ecological models of social organisation. Evol Anthropol 8:101–112.

Cairns SJ, Schwager SJ, 1987. A comparison of association indices. Anim Behav 35:1454–1469.

Chapman CA, Wrangham RW, Chapman LJ, 1995. Ecological constraints on group-size—an analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36:59–70.

Clark M, Young R, 1998. Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. J Mar Biol Assoc 78:623–641.

Connor RC, 2000. Group living in whales and dolphins. In: Cetacean societies: field studies of dolphins and whales, 1st ed (Mann J, Connor, RC, Tyack PL, Whitehead H, eds). Chicago: University of Chicago Press; 199–218.

Defran RH, Weller DW, 1999. The occurrence, distribution, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in San Diego, California. Mar Mamm Sci 15:366–380.

Defran RH, Weller DW, Kelly DL, Espinoza MA, 1999. Range characteristics of Pacific bottlenose dolphins within the Southern California Bight. Mar Mamm Sci 15:381–393.

Doran D, McNeilage A, 1998. Gorilla ecology and behavior. Evol Anthropol 6:120–131.

Doran D, McNeilage A, 2001. Subspecific variation in gorilla behavior: the influence of ecological and social factors. In: Mountain gorillas, 1st ed (Robbins MM, Sicotte P, Stewart KJ, eds). Cambridge: Cambridge University Press; 123–149.

Friday N, Smith TD, Stevick PT, Allen J, 2000. Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. Mar Mamm Sci 16:355–374.

Gailey GA, 2001. Computer systems for photo-identification and theodolite tracking of cetaceans (MS thesis). College Station: Texas A&M University.

Galver LM, 2002. The molecular ecology of spinner dolphins, *Stenella longirostris*: genetic diversity and population structure (PhD dissertation). San Diego: University of California.

Ginsberg JR, Young TP, 1992. Measuring association between individuals or groups in behavioural studies. Anim Behav 44: 377–379.

Gittleman JL (ed), 1989. Carnivore behavior, ecology, and evolution, vol. 1. Ithaca: Cornell University Press.

Gowans S, Whitehead H, 2001. Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): sources of heterogeneity from natural marks. Mar Mamm Sci 17:76–93.

Guissamulo AT, Cockcroft VG, 2004. Ecology and population estimates of the Indo-Pacific humpback dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique. Aquat Mamm 30:94–102.

Hemelrijk CK, 1990. Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Anim Behav 39:1013–1029.

Hohmann G, Gerloff U, Tautz D, Fruth B, 1999. Social bond and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136:1219–1235.

Johnson CM, Norris KS, 1994. Social behavior. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, eds). Berkeley: University of California Press; 243–286.

Kano T, 1992. The last ape: pygmy chimpanzee behavior and ecology. Stanford: Stanford University Press.

Kappeler PM, 1999. Convergence and divergence in primate social system. In: Primate communities, 1st ed (Fleagle JG, Janson C, Reed KE, eds). Cambridge: Cambridge University Press; 158–170.

Karczmarski L, 1999. Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. J Zool Lond 249: 283–293.

Karczmarski L, Cockcroft VG, 1998. Matrix photo-identification technique applied in studies of free-ranging bottlenose and humpback dolphins. Aquat Mamm 24:143–147.

Karczmarski L, Cockcroft VG, McLachlan A, 1999a. Group size and seasonal pattern of occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. S Afr J Mar Sci 21:89–97.

Karczmarski L, Winter PED, Cockcroft VG, McLachlan A, 1999b. Population analyses of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, Eastern Cape, South Africa. Mar Mamm Sci 15:1115–1123.

Kinzey WG, Cunningham EP, 1994. Variability in Platyrrhine social organization. Am J Primatol 34:185–198.

Lee PC (ed), 1999. Comparative primate socioecology. Cambridge: Cambridge University Press.

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson SM, 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. Can geographic isolation explain this unique trait? Behav Ecol Sociobiol 54:396–405.

Manly BFJ, 1995. A note on the analysis of species co-occurrences. Ecology 76:1109–1115.

Matkin CO, Ellis G, Olesiuk P, Saulitis E, 1999. Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska. Fish Bull 97:900–919.

McGrew WC, Marchant LF, Nishida T (eds), 1996. The great ape societies, 1st ed. Cambridge: Cambridge University Press.

Moehlman PD, 1989. Intraspecific variation in canid social systems. In: Carnivore behavior, ecology, and evolution, vol. 1 (Gittleman JL, ed). Ithaca: Cornell University Press; 143–163.

Nishida T, Hiraiwa-Hasegawa M, 1987. Chimpanzees and bonobos: cooperative relationships among males. In: Primate societies, 1st ed (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds). Chicago: University of Chicago Press; 165–177.

Norris KS, Dohl TP, 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish Bull 77:821–849.

Norris KS, Johnson CM, 1994. Schools and schooling. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J). Berkeley: University of California Press; 232–242.

Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, 1994. The Hawaiian spinner dolphin. Berkeley: University of California Press.

Östman JSO, 1994. Social organization and social behavior of Hawaiian spinner dolphins (*Stenella longirostris*) (PhD dissertation). Santa Cruz: University of California.

Perrin WF, 1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc Biol Soc Wash 103:453–463.

Perrin WF, 1998. *Stenella longirostris*. Mamm Species 599:1–7.

Perrin WF, Gilpatrick JW, 1994. Spinner dolphin *Stenella longirostris* (Gray, 1828). In: Handbook of marine mammals, vol. 5: the first book of dolphins (Ridgway SH, Harrison R, eds). San Diego: Academic Press; 99–128.

Perrin WF, Mesnick SL, 2003. Sexual ecology of the spinner dolphin: geographic variation in mating system. Mar Mamm Sci 19:462–483.

Poole MM, 1995. Aspects of behavioral ecology of spinner dolphins (*Stenella longirostris*) in the nearshore waters of Mo'orea, French Polynesia (PhD dissertation). Santa Cruz: University of California.

Reich A, 1981. The behavior and ecology of African wild dogs in Kruger National Park (PhD dissertation). New Haven: Yale University.

Robbins D, Chapman CA, Wrangham RW, 1991. Group-size and stability: why do gibbons and spider monkeys differ? Primates 32: 301–305.

Robbins MM, Sicotte P, Stewart KJ, 2001. Mountain gorillas, 1st ed. Cambridge: Cambridge University Press.

Robinson JG, Janson CH, 1987. Capuchins, squirrel monkeys and Atelines: socioecological convergence with old world primates. In: Primate societies, (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds). Chicago: University of Chicago Press; 69–82.

Rubenstein DI, Wrangham RW (eds), 1986. Ecological aspects of social evolution: birds and mammals. Princeton: Princeton University Press.

Sakamoto Y, Ishiguro M, Kitagawa G, 1986. Akaike information criterion statistics. Tokyo: D Reidel Publishing Company, KTK Scientific Publishers.

Schnell GD, Watt DJ, Douglas ME, 1985. Statistical comparison of proximity matrices: applications in animal behaviour. Anim Behav 33:239–253.

Sokal RR, Rohlf FJ, 1995. Biometry, 3rd ed. New York: W. H. Freeman.

Sugiyama Y, 1988. Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. Int J Primatol 9:393–407.

Sugiyama Y, 1999. Socioecological factors of male chimpanzee migration at Bossou, Guinea. Primates 40:61–68.

Sussman RW, 2000. Primate ecology and social structure, vol. 2: New World monkeys. Needham Heights: Pearson Custom Publishing.

Symington MM, 1990. Fission-fusion social organization in *Ateles* and *Pan*. Int J Primatol 11:47–61.

van der Jeugd HP, Prins HHT, 2000. Movements and group structure of giraffe (*Giraffa camelopardalis*) in Lake Manyara National Park, Tanzania. J Zool Lond 251:15–21.

Weller DW, 1991. The social ecology of Pacific coast bottlenose dolphins (MA thesis). San Diego: San Diego State University.

Wells RS, 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Dolphin societies: discoveries and puzzles, 1st ed. (Pryor K, Norris KS, eds). Berkeley: University of California Press; 199–225.

Wells RS, 2003. Dolphin social complexity: lessons from long-term study and life history. In: Animal social complexity: intelligence, culture, and individualized societies, 1st ed. (de Waal FBM, Tyack PL, eds). Cambridge: Harvard University Press; 32–56.

Wells RS, Boness DJ, Rathbun GB, 1999. Behavior. In: Biology of marine mammals, 1st ed (Reynolds JE III, Rommel SA, eds). Washington and London: Smithsonian Institution Press; 324–422.

Wells RS, Norris KS, 1994. The island habitat. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, eds). Berkeley: University of California Press; 31–53.

Wells RS, Scott MD, Irvine AB, 1987. The social structure of free-ranging bottlenose dolphins. In: Current mammalogy, vol. 1 (Genoways H, ed). New York: Plenum Press; 247–305.

White F, 1996. Comparative socio-ecology of *Pan paniscus*. In: Great ape societies, 1st ed (McGrew WC, Marchant LF, Nishida T, eds). Cambridge: Cambridge University Press; 29–41.

White FJ, Burgman M, 1990. Social organization of the pygmy chimpanzee (*Pan paniscus*): multivariate analysis of intracommunity associations. Am J Phys Anthropol 83:193–201.

Whitehead H, 1995. Investigating structure and temporal scale in social organizations using identified individuals. Behav Ecol 6: 199–208.

Whitehead H, 1997. Analysing animal social structure. Anim Behav 53: 1053–1067.

Whitehead H, 1999a. Socprog 1.2 (for Matlab 5.1): programs for analysing social structure. Halifax: Dalhousie University.

Whitehead H, 1999b. Testing association patterns of social animals. Anim Behav 57:F26–F29.

Whitehead H, 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology 82: 1417–1432.

Whitehead H, Dufault S, 1999. Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. Adv Study Behav 28:33–74.

Wrangham RW, 1986. Ecology and social relationships in two species of chimpanzee. In: Ecological aspects of social evolution: birds and mammals (Rubenstein DI, Wrangham RW, eds). Princeton: Princeton University Press; 352–378.

Wrangham RW, 1987. Evolution of social structure. In: Primate societies, 1st ed (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds). Chicago: University of Chicago Press; 282–296.

Würsig B, Wells RS, Norris KS, 1994a. Food and feeding. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, eds). Berkeley: University of California Press; 216–231.

Würsig B, Wells RS, Norris KS, Würsig M, 1994b. A spinner dolphin day. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, eds). Berkeley: University of California Press; 65–102.

Würsig B, Wells RS, Würsig M, Norris KS, 1994c. Population structure. In: The Hawaiian spinner dolphin, 1st ed (Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson CM, Solow J, eds). Berkeley: University of California Press; 122–140.

Yamagiwa J, 1999. Socioecological factors influencing population structure of gorillas and chimpanzees. Primates 40:87–104.