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Dolphins and African apes: comparisons of sympatric socio-ecology

Maddalena Bearzi[1], Craig B. Stanford[2]
[1] *Ocean Conservation Society, P.O. Box 12860, Marina del Rey, CA 90292, USA, mbearzi@earthlink.net, www.oceanconservation.org (corresponding author)*
[2] *Departments of Anthropology and Biological Sciences, University of Southern California, Los Angeles, CA 90089-0032, USA, stanford@almaak.usc.edu*

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Abstract

Dolphins and African apes are distantly related mammalian taxa that exhibit striking convergences in their socioecology. In both cetaceans and African apes, two or more closely related species sometimes occur in sympatry. However, detailed reviews of the ways in which sympatric associations of dolphins and apes are similar have not been done. As field studies of dolphins and apes have accumulated, comparisons of how the two groups avoid direct food competition when in sympatry have become possible. In this paper we review sympatric ecology among dolphins and African apes, and examine convergences in species-associations in each taxa. We review evidence for hypotheses that seek to explain avoidance of food competition, and consider whether ape-dolphin similarities in this area may be related to the way in which social groups in both taxa optimally exploit their food resources.

Contents

Introduction

Dolphins and African apes are two distantly related mammalian taxa that have produced socially complex, large-brained nonhuman animals. Comparisons between the two taxa have burgeoned in recent years, as field data on the various species in each group have accumulated. These comparisons have tended to stress parallels between two African apes (*Pan troglodytes* and *P. paniscus*) and dolphins (order Cetacea, suborder Odontocetes, family Delphinidae) in brain and social cognition (Herman, 1980; Marino, 1998; McCowan *et al.*, 2000; De Waal and Tyack, 2003; Johnson and Herzing, 2006, Lefevbre *et al.,* 2006), evidence for cultural traditions (Smolker, Richards, Connor, Mann, and Berggren, 1997; Whiten, *et al.,* 1999; Rendell and Whitehead, 2001, Whitehead *et al.,* 2006), and the influence of ecology on social structure (Connor, Read, and Wrangham, 2000b; Connor, Heithaus, and Barre, 2000c; Anderson *et al.,* 2005). Similarities in the pattern of sympatric associations between the two taxa have not been described, even though chimpanzees, bonobos and some well-studied dolphin species (*e.g.,* bottlenose dolphins *Tursiops truncatus,* spinner dolphins, *Stenella longirostris)* share many characteristics of their socioecologies: fission-fusion polygamy, male coalitions, strong mother-son bonds, and dispersed foraging for high-quality, patchy food resources (Table 1).

Dolphins and African apes both exhibit sympatric species associations. Chimpanzees and gorillas (*Gorilla gorilla*) are broadly sympatric across equatorial Africa, and several field studies have examined the way in which these two apes exhibit ecological overlap and potentially partition resources and habitat use (Jones and Sabater-Pi, 1971; Tutin, 1996; Stanford and Nkurunungi, 2003; Yamagiwa and Basabose, 2006). Although the earliest studies of each ape species seemed to show stark interspecific contrasts (*e.g.,* Goodall, 1986; Fossey and Harcourt, 1977), more recent work has blurred some of these distinctions by providing much evidence of intraspecific variability between both species, especially gorillas (Doran and McNeilage, 1998). Detailed field studies of dolphins have lagged behind those of African apes, largely due to the logistical difficulties of observation in a marine

Table 1. Parallels between dolphins and African apes.

Trait	Dolphins	References	Primates	References
fission-fusion	*Tursiops truncatus*	Würsig, 1978 Wells *et al.,* 1987	*P. troglodytes* *P. paniscus*	Goodall, 1986 Wrangham *et al.,* 1994 Kano, 1992; Furuichi, 1987
large testes	*T. truncatus*	Wells *et al.,* 1987	*P. troglodytes*	Harcourt, 1978
promiscuous mating system	*T. truncatus* *Stenella longirostris*	Connor *et al.,* 2000b (for general review) Perrin and Mesnick, 2003	*P. troglodytes* *P. paniscus*	Goodall, 1986 Tutin, 1979 Furuichi, 1987 Sussman, 1984
rival male aggression	*T. truncatus*	Connor *et al*., 2000abc (for general review)	*P. troglodytes* *G. gorilla*	Goodall, 1986 Fossey and Harcourt, 1977
male dominance over females	*T. truncatus*	Samuels and Gifford, 1997	*P. troglodytes* *G. gorilla*	Goodall, 1986 Fossey and Harcourt, 1977 Harcourt *et al*. 1981
co-ordinated prey capture prey capture	*Tursiops spp*. *Orcinus orca* *S. longirostris*	Bel'kovich *et al.,* 1991 Tayler and Saayman, 1972 Acevedo-Gutierrez, 1997 Norris and Dohl, 1980 Würsig, 1986 Baird and Whitehead, 2000 Benoit-Bird and Au 2003	*P. troglodytes*	Goodall, 1986 Stanford, 1998
large brain/ body size ratio	*T. truncatus*	Marino, 1998	*P. troglodytes*, *G. gorilla*, *P. paniscus*	Dunbar, 1988
cultural transmission	Odontocetes	Rendell and Whitehead, 2001	*P. troglodytes*	Whiten *et al.,* 1999

habitat (Bearzi, 2003). The existing literature contains numerous accounts on the biology and ecology of different species of dolphins worldwide, but only a few sympatric populations of small odontocetes have been well investigated in the field (Table 2a).

In this paper we compare the sympatric ecology of dolphins with that of African apes. By sympatry, we mean the co-occurrence of two or more ape or dolphin species in the same immediate habitat, which might be called direct sympatry, where broad sympatry simply means two or more species occur over the same wider geographic area (Futuyma, 1997). The implication of direct sympatry is that the species in question must subsist on the same resource base. According to the ecological principle of competition and mutual exclusion, without some form of resource partitioning one species or the other would eventually be driven to local extinction. By taxa we mean forms that are genetically and morphologically distinct. Among dolphin species there is some controversy as to weather some species consisting of multiple forms should be regarded as distinct taxa (*e.g.,* transient and resident orcas, *Orcinus orca*, were included in this review because the two forms are genetically and morphologically distinct).

We limit the comparison to the African apes because their societies - chimpanzees and bonobos in particular - display social complexity lacking in the social systems of the lesser apes (Reichard, 2003) and orang-utans (*Pongo pygmaeus*) (Delgado and van Schaik, 2000). Orang-utan sociality has been well demonstrated to be highly restricted by availability of fruit (van Schaik, 2004). The more distantly related gibbons are now known not to be entirely monogamous reproductively, but most of the taxa are socially pair-bonded (Sommer and Reichard, 2000). It is for these reasons that chimpanzees and bonobos in particular have been the focus for using great ape social ecology to reconstruct the possible behaviour of early hominids (Finch and Stanford, 2004; Stanford, 2006). We hope to elucidate parallels in the ways in which the grouping patterns and feeding strategies of large-brained, socially complex mammals may be an evolved response to their environment.

Habitats as dissimilar as tropical forests and oceans appear to have provided some similar ecological context in which natural selection shaped parallel behavioural adaptations. The co-occurrence of two or more closely related species is thought to have been an im-

Table 2a. Field studies of sympatric associations of dolphins.

Species	Site	Reference
O. orca (transient and resident)	Eastern north Pacific	Baird, 1994
		Baird *et al.,* 1992
	British Columbia	Baird and Dill, 1995, 1996
	Vancouver Island	Bigg, 1982
		Baird and Whitehead, 2000
	British Columbia and Alaska	Barrett-Lennard *et al.,* 1996
	British Columbia and Washington State	Bigg *et al.,* 1987, 1990
	Coastal British Columbia and adjacent waters	Ford *et al.,* 1998
	British Columbia	Guinet, 1990; Morton, 1990
	Prince William Sound (Alaska)	Saulitis *et al.,* 2000
T. truncatus, *T. aduncus*	Indian and western Pacific Oceans	Hale *et al.,* 2000
	Chinese waters (Taiwan and south-central China)	Wang *et al.,* 2000
Delphinus delphis and *D. capensis*	Santa Monica Bay, California	Bearzi, 2005a
	southern California Bight	Banks and Brownell, 1969
	eastern north Pacific	Evans, 1975
		Heyning and Perrin, 1994
		Rosel, Dizon, and Heyning, 1994
	Californian coast	Hill and Barlow, 1992
	eastern North Pacific and adjacent waters	Leatherwood *et al.,* 1998
	eastern Pacific	Perrin *et al.,* 1985
Lagenorynchus acutus and *D. delphis*	Scotian Shelf (Nova Scotia)	Gowans and Whitehead, 1995
L. acutus, *D. delphis* and *Globicephala melas*	northeastern United States	Selzer and Payne, 1988
Stenella coeruleoalba and *D. delphis*	eastern tropical Pacific	Polacheck, 1987
		Au *et al.,* 1979
		Au and Perryman, 1985
	Biscay Bay (North-east Atlantic)	Das *et al.,* 2000
		Hobbs 2004
	south-eastern coast of Spain	Sagarminaga and Cañadas, 1995, 1998
S. coeruleoalba, *D. delphis* and *Grampus griseus*	Gulf of Corinth (Greece)	Frantzis and Herzing, 2002
S. longirostris and *Stenella attenuata*	Hawaii (eastern tropical Pacific)	Norris and Dohl, 1980
		Norris *et al.,* 1994
		Perrin *et al.,* 1973
		Psarakos *et al.,* 2003
	western tropical Indian Ocean	Ballance and Pitman, 1998
S. longirostris, *S. attenuata* and *T. truncatus*	Hawaii	Baird *et al.,* 2001
S. longirostris and *Lagenodelphis hosei*	Central Philippines	Dolar, 1999
S. attenuata and *T. truncatus*	Bahamas waters	Herzing and Johnson, 1997
Globicephala macrorhynchus and *D. delphis*	eastern tropical Pacific	Polacheck, 1987
G. macrorhynchus and *T. truncatus*	North-eastern Pacific	Norris and Prescott, 1961
G. macrorhynchus and *G. griseus*	Santa Catalina Island (California)	Shane, 1995
T. truncatus and *D. delphis*	Kalamos Island (Greece)	Ferretti *et al.,* 1998
		Politi, 1998
		Politi *et al.,* 1998
		Bruno *et al.,* 2004
		Bearzi *et al*. 2005
T. truncatus, *D. delphis*, *S. coeruleoalba* and *Sousa sp*.	Cape coast of South Africa	Saayman *et al.,* 1972
Orcaella heinsohni and *Sousa chinensis*	North-east Queensland (Australia)	Parra, 2006

portant ecological influence in hominin evolution (Coppens, 1994) as it has been in many other mammalian taxa. Behavioural, dietary and physiological habitat specializations may have evolved in response to the presence of potential competing species. Reaching a greater understanding of similarities and differences between sympatric dolphin associations and those of African apes may provide a new perspective on the evolutionary context of social complexity and intelligence.

Table 2b. Field studies of sympatric associations of African apes. All studies have been conducted in Africa on chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*).

Site	Reference
Equatorial Guinea	Jones and Sabater-Pi, 1971
Lopé, Gabon (*G. g. gorilla*)	Tutin and Fernandez, 1984, 1993; Tutin *et al.,* 1997
Ndoki, Republic of Congo	Kuroda *et al.,* 1996; Nishihara, 1992
Kahuzi-Biega, Democratic Republic of Congo (*G. g. gorilla*)	Yamagiwa *et al.,* 1996; Yamagiwa and Basabose, 2006
Goualougo Triangle, Republic of Congo (*G. g. gorilla*)	Morgan and Sanz, 2006
Bwindi Impenetrable, Uganda (*G. g. beringei*)	Stanford, 2001; Stanford and Nkurunungi, 2003

The main goal of this paper is, therefore, to compare similar patterns of multi-species associations in dolphins and African apes. We try to identify important ecological variables, and suggest that there may be specific features of both dolphin and ape socio-ecologies that select for the large brains and social complexity that characterize both taxa.

Sympatric species associations

I. Dolphins

Far more studies have been conducted of sympatric associations of dolphins than have been done on African apes (Table 2a,b). The dolphin studies, however, have been less systematic due to the difficulties of obtaining data in an aquatic medium. Therefore, ape-dolphin data are not always comparable. In this paper we seek parallels between the two groups, using parameters of evidence that seem appropriate for comparison (*e.g.,* habitat use, diet, *et cetera*).

The regular presence of bottlenose dolphins along the coastline has made this dolphin one of the best-known cetaceans (*e.g.,* Shark Bay, western Australia: Connor and Smolker, 1985; Connor *et al.,* 1998; the Firth of Tay and Moray Firth, Scotland: Wilson *et al.,* 1993, Wilson, 1995; Sarasota Bay, Florida: Scott *et al.,* 1990; Wells, 1991; Argentine Bay: Würsig, 1978; Croatia, Mediterranean Sea: Bearzi *et al.,* 1999; and in southern California: Weaver, 1987; Hansen, 1990; Weller, 1991; Defran *et al.,* 1999, Bearzi 2005c). Some populations exhibit a fission-fusion grouping pattern where individuals associate in small groups that change more or less frequently in composition (Connor *et al.,* 2000a).

Sympatric species of the genus *Tursiops* have been described by a few investigators (Table 2). Bottlenose dolphins and Indo-Pacific bottlenose dolphins (*T. aduncus*) appeared to be in direct sympatry around the Chinese waters of the Penghu archipelago and were frequently observed in mixed schools with other dolphin species (Yang, 1976; Zhou and Qian, 1985). These two species, however, differed ecologically: bottlenose dolphins preferred the coastal and shallow waters of the continental shelf feeding upon benthic or reef-dwelling fish and cephalopods whereas Indo-Pacific bottlenose dolphins favored offshore waters feeding mostly on schooling epipelagic and mesopelagic species (Wang *et al.,* 2000).

In the Indian and western Pacific Oceans, Hale *et al*. (2000) recorded different preferences in habitat choice for the same species, with bottlenose dolphins frequenting both shallow waters and offshore reefs and Indo-Pacific bottlenose dolphins inhabiting estuaries and costal waters. This study showed that some areas were occupied exclusively by one species, with coastal regions of sympatry in their distribution.

Sympatric bottlenose dolphins and Indo-Pacific bottlenose dolphins also exist in south African waters (Wang *et al.,* 2000), although Ross (1977) described these species as being typically allopatric. Ross (1977) noted different prey in their stomachs, with bottlenose dolphins exploiting deep reefs located offshore and Indo-Pacific bottlenose dolphins preferring shallow inshore waters.

Inshore populations of the genus *Delphinus* have been described for different areas worldwide, including California (Evans, 1975; Bearzi, 2005a), South Africa (Young and Cockroft, 1994), New Zealand (Neumann, 2001ab) and the Mediterranean Sea (Bruno *et al.,* 2004; Bearzi *et al.,* 2005), whereas the ecology of offshore communities remains largely unknown (Evans, 1994). Short-beaked common dolphins (*D. delphis*) and long-beaked common dolphins (*D. capensis*) occur sympatrically in tropical and temperate waters (Heyning and Perrin, 1994; Table 2a).

In Santa Monica Bay, California, the direct sympatric ecology of short-beaked common dolphins and

long-beaked common dolphins was investigated (Bearzi, 2005a). Short-beaked common dolphins and long-beaked common dolphins were sympatric in the bay, but they were never seen in mixed schools (Bearzi, 2005a). The co-existence of these species is probably explained by an abundance of anchovies (*Engraulis mordax*), among their favorite food, and other prey in areas of local upwelling, as also reported by other authors (Mais, 1974; Evans, 1975; Hui, 1979). These sympatric species had similar diet (Fitch and Brownell, 1968), however, slight differences in their prey were observed (Schwartz *et al.,* 1992). This difference in diet might indicate how partitioning of ecological niches may have reduced the occurrence of competition for food resources when the dolphins were in direct sympatry (Bearzi, 2003, 2005a).

In the same bay, the broad sympatric ecology of bottlenose dolphins, short-beaked common dolphins and long-beaked common dolphins was also investigated (Bearzi, 2005a). High abundance and year-round occurrence of the three species appeared to be correlated to prey abundance and, consequently, to the oceanography of this region (Bearzi, 2005a), as also reported for other small odontocetes in different locations (Cockcroft and Peddemors, 1990; Gowans and Whitehead, 1995; Defran *et al.,* 1999). Eighty percent of bottlenose dolphin sightings (n = 157) were found in shallow waters and they were generally separated from the distribution of the two species of common dolphins showing spatial habitat partitioning (Bearzi, 2005a).

Das *et al*. (2000) reported slightly different dietary preferences for sympatric striped dolphins and short-beaked common dolphins in the north-east Atlantic (Bay of Biscay). In this area, both species were quite opportunistic feeders taking advantage of seasonally or locally abundant preys, but striped dolphins were observed displaying more opportunistic trophic habits compared to common dolphins (Das *et al*. 2000).

Habitat partitioning and direct sympatry have been observed for short-beaked common dolphins and other delphinids by Gowans and Whitehead (1995). These authors examined the summer distribution of short-beaked common dolphins, Atlantic white-sided dolphins (*Lagenorhyncus acutus*) and long-finned pilot whales (*Globicephala melas*) in the highly productive waters in and near a submarine canyon of the Scotian Shelf called the Gully. These species were much more abundant inside the Gully than outside, and they used some areas of the Gully slightly differently, showing spatial partitioning of habitat. Atlantic white-sided dolphins and short-beaked common dolphins divided the Gully temporally but not geographically whereas pilot whales ranged widely over the entire study site, preferring locations with flat relief.

Habitat partitioning and direct sympatry were observed for short-beaked common dolphins and bottlenose dolphins in the eastern Ionian Sea near the island of Kalamos (Politi *et al.,* 1998; Bruno *et al.,* 2004). The two sympatric species had adopted different foraging strategies, with common dolphins feeding in the water column or near the surface and bottlenose dolphins focusing on bottom prey (Ferretti *et al.,* 1998). In spite of such sympatry, the two species rarely mixed and showed no direct interactions (Bearzi *et al.,* 2005).

Frantzis and Herzing (2002) observed striped dolphins and short-beaked common dolphins also in mixed-species associations with Risso's dolphins (*Grampus griseus*). Among the accountable factors for mixed-species associations in the Mediterranean Sea there were: 1) the relative abundance of each species, and 2) the potential dependence of common dolphins on striped dolphins when the former could not form single-species groups (Frantzis and Herzing, 2002).

Two forms of killer whales, resident and transient, are distinguished in the eastern north Pacific (Bigg, 1982; Baird and Dill, 1995). Residents and transients show differences in acoustics, morphology, pigmentation patterns, and genetics (Barrett-Lennard, Ford, and Heise, 1996; Ford *et al.,* 1998; Baird, 2000). Besides significant differences, these populations are well known to live sympatrically (Table 2a).

In British Columbian and Washington waters, two communities of northern and southern resident killer whales live in broad sympatry with transient killer whales while displaying remarkable differences in feeding behaviour (Baird, 2000; Saulitis *et al.,* 2000). Resident populations feed primarily on fish, while transient whales prey on marine mammals, mainly pinnipeds (Bigg *et al.,* 1990; Ford *et al.,* 1998; Saulitis *et al.,* 2000). Bigg *et al*. (1990) and Ford *et al*. (1998) observed that resident killer whales of British Columbia, Washington and Alaska ate mostly salmonids, of which 50% were chinook (*Oncorhynchus tshawytscha*), the largest and most energy-rich species present year-round in these areas. Similarly, resident killer whales in Prince William Sound, Alaska, fed primarily on coho salmon (*Oncorhynchus kisutch*), while transient killer whales fed on harbour seals (*Phoca vitulina*) and Dall's porpoises (*Phocoenoides dalli*; Saulitis *et al.,* 2000).

In the various study areas, transients travel and forage more than residents (88.5-94.5% of their time vs. 58-72% of the time), whereas residents socialize and

rest more than transients (Morton, 1990; Felleman *et al.,* 1991; Baird, 1994; Saulitis *et al.,* 2000). Saulitis *et al.* (2000) also reported that different prey choices among populations of killer whales were accompanied by different foraging strategies. Residents foraged in co-ordinated pods swimming at high speed, lunging, encircling and chasing fish at the surface (Similä and Ugarte, 1993; Barrett-Lennard *et al.,* 1996); mammal-eating transients either swam along shorelines or in dispersed formation across open areas (Barrett-Lennard *et al.,* 1996; Saulitis *et al.,* 2000).

Baird and Dill (1995) found high variability in habitat use between resident and transient whales, with transient animals spending far more time in shallow waters. Dissimilarities existed also in diving patterns of these populations, with resident animals spending most of their time in the upper twenty metres of the water column and feeding on salmonids and with transient animals displaying longer mean dive durations between 20-60 m (Bigg *et al.,* 1990; Baird 1994, 2000).

Associations between transient and resident killer whales have rarely been seen (Morton, 1990; Baird and Dill, 1995; Barrett-Lennard *et al.,* 1996). These populations do not associate, most likely because of their strikingly different diet (Ford *et al.,* 1998; Saulitis *et al.,* 2000).

II. African Apes

Chimpanzees live in fission-fusion polygynous societies in which members of a community form temporary foraging associations (parties) of varying sizes (Goodall, 1986). This flexible grouping pattern is thought to be a social adaptation to a reliance on patchily distributed fruit trees (Wrangham, 1977), although the energy value of particular fruits varies widely and may play an important role (Conklin-Brittain *et al.,* 2006). Chimpanzee party size and composition varies widely among study sites (Boesch and Boesch-Achermann, 2000; Pruetz, 2006). Party size is thought to correlate with the size and distribution of fruit patches and with the presence of females with sexual swellings (Chapman *et al.,* 1994; Anderson *et al.,* 2005, 2006), but empirical tests that separate these influences are lacking and the relative influences may vary from site to site (te Bockhorst and Hogeweg, 1994). Chimpanzee communities vary in size from 20 to over 100, depending on the site (Nishida, 1979; Mitani and Watts, 1999). Females spend most of their time with their offspring, rarely joining large foraging parties (Goodall, 1986). Estrous females provide an exception to this pattern, being both highly sociable and strongly attractive to males. The chimpanzee diet is mainly ripe fruit (70% of the diet), but their diet includes leaves, shoots, buds, blossoms, seeds, nuts, bark, invertebrates, birds, eggs, honey and a number of mammal species (Wrangham, 1977; Goodall, 1986; Stanford, 1998). The Kasakela chimpanzees of Gombe National Park use at least 141 species of trees and plants (Wrangham, 1977). However, 95% of feeding time is spent on half of these food types, and foods are selected in proportion to their availability (Wrangham, 1977).

Gorillas occur across a wide range of habitat types, and their ecology varies accordingly (*e.g*, Robbins *et al.,* 2006). Mountain gorillas (*Gorilla gorilla beringei*) from the Parc d'Volcans in the Virunga mountains of Rwanda feed primarily on perennially available foliage and other non seasonal foods (Watts, 1984). Fruit comprises a large percentage of western lowland gorilla diets. In Equatorial Guinea, 40% of the diet was composed of fruit (Jones and Sabater-Pi, 1971; Sabater-Pi and Groves, 1972; Sabater-Pi, 1977). In Cameroon, evidence of fruit was found in 50% of all fecal samples (Calvert, 1985). Studies in Gabon (Tutin and Fernandez, 1985, 1993; Rogers *et al.,* 1988; Williamson, 1988; Rogers, Maisels *et al.,* 1990; Williamson *et al.,* 1990), the Central African Republic (Remis, 1997; Goldsmith, 1999) and the Republic of Congo (Nishihara, 1992, 1995) indicate a large proportion of fruit in the diet. Although large amounts of fruit are consumed during certain times of the year more than 90% of the fecal samples contain fiber and leaf fragments (Rogers and Williamson, 1987; Williamson, 1988) and in one study herbaceous material was eaten in equal amounts throughout the year (Goldsmith, 1999).

Gorilla ranging is strongly influenced by habitat and food availability. The day range of Karisoke gorillas is short; over a period of seventeen months a group traveled between 190 and 3,300 m per day (mean = 570 m; Watts, 1991). Watts found that the effect of group size on time spent feeding is small, which suggests that the costs of social foraging are low for mountain gorillas. Lowland gorillas travel much farther per day. Tutin (1996) found an overall mean day range in Lopé of 1.1 km/day, while Remis (1994) found a mean at Bai Hokou, Central African Republic, of 2.3 km/day. Differences between sites may be related to habitat and group size differences.

Lowland gorillas travel significantly farther during periods of fruit availability. Research in Lopé (Tutin, 1996) and at Bai Hokou (Remis, 1997; Goldsmith, 1999) demonstrates that daily ranging behaviour is in-

fluenced by the degree of frugivory. Tutin *et al*. (1992) suggest that due to their reliance on terrestrial herbaceous vegetation, western lowland gorilla groups do not experience high levels of within-group feeding competition. As a result, they do not need to modify their group size, explaining why their grouping pattern resembled that of mountain gorillas. At Bai Hokou, however, there was a significant positive relationship between group size and daily path length during all seasons, suggesting high levels of within-group feeding competition. In addition, groups were found to form temporary subgroups that fed and slept separately from one another, perhaps as a way of reducing feeding competition (Remis, 1994; Goldsmith, 1999).

Mountain gorilla group size does not seem to influence day range either due to the widespread, abundant foliage on which they feed (Watts, 1996). Mountain gorillas live in relatively stable groups, and a variable number of offspring. Both male and female mountain gorillas tend to emigrate from their natal groups (Harcourt, 1978). Emigrating males either join all-male bands or travel by themselves; females either join a new breeding group or take up with a solitary male (Stewart and Harcourt, 1987). Harcourt *et al*. (1981) reported that 60% of studied groups at Karisoke had only one adult male. Approximately 10% of the groups were all-male bands (Stewart and Harcourt, 1987). An emerging picture of lowland gorilla social organization is of less cohesive groups that are more likely to contain multiple silverbacks (Tutin *et al.,* 1992; Remis, 1994; Olejniczak, 1996; Goldsmith, 1999). Evidence from Lopé (Tutin *et al.,* 1992), the Ndoki (Olejniczak, 1996), and Bai Hokou (Goldsmith, 1999) suggest a mean group size of about 9.5 individuals, with groups not exceeding 18 individuals. Average group size is larger in eastern lowland gorillas (*G. g. graueri*) (10.8; Yamagiwa and Basabose, 2006).

There are a small but growing number of detailed ecological studies of sympatric chimpanzee and gorilla populations (Table 2b). Jones and Sabater-Pi (1971) identified several means of ecological separation between the two species in Equatorial Guinea. During the wet season, gorillas ranged in fairly open areas of regenerating vegetation, while chimpanzees utilized the upper strata of primary forest. During the dry season, gorillas were found in dense vegetation at the edge of forests and occasionally in primary forest adjacent to areas of regenerating vegetation, while chimpanzees ranged mainly in the lower strata and on the ground in primary forest. The gorillas in Jones' and Sabater-Pi's study were reported to feed almost completely terrestrially, whereas chimpanzees were mostly arboreal feeders.

More detailed sympatric ecological studies have been conducted in the Lopé Reserve in Gabon, where chimpanzees and gorillas live at similar population densities (Tutin and Fernandez, 1985, 1993). Lowland gorilla diet at Lopé more closely resembles that of chimpanzees than that of mountain gorillas living in the Virungas (Rogers *et al.,* 1990; Tutin and Fernandez, 1993). It appears that Lopé gorillas satisfy a substantial part of their energy needs from fruit, relying on leaves to provide protein (Rogers *et al.,* 1990). Most gorilla plant foods (69%) are harvested arboreally (Tutin and Fernandez, 1993). Lopé chimpanzees consist of at least 174 food items in their diet, including 111 species of fruit (Tutin and Fernandez, 1993). Approximately 76% of Lopé chimpanzee plant foods are harvested arboreally (Tutin and Fernandez, 1993). There is great overlap in the diets of chimpanzees and gorillas at Lopé with approximately 60-80% of foods being eaten by both species (Williamson *et al.,* 1990; Tutin and Fernandez, 1993). Gorillas are more likely to feed on terrestrial herbaceous vegetation than chimpanzees and are more ready than chimpanzees to concentrate on this vegetation when fruit is scarce. Chimpanzee and gorilla diets diverge most when fruit is not abundant, although it is mainly gorillas that shift foraging strategies while chimpanzees continue to forage extensively for ripe fruit even in periods of low fruit availability (Williamson *et al.,* 1990; Remis, 1997). Direct interspecific interference competition has never been observed.

Research on sympatric gorillas and chimpanzees in the Nouabalé-Ndoki forest of the Congo and Central African Republic have revealed similar patterns of resource use. In Nouabalé-Ndoki, gorillas are more highly frugivorous than any other studied population (Kuroda, 1992; Nishihara, 1995). Their diet consists of over 63% fruit, which is consumed seasonally. Ndoki gorillas make extensive year-round use of swamp forest (Nishihara, 1995) and feed in fig trees in proximity to chimpanzees during times of fruit scarcity (Suzuki and Nishihara, 1992). They also feed extensively on aquatic herbaceous vegetation, perhaps as a fallback food analogous to the use of terrestrial herbaceous vegetation (Magliocca and Querouil, 1997).

Eastern lowland gorillas and chimpanzees are sympatric in Kahuzi-Biega National Park in eastern Democratic Republic of Congo (Yamagiwa *et al.,* 1994; Yamagiwa *et al.,* 1996). Gorillas occur there at a much higher density than chimpanzees. The higher popula-

tion density of gorillas may have been related to the chimpanzee frugivorous diet in a mountainous area of low fruit diversity. Yamagiwa *et al*. (1996) found that gorillas ate a more diverse diet than chimpanzees did. Both species ate fruit over the entire annual cycle, though not necessarily the same species at the same time. They shared at least four important fruit species in their diets and both apes sometimes fed together in the same tree crown. Gorillas found at lower elevations in Kahuzi-Biega ate more fruit than those at higher elevations, apparently related to fruit availability differences (Yamagiwa *et al.,* 1994). Ecologically, this population appears to be intermediate between western lowland and mountain gorilla populations in the degree of frugivory and the plant species diversity in the diet.

Results of the Bwindi Impenetrable Great Ape Project include the first detailed study of Bwindi gorilla feeding and ranging ecology (Nkurunungi, 2005) and preliminary information on Bwindi chimpanzee behavioural ecology (Stanford, 1999; Stanford and Nkurunungi, 2003). Bwindi gorilla diet is seasonally high in fruit; in some months more than 50% of gorilla dung samples contain seeds (Nkurunungi, 2005). In other months, however, the gorilla diet contains no fruit and is similar to the diet of gorillas in the Virungas (Watts, 1984; Stewart and Harcourt, 1987). Gorilla and chimpanzee diets are thus similar in some months, and chimpanzees range farther when fruit is scarce to find fruit. Day range is positively correlated with the percentage of fruit in the diet, although only slightly so. Bwindi gorillas are much more likely to construct nests in trees than their Virungas counterparts, who nest entirely on the ground (Nkurunungi, 2005).

Ecological separation within African ape and dolphin communities

Two closely related, ecologically similar species that share one habitat are presumed to have either diverged from each other in the course of their evolution or else are currently in ecological competition that may lead eventually to the local extinction of one species. This is based on an assumption that the two species are resource-limited. But are African apes and dolphins resource-limited?

Evidence from studies of African apes suggests that they are. Kuroda *et al*. (1996) found that chimpanzees and gorillas in the Ndoki forest practice mutual avoidance, although they occasionally enter the same food trees. Findings that chimpanzee and gorilla diets converge most when fruit and foliage are most abundant indicate that there is some degree of ecological release during times of food abundance (Tutin and Fernandez, 1993; Stanford and Nkurunungi, 2003). Gorillas are likely able to make use of herbaceous foliage as fall back food when fruit is not available, accounting for the dietary divergence in times of food scarcity.

The food limitation question for dolphins is more complicated due to the difficulties of observing animals in the open ocean and obtaining direct evidence of food prey intake. Similar species co-occuring in the same area are thought to compete for resources unless they occupy different physical locations and/or feed on different prey (Roughgarden, 1976; Pianka, 1978). Sympatric species of odontocetes observed worldwide and living in a restricted region where food is limited were reported to adopt a few similar strategies. These strategies include foraging and feeding at different depths and/or inhabiting shallow and deep waters (Saayman *et al.,* 1972; Norris *et al.,* 1994; Baird and Dill, 1995; Ferretti *et al.,* 1998; Wang *et al.,* 2000; Hobbs, 2004; Bearzi, 2005a; Parra 2006) and divergence in diet (Bigg *et al.,* 1990; Ferretti *et al.,* 1998; Baird, 2000; Das *et al.,* 2000; Hale *et al.,* 2000; Saulitis *et al.,* 2000).

Different dolphin species can be found together in the same microhabitat showing prey resource partitioning and, apparently, no competition for resources (Selzer and Payne, 1988; Gowans and Whitehead, 1995; Bearzi, 2005a,b). In these situations where diets frequently overlap, it appears that sympatric species can differ slightly in prey preferences (Gowans and Whitehead, 1995). Many species of odontocetes, such as common dolphins, are well known to be opportunistic feeders that can vary their diet according to the availability of the most abundant and catchable prey (Evans, 1975, 1994; Klinowska, 1991). A small difference in prey preference may be enough to support the feeding requirements of more than one species, allowing them to co-exist (Hoelzel, 1998).

Similar patterns in the sympatric associations of some dolphin species and African apes are outlined in Table 3. As can be seen, ecological separation exists between sympatric species in both taxa based on microhabitat, ranging patterns, and diet.

In all forests in which both chimpanzees and gorillas have been studied, chimpanzees forage at greater heights than gorillas. Although chimpanzees in Bwindi eat far more tree fruits than gorillas do, gorillas forage in the same fruit trees seasonally and also forage high

in trees for epiphytic plants and fungi. Chimpanzees nest at significantly higher forest heights than gorillas do in all months (Stanford and Nkurunungi, 2003). Does competition exist for nesting sites? There is little evidence of this, although two pieces of information are suggestive. First, in the northern section of the study site, the only area of the national park in which gorillas do not occur, chimpanzees nest on the ground at a higher frequency than noted elsewhere. Second, when gorillas nest in trees, they nearly always choose one species, an understory tree that is rarely used as a nest tree by chimpanzees.

Some dolphin species seem to use strategies similar to chimpanzees and gorillas but in an aquatic medium. Foraging at different heights in the forest canopy can be compared with foraging at different depths in the ocean.

A separation of niches based on depth was proposed in the eastern Ionian Sea (Ferretti *et al.,* 1998; Politi *et al.,* 1998). Sympatric species can also display ecological separation utilizing inshore and offshore waters, as observed by Wang *et al*. (2000) for bottlenose dolphins living in Chinese waters, Dolar (1999) for spinner dolphins (*Stenella longirostris*) and Fraser's dolphin (*Lagenodelphis hosei*) in the Sulu Sea, Bearzi (2005a) for bottlenose dolphins in sympatry with short-beaked common dolphins in California waters, and Baird and Dill (1995) for transient and resident killer whales in British Columbia and Washington State. These killer whales also show different diving patterns (Bigg *et al.,* 1990; Baird 1994, 2000).

Chimpanzees and gorillas can occupy the same home ranges and eat overlapping diets but nevertheless harvest their foods differently in ways that may mitigate competition (Morgan and Sanz, 2006). As Yamagiwa (1996) has pointed out, a chimpanzee community uses its home range on a regular basis, traveling to all parts of a range up to 30 km^2, but they canvass it only seasonally, remaining in one small part of the overall range for long periods. Gorillas may be able to forage this way because of their reliance on leafy herbaceous plants, which are more densely and evenly distributed on the landscape than the ripe fruits for which chimpanzees forage (Malenky *et al.,* 1994).

Small odontocetes with overlapping diet in the Gully (Scotian Shelf) occupy the same home ranges in their daily activities but in a slightly different way (Gowans and Whitehead, 1995). Resident and transient killer whales also use the same habitat in British Columbia and Washington State but with different travel routes, sometimes related to the bottom topography (Morton, 1990; Felleman *et al.,* 1991; Gowans and Whitehead, 1995; Baird, 2000). Dietary separation of day and/or during different seasons was observed for Atlantic white-sided dolphins and short-beaked common dolphins in the Gully (Gowans and Whitehead, 1995) and for spotted dolphins and spinner dolphins in the eastern tropical Pacific (Perrin *et al.,* 1973; Norris and Dohl, 1980; Norris *et al.,* 1994; Scott and Cattanach, 1998).

Chimpanzees and gorillas have different diets in the wild, although the degree of difference varies among study sites (Fig. 1b). At all sites where they have been studied, chimpanzees are ripe fruit specialists, traveling long distances in search of new fruit sources. Gorillas, based on Fossey's early work, were thought to be obligate folivores. More recent fieldwork on other gorilla populations living at lower elevations has revealed gorillas to be opportunistic, feeding heavily on fruits when available while using foliage as a fallback food during times of food scarcity (Tutin, 1996). In Bwindi, gorilla and chimpanzee diets converge during periods of heavy fruiting, and the two species share many of the same preferred food species. During times of scarcity, chimpanzees scatter into smaller social units to forage further afield for fruits while gorillas turn to fallback foods, primarily herbaceous groundcover.

Sympatric species of dolphins show different diets with a degree of dissimilarities among study areas. Hale *et al*. (2000) report different preferences in prey for sympatric species of bottlenose dolphins for various areas around the world, and Das *et al*. (2000) give an account of different diet for striped dolphins and short-beaked common dolphins in association with albacore tuna in the north-east Atlantic (Bay of Biscay).

The most striking example of diet divergence is known for resident and transient killer whales (Bigg *et al.,* 1990) and individual populations of this species also specialize in catching specific types of prey (Fig. 1a, Felleman *et al.,* 1991). Like gorillas, many species of odontocetes are opportunistic feeders, able to change their diet based on food availability (Klinowska, 1991). Transient killer whales in Prince William Sound feed almost evenly on harbour seals (*Phoca vitulina*) and Dall's porpoises (*Phocoenoides dalli*), while off British Columbia and south-eastern Alaska, harbour seals are their most favored prey (Saulitis *et al.,* 2000). Off southern Vancouver Island, Baird (1994) reported that transient killer whales killed harbour seals almost exclusively. Attacks by transient killer whales on Dall's porpoises appeared to be more energetically expensive and less successful. These

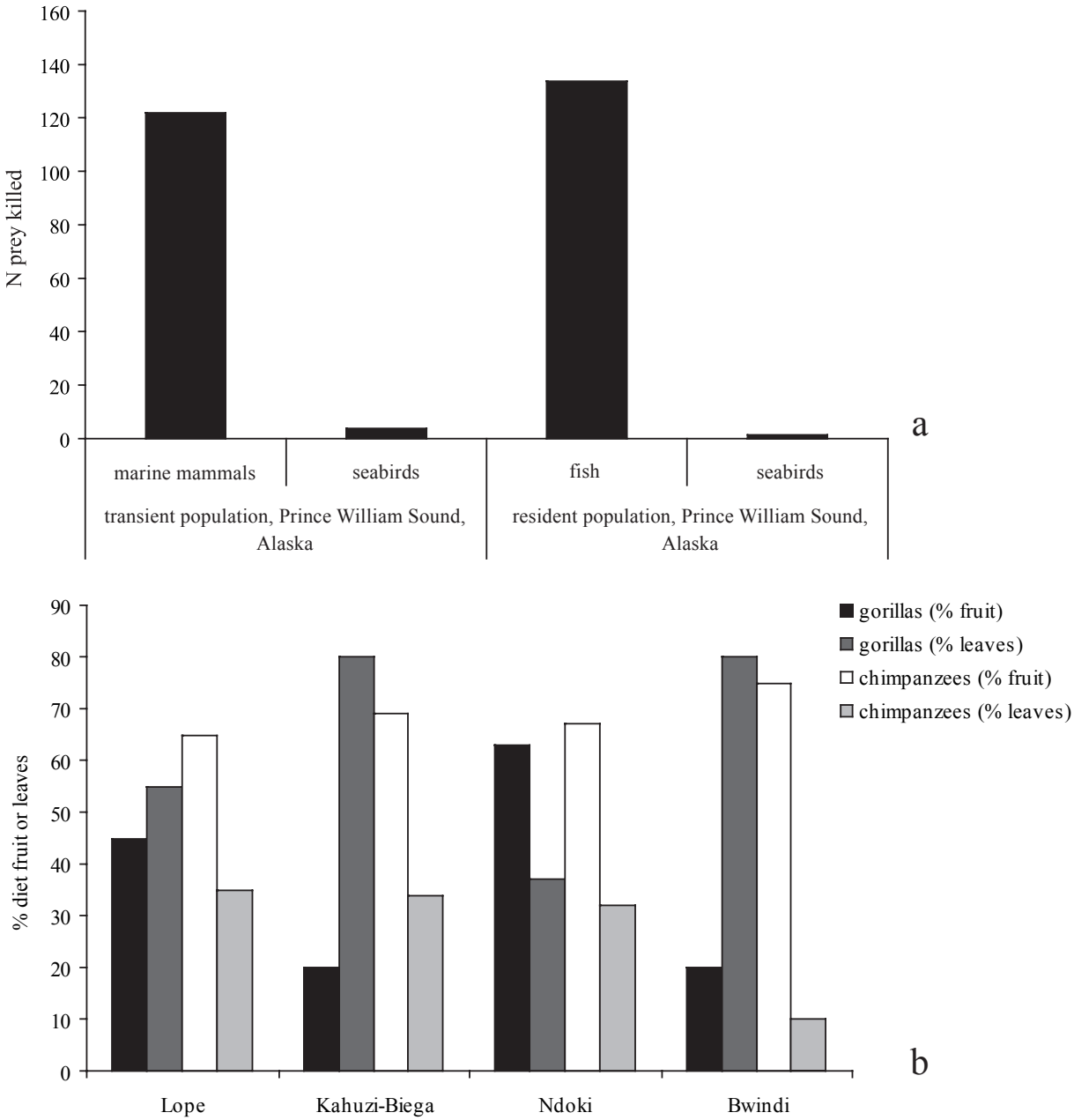

Figure 1a, b. Examples of dietary differences for odontocetes and pongids.
a. Diet of transient and resident populations (Ford *et al.,* 1998).
b. Comparison of gorilla and chimpanzee diets at four sites in which the two species are sympatric (Lopé: Tutin and Fernandez, 1993; Tutin *et al.,* 1997; Kahuzi-Biega: Yamagiwa *et al.,* 1996; Ndoki: Kuroda *et al.,* 1996; Bwindi: Stanford and Nkurunungi, 2003).

differences in transient killer whales' preferential preys in Prince William Sound in comparison with those of British Columbia, Washington and Alaska may been explained by the fact that the former location has a lower number of pinnipeds than the latter locations.

Direct competition and aggressive behaviour between sympatric species of the family Delphinidae has

occasionally ever been observed (Shane, 1995; Ross and Wilson, 1996; Baird, 1998; Patterson *et al.,* 1998; Frantzis and Herzing, 2002; Herzing *et al.,* 2003; Psarakos *et al.,* 2003).

Ross and Wilson (1996) witnessed four violent dolphin-porpoise interactions in the Moray Firth, Scotland, but these authors did not discuss possible reasons for these interactions. In the same study area, Patterson *et al*. (1998) recorded aggressive behaviour by sympatric bottlenose dolphins toward harbour porpoises, suggesting that infanticide may be a factor responsible for this type of behaviour. Baird (1998) also reported aggressive behaviour by a Pacific white-sided dolphin on a neonatal harbour porpoise in Washington State. His study showed that aggression was more the result of an object-oriented play than aggressive behaviour displayed by one species competing for food, mate, or space. In the western edge of Great Bahama Bank, Herzing *et al*. (2003) observed interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins, with male spotted dolphins displaying dominant mounting behaviour towards bottlenose dolphin males. In Hawaiian waters, Psarakos *et al*. (2003) also observed aggressive behaviour between sympatric spinner and spotted dolphins. This type of interaction was accompanied by interspecific copulation. It is clear that by contrasting these occasional examples of interactions, the majority of the investigations conducted worldwide to date show that dolphins under limited food resources conditions tend, whenever possible, to avoid direct competition by using behavioural, dietary and physiological habitat specializations (Table 3).

Researchers have long questioned whether gorillas and chimpanzees in sympatry engage in contest food competition. Kuroda *et al*. (1996) inferred mutual avoidance from the infrequency with which the two species met in the forest despite similar densities and ranging patterns. Although data from Bwindi do not provide systematic evidence of contest food competition, Stanford (pers. obs.) has witnessed one obvious incident, in which a party of nine chimpanzees occupied a fruiting tree, displaying at a gorilla group that attempted to ascend the same tree. The observation that chimpanzees were ecologically dominant, at least in this one encounter, accords with other recent studies of sympatric primates, in which two species assume role of ecological subordinate and dominant (Houle, 2004). Stanford and Nkurununngi (2003) also recorded gorillas and chimpanzees nesting in adjacent trees on the same night, and the home ranges of the gorilla study group and the chimpanzee study community occupied roughly the same area of forest. Rather than direct competition, most sympatric chimpanzee-gorilla associations may partition food resources by having different key food preferences, and through the seasonality of their diets (Stanford and Nkurununngi, 2003). In this way African ape sympatry would resemble sympatric dolphins.

Conclusions

Do sympatric associations among dolphins and African apes reflect convergently evolved social adaptations?

The pattern of ecological divergence described above can be found in a wide variety of associations among terrestrial or marine animals. The most striking ecological parallel between the two taxa is the tendency toward a fission-fusion grouping pattern, in which proximate changes in group size and composition appear to reflect proximate availability and distribution of food resources. The key food resource that may account for this grouping structure in primates is ripe fruit, the occurrence of which is ephemeral and patchy. This pattern is seen in only a few primate species, and in very few non primate mammals. In addition to chimpanzees, bonobos (*Pan paniscus*; Kano, 1992) and spider monkeys (*Ateles sp*.; Symington, 1987) most prominently exhibit fission-fusion. Such a social system may, among other functions, enable the animals to forage for widely dispersed, frequently changing food sources, and to cope with the complexities of group life that follow from such a fluid foraging pattern. In these respects, many dolphin species (*e.g.,* bottlenose dolphins, killer whales, common dolphins, spinner dolphins) offer a striking parallel to chimpanzees and bonobos. If fission-fusion grouping is a response to a complex foraging environment and has placed intelligence and social complexity at a premium in these two distantly related taxa, how may it have affected sympatric associations in the two groups?

Among African apes, sympatry between chimpanzees and gorillas has only recently been studied in detail. In sympatric association with gorillas, chimpanzees utilize many of the same food resources in a different manner, foraging widely on a daily basis while sympatric gorilla group forage more slowly within a smaller area while remaining in cohesive groups. Since these two species and their ancestors have presumably been broadly sympatric for millions of years,

Table 3. Parallels between sympatric associations of dolphins and African apes.

Trait	Species and Locations	References
different habitat use	**dolphins**	
Shallow vs. deep waters and/or inshore vs. offshore populations	*O. orca* (transients and residents) British Columbia and Washington State	Baird and Dill, 1995 Baird, 1994, 2000
	D. delphis, *D. capensis* and *T. truncatus* Santa Monica Bay, California	Bearzi, 2005a
	D. delphis, *T. truncatus* Kalamos Island, Greece	Ferretti *et al.,* 1998, Politi *et al.,* 1998
	D. delphis, *S. coeruleoalba* Western English Channels, Bay of Biscay	Hobbs, 2004
	T. truncatus, *T. aduncus* Chinese waters	Wang *et al.,* 2000
	T. truncatus, *Sousa* sp., *S. coeruleoalba* South-eastern Cape coast of South Africa	Saayman *et al.,* 1972
	S. longirostris, *S. attenuata*, eastern tropical Pacific, Hawaii	Norris and Dohl, 1980 Norris *et al.,* 1994 Perrin *et al.,* 1973
	O. heinsohni, *S. chinensis* North-east Queensland, Australia	Parra, 2006
flat areas vs. steeper areas	*L. acutus*, *D. delphis*, *G. melas* Scotian shelf	Gowans and Whitehead, 1995
different travel routes related to bottom topography	*O. orca* (transients and residents) British Columbia and Washington State	Felleman *et al.,* 1991 Morton, 1990
different habitat use	**pongids**	
forest strata use	tree-nesting (chimpanzees) *vs*. ground-nesting (gorillas)	Jones and Sabater-Pi, 1971 Stanford and Nkurunungi, 2005
different ranging patterns/ travel routes	*P. troglodytes*, *G. gorilla*, Kahuzi-Biega NP, Democratic Republic of Congo	Yamagiwa *et al.,* 1996 Stanford and Nkurunungi, 2005
association	**dolphins**	
rarely or not observed	*O. orca* (transients and residents) British Columbia and Washington State Prince William Sound, Alaska	Morton, 1990; Baird and Dill, 1995 Barrett-Lennard *et al.,* 1996 Saulitis *et al.,* 2000
	D. delphis, *D. capensis* California	Bearzi, 2003, 2005a
	D. delphis, *T. truncatus* Kalamos Island, Greece	Politi *et al.,* 1998
observed	*T. truncatus* and *T. aduncus* Chinese waters	Wang *et al.,* 2000
	S. longirostris, *S. attenuata* eastern tropical Pacific, Hawaii	Norris and Dohl, 1980 Norris *et al.,* 1994 Perrin *et al.,* 1973
	T. truncatus, *Sousa sp*. South-eastern Cape coast of South Africa	Saayman *et al.,* 1972
	Orcaella brevirostris, *Neophocaena phocaenoides*, *S. longirostris*, *S.l. roseiventris*, *T. truncatus*, *T. aduncus*, *S. attenuata*, *Pseudorca crassidens*, *Peponocephala electra* Berau Archipelago and coast off East Kalimantan, Indonesia	Kreb and Budiono, 2005
association	**pongids**	
observed	*P. troglodytes* and *G. gorilla* Ndoki Forest, Republic of Congo Bwindi Impenetrable National Park, Uganda	Kuroda *et al.,* 1996 Stanford and Nkurunungi, 2005
aggression	**dolphins**	
rarely or not observed	*O. orca* (transients and residents) British Columbia and Washington State	Baird and Dill, 1995
	T. truncatus, *Sousa sp*. South-eastern Cape coast of South Africa	Saayman *et al.,* 1972

	D. delphis, *D. capensis*, *T. truncatus* California	Bearzi, 2005a
	D. delphis, *T. truncatus* Kalamos Island, Greece	Politi and Bearzi, pers. comm.
observed	*T. truncatus*, *P. phocoena* Moray Firth, Scotland	Ross and Wilson, 1996 Patterson *et al.,* 1998
	L. obliquidens, *P. phocoena* San Juan Island, Washington State	Baird, 1998
	S. frontalis, *T. truncatus* Great Bahama Bank, Bahamas	Herzing *et al.,* 2003
	S. longirostris, *S. attenuata* Hawaii (eastern tropical Pacific)	Psarakos *et al.,* 2003
	G. griseus, *S. coeruleoalba* Gulf of Corinth, Greece	Frantzis and Herzing, 2002
	D. delphis, *G. griseus*, *G. melaena* California	Shane, 1995
aggression	**pongids**	
not observed	*P. troglodytes* and *G. gorilla* Kahuzi-Biega NP, Democratic Republic of Congo	Yamagiwa *et al.,* 1996 Stanford and Nkurunungi, 2005
dietary divergence within habitat	**dolphins**	
different prey preference	*O. orca* (transients and residents) British Columbia, Alaska and Washington State Felleman *et al.,*1991	Bigg *et al.,* 1990 Saulitis *et al.,* 2000
	D. delphis, *T. truncatus* Kalamos Island, Greece	Ferretti *et al.,* 1998 Politi *et al.,* 1998
	Tursiops sp. (two forms) various areas around the world	Hale *et al.,* 2000
	D. delphis, *S. coeruleoalba* North-east Atlantic	Das *et al.,* 2000
diet overlap/ slightly different diet	*D. delphis*, *D. capensis* California	Bearzi, 2003,2005a
	L. acutus, *D. delphis*, *G. melas* Scotian shelf	Gowans and Whitehead, 1995
	L. acutus, *D. delphis* continental shelf of the northeastern United States	Selzer and Payne, 1988
diet overlap/different seasons or time	*L. acutus*, *D. delphis*, *G. melas* Scotian shelf	Gowans and Whitehead, 1995
	S. longirostris, *S. attenuata* eastern tropical Pacific, Hawaii	Norris and Dohl, 1980 Norris *et al.,* 1994
	S. longirostris, *S. attenuata* eastern tropical Pacific	Perrin *et al.,* 1973
dietary divergence within habitat	**pongids**	
diet overlap/slightly different diet and seasons	*P. troglodytes* and *G. gorilla* Lopé, Gabon, Kahuzi-Biega National Park, Democratic Republic of Congo, Rio Muni, Bwindi Impenetrable National Park, Uganda	Tutin and Fernandez, 1984, 1993 Yamagiwa *et al.,* 1996 Jones and Sabater-Pi, 1971 Stanford and Nkurunungi, 2005
	Ndoki Forest, Republic of Congo	Stanford, 2001; Kuroda *et al.,* 1996

the possibility exists that chimpanzee-gorilla foraging differ at least to avoid direct competition for food and other resources. Such a divergence may have been facilitated by the tendency of chimpanzees to adopt a far-ranging foraging strategy that relies on their ability to remember the locations and timings of ripe fruit patches from seasons and even years past. Even though many more field studies have been conducted on dolphin sympatric ecology than have been done on African apes, we have less detailed ecological information about their associations. However, the socio-ecology of at least some species shows striking parallels to those of African apes (Marino, 1996, 1998; Reiss *et al.,* 1997).

Although apes and dolphins are only distantly related, the ecological convergence of the way in which food resources are shared when two or more species are in sympatry is striking. The behavioural flexibility associated with switching prey items and foraging patterns, and coordinating these dynamics with a sympatric species, characterizes both primates and dolphins. This behavioural flexibility may contribute to avoidance of interspecific food competition. Further studies focusing on behavioural ecology in each taxon may elucidate the role of social adaptations that allow multiple species of each group to co-exist.

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