7-1-2013

Decades-long social memory in bottlenose dolphins

Jason N. Bruck
Stephen F Austin State University, Jason.Bruck@sfasu.edu

Repository Citation

Bruck, Jason N., "Decades-long social memory in bottlenose dolphins" (2013). *Faculty Publications*. 172.
https://scholarworks.sfasu.edu/biology/172

PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Bruck JN. 2013 Decades-long social memory in bottlenose dolphins. Proc R Soc B 280: 20131726.
http://dx.doi.org/10.1098/rspb.2013.1726

Received: 4 July 2013
Accepted: 15 July 2013

Subject Areas:
behaviour, cognition, ecology

Keywords:
cognition, long-term memory, signature whistles, social memory

Author for correspondence:
Jason N. Bruck
e-mail: jbruck@uchicago.edu

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2013.1726 or via http://rspb.royalsocietypublishing.org.

Royal Society Publishing
Informing the science of the future

Decades-long social memory in bottlenose dolphins

Jason N. Bruck

Department of Comparative Human Development, Institute for Mind and Biology, University of Chicago, Chicago, IL 60637, USA

Long-term social memory is important, because it is an ecologically relevant test of cognitive capacity, it helps us understand which social relationships are remembered and it relates two seemingly disparate disciplines: cognition and sociality. For dolphins, long-term memory for conspecifics could help assess social threats as well as potential social or hunting alliances in a very fluid and complex fission–fusion social system, yet we have no idea how long dolphins can remember each other. Through a playback study conducted within a multi-institution dolphin breeding consortium (where animals are moved between different facilities), recognition of unfamiliar versus familiar signature whistles of former tank mates was assessed. This research shows that dolphins have the potential for lifelong memory for each other regardless of relatedness, sex or duration of association. This is, to my knowledge, the first study to show that social recognition can last for at least 20 years in a non-human species and the first large-scale study to address long-term memory in a cetacean. These results, paired with evidence from elephants and humans, provide suggestive evidence that sociality and cognition could be related, as a good memory is necessary in a fluid social system.

1. Introduction

Long-term social recognition (LTSR) provides specific survival benefits to the organisms shown to possess it [1–3]. The recognition of kin or potentially aggressive conspecifics can, among other things, help identify whom to give resources in acts of reciprocal altruism and whom to avoid [4], as well as help in the maintenance of social hierarchies in complex social environments [5] and avoid inbreeding [6]. When patterns of association become fluid and complex, it is the retention of social memories over long periods of time that potentially confers survival and reproductive advantages, as memories of past interactions are essential for the maintenance of reciprocal altruism as well as social threat assessment [7]. Many studies have focused on social recognition [8–10], but very few have addressed how long conspecifics are remembered in the absence of ongoing associations.

LTSR is important as an ecologically relevant test of cognitive capacity, which is useful in comparative study. With research across multiple taxa and various types of social systems, one can determine how sociality might play a role in the evolution of cognitive traits, hypothesizing that complex social systems might lead to better social memory just as dispersal patterns of offspring may lead to strong mother–offspring social memory, as a mechanism to avoid inbreeding [11,12].

(a) The possible role of sociality in cognition

LTSR is not precisely defined in terms of a set time or percentage of lifespan, but it is possible that animals, which have a social system characterized by frequent associations bookmarked by unpredictably long periods of separation, as in a fission–fusion system, remember *unrelated* conspecifics at least in the order of years. For fission–fusion species most likely to have persistent kin-independent social memories, relatively few species have been examined. Systematic studies have been conducted on corvids [3,13], monkeys (*Macaca fuscata* [14] and *Cercopithecus* *campbelli* [15,16]) humans [17], and there are anecdotal observations on elephants [18,19] and spotted hyenas (*Crocuta crocuta*) [20] (3 years for corvids and Japanese monkeys, possibly 4 years for Campbell's monkeys, 40+ years for humans, 10+ years for elephants and at least 1 year for hyenas), but there is no information for non-human apes, parrots or dolphins. Currently, kin-independent social memory studies are restricted to fission–fusion species, but they should be extended to non-fission-fusion species as well to further examine the potential relationship between sociality and LTSR.

From the limited information available, it appears that fission–fusion species are good candidates for the study of LTSR, but this is not to say that only socially complex species may possess excellent social memory. At least two otariid species (fur seals and Australian sea lions) and one species of tamarin (*Saguinus oedipus*) are known to have long memories for offspring or other kin [12,21–23], and male warblers have surprisingly long social memories (at least eight months) for conspecific rivals bordering their territory [24]. Although, in the case of male warblers (*Wilsonia citrina*), migration to Central America during winter and from the breeding territories in North Carolina causes the breakup and reformation of social partners, so the natural behaviour approximates fission–fusion [25]. However, it is clear that factors potentially unrelated to the cognitive social demands of fission–fusion sociality, such as inbreeding avoidance and the reduction of territorial hostilities, can also factor towards the evolution of LTSR.

(b) Bottlenose dolphins

Bottlenose dolphins (*Tursiops truncatus*; hereafter referred to as 'dolphins') are an intelligent, long-lived species shown to have complex fission–fusion social patterns, individual recognition capabilities [10,26–30] and procedural memories that last for years [31]. Females tend to stay within a pod, whereas males typically leave at 1–3 years of age and sometimes form bachelor pods of two to three individuals, which compete for access to females [32,33]. Their mating system is principally defined as hierarchical promiscuous, meaning there are no strong pair bonds between individuals and mating is determined by dominance [29]. Despite the fact that so much is known about bottlenose dolphin sociality, they have not previously been shown to have LTSR, even though by comparative standards they are good candidates for it.

(c) Long-term social recognition: a relevant test of memory

Investigating LTSR provides a unique, ecologically relevant test of memory. There is some information on dolphin procedural and working memory capacity from studies done on relatively few individual animals under human care [28]. However, there has been no large-scale evaluation of cetacean long-term memory [27]. Bottlenose dolphins experience complex patterns of association that may warrant sophisticated LTSR [29]. Using the relationships of 56 animals (43 of which were subjects) moved between facilities in a six-institution breeding programme (including the Brookfield Zoo, Indianapolis Zoo, Minnesota Zoo, Dolphin Quest: Bermuda, Texas State Aquarium and *The Seas* at Walt Disney World) as well as archived recordings of 20 additional individuals collected by researchers at the Woods Hole Oceanographic Institution in the 1980s and 1990s, I tested how long dolphins can recall familiar signature whistles. Signature whistles are individual-specific contact calls given by dolphins most often during periods of separation [34]. Using multiple methods (see the electronic supplementary material), I was able to determine the signature whistle for each animal in this study. I also tested long-term recognition of whistles based on sex, age, kinship and length of association. This study not only represented, to my knowledge, the first test of LTSR in a cetacean, but is also the first to systematically test decades-long social memory in a non-human animal. Ultimately, this study was focused on determining whether dolphins as a study species support the prediction that complex social patterns co-occur with extensive (even lifelong) kin-independent LTSR.

2. Material and methods

(a) Subjects

Dolphins ($n = 43$) ranged in age from four months to 47 years and had a sex ratio of 1 : 1.15. Age classes were defined as calf (under 1 year), juvenile (1–6 years) and adult (over 6 years). Animals were group housed for as little as three months to as much as 18.5 years before relocation and were housed at different facilities for as little as six months to as much as 20.5 years before playback presentation. The average duration of group housing was approximately 4 years, the average length of time the animals were separated from one another before testing was 6 years, and animals were moved on average 1.48 times in their lives. Pairs of animals were defined as kin if their coefficient of relatedness was greater than or equal to 0.25 (mostly included parents and siblings). After their relocation and prior to any playbacks for this study, the dolphins were not exposed to other human-facilitated presentations of former tank mates' calls.

(b) Experimental design

A modified version of a habituation–dishabituation design using signature whistle playbacks (fundamental frequency 800 Hz–28.5 kHz [35]) was used to assess response differences to familiar and unfamiliar calls (see the electronic supplementary material for recording methods). All vocalizations were presented singly (consisting of one presentation of the contour if the shape was repeated or 'looped', usually no longer than 1 s [34,35]) with a Lubell Labs (Columbus, Ohio; model LL9816) underwater speaker (range: 0.2–20 kHz). Calls were triggered after the focal dolphin swam past the submerged speaker (head within 1 m; see the electronic supplementary material for diagram). All playbacks were spaced 5 min apart and the observation continued until the animals stopped responding for 30 continuous seconds. Each playback session was defined as having a habituation phase followed by a test whistle, then a second habituation phase followed by a second test whistle. Each whistle in the habituation phase was unique and unfamiliar to the listener (each from a different dolphin). Presentations of unfamiliar habituation whistles from different dolphins would persist until the animals stopped responding to them. This mechanism was effective for removing whistle novelty as a motivation for responses to test whistles (see the electronic supplementary material for more detail). Therefore, the first habituation process of the session ended when the respondent ignored an unfamiliar playback, after which the animal was presented with the first test whistle (from a familiar or unfamiliar dolphin). Five minutes after the first test whistle, dolphins were again presented with different habituation whistles until they no longer responded, receiving the second test whistle after habituation. If the first test whistle presented in the session was familiar, then the second test whistle presented in the same session was unfamiliar (matched in age and sex to the familiar) and vice versa. If the dolphins showed a response, then their behaviour was classified into one of four levels (see the electronic supplementary material for scoring method).

(c) Response levels

Dolphin playback response levels included: (i) head turned towards the speaker but no approach, (ii) approached the speaker but maintained 1 m proximity for less than 2 s, (iii) approached the speaker and maintained 1 m proximity for more than 2 s, and (iv) either made forceful contact with gate protecting the speaker or engaged in rapid swimming behaviours (see the electronic supplementary material). For a response to be measured, dolphins needed to respond within 2 s of the playback. For all dolphins (even those less than 1 year of age), efforts were taken to trigger playbacks when the animals were self-separated to mitigate the effects of social facilitation (see the electronic supplementary material).

(d) Statistical analysis

With R v. 2.14.0, I used a generalized linear mixed-effects model (GLMM) to test how dolphins' responses to playback calls were affected by the call's familiarity, the length of separation between the caller and the subject and the subject's age category. Calls were either familiar or unfamiliar to the subject, and separation time was broken into four categories: 0–4.75 years, 5–9.75 years, 10–14.75 years, and 15 or more years of separation, and subjects were assigned to calf, juvenile or adult age categories (for model details see the electronic supplementary material). These data represent over 250 different sessions (including those with no responses to either the familiar or unfamiliar caller) from over 1200 total playbacks (adding habituation and test whistles).

3. Results

Overall, dolphins showed significantly higher response scores to familiar whistles than to unfamiliar ones (mean response score: familiar = 2.185 ± 0.285, unfamiliar = 0.307 ± 0.115, $z = 6.377$, $p < 0.001$). There was no significant effect of time separated on response scores (model test $\chi^2_6 = 7.368$, $p = 0.288$), even after 15 or more years (up to 20 years; figure 1). The interaction between familiarity and separation time was also not significant (model test $\chi^2_3 = 3.867$, $p = 0.276$). The interaction between familiarity and dolphin age was significant (model test $\chi^2_2 = 22.57$, $p < 0.001$; figure 2), with calves showing a weaker response difference than adults (mean response score of calves: familiar = 1.623 ± 0.720, unfamiliar = 0.754 ± 1.195, $z = 3.079$, $p = 0.002$) and juveniles showing a stronger response difference than adults (mean response score of juveniles: familiar = 2.478 ± 0.750, unfamiliar = 0.036 ± 0.122, $z = -2.223$, $p = 0.026$). Male subjects had marginally higher mean responses than those of females (mean response score = 2.649 ± 0.698, $z = 1.734$, $p = 0.083$). None of the other effects were significant, including kinship ($z = 1.61$, $p = 0.107$), the sexes of caller and respondent interaction ($z = -1.530$, $p = 0.126$), or the number of years that the animals were housed together ($z = 0.367$, $p = 0.714$).

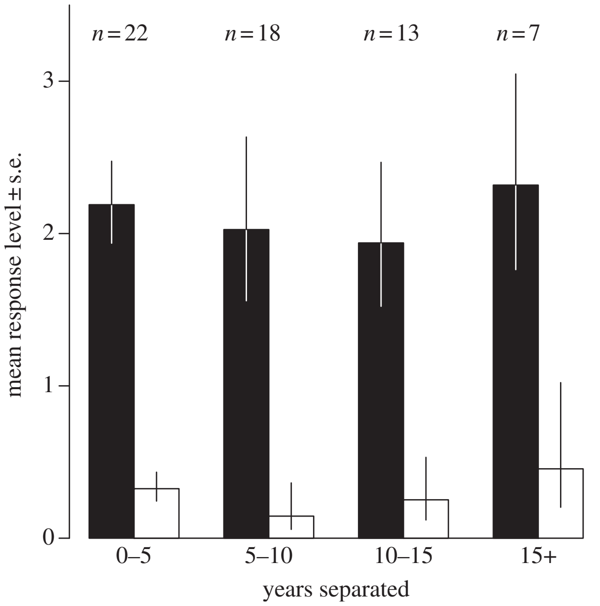

Figure 1. Mean response level for both familiar (black bars) and unfamiliar (white bars) playbacks (± s.e.) was calculated for separations lasting 0–5, 5–10, 10–15, and 15 or more years. Means and standard errors generated from a GLMM with Poisson-distributed errors. At all separation timespans, significant differences have $p < 0.001$. Numbers of dolphins in each testing group are displayed above bars (*n* of sessions: 0–5 = 125; 5–10 = 61; 10–15 = 44; 15+ = 27).

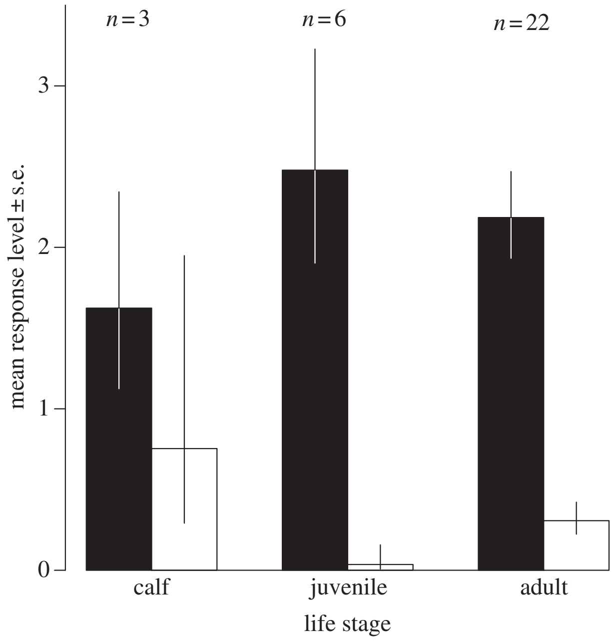

Figure 2. Mean response level for both familiar (black bars) and unfamiliar (white bars) playbacks (± s.e.) was calculated for calf, juvenile and adult age classes. Means and standard errors generated from a GLMM with Poisson-distributed errors. Calf responses to unfamiliar calls are significantly greater than that of adults ($p = 0.002$) and juvenile response to unfamiliar calls are significantly weaker than that of adults ($p = 0.026$). Numbers of dolphins in each testing group are displayed above bars (*n* of sessions: calves = 15; juveniles = 27; adults = 217).

4. Discussion

(a) The extent of long-term social recognition in dolphins

In this study, I sought to determine the extent of common bottlenose dolphin LTSR. Specifically, I predicted that given the highly social nature of bottlenose dolphins, LTSR would not only be present, but also persistent. The results have matched this expectation, as I have shown that dolphins were capable of remembering each other's whistles for 15 or more years (up to 20) with no decay (figure 1). Duration of association did not affect recognition, meaning long periods of association were not required for long-term recognition. Interestingly, calves of less than 1 year are behaviourally less discriminating than adults or juveniles (figure 2).

(b) Sex and kinship differences

Sex (both respondent and caller) and kinship status did not affect recognition. This is expected given that both males and females inhabit socially complex groups, and both kin and non-kin would need to be remembered in networks of at least 60–70 individuals with whom they cooperatively hunt and engage in predation defence [29,30]. In elephants, females are the repositories of social knowledge, and therefore they seem to be better at LTSR [2]. But male bottlenose dolphins in Shark Bay live in an open social network (with overlapping ranges comprised males and females) and exhibit social complexity on the magnitude of two to three levels of shifting alliances involving 14 or more animals (a level of complexity not seen outside of humans) [26,30]. Furthermore, mixed sex philopatry is common to the two most-studied dolphin populations in the world (Sarasota Bay and Shark Bay) indicating that both kin and non-kin are part of an individual dolphin's association matrix [29,36]. There is an overall marginal increase in male responses to signature whistles (both familiar and unfamiliar), which could be related to territory defence [37].

(c) Extreme stability and longevity in dolphin recognition systems

For LTSR to be useful to dolphins, signature whistles must be stable. Sayigh *et al*. [38] demonstrated through spectrographic analyses that signature whistles are acoustically stable for more than 12 years. My results would probably not be possible without whistle stability, and given this lack of change and the fact that dolphins remember each other's signature whistles, this system may be the longest-lasting recognition system in nature (in contrast to human faces, bodies and voices that change over time [39]). It is possible that free-living dolphins may experience long separations [29], and my data show that they would be capable of remembering each other after a delay that would amount to at least 75%–100% of their average total lifespan [40].

(d) Sociality and cognition

Systematically, humans and dolphins (and possibly elephants) have been shown to have both decades–long social recognition and complex sociality [1,17,18]. In addition, there is some comparative evidence that extensive social networks correlate with and could promote cognitive development [30,41]. With further evidence from more species (differing in degrees of social complexity and recognition capacity), the trait of LTSR may highlight directly how the evolution of memory is advanced by an animal's social system, similar to how food caching is shown to enhance spatial abilities [42]. For example, testing LTSR in animals without fission–fusion dynamics will help us understand whether complex sociality (either in extant animals or in the ancestors of animals who are now socially less complex) is necessary to drive cognitive development. However, social complexity may not need to be the only selective pressure in operation and is not mutually exclusive with other factors, for example inbreeding avoidance. Fission–fusion dynamics would not be necessary for the development of the trait in this case [11,12,21], which is why kin-independent LTSR should be a particular focus for this type of research. These results are by no means definitive proof of the link between complex sociality and advanced cognitive abilities. Instead, this study is only a data point in a larger picture, and it should hopefully motivate further research in other species with varying degrees of social complexity with the goal of elucidating the potential connections between sociality and cognition.

(e) Early development of dolphin recognition systems

In general, calf responses seem to be less organized and less focused than adult or juvenile responses, but I would not be surprised if calves were capable of discrimination of signature whistles based on familiarity. Calves do show adult and juvenile-like responses to familiar callers. However, calves are also much more interested in unfamiliar whistles than the other age classes (figure 2). One should consider that this pattern in young dolphins may serve a function in whistle learning and development, which could have adaptive value for calves formulating their own signature whistles [43].

(f) Candidate species for long-term social recognition based on comparative sociality

This study was conducted in zoos and aquariums, but it is likely that these abilities exist in free-living animals, as both groups share complex social traits [44], and the animals in this study have a social environment that approximates fission–fusion owing to movement between facilities for breeding–separating and reuniting social partners throughout life. It is possible that reduced social partners in human-care facilities might improve social memory, because there are fewer dolphins to remember which reduces cognitive load. Therefore, despite the methodological difficulties, a study looking at LTSR in free-living animals could confirm that social memories are virtually lifelong in dolphins.

Bottlenose dolphins' social recognition has implications for other relatively long-lived, large-brained, socially complex systems for which long-term social memory has not been systematically studied, including chimpanzees (and other ape species), hyenas and elephants (for which only anecdotal evidence exists for long-term social memory [18–20]) and birds (including parrot species). We need to further address animal long-term memory to see whether non-social information will also show the same level of resilience or whether social content is more salient and therefore more resistant to decay. The broad implications of this work, however, suggest that at least social memory in non-human animals is perhaps more resilient than previously thought, as no systematic study so far to my knowledge has shown such long retention of information in a species outside of humans.

This study was approved by the IACUCs of the Chicago Zoological Society, Disney's Animals, Science and Environment, Indianapolis Zoological Society, Minnesota Zoo, Texas State Aquarium and Dolphin Quest: Bermuda.

Acknowledgements. I thank B. Taft for assistance in statistical analysis and J. Mateo, M. McClintock, S. Pruett-Jones, L. Sayigh, J. Watters, R. Stacey-Vondra, M. Pruett-Jones, W. Fellner, M. A. Stamper, M. Campbell, N. O'Donnell, H. LaRock, D. Fusco, D. Merritt,

J. Baker, M. Heintz, C. Loomis, C. Dodge, P. Tyack, R. Wells, V. Janik, A. Kuczynski, M. Wirthlin, J. Cacciopio, B. Tang, T. Jachimczak, D. Guilloton, H. Williams, A. Hribar, A. Samuels and D. Hill. I also thank the staff and administrators of Brookfield Zoo, Disney's Animals, Science and Environment, Indianapolis Zoo, Minnesota Zoo, Texas State Aquarium and Dolphin Quest: Bermuda.

Funding statement. Funding was provided by grants from the University of Chicago divisions of Social and Natural Sciences.

References

1. Moss CJ, Poole JH. 1983 Relationships and social structure of African elephants. In *Primate social relationships* (ed. RA Hinde), pp. 315–325. Sunderland, MA: Sinauer.
2. McComb K, Moss C, Durant S, Baker L, Sayailel S. 2001 Matriarchs act as repositories of social knowledge in African elephants. *Science* **292**, 491–494. (doi:10.1126/science.1057895)
3. Boeckle M, Bugnyar T. 2012 Long-term memory for affiliates in ravens. *Curr. Biol.* **22**, 801–806. (doi:10.1016/j.cub.2012.03.023)
4. Hamilton WD. 1964 The genetical evolution of social behaviour, I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)
5. Smuts BB, Cheney DW, Wrangham RW, Struhsaker TT. 1987 *Primate societies*. Chicago, IL: University of Chicago Press.
6. Sayigh LS, Tyack PL, Wells RS, Scott MD, Irvine AB. 1995 Sex differences in signature whistle production of freeranging bottlenose dolphins, *Tursiops truncatus*. *Behav. Ecol. Sociobiol.* **36**, 171–177. (doi:10.1007/BF00177793)
7. Axelrod R, Hamilton W. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)
8. Mateo JM. 2006 The nature and representation of individual recognition odours in Belding's ground squirrels. *Anim. Behav.* **71**, 141–154. (doi:10.1016/j.anbehav.2005.04.006)
9. Boysen ST, Berntson GG. 1989 Conspecific recognition in the chimpanzee (*Pan troglodytes*): cardiac responses to significant others. *J. Comp. Psychol.* **103**, 215–220. (doi:10.1037/0735-7036.103.3.215)
10. Sayigh LS, Tyack PL, Wells RS, Solow AR, Scott MD, Irvine AB. 1998 Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Anim. Behav.* **57**, 41–50. (doi:10.1006/anbe.1998.0961)
11. Charrier I, Mathevon N, Jouventin P. 2003 Fur seal mothers memorize subsequent versions of developing pups' calls: adaptation to long-term recognition or evolutionary by-product? *Biol. J. Linnean Soc.* **80**, 305–312. (doi:10.1046/j.1095-8312.2003.00239)
12. Insley SJ. 2001 Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* **61**, 129–137. (doi:10.1006/anbe.2000.1569)
13. Marzluff JM, Walls J, Cornell HN, Withey JC, Craig DP. 2010 Lasting recognition of threatening people by wild American crows. *Anim. Behav.* **79**, 699–707. (doi:10.1016/j.anbehav.2009.12.022)
14. Murai C, Tanaka M, Tomonaga M, Sakagami M. 2011 Long-term visual recognition of familiar persons, peers, and places by young monkeys (*Macaca fuscata*). *Dev. Psychobiol.* **53**, 732–737. (doi:10.1002/dev.20548)
15. Lemasson A, Hausberger M, Zuberbühler K. 2005 Socially meaningful vocal plasticity in adult Campbell's monkeys (*Cercopithecus campbelli*). *J. Comp. Psychol.* **119**, 220–229. (doi:10.1037/0735-7036.119.2.220)
16. Lemasson A, Gautier JP, Hausberger M. 2003 Vocal similarities and social bonds in Campbell's monkey (*Cercopithecus campbelli*). *C. R. Biol.* **326**, 1185–1193. (doi:10.1016/j.crvi.2003.10.005)
17. Bahrick HP, Bahrick PO, Wittlinger RP. 1975 Fifty years of memory for names and faces: a cross sectional approach. *J. Exp. Psychol. Gen.* **104**, 54–75. (doi:10.1037/0096-3445.104.1.54)
18. Rasmussen LEL. 1995 Evidence for long-term chemical memory in elephants. *Chem. Senses* **20**, 762.
19. McComb K, Moss C, Sayailel S, Baker L. 2000 Unusually extensive networks of vocal recognition in African elephants. *Anim. Behav.* **59**, 1103–1109. (doi:10.1006/anbe.2000.1406)
20. Holekamp KE, Sakai ST, Lundrigan BL. 2007 Social intelligence in the spotted hyena (*Crocuta crocuta*). *Phil. Trans. R. Soc. B* **362**, 523–538. (doi:10.1098/rstb.2006.1993)
21. Insley SJ. 2000 Long-term vocal recognition in the northern fur seal. *Nature* **406**, 404–405. (doi:10.1038/35019064)
22. Pitcher BJ, Harcourt RG, Charrier I. 2010 The memory remains: long-term vocal recognition in Australian sea lions. *Anim. Cogn.* **13**, 771–776. (doi:10.1007/s10071-010-0322-0)
23. Matthews S, Snowdon CT. 2011 Long-term memory for calls of relatives in cotton-top tamarins (*Saguinus oedipus*). *J. Comp. Psychol.* **125**, 366–369. (doi:10.1037/a0023149)
24. Godard R. 1991 Long-term memory of individual neighbors in a migratory songbird. *Nature* **350**, 228–229. (doi:10.1038/350228a0)
25. Rappole J, Warner D. 1980 Ecological aspects of avian migrant behavior in Veracruz, Mexico. In *Migrant birds in the Neotropics* (eds A Keast, E Morton), pp. 353–393. Washington, DC: Smithsonian Institute.
26. Randić S, Connor RC, Sherwin WB, Krützen M. 2012 A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network. *Proc. R. Soc. B* **279**, 3083–3090. (doi:10.1098/rspb.2012.0264)
27. Mercado E, DeLong C. 2010 Dolphin cognition: representations and processes in memory and perception. *Int. J. Comp. Psychol.* **23**, 344–378.
28. Herman LM. 1980 Cognitive characteristics of dolphins. In *Cetacean behavior: mechanisms and functions* (ed. LM Herman), pp. 363–429. New York, NY: Wiley-Interscience.
29. Connor RC, Wells RS, Mann J, Read AJ. 2000 The bottlenose dolphin, *Tursiops* spp: social relationships in a fission–fusion society. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 91–126. Chicago, IL: University of Chicago Press.
30. Connor RC. 2007 Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Phil. Trans. R. Soc. B* **362**, 587–602. (doi:10.1098/rstb.2006.1997)
31. Reiss D, McCowan B. 1993 Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *J. Comp. Psychol.* **107**, 301–312. (doi:10.1037/0735-7036.107.3.301)
32. Connor R, Whitehead H. 2005 Alliances. II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. *Anim. Behav.* **69**, 127–132. (doi:10.1016/j.anbehav.2004.02.022)
33. Owen ECG, Wells RS, Hofmann S. 2002 Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Can. J. Zool.* **80**, 2072–2089. (doi:10.1139/z02-195)
34. Caldwell MC, Caldwell DK, Tyack PL. 1990 Review of the signature whistle hypothesis for the Atlantic bottlenose dolphin (*Tursiops truncatus*). In *The bottlenose dolphin* (eds S Leatherwood, R Reeves), pp. 199–234. New York, NY: Academic Press.
35. Janik VM. 2009 Acoustic communication in delphinids. *Adv. Study Behav.* **40**, 123–157. (doi:10.1016/S0065-3454(09)40004-4)
36. Wells RS. 2003 Dolphin social complexity: lessons from long-term study and life history. In *Animal social complexity* (eds FBM de Waal, PL Tyack), pp. 32–56. Cambridge, MA: Harvard University Press.
37. Gowans S, Würsig B, Karczmarski L. 2007 The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar.*

Biol. **53**, 195–294. (doi:10.1016/S0065-2881(07)53003-8)

38. Sayigh LS, Tyack PL, Wells RS, Scott MD. 1990 Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother–offspring comparisons. *Behav. Ecol. Sociobiol.* **26**, 247–260. (doi:10.1007/BF00178318)
39. Xue S, Deliyski D. 2001 Effects of aging on selected acoustic voice parameters: preliminary normative data and educational implications. *Educ. Gerontol.* **27**, 159–168. (doi:10.1080/03601270151075561)
40. Duffield DA, Wells RS. 1991 Bottlenose dolphins: comparison of census data from dolphins in captivity with a wild population. *Soundings* **16**, 11–15.
41. Dunbar R. 1998 The social brian hypothesis. *Evol. Anthropol.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5,178:AID-EVAN5.3.0.CO;2-8)
42. Pravosudov VV, Clayton NS. 2002 A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behav. Neurosci.* **116**, 515–522. (doi:10.1037//0735-7044.116.4.515)
43. Tyack PL, Sayigh LS. 1997 Vocal learning in cetaceans. In *Social influences on vocal development* (eds CT Snowden, M Hausberger), pp. 208–233. Cambridge, UK: Cambridge University Press.
44. Samuels A, Gifford T. 1997 A quantitative assessment of dominance relations among bottlenose dolphins. *Mar. Mamm. Sci.* **13**, 70–99. (doi:10.1111/j.1748-7692.1997.tb00613.x)