Animal Behaviour 84 (2012) 1347–1362

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins

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ARTICLE INFO

Article history:
Received 25 November 2011
Initial acceptance 16 December 2011
Final acceptance 6 August 2012
Available online 6 October 2012
MS. number: 11-00943R

Keywords:
bottlenose dolphin
dating
fitness benefit
individual-based model
innovation rate
learning fidelity
social learning
sponging
Tursiops sp.

An apparently vertically, socially transmitted foraging specialization ('sponging') in bottlenose dolphins (*Tursiops* sp.) is observed in two adjacent gulfs within Shark Bay, Western Australia, where sponging has possibly spread from independent innovations. We designed an individual-based model based on empirical data, to investigate the conditions (of learning fidelity and fitness benefits for spongers) under which sponging could be established and maintained. Simulations show that sponging is unlikely to be established from a single innovation event but the probability increases with independent innovation events. Once established, however, it can be maintained in the absence of fitness benefits for spongers, if learning fidelity of daughters is virtually 100%. Smaller learning fidelities can be compensated for with fitness benefits for spongers, but these benefits must be 5% and 10%, respectively, to compensate for learning fidelities of 96.25% and 92%. Furthermore, we estimated the time since the emergence of sponging by tracking the average pairwise relatedness among spongers over time and comparing it to empirical estimates. For the eastern gulf of Shark Bay, we show that sponging might have been in place for at least 120 years if it originated from a single innovation event. For comparison of vertical, social transmission to other trait acquisition methods, we ran simulations in which sponging was either a genetic trait or acquired solely by innovation. In these simulations, sponging could be maintained but the simulation results and empirical data did not match. Hence vertical social transmission is a more feasible mechanism to explain the spread of sponging.

Socially learnt behaviours influence many domains of life in numerous animal species (reviewed in Galef & Laland 2005): predator avoidance (Cook & Mineka 1989); courtship behaviour (Noad et al. 2000); migratory routes (O'Corry-Crowe et al. 1997) and a growing body of literature describes foraging strategies that seem to be transmitted vertically (i.e. from parent to offspring). The diets or foraging strategies of offspring have been shown to resemble their mother's in sea otters, *Enhydra lutris* (Estes et al. 2003), orang-utans, *Pongo pygmaeus wurmbii* (Jaeggi et al. 2010) and bottlenose dolphins, *Tursiops* sp. (Mann & Sargeant 2003; Sargeant & Mann 2009), which indicates vertical transmission, possibly by social learning (Galef & Laland 2005).

Mathematical modelling shows that the establishment and maintenance of a socially transmitted trait is very unlikely if naïve individuals learn from only one cultural parent (Enquist et al. 2010). Reasons for this conclusion are, first, that cultural drift (Koerper & Stickel 1980), analogous to random genetic drift, is likely to eliminate new innovations and, second, that it is unrealistic to assume that social learning is perfect (i.e. not all observers learn the behaviour). Under these conditions, fitness benefits assigned to bearers of socially learnt traits must be very high in order to maintain the trait in the population (Enquist et al. 2010). Therefore, the frequency of trait bearers in the population would be expected to decrease over time and the trait would be lost. However, Enquist et al.'s (2010) modelling was rather generic, and further development would be possible, especially the addition of full stochasticity and use of values from real populations. Individual-based stochastic modelling would allow use of more biological details of the system.

The Sponging Behaviour

Despite the low likelihood predicted for vertically, socially transmitted behaviours to be established and maintained, at least one such behaviour ('sponging') has been established in each of the two gulfs of Shark Bay, Western Australia (Smolker et al. 1997; Mann et al. 2008; Bacher et al. 2010). A subset of the bottlenose dolphin population wears conical marine sponges on their rostra when apparently foraging along the seafloor (Smolker et al. 1997;

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http://dx.doi.org/10.1016/j.anbehav.2012.08.029

Mann et al. 2008). This behaviour appears to be based on a pattern of vertical social transmission without apparent genetic determination (Krützen et al. 2005; Ackermann 2008; Mann et al. 2008; Bacher et al. 2010). Within each gulf, spongers share maternally inherited mitochondrial DNA (mtDNA) haplotypes, with one exception of a male sponger with a different haplotype in the eastern gulf (Krützen et al. 2005; Ackermann 2008). This male indicates that horizontal/oblique transfer or individual learning of sponging may occur very rarely (Krützen et al. 2005). Sponging haplotypes differ between the gulfs (Ackermann 2008), which suggests that either sponging has been established from two independent innovation events in each of the two gulfs of Shark Bay (Ackermann 2008) or else that other horizontal transmission has occurred. We do not know how stable the sponging behaviour is over long time periods in either of the gulfs. Sponging was first observed in the eastern gulf in 1984 (Smolker et al. 1992), shortly after the long-term study of bottlenose dolphins in Shark Bay was launched (Connor & Smolker 1985). Since then, 41 spongers have been identified in the eastern gulf of Shark Bay (Mann et al. 2008) and, since 2007, 40 spongers have been identified in the main study area in the western gulf (Useless Loop, Kopps 2012). Learning of sponging is not perfect in the eastern gulf: 91% of daughters and 25% of sons born to spongers sponge (Mann et al. 2008). Hereafter, we refer to the probability that an offspring born to a sponger becomes a sponger as ‘learning fidelity’. Based on the sample sizes reported in Mann et al. (2008), the binomial 95% confidence levels around the 91% learning fidelity for daughters are 59%–100%. Sponging is habitat dependent and only observed in deep water (channels > 6 m in the eastern gulf, Sargeant et al. 2007; >10 m in the western gulf, Tyne et al. 2012) where the majority of females sponge (Mann et al. 2008; Kopps 2012).

Because sponging appears to have been established and maintained once or more in Shark Bay, it appears that additional modelling is required. The next stage in advancing our understanding of the establishment and maintenance of vertical social transmission is to develop individual-based models informed by biological data, thus providing models that are specific to a species and context. Individual variation in both attributes and experience results in stochastic processes, which are difficult to approach by analytical models. Simulations are run on a time axis where individuals follow probability-based rules of reproduction, migration or other behaviours implemented in the simulation (DeAngelis & Mooij 2005).

Time of Emergence of Culture

Modelling not only allows examination of the maintenance of sponging, but also estimation of the time since its establishment. It is difficult to date innovation events. Their low frequencies mean that, in wild populations, it is rather unlikely that innovation events will be witnessed. However, innovation and extinction of conventions (e.g. hand sniffing) have been documented in capuchin monkeys, *Cebus capucinus*, where these behaviours lasted for up to 10 years (Perry et al. 2003). If innovations are not observed, they can be tentatively dated by indirect methods. Based on archaeological dating methods on stone tools or bones with cut marks, the emergence of hominid tool use was dated to 2.6 million years (Semaw et al. 2003). Excavated flaked stone assemblages that derive from chimpanzee, *Pan troglodytes*, nut cracking have proved that durable records can shed light into past activity (Mercader et al. 2002). The excavated site was dated to 3400 years, indicating that tool use in chimpanzees has been transmitted for more than 200 generations (Mercader et al. 2007).

Indirect dating is more difficult in aquatic habitats because it is difficult to find material evidence of historical tool use. However, modelling of pairwise genetic relatedness provides a tool for indirect estimation of the emergence time of a vertically transmitted trait. If there are no competing influences on relatedness, then genetic relatedness among spongers is expected to decline over time since the common sponging ancestor (Krützen et al. 2005). Spongers in the eastern gulf of Shark Bay are more related than expected by chance (Krützen et al. 2005). Therefore, it was suggested that sponging in the eastern gulf derived from a more recent innovation event than in the western gulf, where the spongers are not more related than the population average (Ackermann 2008). These relatedness estimates were based on average pairwise relatedness based on biparentally inherited microsatellite DNA (e.g. Queller & Goodnight 1989).

This Study

In this study, we used bottlenose dolphin field data on life history, behaviour and genetics to build an individual-based model of establishment and maintenance of sponging in the eastern and western gulfs of Shark Bay (Appendix Fig. A1). This included the examination of learning fidelity and fitness effects necessary for establishment and maintenance of sponging, and the likely time since establishment. By comparison with observed patterns in Shark Bay, we also investigated the possibility of horizontal transmission or multiple innovations. Based on the simulation, we addressed the following questions. (1) Under what conditions of vertical social transmission is sponging stable? (2) How likely is it that sponging is established from a single innovation event? (3) Are spongers biparentally more related than the population average? (4) Can we estimate the time since the emergence of sponging based on average pairwise relatedness among spongers? (5) Can the actual number of spongers give information about the time since the emergence of sponging? (6) How many spongers would we expect and how genetically related would they be if sponging is a genetic trait or only individually innovated?

METHODS

The Model

We built an individual-based model of a diploid, sexually reproducing dolphin population in Matlab R2010a (MathWorks, Natick, MA, U.S.A.). Simulations were run and then compared to empirical results from the eastern and western gulfs of Shark Bay independently. The two populations are connected by high dispersal (number of migrants is much greater than one; Crow & Kimura 1970; Krützen et al. 2004a); however, the 110 km separation between the study sites has led to low, but significant, genetic differentiation between the gulfs (Krützen et al. 2004a). In Shark Bay, male and female dolphins are philopatric, with males extending their natal range (Tsai & Mann 2012). Therefore, dispersal between the gulfs was not implemented in the model.

The population size was set to 600 at the start of the simulation. In three field seasons in the western gulf (Appendix Fig. A1) we identified almost 500 individuals, and unknown individuals have been encountered since (Kopps 2012). However, 500 dolphins is more than the 229 ± 42 dolphins estimated based on an aerial survey in 1994 for the study area in the western gulf of Shark Bay (Preen et al. 1997). The same survey estimated the number of dolphins in the study area in the eastern gulf to be 530 ± 146.

Virtual dolphins had the following attributes (Appendix Table A1): a unique individual number, sex, age class, habitat, whether sponger or nonsponger (which could also represent any other maternally transmitted trait), mtDNA haplotype, and genotypes for 10 neutral, polymorphic, biparentally inherited loci. Sex