

Solitary bottlenose dolphins in comparative perspective

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Abstract

Many mammal populations include solitary individuals. These individuals could be solitary for short or long periods and involve more or less spatial separation from conspecifics. A variety of accepted socio-ecology variables such as food availability, predator pressure, and reproductive strategies can account for much solitary behaviour. However, other factors, such as human interference, disease and the individual variability evident in many mammals may also be significant in some cases. The reasons dolphins become solitary are common to many mammalian species, but the response of some dolphins to the solitary state, including a redirection of social responses to humans or other species, could be unique to the Delphinidae.

Key words: Delphinidae, *Tursiops truncatus*, bottlenose dolphin, solitary behaviour, social organization, individual variability, reproductive strategies, food availability, predator pressure.

Introduction

The Delphinidae are gregarious and most behavioural studies have focused on aspects of group structure and function. However, a sizable literature describing the behaviour of individuals which seem to spend most or even all of their time without other conspecifics also exists (Lockyer & Morris, 1986; Bearzi, 1996). Some of these individuals have formed close associations with humans (Lockyer, 1990) or other cetacean species (Pilleri & Knuckey, 1967; Kraus & Gihir, 1971; Wells *et al.*, 1990; Müller *et al.*, 1998)

Reports of dolphins swimming alone range from less than an hour (Bel'kovich, 1991) to several days or months (Hansen, 1990) or even several years (Lockyer, 1990). Unfortunately, a clear definition of the spatial and temporal parameters of the solitary state is absent in many relevant studies. Despite the well-documented existence of solitary

individuals there appears to have been no attempt to understand the behaviour in a socio-ecological context. Several commentaries on the behaviour appear to conceive of solitary dolphins as 'aberrant', that is diverging from normal behaviour of the species (e.g., Cousteau & Dirole, 1975; Bradbury, 1986; Ferrero & Tsunoda, 1989). A notable exception to this view is by Lockyer (1990), who suggested solitary dolphins could be the victims of circumstances, rather than 'misfits'.

The ascription of solitary dolphins as 'aberrant' is curious given that behavioural studies of many other mammalian species have revealed a similar phenomenon. Thus chimpanzee populations, (*Pan troglodytes*) whose social structure often has been compared to that of the bottlenose dolphin (*Tursiops truncatus*) (McBride & Hebb, 1948; Tayler & Saayman, 1972; Würsig, 1978), are also known to include solitary individuals (Goodall, 1986; Newton-Fisher, 1999). Goodall (1986) noted at least two forms of such solitary behaviour, one temporary and one virtually permanent.

There are many reports of other mammalian species whose populations include solitary individuals, including the metaphoric 'lone wolf' of *Canis lupus* (Zimen, 1976) as well as spider monkeys (*Ateles* sp., McFarland Symington, 1990), gorillas (*Gorilla gorilla*, Harcourt *et al.*, 1976), African wild dogs (*Lycyaon pictus*, Frame & Frame, 1976), African elephants (*Loxodonta africana*, Barnes, 1982; Moss, 1983), lions (*Panthera leo*, Packer, 1986), sperm whales (*Physeter macrocephalus*, Whitehead, 1993), and many other species. Camenzind's (1978) description of coyote (*Canis latrans*) social structure noted that 15% of the population was made-up of solitary animals he called 'nomads'.

The widespread existence of solitary individuals within a normally sociable species indicates it is inappropriate to conceive of solitary dolphins as in any way biologically aberrant. The range of mammalian species exhibiting the existence of solitary individuals suggests the phenomenon could be amenable to conventional socio-ecological analysis.

Variables operating at the level of individual variability may also be involved. This paper will examine the phenomenon of solitary mammals in comparative perspective from both socio-ecological and individual difference perspectives, with special reference to solitary bottlenose dolphins.

Consequences of group living

Mammals display the full spectrum of social organization, from highly social species such as most primates and cetaceans (Connor *et al.*, 1992) to solitary species such as the hamster (*Cricetus cricetus*) and squirrel (*Sciurus vulgaris*) (Eisenberg, 1966). Solitary species normally avoid conspecifics except during mating, and individual social relations exist almost exclusively between females and their dependent offspring (Bischof, 1985).

The social life style affords both advantages and disadvantages to an individual (Krebs & Davies, 1993). For example, living in a social group has the disadvantages of energy expenditure in maintaining social relations such as dominance hierarchies, increased competition for food, and an increased vulnerability to disease or parasite transmission, infanticide and cannibalism (Wrangham & Rubenstein, 1986; Silk *et al.*, 1999). A significant advantage of group life is protection against predation, both in terms of mathematical probabilities of becoming prey and in terms of group vigilance (Hill & Dunbar, 1998; Janson, 1998).

The forces in favour of social versus solitary life styles must be finely balanced (Pulliam & Caraco, 1984). The behavioural plasticity characteristic of most mammal species sometimes reflects this changing balance and in so doing demonstrates the importance of external forces in shaping social behaviour (Lott, 1991). In evolutionary time scales, the social environment could actually increase levels of behavioural plasticity (Silk *et al.*, 1999).

Ecological factors

Group size is an important factor in socio-ecological explanations of how populations adapt to food availability. In general, the solitary life style occurs where food sources are dispersed and prey size is small relative to the predator. Conversely, where food resources are concentrated and prey is large, grouping of animals is advantageous (Krebs & Davies, 1993). Gautier (1982) illustrated these factors operating within the antelopes: the small, highly selective feeder dik-dik (*Madoqua kirki*) concentrates on a dispersed food resource and is found in small groups or totally solitary, whereas the large hartebeest (*Connochaetes t. taurinus*) feeds on an abundant resource and is found in very large groups.

The same forces can be observed operating within a species. Zimen (1976) noted that in wolves

(*Canis lupus*) the availability of prey influenced intra-group aggression. When prey was freely available there were low levels of aggression within the group, but as prey availability declined the aggression levels increased, apparently predisposing individuals to leave the group to forage alone. Solitary individuals are forced to rely on smaller prey because large prey requires cooperative hunting.

Other species in which the appearance of solitary individuals increases in relation to reduced prey availability include coyotes (*Canis latrans*) (Bekoff & Wells, 1986), hyenas (*Crocuta crocuta*) (Kruuk, 1972), red foxes (*Vulpes vulpes*) (Baker *et al.*, 1998), the European brown hare (*Lepus europaeus*) (Lott, 1991), lions (*Panthera leo*) (Owens & Owens, 1984), and the badger (*Meles meles*) (Kruuk & Parish, 1982).

Dolphins also display high levels of behavioural plasticity in relation to food availability. Group size and hence hunting technique has been demonstrated to reflect prey availability (Leatherwood & Reeves, 1983; Shane *et al.*, 1986; Leatherwood, 1975; Caldwell & Caldwell, 1972). Cockroft & Ross (1990) suggested the 'fission-fusion' social structure (Kummer, 1968) of bottlenose dolphins probably evolved to reduce intra-specific competition for food resources. Inter-specific aggregations (e.g., Herzing & Johnson, 1997) also correlate with increased food availability.

Prey selection is variable in the bottlenose dolphin. The catholic tastes of this species probably moderate the impact of prey availability on group size. This assumption is supported by the observation that dolphins do not appear to defend food territories (Wells *et al.*, 1987; Robineau *et al.*, 1994). Food availability clearly influences dolphin social structure (Wells *et al.*, 1999) and could produce solitary behaviour. This could be short-term in the form of individuals adopting solitary hunting techniques to suit the prey of the moment or of longer duration due to a chronic reduction in food availability.

The protection from predators afforded by group living is widely accepted (Janson 1998, Krebs & Davies, 1993; Hamilton, 1971; Alexander, 1974). Higher mortality for solitary individuals have been described for chimpanzees (Wrangham, 1986), lions (Packer, 1986), African wild dogs (Frame & Frame, 1976), and wolves (Jordan *et al.*, 1967).

Predator pressure also is related to habitat characteristics, closed habitats usually offering better protection. Gautier's (1982) analysis of African antelopes revealed forest dwelling species lived singly or in small groups (making use of protection via immobility, cryptism or silence to avoid predators). Species in open habitats lived in large groups and used vigilance and flight to avoid predators. Similarly, river dolphins, which experience

minimal predator pressure, are usually found alone or in very small groups (Layne, 1958; Smith, 1993). Even within a particular species the effects of habitat/predator pressure have been shown to influence social structure, e.g., the mountain goat (*Oreamus americanus*) is solitary or lives in small groups in cliff environments but aggregates into larger groups when living in flatter habitat (Lott, 1991).

The influence of predators (such as sharks and killer whales) on group size in dolphins is still unclear (Corkeron *et al.*, 1987), but the notion that in the open ocean there is more predator pressure from sharks is widely believed to account for the large group sizes found there (Connor & Norris, 1982; Wells *et al.*, 1980; Shane *et al.*, 1986; Robineau *et al.*, 1984). Unfortunately, establishing the level of shark attack on dolphins is difficult. The usual measure, the frequency of scarred animals in a population, is strictly only indicative of survival rate following attack rather than attack frequency *per se* (Herzing & Johnson, 1997; Shane *et al.*, 1986).

Most solitary bottlenose dolphins described to date inhabit protected coastal waters (Lockyer, 1990; Müller, 1998). This supports the view that the open ocean is more hazardous to single animals, though this observation could merely reflect observer effort. Consistent with this view is the observation that single bottlenose dolphins sometimes swim with open water pelagic species, such as pilot whales (*Globicephala melas*) (Pilleri & Knuckey, 1967; Kraus & Gahr, 1971; Wells *et al.*, 1990). The apparent high frequency of solitary dolphins in the Mediterranean (Bearzi *et al.*, 1997; Müller, 1998), an environment unlikely to produce high levels of predation pressure from sharks, also supports the view that predation favours larger aggregations.

It is highly unlikely one factor would determine the size of groups in any mammalian species. Krebs & Davies (1993) suggested hunger and fear are opposing factors: the former leading to smaller groups, the latter larger. Behavioural plasticity maintains the two factors in a state of dynamic equilibrium (Lott, 1991; Hill & Dunbar, 1998; Janson, 1998).

Human impacts can substantially alter social dynamics. Andelet (1985) described reduced group size of a persecuted coyote population and a substantial increase in the proportion of solitary individuals compared to non-persecuted populations.

Severe population decrease due to human hunting has occurred in several pinniped species. In two species the reduced population density was associated with changes in reproductive strategy involving a shift from polygamy to monogamy (Jouventin

& Cornet, 1980). Other behavioural consequences of human exploitation include fear and aggression (e.g., in elephants, Douglas-Hamilton & Douglas-Hamilton, 1975), stressful responses that probably influence intra-specific social behaviour.

In Europe, whole populations of dolphins are known to have disappeared, probably from intentional persecution by humans (Müller, 1998). The remaining small groups probably represent remnants of past populations. These include small populations around certain Mediterranean Islands (Dhermain, 1996a; Bearzi *et al.*, 1997), the Brittany coast of France (Hussenot, 1980; Liret & Ridoux, 2000), in coastal lagoons (Ferrety *et al.*, 1993, 1998), the Sado Estuary of Portugal (Dos Santos & Lacerda, 1987), and the Moray Firth in Scotland (Thompson & Wilson, 1994).

The decimation of dolphin populations in European waters could increase the probability of finding solitary dolphins in several ways. In areas where dolphin populations exist in more or less their original form there are usually several populations with overlapping home ranges, thus providing a ready avenue of dispersal to a neighbouring population. A dolphin in the process of dispersing will be solitary probably for only a short time. In areas with depleted numbers living in widely separated populations there could be less incentive for dispersal, and an individual may be solitary for a much longer time as it seeks-out another population.

There has been widespread and sustained persecution of dolphins in European waters even in recent times. Small cetaceans were systematically hunted and persecuted from the beginning of the twentieth century until 1965. During this period, small cetaceans in many areas were considered a pest to be destroyed (Thomazi, 1947; MAP, 1993). This sustained persecution seems to have resulted in a high level of avoidance behaviour towards humans in several of the surviving groups, making observations difficult (Pilleri, 1967; Ferrey *et al.*, 1993). This is particularly the case in certain areas where local fishermen have attacked dolphins in recent times and could, indeed, continue the practice to this day.

The contrast between avoidance behaviour to humans shown by many dolphins in European waters and the high levels of habituation shown by some solitary dolphins could be more exaggerated in Europe than elsewhere. This could have caused some observers to conclude the animals are more anomalous than they really are and given rise to the view solitary dolphins are biologically aberrant.

Pollution could effect social structure by affecting the fecundity and morbidity of a population, or by impacting on the habitat and affecting food availability. Toxic products, such as pesticides, could

accumulate in the food chain and can directly or indirectly reduce the density of prey species and consequently top order predators (Helle, 1980; Martineau *et al.*, 1994; Johnston *et al.*, 1996). In the long-term, environmental pollution works against animals associating in larger groups and favours small groups or solitary individuals (Lott, 1991).

Reproduction and social organization

The social structure of bottlenose dolphin society displays some apparently contradictory characteristics. At the overall society level, the dynamics of the species is a fission-fusion society (Kummer, 1968) with typically fluid association patterns. At a closer level of analysis, very stable associations among individuals are found. Bottlenose dolphin society can thus be seen to include a complex mixture of associations. The existence of solitary individuals can be viewed as representing one end of the wide continuum of sociability characterizing bottlenose dolphin society. The degree of fluidity evident in bottlenose dolphin social structure appears to be greater than that found in other species with fission-fusion social systems (e.g. Kummer, 1968; Symington, 1990; Smolker *et al.*, 1992).

Bottlenose dolphin mating involves short-term polygamy, i.e., for the duration of the female's oestrous season (Irvine *et al.*, 1981; Connor *et al.*, 1992, 1993). In many areas this pattern is overlaid by the development during adolescence of enduring male coalitions. The individuals forming these coalitions, usually two animals, could cooperate in sequestering females in oestrous as well as aiding each other in achieving intromission. Higher order coalitions could also form (Connor *et al.*, 1999).

Females in several species of primates are more solitary than the males. Wrangham (1986) observed female chimpanzees spent 65% of their time alone whereas males are rarely observed without conspecifics. Similarly, Symington's (1990) observations of spider monkeys found females spend 37% of their time alone compared to only 15% in males.

Female bottlenose dolphins display a wide range of sociability, from virtually solitary through to individuals who are almost never seen alone (Smolker *et al.*, 1992). Males also display the full spectrum of sociability. Wells *et al.*, (1987) observed most adult males in the Florida (Sarasota) population were either solitary or in coalition pairs when they were in areas frequented by females. In Australia (Shark Bay), males are usually found in coalitions though, in older males, if one individual of a pair dies, the other will often remain solitary (Smolker *et al.*, 1992). These observations indicated that observed sociability of older males might decrease considerably if contact with their habitual partner is severed. It is also possible that older animals are restricted by their condition from

associating in vigorous activities such as group feeding and resort to alternative, solitary feeding strategies (Doak, 1995; Müller, 1998). Male chimpanzees also have been reported to spend more time alone if they lose a coalition partner (Newton-Fisher, 1999).

A number of features of the reproductive strategies in bottlenose dolphins thus can increase the probability of individuals becoming solitary. The distribution of individuals in geographic space as part of the population dispersal process is a basic component of mammalian biology (Stenseth & Lidicker, 1992; Krebs & Davies, 1993). This can take one of two forms: dispersal of individuals in a pre-reproductive state and dispersal of reproductive individuals to neighboring populations (Blondel, 1995).

Dispersal has advantages at the population level (e.g., reduction of intra-group competition, avoidance of inbreeding and increasing genetic diversity), but can be hazardous at the individual level (unknown habitat, unknown food resources, competition with local rivals) (Lidicker, 1962; Greenwood, 1980; Stenseth & Lidicker, 1992; Blondel, 1995). It is also clear that in many instances of natal dispersal individual animals leave their group in search of a new group or home range (Stenseth & Lidicker, 1992) and thus, contribute to the proportion of solitary individuals in that population.

In most mammalian species, males disperse more than females (Stenseth & Lidicker, 1992), but there are notable exceptions, including chimpanzees (Goodall, 1986; Gagneux *et al.*, 1999), bonobos (*Pan paniscus*) (Wrangheim, 1986) and African wild dogs (Frame & Frame, 1976). In some species both sexes disperse as in mice (*Mus musculus*) (Lidicker, 1976), southern elephant seals (*Mirounga leonina*) (Nicholls, 1970), fur seals (*Arctocephalus pusillus*) (Kenyon, 1960) or dik-dik (Hendrichs & Hendrichs, 1971).

Male dolphins appear to travel longer distances than females. Wells (1991) observed males often disappeared from their normal home range for several weeks. This behaviour, which could aid in genetic mixing (Duffield & Wells, 1991), would have the incidental effect of increasing the probability of finding solitary individuals in a population.

In bottlenose dolphins, at least those belonging to large populations, both sexes leave their natal group as subadults between 4 and 10 years old (Leatherwood, 1977; dos Santos & Lacerda, 1987; Wells *et al.*, 1987; Tyack, 1991; Duffield & Wells, 1991). However, observations of the Sarasota population in Florida and of that of Shark Bay in Australia indicate males also travel for to reproduce with females of neighboring communities (Felix, 1997). Young females become members of mixed

subadult groups and then normally join groups of adult females or even rejoin their natal group (Duffield & Wells, 1991). However, in one case a solitary female left her home range and travelled 600 km to an environment frequented by conspecifics, and subsequently became pregnant (Müller 1998; Müller *et al.*, 1998). Reproductive dispersal in bottlenose dolphins is clearly one source of solitary animals, although the solitary state could be of only short duration if the individual migrates to a new group.

Individual variability

All populations show morphological variations in an approximately Gaussian distribution. It is evident behavioural variations also exist in any population, although problems in quantifying these differences makes it difficult to know whether they too are Gaussian in distribution. The behavioural variations observed are known variously as 'individual differences', 'temperament', or 'personality', depending on the author (Mather & Anderson, 1993).

Individual differences in behaviour have been described for many species (Schleidt, 1976; Slater, 1981; Lott, 1991). Based on his observations of Canidae, Bekoff (1977) suggested behavioural differences between individuals are responsible for the development of solitary behaviours in some individuals.

Several studies on large-brained mammals report major behavioural differences among individuals. These include chimpanzees (Goodall, 1986), elephants (Douglas-Hamilton & Douglas-Hamilton, 1975), and bottlenose dolphins (Smolker *et al.*, 1992). In the latter case, at least, individual differences can occur in both spatial and social behaviour (Lockyer, 1990). The nature/nurture debate has long been relegated to the status of a non-issue, with both inevitably influencing the developing organism (Hinde, 1966). It is almost impossible to disentangle the effects of heredity and experience via experimentation, but the impact of experience is now well-established via studies of classical and operant conditioning, observational learning, and imprinting (Immelmann *et al.*, 1996).

In several studies reporting differential levels of sociability the effects are clear if ambiguous as to cause. Hirth (1977) observed that the offspring of white-tailed deer (*Odocoileus virginianus*) living in open habitat spend more time together and that in adult life these individuals are more sociable than those living in closed habitats. Similarly, Bekoff (1977) found coyotes that socialized less as pups also socialized less as adults. Brandt (1992), in an ingenious experiment with marmots (*Marmota flaviventris*), demonstrated that the offspring of less

sociable mothers were much more prone to disperse than the young of more sociable mothers.

There is some direct evidence for the impact of experience on social behaviour in bottlenose dolphins. Smolker *et al.* (1997) described how several female dolphins in the Shark Bay area demonstrated a unique feeding strategy involving carrying sponges in their mouths, possibly as protection for the rostrum. Animals using this technique were largely solitary. Calves learned to carry sponges at a young age and also grew up to be solitary.

Circumstances which might result in a dolphin becoming solitary also include the death of a male's coalition partner or even the individual's whole group; poor health could make it impossible for an animal to keep-up with the rest of the group; or there could be more general developmental reasons. For example, separation of old animals from the main group has been reported in several mammalian species. These include elephants (Douglas-Hamilton & Douglas-Hamilton, 1975), chimpanzees (Goodall, 1986), lions, and buffalos (*Bison bison*, Gautier, 1982). Smolker *et al.* (1992) and Müller (1998) described bottlenose dolphins becoming more solitary in old age.

Disease can produce reductions in group size if it is serious enough to be fatal. For example, Baker *et al.* (2000) recently described the reduction in group size in a red fox population suffering from mange. The decimation of dolphin groups via epidemic also is well-documented (Dhermain, 1966b; Kennedy, 1996). This phenomenon could result in a sole survivor becoming solitary. In recent years, a number of epidemic events have resulted in major marine mammal die-offs. One such event occurred in the Mediterranean in 1990/1991 and resulted in smaller school sizes in striped dolphins (*Stenella coeruleoalba*) during the period of the epidemic, although following the epidemic the school sizes returned to their pre-epidemic levels (Forcada *et al.*, 1994). These smaller school sizes probably represent the survivors of larger schools which, following the epidemic, recongregated into schools of optimum size. In groups hard hit by the epidemic it is conceivable there would be only one survivor, leading to a solitary animal, at least until it could find other animals with which to group.

Dolphins are well-known for practicing epimeletic behaviour in the event of sick and injured individuals (Connor & Norris, 1982; Norris & Prescott, 1961). This can take the form of remaining close to a distressed individual or even actually supporting it in the water (Caldwell & Caldwell, 1966). However, the duration of this epimeletic behaviour must have limitations. If a sick or injured individual does not recover its companions will eventually leave it and move on (Mannion, 1991). The high proportion of single dolphins that

strand (both dead and alive) is further evidence that the epimeletic response has its limits (Donoghue, 1996).

Sick or injured dolphins also have been reported to seek-out protected coastal environments until they recover and thus become solitary during their recuperation (Doak, 1995; Hansen, 1990). Alternatively, dolphins which have suffered serious injury (e.g., shark attack) may be actively avoided by others. This response is presumably a self-protective response because injured animals could attract predators (Bischof, 1985).

If a calf becomes orphaned and its mother is not part of a group it will effectively become solitary. In addition, dolphin calves tend to stray from their mothers as they mature (Würsig, 1978; Leatherwood, 1977; Bel'kovich *et al.*, 1991; Connor *et al.*, 1993; Mann & Smuts, 1988).

Chimpanzee orphans have been reported to avoid contact with conspecifics, at least for a time (Goodall, 1986) and other behavioural disturbances have been described in other primates (Kaufmann & Rosenblum, 1969; Hinde & Spencer-Booth, 1971). Stereotypical behaviour involving protracted circling of a boat was described in an orphaned dolphin by Doak (1995). Similar stereotypical responses were described by Bel'kovich (1991). Such responses to trauma could facilitate the individual becoming solitary, if not actually cause it. There are many recorded cases of solitary dolphins focusing their social behaviour on humans and other species. However, this reorientation of social response toward another species is clearly a consequence of the solitary life style, rather than a cause of it (Müller, 1998). The above observations suggest that either a response to trauma or the occurrence of special circumstances might result in a dolphin becoming solitary.

It has been suggested the behaviour of solitary dolphins is biologically aberrant. However, a comparative review of social behaviour reveals the existence of solitary individuals in many mammalian species. In fact, it would appear to be normal for even highly social species to include at least some individuals who spend at least part of their time in a solitary state.

Simple causal relations are seldom the case in biology (Gautier, 1982) and the case of solitary behaviour in dolphins is unlikely to be an exception to this rule. The evidence cited above suggests the solitary state in dolphins could have a variety of causes. These include socio-ecological factors such as food availability; reproductive dispersal and social dynamics; as well as causation operating at the individual level, such as inherent intra-specific variability, behavioural plasticity, and individual experience. None of these factors are unique to dolphins.

The individual experiences of some solitary dolphins could have been traumatic (e.g., becoming orphaned) and result in abnormal behaviour. However, there are many other potential causes of a solitary state which do not invoke the attribution of abnormal behaviour. Whether the solitary lifestyle results in stresses that, in turn, produce abnormal behaviour is difficult to determine, but such consequences for any highly social species would seem a plausible assumption.

The reduced home range apparent in many solitary dolphins (Müller, 1998) does not seem to occur in other mammalian species. The many cases of solitary dolphins that focus their social behaviour on humans also appear to be unique to dolphins. Why these responses to a solitary state are not found in other species is unclear.

One of the most difficult aspects of reviewing the work on solitary dolphins is the absence of an accepted definition of the term 'solitary'. In an attempt to overcome this problem it would be beneficial for future researchers to clearly specify the temporal and spatial parameters of both dolphin groups and individual animals. If this is done it is likely a variety of types of solitary dolphin will be apparent, each with its own spatio-temporal parameters, antecedents, and associated behaviours. It follows that any single definition for a solitary dolphin is likely to be simplistic and perhaps confusing.

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