Facultative river dolphins: conservation and social ecology of freshwater and coastal Irrawaddy dolphins in Indonesia

Kreb, D.

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
CHAPTER 9

Social dynamics of facultative Irrawaddy river dolphins (Orcaella brevirostris) in Borneo: Impacts of habitat

Submitted manuscript

Coastal Irrawaddy dolphins mating in Balikpapan Bay. This particular mating event lasted about 1.5 h and involved several groups totaling 13 individuals. The individual in the center has its belly turned up.
ABSTRACT

Information on social structures and breeding strategies within cetaceans and especially (facultative) river dolphin species is sparse. The impacts of habitat on social structures of coastal and freshwater populations of Irrawaddy dolphins, *Orcaella brevirostris*, in East Kalimantan were studied between 1999 and 2002. River and bay habitats differed in three aspects, respectively; 1) constrained vs open geographical shape; 2) year-round vs seasonal high food abundance and 3) clumped vs scattered food resources. These conditions favored a lesser degree of sociality of “bay” dolphins indicated by smaller groups and less frequent inter-group interactions; seasonal breeding and a lesser degree of sexual dimorphism, which may result in less competition among males and probably in one, polyandrous mating system. Inter-group interactions of “bay” dolphins were mostly functional, *i.e.*, feeding, whereas river dolphin inter-group interactions were of varying nature, *i.e.*, feeding, traveling, socializing, agonistic interactions. River dolphins display year-round breeding; congregation in a few preferred feeding sites; lower site fidelity of males; overall high association values among individuals but fluid association patterns amongst sexes; existence of preferred male companionships; and a higher degree of sexual dimorphism. These result in high competition among males and two (polyandrous) mating strategies seem to apply: 1) roving-male strategy (single and in alliances) for early detection of females in estrus and to abduct them from other males, and 2) residing-male strategy in feeding sites of females and joining the open, direct competition if a female is in estrus whereas the female ultimately chooses (a) mating partner(s).

RINGKASAN

berkembangbiak sepanjang tahun, berkumpul di beberapa tempat yang mereka sukai
untuk makan, bagi jantan tingkat kesetiaan pada suatu tempat rendah, secara
keseluruhan nilai hubungan antar individu adalah tinggi tetapi nilai hubungan antara
jenis kelamin lebih rendah. Adanya hubungan dengan jantan yang disukai, dan
tingginya tingkat perbedaan jenis kelamin. Akibatnya adalah kompetisi yang tinggi
antara para jantan dan dua strategi perkawinan dengan banyak pasangan terjadi yaitu:
1) seekor atau lebih jantan mengambil betina dari kelompok pada awal masa
reproduksi untuk dijauhkan dari jantan lain, dan 2) jantan yang ikut dalam kompetisi
langsung dan terbuka dalam mencari pasangan dimana pada akhirnya betina akan
memilih satu atau lebih jantan sebagai pasangannya.

INTRODUCTION

Social structures of odontocetes are usually characterized by long-lasting associations
among individuals (mostly mother/calf, females, and (sub)adult male bands) and
mating systems are typically described to be promiscuous (in this study further, more
properly referred to as polyandrous) (Berta & Sumich, 1999). Best studied groups of
oceanic dolphins (Delphinidae) in terms of social ecology are bottlenose dolphins,
*Tursiops truncatus*, spinner dolphins, *Stenella longirostris*, Hectors’ dolphins,
*Cephalorhynchus hectori*, Indo-Pacific Humpback dolphins, *Sousa chinensis* and killer
whales, *Orcinus orca*. Least studied of species in terms of social organization include all
river dolphin species.

Long-term studies on the social organization of bottlenose dolphins were
described for Florida (Wells, 1991), Western Australia (Smolker et al., 1992), Scotland
(Wilson, 1995) and the Northern Adriatic Sea, near Croatia (Bearzi et al., 1997). School
composition in bottlenose dolphin societies in a short-term is predominantly fluid
(fission-fusion), but many associations are relatively long-term (Connor et al., 2000a).
Common mating strategies involve (super) male alliances attending or even sometimes
abducting adult females until estrus occurs (Connor et al., 1999; 2001). Mating within
spinner dolphins is seasonal and polyandrous and also male coalitions do occur
(Johnson and Norris 1994). Hectors’ dolphins and Indo-Pacific hump-backed
dolphins also appeared to have a typical fission-fusion society and they are
hypothesized to have either a polyandrous (Bräger, 1999; Slooten et al., 1993), or mate
searching mating system (Karczmarski, 1999; Jefferson, 2000), respectively. Resident
killer whales live in small stable social pods of two to nine individuals. These pods are
matrilineal consisting of an older mature female and her first and second generation’s
offspring (Olesiuk et al., 1990). Matrilineal groups may travel together in larger pods of
three to 59 individuals. Inter-pod matings occur during pod encounters in shared or
resting areas and seem to be seasonal (Ford et al., 1994). Transient killer whales also
associate in fairly stable pods, equivalent to a single matrilineal group with one to two
generations present existing of one to four individuals, and individual associations
over fifteen years have been documented (Baird, 1994; Baird & Whitehead, 2000; Baird & Dill, 1996). Dispersal by members of the native group has been recorded of both males before they reach, and females once they reach sexual maturity (Baird, 1994). One-third of groups encountered consisted of single, male individuals (Baird & Dill, 1996).

River dolphins are least documented as to their individual associations and mating strategies. The mating system of the boto (*Inia geoffrensis*) was hypothesized to be monogamous based on the relatively small testis size and lack of sexual dimorphism (Best & Da Silva, 1984), although Connor *et al.* (2000) found a moderate sexual dimorphism (1: 1.11) for the same species. Male-biased sexual dimorphism (length, weight) was found in hump-backed dolphins in South Africa in contrast to hump-backed dolphins in Hong Kong for which no evidence was found for sexual dimorphism (Jefferson, 2000; Cockcroft, 1989). In Hectors’ dolphins, females are larger than males (Slooten *et al.* 1993). Sexual dimorphism in both bottlenose and spinner dolphins in length is minimal, although males may be heavier up to 39% in large bottlenose dolphins (Read *et al.*, 1993; Tolley *et al.*, 1995). In contrast, a high degree of sexual dimorphism occurs in killer whales.

Social structures (group formation) in general are affected by prey availability and predator and parasites avoidance (Connor, 2000). The most distinct intra-species differences of social structures due to prey resources are demonstrated for killer whales. Fish-eating “resident” killer whales do not disperse from their maternal pod, whereas some female and male mammal-eating “transient” killer whales do disperse from their natal pod of which the males associate with other individuals to a lesser degree than females do (Baird & Whitehead, 2000).

In this study, social structures are compared of two populations of the same delphinid species, *Orcaella brevirostris*, commonly described as an elusive species (Lloze, 1973; Dhandapani, 1992; Kreb, 1999), *i.e.* a coastal population in Balikpapan Bay and a freshwater population in the Mahakam River, both occurring in East Kalimantan, Indonesia. These habitats not only differ in prey availability and presence of predators, but also in geographical shape, which affect dolphin movement patterns and bioacoustics, and which in their turn may affect social structures. For example, the chance that different dolphin groups meet unintended is much higher in a river habitat than in an open bay habitat due to constrained area size in rivers and clumped food resources in confluence areas (Kreb, 2002; Smith, 1993). Also, the confined river shape and many river bends limits the free passage of dolphin sounds over large distances and thus favors physical nearness of individuals to maintain social relationships. In contrast, clicks of sperm whales, *Physeter macrocephalus* may travel over several kilometers and individuals may keep track of each other over larger distances (Berta & Sumich, 1999). A study on bottlenose dolphins living at the southern extreme of the species’ range showed that ecological constraints were important factors in shaping social interactions within cetacean societies as they showed in contrast to bottlenose dolphins in other areas, a temporally stable community structure (Lusseau *et al.*, 2003).
The objectives of the present study are to assess the impacts of ecological differences on shaping social structures within coastal and river populations of the same dolphin species in terms of group size and composition, and social interactions among groups. In addition, I wanted to determine which breeding strategies might apply for both populations based on the degree of sexual dimorphism, extent of home ranges, dolphin distribution, inter-group interactions, breeding seasonality. Finally, individual association patterns and site fidelity are being analyzed for the river dolphin population. Individual associations of the Irrawady river dolphin population will be analyzed using the simple ratio-index as recommended by Ginsberg and Young (1992), when association is defined by presence in the same group. This population is listed as Critically Endangered following IUCN criteria (Reeves et al., 2003) and the population is estimated to exist of less than 75 individuals (Kreb, in press). A better understanding of their social ecology may aid in their conservation. Other studies on association patterns, which used association indices, only involved coastal dolphins. Most studies were on Hector's dolphins in New Zealand (Slooten et al., 1993; Bejder et al., 1998; Bräger, 1999). Association patterns of bottlenose dolphins were studied in Texas and New Zealand (Bräger et al., 1994; Lusseau et al., 2003). Transient and resident killer whales were studied in Canada and Alaska (Baird & Whitehead, 2000; Matkin, 1999). Indo-Pacific Humpback dolphins were studied in Hong Kong and South Africa (Jefferson, 2000; Karczmarski, 1999). Half-weight indices were most frequently used, than the simple-ratio association index, whereas Cole’s index and point correlation coefficient index were only used in one study.

METHODS

Study area

Balikpapan Bay stretches from 116°42' to 116°50' E and 1° to 1°22' S (Figure 1). Water surface area of the bay is approximately 120 km². Maximum width of the bay is approximately 7 km, and the surrounding shorelines within the bay consisted mainly of mangrove vegetation. Dolphin densities were more or less equally distributed over all the strata in the bay (Kreb, unpublished data). Food ecology is regulated seasonally and four different seasons can be distinguished based on wind prevalence. December until February is governed by northern wind with varying but mainly low fish availability, and many waves. From March until May an eastern wind prevails with high fish abundance. From June until August southern wind is dominant, with many waves at sea, but high abundance of fish in the bay. Finally, September until November is characterized by the highest waves, with low fish abundance in the bay due to fish spawning in mangrove vegetation.

The Mahakam River is one of the major river systems of Borneo and runs from 118° east to 113° west and between 1° north and 1° south (Figure 1). Regional climate is characterized by two seasons, i.e., dry (from July-October, southeast monsoon) and
Figure 1. Map of both study areas, the Mahakam River and Balikpapan Bay. Four dolphin distribution areas in the river are encircled and high dolphin density areas are indicated by square boxes named “core”.
Social dynamics of facultative river dolphins

wet (November-June, northwest monsoon) (MacKinnon et al., 1997). However, dry and wet periods alternate during the wet season as well. The river measures about 800 km from its origin in the Müller Mountains to the river mouth and crosses two districts, West and Central Kutai. Average river width between Samarinda (80 km from the mouth) and Long Bagun (c. 560 km from the mouth) at medium water levels is 200 m. Three major lakes, Semayang (10,300 ha), Melintang (8,900 ha), and Jempang (14,600 ha) are connected to the main river system in the Middle Mahakam Area (MMA) between 180 km and 375 km from the mouth. In addition, nearly all the major tributaries connect with the main river in the MMA, together with many smaller swamp lakes that are connected to these (some only seasonally through flooding). These lakes are very important fish-spawning grounds and replenish the main river seasonally. Rapids start upstream at c. 600 from the mouth, which limit the dolphins from moving further upstream. In the dry season, dolphins congregate in deep, confluence areas. At the onset of the rainy season, fish spawn upstream tributaries and dolphins migrate accordingly (Kreb, 2002).

Field techniques

From February 1999 until August 2002, we surveyed the Mahakam River for a total of 750 hr with transects totaling 7933 km. In total, 12 extensive surveys (= six replicated up-and downstream surveys) were conducted that covered the entire distribution range (mean duration = 10 days; SD ± 2 days) during all types of water levels (high, low, medium, increasing, decreasing). Another six intensive surveys were conducted in areas of high dolphin density (average duration 12 days; SD ± 3 days). River dolphins were observed for a total of 545 h. Four coastal surveys were conducted in the Balikpapan Bay survey area from May 2000 until October 2001, and a total distance of 1360 km during 127 h was covered in 36 days. Coastal dolphins were observed during 60 h. Of the river dolphin population, 775 photographs were made representing identifiable dorsal fins and a total number of 66 dolphins identified. Observation- and survey procedures, and photo-identification techniques are described in Kreb (2002; in press).

Along the river, 58 focal groups distributed over the entire dolphin range were followed for 321 h in total (hereafter referred to as “focal follows”) and each group on average 5.5 h (range = 1.5 – 13 h). In the bay, 21 coastal focal groups were followed each for on average 3 h (range = 1.5 – 8.5 h) and for a total of 64 h. General group behaviour was recorded from the start of observation and ended when changes occurred in group behaviour or when dolphins left or joined the group. Then, a new recording session would start. Group behaviour involved general behaviour in which > 50% of dolphins were engaged. When new individuals joined the focal group after the first 15 minutes of observation time, these were recorded as inter-group interactions and lasted until these individuals left the focal group or until the end of
observation time. If the focal group was observed to split during observation time without any new individuals joining the group at first then the largest group was still followed and regarded as focal group. The observation time until the groups split was then recorded as inter-group interaction time.

Sex was determined visually from the presence or absence of a neck crest. Males have prominent neck crests and females have smooth necks with no crest. This distinction was based on a preliminary study in the Mahakam (Kreb, 1999) during which individual differences in sizes of neck crests irrespective of body length were noticed. Also, individuals with calves always had a smooth, thin neck shape as had one dead female dolphin. To double check if differences in neck sizes were related to sex, a control group of 12 captive Irrawaddy dolphins of known sex in Oasis Seaworld, Thailand were examined. All these dolphins were six years or older. Four dolphins with no crest at all were females. Males always had a neck crest, varying from slight to conspicuous. However, crests of these Irrawaddy dolphins, which were caught from the Gulf of Thailand, never attained the same size as those observed for dolphins in the Mahakam River.

**Data analysis**

All tests involved non-parametric statistics since sample populations were not always normally distributed nor had similar variances. Only once, a parametric Z-test was used to compare group sizes between both populations, because a large data set was available that complied with the set restrictions for parametric tests (Fowler & Cohen, 1990).

**Group size and composition**

Mean group size in the Mahakam was based on all on-effort sightings made during 9 extensive abundance surveys covering the entire distribution range. Likewise, mean group size in Balikpapan Bay employed on-effort sightings made during 4 surveys with equal survey effort in all segments of the bay. Groups were considered different if a group joined after 15 min of observation or groups split during observation time. The proportion of adult males in groups were determined only for those groups for which the number of individuals and males could be determined with a high certainty, i.e., was agreed upon by all observers who had been assigned the special task to determine group composition (2-3 observers).

In order to find the maximum, optimum group sizes for various general behaviors only interacting groups were used.

**Movement patterns and site fidelity**

Overall home ranges of photo-identified dolphins were only determined for river dolphins, since we had no photo-identification data for the coastal population. Home ranges were estimated by measuring the distance between the two most widely
separated sighting locations for each individual photographed during surveys that covered the entire dolphin distribution range. This linear distance was then multiplied by the average width for the different river sections. Since we did not always get a positive photo-identification during each survey period for each of the photo-identified dolphins and the photographic effort was not equally spread over the different years, we calculated overall home ranges based on sightings made during the entire study period (3.5 years) and not per year.

To assess site fidelity, the locations of photo-identified river dolphins were mapped according to different zones in the river (Figure 1). The core areas 1 & 2 represented high dolphin density regions, which included confluence areas of tributaries, lakes and main river (Kreb, 2002). In addition, residence indices (RI) were calculated for 13 females and 9 males, excluding known juveniles and sightings made < 3 days, following a formula, which was thought to reflect best the extent of site fidelity for the river dolphin situation (Eqn. 1). Residence indices were calculated for each individual by distracting the number of periodical sightings in the area where most sightings were made ($x_i$), with the combined number of periodical sightings in other areas ($\sum x_i$). The distribution areas of dolphins to this end were divided in 40 km river strips and only sighting was calculated per area per survey period (≡ periodical sighting). This value then was divided by the total number of survey periods, in which each individual was sighted ($s$). Index values could range between -1 (low site fidelity) and 1 (high site fidelity).

Eqn 1.
\[
RI = \frac{x_i - \sum x_i}{s}
\]

**Social interactions and behaviours**

Interactions between groups were described either as non-interactions when dolphins moved in different directions (zero interaction time), or low level-interactions if groups were traveling in the same direction but kept a distance of > 50 < 500 m. In a pure sense dolphins of the latter category probably interacted to some extent with each other through their acoustics, since click trains of dolphins in the river could be detected at least over 500 m at straight stretches using a High Tech Inc.- 94-SSQ hydrophone (frequency range: 2Hz - 30 KHz at –168 dB re 1V/μPa), which hung 1.5 m deep into the water).

When assessing the mean interaction time between the focal and newly encountered groups, only those interactions were included in which the new groups were encountered during the focal follow time and also separated from the focal group before the end of the follow time. However, these interactions were included when assessing how many group interactions lasted > 1 hour.
**Individual associations**

In this study, associations were analyzed using SOCPROG 1.3, a program developed in MATLAB (The Mathworks, Inc., Natick, Mass., U.S.A.) by Hal Whitehead for analyzing social structure. In this study, the MATLAB 6.5.1 version was used.

Individuals were considered associated if they were seen together in the same group (total no. groups = 95). Only photo-identified individuals were used \((n = 50)\) of total identified \(n = 66\), which were sighted in 3 or more groups and 2 or more sampling periods (years). Groups were newly defined when a new sighting started and every 3 h when groups were followed > 3 h. Minimally 2 individuals were photo-identified within each group.

Simple-ratio association indices (Equation 1) were used to measure associations, which are thought most appropriate when association is defined by presence in the same group, here referred to simply as association index (AI). Also, since sampling biases vary among pairs of individuals, the association indices which use arbitrary weightings only reflect the direction, but not the extent of sampling biases (Ginsberg & Young, 1992). The simple ratio indices provided values between 0 (if individuals were never seen together) and 1 (if two individuals were always seen together).

\[
\text{Eqn 2} \quad \text{AI} = \frac{x}{x + y_A + y_B}
\]

Where \(x\) = number of sightings in which both dolphin \(A\) and \(B\) were seen in the same group, \(y_A\) = total number of sightings of individual \(A\) excluding individual \(B\), and \(y_B\) = number of sightings in which only individual \(B\) was sighted and not \(A\).

Association patterns were displayed in two ways: 1) by an average-linkage cluster analysis showing the average level of association between hierarchically formed clusters and 2) by a principal coordinates analysis, which makes a metric scaling and produces an arrangement of points, each representing an individual, so that the distance between them is inversely proportional to the square-root of their association.

Real association values were also randomly permuted 50,000 times following Bejder et al. (1998), Manly (1995) and a modification of Whitehead (1999) in order to test if the mean, SD, and proportion of non-zero association indices were different than would be expected from random associations. For detection of diads (pairs) that have significantly large or small associations, a 2-sided significance level of 0.05 was selected. Two types of random permutations were performed: 1) permuting groups within samples, which test accounts for situations in which not all individuals are present in each sampling interval (because of birth, death, migration etc.) and tests both long-term (between sampling periods) as well as short-term (within sampling
RESULTS

Group sizes

Mean group size of dolphins in the Mahakam (covering the entire dolphin distribution range) is 4.4 and most dolphins (29% of total $n$) occurred in group sizes of 5 individuals ($n = 75$; SD = 2.2; range = 1-10). Mean group size in Balikpapan Bay was significantly smaller, i.e., 3.2 ($n = 79$; SD = 2.1, range = 1-9; Test equal variances, $F = 1.13, P > 0.05$; Z-test, $z = 3.43, P < 0.01$). Frequencies of group size occurrences are in Figure 2. Most coastal dolphins moved about solitarily (27% of total $n$).

Within the river dolphin population, lowest mean group sizes of interacting groups were found when groups were feeding (mean = 6.4, SD = 2.4) or traveling (mean = 6.6, SD = 2.6) together (Table 1). Interacting groups, which were feeding or

![Figure 2. Frequency of group size occurrence of coastal ($n = 75$ groups) and freshwater ($n = 79$ groups) Irrawaddy dolphins](image-url)
Table 1. Predominant inter-group activities, interaction time and group sizes for coastal and river Irrawaddy dolphin populations

<table>
<thead>
<tr>
<th>Predominant inter-group activities</th>
<th>% of total interactions</th>
<th>*Mean *interaction time (min)</th>
<th>Mean group size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bay (n = 20)</td>
<td>River (n = 76)</td>
<td>Bay (n = 8)</td>
</tr>
<tr>
<td>Heading in one direction</td>
<td>10%</td>
<td>18%</td>
<td>-</td>
</tr>
<tr>
<td>Feeding</td>
<td>75%</td>
<td>34%</td>
<td>30</td>
</tr>
<tr>
<td>Intensive socializing</td>
<td>10%</td>
<td>25%</td>
<td>181</td>
</tr>
<tr>
<td>Agonistic displays</td>
<td>0%</td>
<td>8%</td>
<td>-</td>
</tr>
<tr>
<td>Low level interaction</td>
<td>5%</td>
<td>8%</td>
<td>19</td>
</tr>
<tr>
<td>No interaction</td>
<td>0%</td>
<td>7%</td>
<td>-</td>
</tr>
</tbody>
</table>

- = only one or no interactions available; * only interaction used, which formed and split during observation time

traveling, were significantly smaller than groups engaged in any of the other behaviors (median group sizes of each behavioral category were compared with one another using Mann-Whitney U test; all p < 0.05 except for one pair, i.e., travel and low level interaction p > 0.05). The mean group sizes associated with feeding or traveling are considered the optimal group sizes for these types of behaviors. If interacting groups are larger in size than the standard deviation, the interaction is characterized by intensive socializing or gets a less desirable character. Groups either avoid each other (low level interaction and no interaction), or become agonistic if groups just happened to encounter each other unintended, whereas they actually intended to feed. For the bay population we found that the median optimum group size for interacting feeding groups (mean = 6.1, SD = 2.1) was not significantly different from the median feeding group size in the river population (Mann-Whitney U-test, U= 196.5, P > 0.05).

Group composition

A positive correlation was found between group size and the relative percentage of calves within the river dolphin population \((r = 0.81, \text{df} = 8, P < 0.01)\), but not within the coastal population \((r = 0.11, \text{df} = 7, P > 0.05)\). The largest relative proportion of river calves in relation to juveniles and adults occurred within group sizes of 8-10 individuals. The relative proportions of coastal calves were normally distributed over different group size classes with the largest proportion of calves found in groups of 4-5 individuals. Significant relatively larger proportions of calves for the coastal population in comparison to the river population were found in small groups of two to three individuals \((G = 28.4, \text{df} = 2, P < 0.01)\). Most river dolphin groups sighted \((54 \% \text{ of } n = 75)\) involved adults with their offspring; 29% were adult groups; 4% involved groups consisting of juveniles exclusively \((6-7 \text{ individuals})\); 13% were single...
individuals. Proportions differed significantly from those in the coastal population with percentages in the same sequence of 34%, 30%, 0% and 21% \((G = 7.906, \text{df} = 3, P < 0.05)\). Especially more single individuals were recorded in the coastal area and there were no juvenile groups.

### Sexual dimorphism

In both the Mahakam River and Balikpapan Bay, Irrawaddy dolphins that lacked neck crests and dolphins with slightly to more prominent neck crests were observed, irrespective of body length. Individuals with calves had smooth necks with no crest. However, neck crests of coastal Irrawaddy dolphins never attained the same size as those observed for dolphins in the Mahakam River.

The proportion of adult males and females within groups for coastal and river populations are presented in table 2, single groups excluded. The proportion of males in both coastal and river dolphin groups significantly less often exceeded the proportion of females in groups \((X^2 = 7.922 \& X^2 = 18.54, \text{df} = 2, P < 0.05 \& P < 0.01)\). No differences in the proportion of adult males in groups was found between both populations \((G = 3.59, \text{df} = 2, P > 0.05)\). Two cases in the coastal population where the proportion of males exceeded females in groups involved groups that exclusively consisted of males \((n = 3 \& 5)\). Two single coastal and river ‘groups’ of which the sex could be determined involved males. Groups of river and coastal dolphins consisting of minimally one adult female and maximally 7 females were mostly escorted by single adult males \((56 - 60\% \text{ of groups } n = 36 \& 25)\) and up to a maximum of 4 adult males. Two river dolphin groups \((6\%)\) consisted each exclusively of two adult females. Five coastal groups \((20\%)\) involved single-parent groups of one adult female and her offspring, whereas no single-parent groups were found in groups of river dolphins. Coastal adult female groups were significantly more often unescorted by males in comparison to river dolphins \((G_{adj} = 11.75, \text{df} = 1, P < 0.01)\).

A total of 66 river dolphins were photo-identified during the study period for which the sex could be identified for 27 individuals \((41\%)\); 15 were females and 12 were males, of which 1 female juvenile and 2 male juveniles.

### Spatial distribution

#### Home ranges

In order to assess daily home ranges, 58 river and 21 coastal focal groups were followed for a total of 321 and 64 h and on average 5.5 and 3.0 h daily \((\text{range } 1.5 - 13 \text{ h}; 1.5 - 8.5 \text{ h})\), respectively. Daily home ranges of 27 river focal groups, which were
Table 2. Proportion of adult males in groups

<table>
<thead>
<tr>
<th>Proportion of adult males per group</th>
<th>Coastal bay No. of groups</th>
<th>%</th>
<th>River No. of groups</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males &gt; females</td>
<td>2</td>
<td>8%</td>
<td>3</td>
<td>8%</td>
</tr>
<tr>
<td>Males = females</td>
<td>13</td>
<td>50%</td>
<td>10</td>
<td>27%</td>
</tr>
<tr>
<td>Males &lt; females</td>
<td>11</td>
<td>42%</td>
<td>24</td>
<td>65%</td>
</tr>
<tr>
<td>Total groups</td>
<td>26</td>
<td>37</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

followed > 6 h were small, i.e., 10 km river strip (SD = 8.6 km, range 1-45 km) and 1.1 km² in area (SD = 1.8 km, range 0.1 – 9 km²). Daily ranges of 3 coastal focal groups, followed > 6 h were all in a mangrove river strip and were very small, i.e., 2 km length and 0.4 km² (n = 3), respectively. The average daily home ranges of 27 groups, followed > 6 h were 10 km in length (SD = 8.6 km, range 1-45 km) and 1.1 km² in area (SD = 1.8 km, range 0.1 – 9 km²).

Home ranges throughout the year were only calculated for the 53 river dolphins that were photo-identified during the 3.5 years study period during a mean number of 12.5 sightings (SD = 9.5, range = 2 – 39), 6.2 different survey days (SD = 3.7, range = 2 – 20) and 4.4 survey periods (SD = 2.0, range = 1 - 9). No correlation was found between the number of survey days or periods and home range length (r = 0.071, df = 51, P > 0.05 & r = 0.085, df = 51, P > 0.05). These dolphins moved freely in a river strip of on average 61 km in length (SD = 44 km, range = 4 – 181 km) and of 10 km² of river area (SD = 9.1 km², range = 0.3 – 35.5 km²). Female overall home ranges (n = 15) were significantly smaller (mean = 44 km; range = 4-103 km) than male overall home ranges (n = 12; mean = 103 km; range = 15-163 km) (U = 142, P < 0.05) (Figure 3).

Site fidelity of river dolphins
Two center areas of high dolphin density could be distinguished in the river with their peripheral zones (Figure 1). Sighting locations were mapped for all photo-identified individuals sighted on more than one day (n = 53 individuals) and on average 7 days (range = 2 – 22 days) and 4 survey periods (range = 2-10 periods). Eight individuals were exclusively sighted in area 1, and 30 individuals in area 2. Individuals exclusively occurring in either area 1 or 2 with known sex (n = 16), were mostly females (81%). The remaining 12 individuals had an overlap of sightings with peripheral zones of other areas, of which the sex could be identified for 10 individuals. Ten percent of individuals, which showed overlap with peripheral zones of other areas, were females and 90% were males. Three individuals were sighted in both center areas of areas 1 and 2 and were identified to be males (Table 3).
Social dynamics of facultative river dolphins

One group of 6 individuals occurred in an isolated area, being ‘trapped’ in between two rapids since a big flood in 1998 until the end of the study period (August 2002).

Residence indices for females (median = 0.88) were significantly higher than for males (median = 0.37) ($U = 16.5$, $n_1 = 13$ & $n_2 = 10$, $P < 0.01$), indicating a higher degree of site fidelity by females.

\textbf{Figure 3.} Male and female home ranges sizes (km river strip)

\begin{table}[h]
\centering
\begin{tabular}{ll}
\hline
River areas & Number of individuals (N) & Sex of > 75\% of N \\
\hline
Area 1 (core + periphery) & 8 & F \\
Area 2 (core + periphery) & 30 & F \\
Core 1- periphery 2\textsuperscript{2} & 3 & M \\
Core 2- periphery 1 & 5 & M \\
Cores 1 & 2 & 3 & M \\
Peripheries 1 & 2 & 1 & M \\
Core 2- periphery 3 & 2 & M \\
Area 1,2,3 & 1 & M \\
Total photo-id sightings\textsuperscript{3} & 53 & \\
\hline
\end{tabular}
\caption{Distribution of photo-identified individuals and adult sexes in different river areas}
\end{table}

\textsuperscript{1} Corresponding to areas indicated in Figure 1; \textsuperscript{2} Example; most sightings made in core area of area 1, but also sightings made in periphery of area 2; \textsuperscript{3} Only individuals used that were sighted > 1 day

F = females; M = males
Inter-group interactions

Number and duration of interactions
In total 58 river and 21 coastal focal groups were followed each for > 90 min (mean = 5.5 h, range = 1.5 – 13 h & mean = 3 h, range = 1.5 – 8.5 h) and for a total of 321 h and 64 h, respectively. A high percentage (71%) of 58 river focal groups had interactions with other groups on 74 occasions during the follow time. Each group encountered other groups on average 1.8 times (SD = 0.95; range = 1 - 4). Coastal dolphin focal groups interacted less frequently than river dolphins, i.e., only 48% of 21 coastal focal groups had inter-group interactions (mean number of interactions per group = 2, SD = 0.94; range-1 - 4), but not significantly ($G_{adj} = 3.45$, critical value = 3.84). Number of interactions was positively correlated with the focal group follow time in the river population ($r = 0.34, df = 40, P = 0.03$), but no correlation existed in the coastal population ($r = 0.13, df = 8, P > 0.05$) (Figure 4).

River dolphins followed for an average 8 h (range = 6 - 10 h) encountered a mean number of two other groups (range = 1 – 4 h). Inter-group interactions of river dolphins lasted on average 62 min (SD = 67 min; range = 10 - 325 min), and more than half the number of total inter-group interactions (53%) lasted > 1 hour. Mean duration time of interactions of coastal dolphins is 47 min (SD = 56 min; range = 10 – 181 min). Significantly more interactions lasted longer than 1 hour in the Mahakam river as compared to Balikpapan Bay where 6 interactions (30%) of 20 interactions lasted > 1 hour ($G_{adj} = 16.02, df = 1, P < 0.01$). Interactions that lasted longest (nearly 3 h) were socializing in both populations and traveling (Table 1). Feeding lasted shortest (< 1 h) and significantly shorter in the bay than in the river ($X^2 = 8.3, df = 1, P < 0.01$). Agonistic encounters lasted quite long, nearly 1 h.

Nature of interactions
Six main behavioral categories were distinguished of interacting groups: 1) traveling as primary activity, 2) (combination of) feeding (and traveling), 3) intensive socializing (in combination with traveling), 4) agonistic behavioral displays, 5) low level interaction (mean distance between two groups > 50 m < 500 m), 6) no interaction (groups heading in different directions). Predominant inter-group activity (> 50% of interaction time) in both the Mahakam River and Balikpapan Bay was feeding together (34% & 75% of encounters, respectively), which was observed significantly more often than the other behaviors ($X^2 = 28.99, df = 5, P < 0.01$) (Table 1). The proportions of different inter-group activities varied significantly between coastal and river populations ($G_{adj} = 33.26, df = 5, P < 0.01$). Although feeding was the dominant activity, in the river populations other behaviors, such as intensive socializing and traveling were also often displayed, whereas in the coastal population these activities were less common. In Balikpapan Bay, dolphins only socialized during 10% of encounters among groups. Also, nearly one-fourth (23%) of river group interactions
involved agonistic-, low level- and non-interactions, whereas these behaviors were only displayed in 5% of total number of interactions in coastal groups.

Breeding

Mating events \( (n = 3) \) in the Mahakam were observed during the months July and August at low water levels. However, behaviors associated with mating were observed throughout the year and at all water levels. Mating events took place between 2 to 3 subgroups with total group sizes ranging between 5 until 12 adult individuals per mating event. Mating most probably only occurs among different groups, since each time after mating interactions had finished (duration time = 9-80 min) the groups were observed to split into subgroups. Matings were characterized by vocal and behavioral dominance displays: loud blows, fast swimming, rolling along the axis of the dolphin’s body, swimming side-wards and with belly up, group swimming in small circles and speeding up (chases), jumps, many fin and fluke waves and slaps, and intensive body contact. Behaviors associated with mating were not as intensive as mating events, less speeding, rolling activity and body contact compared to the mating events. After a mating event groups were observed to split and mating behavior continued in one group. Newborns (< 1 month of age) were observed in all different months and water levels, so it is likely that matings also take place throughout the year. During all mating events, several males were identified, which during the study period occurred in both core areas of area 1 and 2.

In Balikpapan Bay, one mating event and behaviors associated with mating were only observed during the month October. The mating event lasted 1.5 h and involved 13 adult individuals (and 1 juvenile). After 79 min, the group split in two subgroups of 5 and 9 individuals. The latter group continued mating until they started moving fast and disappeared. Newborns were only observed during the months June and July in 2001 and 2002, respectively. The weather conditions in these months are governed by a southern wind, which causes a high fish availability in the bay due to high waves in the open sea, whereas waves in the bay are moderate.

Individual associations of the river dolphin population

Random permutations of real association values of groups and associations within samples (testing both short- and long-term companionships) were performed for all identified individual dolphins, that were sighted in 2 or more sampling periods \( (n = 50 \) = 79% of \( N \) identified) in a total of 95 groups. Individual dolphins showed clear preferences for association with certain individuals and had long-term preferred companionships both indicated by a significantly higher SD of the real association indices than the random value \( (P = 0.99) \). The mean real simple-ratio association index (AI) value of non-zero elements was 0.42 (SD = 0.18), which was also
Figure 4. Average linkage dendogram of the Irrawaddy dolphin population in the Mahakam River showing associations among individuals in between the period of February 1999 until August 2002. On the y-axis are all individuals, which are identified in more than 2 groups and during 2 or more sampling periods (years). The letters M and F in the ID names correspond with male and female respectively, whereas the numbers with which the ID names begin correspond to the areas in which the individuals have been sighted. The three clusters described in the text are indicated.
significantly higher than the random mean value \((P = 0.99)\). The significantly lower proportion of non-zero associations \((p = 0.37)\) than randomly excepted indicates that some individuals avoided others \((P < 0.01)\). This can be seen from figure 4, where 3 clusters can be distinguished, the first and second existing of individuals with a high site fidelity in areas 1 and 2 (mostly females), respectively mixed with males with overlapping ranges in both areas, and a third cluster representing individuals, which are ‘trapped’ in between two rapids in area 4 (Figure 1). Within sampling periods 20 significant diads were found, whereas between sampling periods 30 significant long-term diads were detected. Mean individual association values (including zero-elements) were found significantly higher for individuals exclusively sighted in one area \((AI = 0.18)\) than for those individuals, which moved in between 2 or more areas \((AI = 0.13)\) (Mann-whitney U-test, \(U = 142; n_2 = 35 \& n_2 = 13; P < 0.05\)). Also, the mean, maximum association values were significantly higher for individuals, which occurred in one area \((mean AI_{max} = 0.75)\) than for individuals occurring in both areas \((mean AI_{max} = 0.65)\) \((U = 80; P < 0.05)\).

All females occurring in area 2 \((n = 11)\) associated with each other relatively intensively \((mean AI = 0.41; SD = 0.16)\), but no preferred companionships were detected as indicated by a significantly lower mean and SD of the real association indices compared to the random values \((P < 0.05)\). The proportion of non-zero associations \((p = 0.85)\) was significantly higher than that of the random values \((P = 0.95)\) indicating that most females associated with other females within sampling periods and also maintained these associations between sampling periods, although not significantly \((P = 0.92)\).

The proportion of 12 individual males that associated with other males \((p = 0.55)\) was much lower compared with the proportion of associations among females \((p = 0.85)\). Mean association values (including zero-elements) were also significantly smaller for males \((AI = 0.20)\) than for females \((AI = 0.36)\) \((U = 120; n_1 = 11 \& n_2 = 12; P < 0.01)\), whereas maximum association values \((mean AI_{max} = 0.55)\) were also significantly smaller than those of females \((mean AI_{max} = 0.68)\) \((U = 103; n_1 = 11 \& n_2 = 12; P = 0.01)\) (Figure 5). No significant short- or long-term preferred companionships were found, except for one diad within one sampling period (Figure 6).

Finally, most associations among sexes were fluid both within and between sampling periods as no significant deviations of real association indices from random values were found, which should indicate short- or long-term preferred companionships. However, the mean association indices of non-zero elements were just as high as found within intra-female associations \((mean = 0.41; SD = 0.17)\), indicating that most males and females associated with each other. One significant male-male diad was found within one sampling period and 3 female-male diads, 2 male-male diads and one female-female diad were found in between sampling periods. The proportion of individuals, which associated with others \((p = 0.59)\) was significantly lower than randomly expected \((P < 0.01)\), indicating that some individuals avoided others.
Figure 5. Mean and maximum simple-ratio indices of female-female ($n = 11$) and male-male ($n = 12$) associations (A.I.)

Figure 6. Principal coordinates analysis plot showing strong (small circles close together, such as trio 2.3MP27, 2MP10 & 1-2MP42) and one looser male consort-ships through time (between sampling periods). Males 2MP10 and 1-2MP42 formed a significant alliance within one sampling period (year).
DISCUSSION

Methodological constraints

Regarding the calculation of association indices, the estimates of the total number of sightings of individual A excluding individual B (and vice versa) may not be accurate, since a successful photo-id picture is not always obtained from each individual in the group. So, dolphin pairs may actually occur together during a sighting, but only one individual may be photo-identified. No photo-identification data for the coastal dolphin population was available, since only a low proportion was found to have characteristic dorsal fins during a preliminary survey.

Social organization

Group sizes are described to be mainly affected by prey availability and predator avoidance (Connor, 2000). In this study, both populations did not seem to be affected by predators. In the sheltered bay area, there are no sharks, only marsh crocodiles, Crocodylus porosus, which do not seem to pose a real threat to the dolphins as inferred from the absence of predator defense mechanisms (formation of large groups) as a high proportion of ‘groups’ exists of single individuals. Similarly, in the river two species of crocodiles, the false gavial, Tomistoma schlegeli, and the Siamese crocodile, Crocodylus siamensis, do not seem to pose a threat to the dolphins because of their rounded body shape, which would be difficult to handle for these relatively small crocodiles. Differences found in coastal and river group sizes are most likely to be related to the distribution of food resources, which are more clumped in the river and more equally distributed in the bay.

The high percentage of more or less unwanted interactions, i.e., agonistic, low-level or non-interactions (23% of total interactions) are typical for the Mahakam situation in which groups compete for confluence areas and many unintended encounters are more a result of the same preferences for specific feeding areas, mostly confluence areas with tributaries and lakes (Kreb, 2002). These types of interactions are unknown for botos, which also occupy a limited range for part of the year but for which no avoidance or aggressive behaviors were found (Schnapp & Howroyd, 1992). A similar large proportion of social interactions (25% of total interactions) as the “negative” interactions take place among different river dolphin groups. Since social interactions among groups may last for 2.8 h; this indicates that these interacting groups are not an aggregation of loose groups but represent a true social unit. In this aspect the Mahakam dolphins, although not as comprehensively studied, resemble the pods of their closest relatives (resident) killer whales (LeDuc et al., 1999), which are composed of several intra-pod groups and form stable relationships based on high
association indices within intra-pods in resident killer whales (Matkin et al., 1999). They also have similar group sizes consisting of 4 individuals on average (Bigg et al., 1990). In the Mahakam, three distinct pods could be distinguished based on individual site fidelity corresponding with downstream core area 1 and upstream core area 2, and the trapped group occurring in Ratah tributary. The Mahakam population also resembles a population of bottlenose dolphins living in a fjord in New Zealand in their geographical isolation, their small population size of both less than 75 individuals, and similar temporally stable community structure with high association values among all members in the population. However, they were dissimilar in group sizes amongst others, which were much larger for these bottlenose dolphins with 17 individuals on average. Association values among individuals of studies on humpback dolphins in Hong Kong and South Africa (Jefferson, 2000; Karczmarski, 1999), bottlenose dolphins in Galveston Bay, Texas (Bräger et al., 1994). Hectors’ dolphins in New Zealand were all low and dolphins appeared to have relatively fluid associations, associating with many individuals rather than with very close associates (Brager, 1999; Slooten et al., 1993). Transient female killer whales had a high average but low maximum association rates indicating that they are not only gregarious, but also socially mobile. Male transient killer whales have no strong or long-term relationships with any individuals (Baird & Whitehead, 2000).

Coastal Irrawaddy dolphins were very similar to transient killer whales with respective small group sizes of 3 and 2 individuals on average. Also, single-individual encounters occurred just as frequent in 27% and 31% of total number of encounters with coastal Irrawaddy dolphins and transient killer whales, respectively (Baird and Dill 1996). A possible explanation for the apparent smaller social units of coastal Irrawaddy dolphins may be the fact that social contact among pods may be maintained over longer distances by means of acoustics, instead of physical contact by the less restrained geographical environment.

**Breeding strategies**

Matings of dolphins in the Mahakam were also similar to the resident killer whales because in both species matings occurred outside the intra-pod groups and possibly among pods when pods encounter each other in shared foraging or resting areas (Berta & Sumich, 1999; Bigg et al., 1990; Ford et al., 1994). Inter-pod matings in Balikpapan Bay occur seasonally and estrus periods of females may be more or less synchronized, which could explain the less marked sexual dimorphism in coastal Irrawaddy dolphins. Since distribution of females in the bay was found to be equally spread over different segments in the bay and estrus of females is seasonal, males may also be more distributed over the bay (daily home ranges were found to be rather small) and competition for males may not be too fierce, favoring a polyandrous or “multi-mate” mating system like those found for other species, e.g. spinner dolphins in Hawaian waters, which mate seasonal (Johnson & Norris, 1994). However, also in
bottlenose dolphins, which are poly-estrous, matings are suggested to be polyandrous (Berta & Schumich, 1999).

River dolphins in the Mahakam on the other hand bred throughout the year and estrus females are easily detected by males since most groups co-occur in favorite feeding areas and encounter other groups twice on average during day time. Female distribution is most likely defined by resource availability, and male distribution is most likely affected by female availability (Davies, 1991). Since the groups are clumped in one area and frequently interact, it seems unlikely that males monopolize females. Rather, a roving male or resident male strategy may be more prevalent. In the roving strategy, males wander from group to group to find receptive females such as was found in Hector’s dolphins and bottlenose dolphins for example (Slooten et al., 1993; Connor et al., 1992). Strongly bonded male groups were also found in spinner dolphins (Östman, 1994), spotted dolphins (Pryor & Schallenberger, 1991), resident killer whales (Baird, 2000), and northern bottlenose whales (Gowans, 1999). The following data confirms the existence of roving males. 1) Ten out of 75 sightings in the Mahakam during the study period occurred of single individuals, which in two cases could be identified and appeared to be males (one juvenile and one adult). 2) Three male diads were identified, of which two had long-term preferred companionships and one pair associated within one sampling period. 3) Overall, males maintained frequent but fluid associations with females. In addition, of the 15 identified males, 9 males had overlap with peripheral zones of other areas, and 3 males were sighted in both core areas of dolphin distribution, whereas females always remained in their core areas. The goal of roving males, whether single or in alliances, may be an early detection of estrus females by males and to herd or guard them, such as observed in bottlenose dolphins (Connor et al., 2000b). The roving technique may apply to juveniles and less dominant males, whereas resident males may be dominant adults, with a high success rate in female mating access. Three identified males were exclusively sighted in one core area during the entire study period and maybe resident males. A receptive female is likely to be soon detected by other males (alliances) since groups frequently meet and a direct competition may occur, in addition to which resident males participate, and in which the female may ultimately choose her mate. Female choice may be based on the multi-variety in behavioral displays observed during the matings in this study (see, results) similarly to many bird species (e.g. Foster, 1981). Also, active mate avoidance behavior of females was observed in this study by speeding up away from other individuals and rolling around the axis of their bodies. It has been suggested that female cetaceans, in contrast to terrestrial female mammals, may more easily avoid unwanted matings due to the three-dimensional fluid structure of the marine or river environment (Whitehead & Mann, 2000).

Because three distinct pods were identified in the Mahakam, which display an apparent, site fidelity for preferred dolphin sites, such as confluence areas where they have frequent social interactions, a site-protection-based conservation strategy is recommended in three core areas. This study attempted to fill in the gap in our knowledge of social ecology of river dolphins in general and more specifically of
facultative river dolphin species that consist both of freshwater as well as coastal dolphin populations.

**ACKNOWLEDGEMENTS**

I would like to thank the Indonesian Institute for Sciences (LIPI), the provincial wildlife conservation department (BKSDA) and local governments of Central- (KUKER) and West Kutai (KUBAR) for granting permission to conduct field research. All field assistants, particularly Ahang, Arman, Budiono, Karen Damayanti and Syachrani, and boatsmen are thanked gratefully as well as local fishermen that participated in the interviews. Funding for fieldwork was provided by Ocean Park Conservation Foundation, Hong Kong; Martina de Beukelaar Stichting; Stichting J.C. van der Hucht Fonds; Gibbon Foundation; Netherlands Program International Nature Management (PIN/ KNIP) of Ministry of Agriculture, Nature Management and Fisheries; Van Tienhoven Stichting; World Wildlife Fund for Nature (Netherlands); Amsterdamse Universiteits Vereniging; Coastal Resource Management Program/ Proyek Pesisir. The University of Mulawarman in Samarinda (UNMUL), Plantage Library, Achmat Ariffien Bratawinata, Frederick R. Schram, Peter J.H. van Bree, Thomas A. Jefferson, Martjan Lammertink and Vincent Nijman are thanked for their support throughout the study. Hal Whitehead is thanked for allowing the use of the SOCPROG software and The Mathworks for providing an evaluation copy of MATLAB 6.5.1. Bernd Würsig and two anonymous reviewers are thanked for their comments on the manuscript.

Fieldwork complied with the current laws in Indonesia, where the study was conducted.

**REFERENCES**


