Original Article

Mothers teach daughters because daughters teach granddaughters: the evolution of sex-biased transmission

Matthew R. Zefferman[a,b]

[a]National Institute for Mathematical and Biological Synthesis, University of Tennessee, 1122 Volunteer Blvd., Suite 106 Knoxville, TN 37996-3410, USA and [b]School of Human Evolution and Social Change, Arizona State University, 900 S. Cady Mall, Rm. 233, Tempe, AZ 85287-2402, USA

Cultural transmission in nonhuman animals is often sex biased, with females more frequently or efficiently learning cultural behaviors than males. The evolutionary origins of sex-biased cultural transmission have been a mystery, though it has been proposed that female offspring may gain greater reproductive benefit from cultural traits than sons—the "disparate benefits" hypothesis. I propose a different, "uniparental teaching," hypothesis where sex-biased transmission evolves in uniparental species if mothers teach, that is, invest in their offsprings' learning. I show, with theoretical models, that mothers evolve to invest more in teaching daughters than sons because teaching daughters results in greater inclusive fitness benefits. Teaching a son gives him a reproductive benefit for one generation. However, I show that because daughters may teach future generations, teaching a daughter can be a better long-term investment. I also model the disparate benefits hypothesis and show that the uniparental teaching hypothesis better fits the empirical patterns of sex-biased transmission in the well-studied example of "sponging" in bottlenose dolphins. Uniparental teaching may also explain sex-biased transmission in other species, including chimpanzees. My findings suggest that controversial mechanisms of cultural transmission in nonhumans, such as teaching, may be inferred from population-level patterns of transmission even when it is difficult to observe transmission directly in the field or laboratory.

Key words: **cultural evolution, gene-culture coevolution, sex-biased transmission, social learning, teaching, tool use.**

INTRODUCTION

In many nonhuman cultural species, cultural behaviors are transmitted with a sex bias—they are more faithfully transmitted to females than males. The reason for sex-biased transmission is a puzzle because many of the transmitted behaviors would be beneficial to both sexes. In well-documented examples of sex-biased transmission in species, such as "sponging" in bottlenose dolphins (*Tursiops* sp.) and "nut-cracking" and "termite fishing" in chimpanzees (*Pan troglodytes*), the behavior is transmitted disproportionately from mothers to their female offspring. In this article, I propose that uniparental care and sex-biased transmission are intimately related. Specifically, I propose that uniparental care sets the stage for the evolution of sex-biased transmission when mothers make investments in their offsprings' learning, that is, if mothers teach their children.

Teaching is broadly defined as "behavior that evolved to facilitate learning in others" (Kline 2015). In teaching, as opposed to purely observational learning, the teacher modifies its behavior to

better transmit information to the target. This behavioral modification is often costly for the teacher and, therefore, may have negative direct fitness consequences (Caro and Hauser 1992) and can be considered a form of altruism (Thornton and Raihani 2010). Mathematical models show that teaching more easily evolves, like other altruistic behavior, to be directed toward close genetic kin, including offspring (Cavalli-Sforza and Feldman 1983), but only if the taught behavior is not easily acquired without teaching (Fogarty et al. 2011). Although there is good evidence for teaching in humans, its importance for nonhuman species is hotly debated (Hoppitt et al. 2008; Thornton and Raihani 2008, 2010; Byrne and Rapaport 2011; Thornton and McAuliffe 2012; Rapaport and Byrne 2012; Kline 2015). Teaching does not need be the type of "active teaching" associated with human classroom instruction, but can take less overt forms including stimulus enhancement or social tolerance (Kline 2015).

Parents who invest resources in teaching their offspring can increase their offsprings' direct fitness, but the parents will have fewer resources to invest in their own direct fitness. In this article, I will show why, in a species with uniparental care, teaching

Address correspondence to M.R. Zefferman. E-mail: zefferman@asu.edu.

offspring of the caregiving sex is a better investment than teaching the non-caregiving sex. Teaching a beneficial behavior to offspring of the non-caregiving sex may give them a fitness advantage over competitors of the same sex, but because they do not teach their offspring, the transmitted behavior will only provide benefits for one generation. Teaching offspring of the caregiving sex is a better long-term investment because they can pass the beneficial behavior on to future generations. Thus, in species where only females provide parental care, mothers who teach daughters should, all else equal, have greater inclusive fitness than mothers who teach sons. Selection should, therefore, drive mothers to preferentially teach daughters over sons. I call this the "uniparental teaching hypothesis" and posit that this process could lead to the evolution of sex-biased transmission.

A competing hypothesis for sex-biased transmission, which I will label the "disparate benefits hypothesis," assumes that learning is purely observational and posits that daughters more frequently or effectively learn transmitted behaviors because they obtain greater fitness benefits from these behaviors than sons. For example, it has been suggested that female bottlenose dolphins gain more from specific culturally transmitted behaviors than males because they are responsible for provisioning future offspring (Krützen et al. 2005) or because males dolphins have access to alternative, superior, techniques for obtaining needed resources (Boesch C and Boesch H 1981, 1984; Krützen et al. 2005). Sex-biased transmission occurs, according to the disparate benefits hypothesis, not because mothers preferentially teach daughters, but because daughters spend more effort than sons learning from their mothers. Although it is possible that daughters receive greater benefit from specific cultural behaviors, I will show that the disparate benefits hypothesis is neither necessary nor sufficient to explain observed empirical patterns of sex-biased transmission.

In this article, I model both the uniparental teaching hypothesis and the disparate benefits hypothesis as processes of gene-culture coevolution (Boyd and Richerson 1985; Richerson and Boyd 2005) where beneficial cultural traits are transmitted uniparentally. In the models, either alleles for teaching (in the uniparental teaching hypothesis) or alleles for observational learning (in the disparate benefits hypothesis) coevolve with the cultural trait. I compare the results of both models to empirical patterns of sex-biased cultural transmission in the intensively studied case of "sponging" in bottlenose dolphins. Finally, I suggest that uniparental teaching may help explain sex-biased transmission in other species and that the existence of teaching may be inferred from population-level patterns of transmission even when teaching behaviors are difficult to observe in the laboratory or the field.

Sponging in bottlenose dolphins: a case study

Bottlenose dolphins learn many foraging behaviors from their mothers. For example, in just 2 populations in Shark Bay, Australia, dolphins employ at least 13 foraging behaviors that seem to be culturally transmitted primarily from mothers to offspring, often with a bias toward daughters (Mann and Sargeant 2003). One of these, sponging, is intensely studied because it is a rare example of tool use by nonhuman mammals. Sponging dolphins remove sponges from the bottom of the bay and use them to protect their rostrum while probing the murky substrate to dislodge prey not easily detected by echolocation. This behavior is thought to give sponging dolphins access to an ecological niche not exploited by dolphins who do not sponge (Smolker et al. 1997; Mann et al. 2008; Patterson and Mann 2011).

The evidence that exploiting this niche leads to greater reproductive benefits is mixed. Mann et al. (2008) observed that sponging bottlenose dolphins had 18% greater calving success than nonspongers though the finding was not statistically significant (at α = 0.05). However, a power analysis (Supplementary Appendix D) indicates that sponging would have had to provide 43% greater calving success to be detectable (at $1 - \beta = 0.8$) given the variation in the data. Previous theoretical modeling supports the idea that sponging provides a reproductive benefit with Kopps and Sherwin (2012) estimating that maintaining the observed frequencies of sponging requires a minimum selection advantage of at least 5–10%. Additional analysis indicates that benefits increase as dolphins age (Patterson et al. 2015).

Despite the potential fitness advantages of sponging, less than 10% of dolphins in Shark Bay sponge (Mann et al. 2008; Mann and Patterson 2013). At least part of the reason is that sponging is transmitted almost exclusively from mothers to offspring. Mitochondrial DNA analysis has shown that within each population, all sponging dolphins are part of the same maternal line (Krützen et al. 2005) and the mother of every sponging dolphin (with known parentage) also sponges. Further analysis determined that genetic transmission and environmental factors do not adequately explain sponging behavior (Krützen et al. 2005; Bacher et al. 2010; Mann et al. 2012), leaving cultural transmission as a likely requirement.

Previous theoretical modeling suggests that uniparentally transmitted cultural traits can only be maintained in a population if the trait has a sufficiently high reproductive benefit or if the trait is independently innovated with sufficient frequency (Enquist et al. 2010). The former mechanism seems important in maintaining sponging behaviors in the Shark Bay dolphin population (Kopps and Sherwin 2012) as it seems to be transmitted primarily from mothers to offspring. However sponging occurs in at least 2 maternal lines, one in each of 2 populations in Shark Bay, suggesting either separate inventions or a case of horizontal transmission between migrants from one population to another.

An unsolved puzzle is why sponging is transmitted at much higher frequencies from mothers to daughters than from mothers to sons. In Shark Bay, more than 90% of female spongers' daughters, but only about 50% of female spongers sons, sponge (Mann et al. 2008; Mann and Patterson 2013).

What explains this discrepancy? One existing hypothesis, the disparate benefits hypothesis, posits that both males and females imitate their mothers, but females invest more in learning specialized foraging behaviors because they gain greater reproductive benefits. This might be because females need more energy to birth and wean offspring (Mann et al. 2008) or because males get smaller benefit from niche-specific foraging behaviors because they have a larger and more ecologically diverse range than females (Mann et al. 2008). However, neither of these hypotheses explains why, if sponging does not give males sufficient reproductive benefit, such a large fraction of spongers' sons do sponge.

The hypothesis I develop in the article suggests that the population-level patterns of sponging in bottlenose dolphins are the result of teaching in a species with uniparental care. The evidence for teaching in cetaceans is mixed and, because teaching is rare in nonhuman mammals, contentious. Observational reports of teaching in cetaceans (Guinet 1991; Guinet and Bouvier 1995; Rendell and Whitehead 2001; Bender et al. 2009) have generated a good deal of controversy (Galef 2001; Herman and Pack 2001; Kuczaj 2001; Maestripieri and Whitham 2001; Mann 2001; Mitchell 2001; Premack and Hauser 2001), especially because teaching has

not been demonstrated in controlled experiments (Galef 1992; Maestripieri and Whitham 2001). However, it is difficult to conduct controlled experiments with large wide-ranging animals such as dolphins and whales (Rendell and Whitehead 2001). Even observational evidence of cetacean teaching behavior is difficult to obtain because cetaceans have large ranges and much of their behavior occurs in deep, murky underwater environments. I propose that an indication of teaching in cetaceans, and other hard-to-study taxa, is if teaching better explains patterns of cultural transmission than other explanations.

THE MODELS

To find out whether the uniparental teaching hypothesis better explains patterns of sex-biased transmission than the disparate benefits hypothesis, I constructed a numerical simulation of each hypothesis. To assess each model, I determined how well it explains the 3 observed patterns of sponging frequency in the dolphins of Shark Bay: 1) The frequency of sponging in the population is low; 2) the transmission rate of sponging from mothers to daughters is high; and 3) the transmission rate of sponging from mothers to sons is positive, but substantially lower than the transmission rate to daughters.

In the following model descriptions, I assume that uniparental care is provided by females and cultural traits are transmitted only through mothers by teaching or observational learning. In species where uniparental care is provided by males, the sexes in the model descriptions and results would be reversed. Strategies for learning and teaching are inherited genetically from both parents.

Uniparental teaching model

The uniparental teaching hypothesis posits that mothers pay a cost to teach their offspring and that they preferentially invest in daughters because daughters might teach beneficial cultural traits to future generations. Sons do not transmit cultural traits because they do not raise their offspring. To determine whether mothers in a uniparental species evolve to transmit beneficial cultural traits preferentially to daughters, I created numeric simulations where genetic alleles for teaching a beneficial cultural trait coevolve with the culturally transmitted traits themselves. I then find conditions where the population settles to the empirical pattern of transmission described above.

In the model, individuals are haploid and of sex s, which is either female, f, or male, m. They also have a genetic locus A_k which, in encultured females (those who have learned the beneficial trait), determines which offspring they teach. Table 1 gives the teaching rules for each allele where τ_{sk} indicates that encultured A_k mothers teach offspring of sex s and $\tau_{sk} = 0$ indicates that mothers with allele k do not teach offspring of sex s. Females with the A_1 allele teach offspring of both sexes. Females with the A_2 allele teach only daughters. Females with the A_3 allele teach only sons. Females with the A_4 allele do not teach their offspring. Males and unencultured females do not teach regardless of their allele.

An individual's fitness, w_{skc}, depends on its sex, its teaching allele, and whether it knows the beneficial cultural trait. Enculturation is indexed by c where $c = 1$ indicates that an individual knows the trait and $c = 0$ indicates that it does not. Because teaching is costly, mothers who teach limit their reproductive potential after their first offspring. In the model, encultured females who teach offspring of only one sex pay a reproductive cost of κ. Because females are as likely to have sons as daughters, females who teach offspring of

both sexes pay twice the reproductive cost (2κ). Individuals of both sexes who learn the cultural trait gain a fitness benefit of b. All individuals have a baseline fitness of 1. Table 2 gives the expected fitnesses for individuals of every combination of sex, allele, and state of enculturation.

Following Boyd and Richerson (1985), I define x_{skc} as the frequency of individuals of sex s, with allele A_k, and enculturation c before genetic selection, x'_{skc} as the frequency after genetic selection, x''_{skc} as the frequency after cultural transmission, and x'''_{skc} as the frequency after innovation. Therefore, if x_{skc} represents the frequency of individuals in one generation, x'''_{skc} represents it in the next.

Genetic selection occurs through reproductive competition, with the fraction of individuals of each type contributing to the next generation determined by that type's fitness relative to other types of the same sex, as described in Equation 1.

$$x'_{skc} = \frac{x_{skc} w_{skc}}{\sum_i \sum_j x_{sij} w_{sij}} \qquad (1)$$

An individual is only taught the cultural trait if its mother both knows the trait and has an allele for teaching offspring of the individual's sex. Equation 2 gives the frequencies of encultured individuals after teaching (x''_{sk1}), and Equation 3 gives the frequencies of unencultured individuals after teaching (x''_{sk0}). These sum to the frequency of allele k in sex s after teaching (i.e., $x''_{sk1} + x''_{sk0} = x''_{sk}$).

The first term on the right side of Equation 2 accounts for encultured individuals of sex s and allele k where the teaching allele is inherited genetically from the mother. This is the frequency of the encultured females with the k allele after selection multiplied by the teaching rule which is one if females of allele k teach offspring of

Table 1

Teaching rules for each allele where $\tau_{sk} = 1$ indicates that encultured A_k mothers teach offspring of sex s

Allele	Daughter Rule	Son Rule
A_1	$\tau_{f1} = 1$	$\tau_{m1} = 1$
A_2	$\tau_{f2} = 1$	$\tau_{m2} = 0$
A_3	$\tau_{f3} = 0$	$\tau_{m3} = 1$
A_4	$\tau_{f4} = 0$	$\tau_{m4} = 0$

When $\tau_{sk} = 0$ mothers with allele k do not teach offspring of sex s. These rules are used in Equations 2 and 3.

Table 2

Expected fitnesses (w_{skc}) for encultured ($c = 1$) and unencultured ($c = 0$) individuals of each genetic allele ($A_k = \{A_1, A_2, A_3, A_4\}$) and sex ($s = \{m, f\}$)

Allele	Female expected fitness		Male expected fitness	
	With trait	Without trait	With trait	Without trait
A_1	$w_{f11} = 1 + b - 2\kappa$	$w_{f10} = 1$	$w_{m11} = 1 + b$	$w_{m10} = 1$
A_2	$w_{f21} = 1 + b - \kappa$	$w_{f20} = 1$	$w_{m21} = 1 + b$	$w_{m20} = 1$
A_3	$w_{f31} = 1 + b - \kappa$	$w_{f30} = 1$	$w_{m31} = 1 + b$	$w_{m30} = 1$
A_4	$w_{f41} = 1 + b$	$w_{f40} = 1$	$w_{m41} = 1 + b$	$w_{m40} = 1$

sex s. The second term accounts for the contribution to encultured individuals of sex s and allele k, where the teaching allele is inherited genetically from the father. This is the frequency of the k allele in males after selection multiplied by the frequency of encultured females of all alleles that teach offspring of sex s.

$$x''_{sk1} = \frac{1}{2}\left(\underbrace{\tau_{sk}x'_{fk1}}_{\substack{\text{Teaching allele}\\\text{from mother}}} + \underbrace{\left(x'_{mk0}+x'_{mk1}\right)\sum_h \tau_{sh}x'_{fh1}}_{\text{Teaching allele from father}}\right)\quad(2)$$

The first 2 terms in Equation 3 account for unencultured individuals of sex s and allele k where the allele is inherited from the mother. The first of these terms accounts for cases where the mother is not encultured and the second term accounts for cases where she is encultured but does not teach offspring of sex s. The third term in Equation 3 accounts for unencultured individuals of sex s and allele k where the allele is inherited from the father. This is the frequency of the k allele in males after selection, multiplied by the frequency of females of all alleles who are either unencultured or do not teach offspring of sex s.

$$x''_{sk0} = \frac{1}{2}\left(\underbrace{x'_{fk0}+\left(1-\tau_{sk}\right)x'_{fk1}}_{\text{Teaching allele from mother}} + \underbrace{\left(x'_{mk0}+x'_{mk1}\right)\sum_h\left(x'_{fh0}+\left(1-\tau_{sh}\right)x'_{fh1}\right)}_{\text{Teaching allele from father}}\right)\quad(3)$$

Unencultured individuals also innovate the trait with a probability of ν, decreasing the fraction of unencultured individuals (Equation 4) and increasing the fraction of encultured individuals (Equation 5).

$$x'''_{sk0} = (1-\nu)x''_{sk0}\quad(4)$$

$$x'''_{sk1} = x''_{sk1}+\nu x''_{sk0}\quad(5)$$

Because the model is intended to be general and applicable to a wide range of potential behaviors, including those in species other than dolphins, I ran a series of numeric simulations of this system with teaching costs uniformly distributed over a wide range of 288 values from $\kappa = 0$ to $\kappa = 0.25$ and trait benefits uniformly distributed over 288 values from $b = 0.01$ to $b = 0.5$. For dolphin sponging, the estimated net benefits (direct benefits minus teaching costs) of 18% (Mann et al. 2008) are likely to be in this range. I set the innovation rate at $\nu = 0.005$.

For each of the 288^2 parameter combinations, I ran 4 simulations each starting at different initial conditions (where one of each allele started at 5% frequency and the rest started at just under 31.7% frequency). Each simulation began with the cultural trait absent from the population where it was subsequently introduced through innovation. I continued the simulations for each parameter combination until the allele and cultural trait frequencies from each starting condition converged to an equilibrium. In the very rare (<0.1%) of the parameter combinations where the simulation did not converge after 10 million generations I stopped the simulation and recorded the mean frequencies between the simulations. These instances occurred close to phase transition boundaries where selection was extremely weak because the cultural trait was not maintained in the population. These rare occurrences did not change the key findings of the model.

I also ran 2 additional variations on the uniparental teaching model, described in Supplementary Appendix C. In the first variation, teaching behavior is determined by 2 loci each with 2 alleles instead of 1 locus with 4 alleles. One locus is for teaching daughters and the other for teaching sons. In the second variation, teaching is imperfect with an error rate of 10%, the maximum empirically plausible error rate for bottlenose dolphins since mothers transmit sponging to daughters at greater than 90% frequency. I also, conservatively, use the same error rate for males to not bias the results toward lower male transmission rates.

Disparate benefits model

The disparate benefits hypotheses assume that cultural traits are transmitted through observational learning by offspring with no investment from either parent. It posits that sex-biased transmission results from daughters putting more effort into learning than sons because daughters gain more reproductive benefit from the transmitted trait (Boesch C and Boesch H 1981, 1984; Krützen et al. 2005). To determine whether females and males both evolve to invest in learning a beneficial cultural trait, but females evolve to invest at a greater frequency, I created numeric simulations where genetic alleles for observational learning coevolve with the cultural traits themselves. I then compare the results of the simulation to the empirical pattern of transmission described above.

As in the uniparental teaching model, individuals are haploid and of sex s, which is either female, f, or male, m, and enculturation is indexed by c. However, mothers do not pay a teaching cost. Instead, individuals have one of 4 alleles at genetic locus B_k. Both males and females with the B_1 allele learn their mother's cultural trait. Females, but not males, with the B_2 allele learn their mother's cultural trait. B_3 males, but not females, learn their mother's trait. B_4 individuals do not learn cultural traits. Table 3 summarizes the learning rules for each sex and allele. If an individual of allele B_k and sex s learns, then $r_{sk} = 1$. Otherwise $r_{sk} = 0$.

All individuals have a baseline fitness of 1 and imitators of both sexes with an encultured mother pay an imitation cost, μ, to learn a trait. Cultural traits give a reproductive benefit of b_f to females and b_m to males. I define w_{skc} as the expected fitness of an individual of sex s and allele k who is either encultured ($c = 1$) or not ($c = 0$), Table 4.

Similar to the uniparental teaching model, I define y_{skc} as the frequency of individuals of sex s, the genetic allele B_k, and enculturated state c before selection. y'_{skc} is the frequency after selection, y''_{skc} is the frequency after cultural transmission, and y'''_{skc} is the frequency after innovation.

As in the uniparental teaching model, an individual's contribution to the next generation is relative to its fitness compared with other members of its sex as described in Equation 6.

Table 3

Learning rules for each allele

Allele	Female Rule	Male Rule
B_1	$r_{f1} = 1$	$r_{m1} = 1$
B_2	$r_{f2} = 1$	$r_{m2} = 0$
B_3	$r_{f3} = 0$	$r_{m3} = 1$
B_4	$r_{f4} = 0$	$r_{m4} = 0$

$r_{sk} = 1$ indicates individuals of sex s and allele B_k learn from their mother and $r_{sk} = 0$ indicates they do not.

Table 4

Expected fitnesses (w_{skc}) for encultured ($c = 1$) and unencultured ($c = 0$) individuals of each allele ($B_k = \{B_1, B_2, B_3, B_4\}$) and sex ($s = \{m, f\}$)

Allele	Female expected fitness		Male expected fitness	
	With trait	Without trait	With trait	Without trait
B_1	$w_{f11} = 1 + b_f - \mu$	$w_{f10} = 1$	$w_{m11} = 1 + b_m - \mu$	$w_{m10} = 1$
B_2	$w_{f21} = 1 + b_f - \mu$	$w_{f20} = 1$	—	$w_{m20} = 1$
B_3	—	$w_{f30} = 1$	$w_{m31} = 1 + b_m - \mu$	$w_{m30} = 1$
B_4	—	$w_{f40} = 1$	—	$w_{m40} = 1$

Horizontal lines indicate allele and trait combinations that do not occur in the model.

$$y'_{skc} = \frac{y_{skc} w_{skc}}{\sum_i \sum_j y_{sij} w_{sij}} \quad (6)$$

Individuals acquire cultural traits by imitating their mother, which changes the type frequencies in the population as described in Equations 7 and 8. Equation 7 describes the frequency of encultured individuals after imitation. Equation 8 describes the frequency of unencultured individuals.

In Equation 8, individuals only learn if they have an allele for imitating their mother (i.e., $r_{sk} = 1$). If an individual has such a trait, the first term in parentheses accounts for encultured individuals of sex s and allele k where the allele is inherited from the mother, which is the frequency of the encultured females with the k allele after selection. The second term accounts for the contribution to encultured individuals of sex s and allele k, where the allele is inherited from the father. This is the frequency of the k allele in males after selection multiplied by the frequency of encultured females of all alleles.

$$y''_{sk1} = \frac{1}{2} r_{sk} \left(\underbrace{y'_{fk1}}_{\substack{\text{Learning allele} \\ \text{from mother}}} + \underbrace{(y'_{mk0} + y'_{mk1}) \sum_h y'_{fh1}}_{\text{Learning allele from father}} \right) \quad (7)$$

The first 2 terms in Equation 8 account for unencultured individuals of sex s and allele k where the allele is inherited from the mother. The first term accounts for cases where the mother is not encultured and the second accounts for cases where she is encultured but offspring of sex s do not imitate. The third term accounts for unencultured individuals of sex s and allele k where the allele is inherited from the father. This is the frequency of the k allele in males after selection, multiplied by the frequency of females of all alleles who are either unencultured or are not imitated by offspring of sex s.

$$y''_{sk0} = \frac{1}{2}\left(\underbrace{y'_{fk0} + (1 - r_{sk}) y'_{fk1}}_{\text{Learning allele from mother}} + \underbrace{(y'_{mk0} + y'_{mk1}) \sum_h \left(y'_{fh0} + (1 - r_{sk}) y'_{fh1} \right)}_{\text{Learning allele from father}} \right) \quad (8)$$

Individuals also innovate the trait with a probability of ν, decreasing the fraction of unencultured individuals (Equation 9) and increasing the fraction of encultured individuals (Equation 10).

$$y'''_{sk0} = (1 - \nu) y''_{sk0} \quad (9)$$

$$y'''_{sk1} = y''_{sk1} + y''_{sk0} \nu \quad (10)$$

I ran numeric simulations of the above model with the innovation rate set to $\nu = 0.005$ and varied the net benefits of learning for each sex ($b_f - \mu$ and $b_m - \mu$) over 285 values distributed uniformly from -0.25 to 0.25. For each combination of these parameters, I started the population at 4 different initial gene frequencies (where one allele was at 5% frequency and the rest were each at just under 31.7%) and ran the simulation until the distribution of genetic and cultural traits converged to an equilibrium. In each simulation, the population began with only unencultured individuals, so that the cultural trait was introduced slowly through innovation.

I also ran an additional variation on the disparate benefits model, described in Supplementary Appendix C, where learning is imperfect with an error rate of 10%, the maximum empirically plausible error rate since mothers transmit sponging to daughters at greater than 90% frequency. As in the previous model, I conservatively use the same error rate for males to not bias the results toward lower male transmission rates.

RESULTS

I found that the uniparental teaching model better describes the patterns of cultural transmission observed in the Shark Bay bottlenose dolphin population than the disparate benefits model.

Uniparental teaching model results

In the range of parameters where a cultural trait's reproductive benefit is roughly twice the cost of teaching, the uniparental teaching model explains the empirical patterns of transmission in bottlenose dolphins (Figure 1). The cultural trait is maintained at a low frequency in the population, cultural transmission to daughters is maintained at a high rate, and cultural transmission to sons is maintained at a substantially lower rate.

The pattern is apparent from the equilibrium allele frequencies shown in Figure 2. When teaching costs are sufficiently low, the allele for teaching offspring of both sexes goes to fixation and the cultural trait is maintained at a high frequency in the population. At higher teaching costs, there are fewer alleles for teaching sons, but still more alleles for teaching daughters. When teaching costs are even higher, alleles for teaching sons and for teaching daughters are selected out of the population. There is a corresponding decrease in the frequency of the cultural trait in the population. Alleles for teaching daughters are maintained at a higher rate than alleles for teaching sons for most of this range until costs are high enough that mothers stop teaching offspring of either sex and the cultural trait is only maintained through innovation.

For the parameter values that reflect the empirical pattern of cultural transmission, alleles for teaching reach a polymorphic equilibrium because there is a reproductive conflict between a mother's fitness and that of her offspring. As the beneficial cultural trait becomes more common, the marginal relative fitness benefit it gives decreases Haldane (1962), eventually balancing with the marginal relative fitness cost incurred by the mother for teaching. This balance occurs at a higher allele frequency for teaching daughters than for teaching sons because a son's reproductive advantage over other males lasts for only one generation, while a daughter may teach the beneficial trait to her offspring who will also gain the benefit. As shown in Figure 2, this leads to an equilibrium where alleles for teaching daughters are more common than alleles for teaching sons.
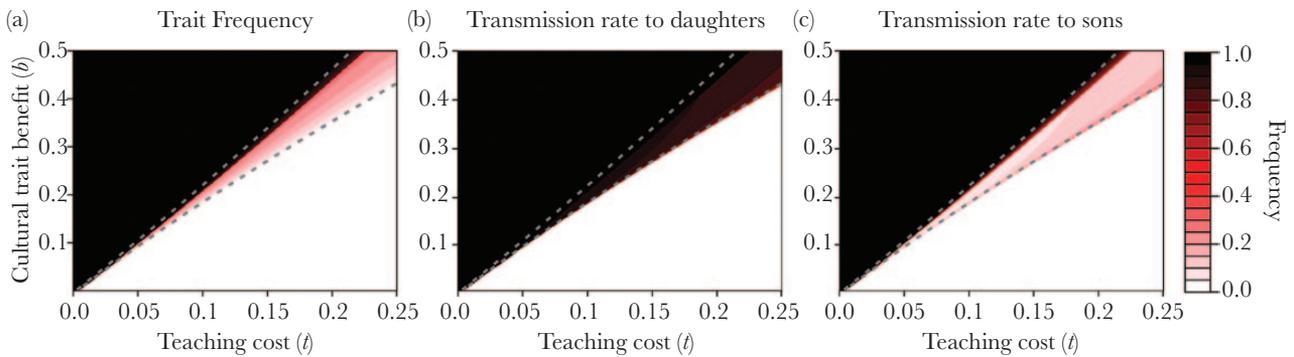
Figure 1

The modeled patterns of cultural transmission match the empirical patterns when the cultural trait's reproductive benefit is roughly twice its teaching cost (between the dotted lines). (a) A region where the cultural trait is maintained at a low, nonzero, frequency in the population. (b) Over the same parameter space, there is a high frequency of transmission from encultured mothers to daughters. (c) Also, over this parameter space, there is a much lower, but nonzero, transmission rate from encultured mothers to sons. This pattern holds even when teaching costs and reproductive benefits are substantially lower than the maximum shown in the figure.
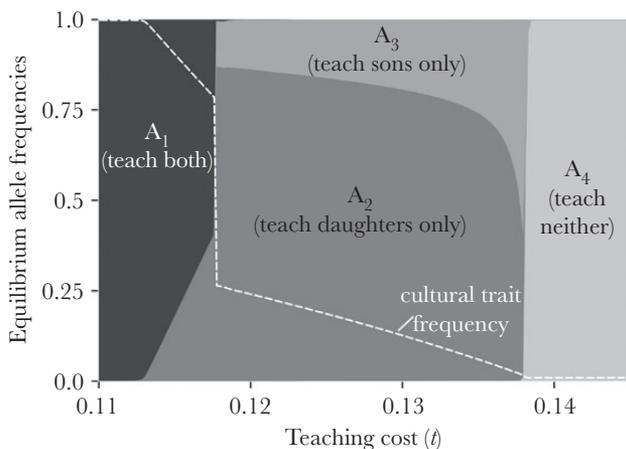
Figure 2

For intermediate teaching costs, alleles for teaching daughters are maintained at high frequency and alleles for teaching sons are maintained at lower frequency. Allele frequencies are shown stacked and always sum to one. Over this intermediate range, the frequency of the cultural trait in the population (dotted line) is low and approaches zero for higher teaching costs. Cultural trait benefits are held constant at $b = 0.25$.

All 3 aspects of the empirical pattern of sponging in Shark Bay occur over the range where teaching costs are intermediately high relative to benefits. First, the trait is maintained at a fairly low frequency, often less than 10%. Second, the transmission rate from mothers to daughters is high, typically over 90%. Third, the transmission rate from mothers to sons is greater than zero, but substantially lower than from mothers to daughters. It is typically lower than the 50% frequency observed in the Shark Bay population, but some deviation from the empirical measurements is unsurprising given the simplicity of the model and the uncertainty of the empirical measurement. The male transmission rate falls within the 95% confidence interval of 3–65% for the measurements reported in (Mann et al. 2008). Ecological variation, overlapping generations, nonlinear fitness effects, finite population effects, out-of-equilibrium dynamics, sampling error, and stochastic factors may also account for the difference. The key qualitative result is that there are polymorphisms for teaching both males and females, and females are taught at a much higher rate than males. The model shows that this pattern can be generated solely by adding a teaching cost to a system with uniparental transmission.

Results for the 2 additional variations of the uniparental teaching model are described in Supplementary Appendix C. Both variations, one with separate loci for teaching males and females and one with transmission errors, result in a similar patterns of cultural and genetic transmission. Both variations result in a zone where the frequency of the cultural trait in the population is low, cultural transmission from mothers to daughters occurs at a high rate, and transmission from mothers to sons occurs at a much lower rate. However, the shape of this zone is slightly different than in the text. In the model with transmission errors, the frequency of the cultural trait in the population is low over a larger range than the case without transmission errors when teaching is small relative to the benefits.

I conducted a stability analysis of this model's monomorphic equilibria. The results of this analysis show a close correspondence with the results of the numeric simulation and are presented in Supplementary Appendix A.
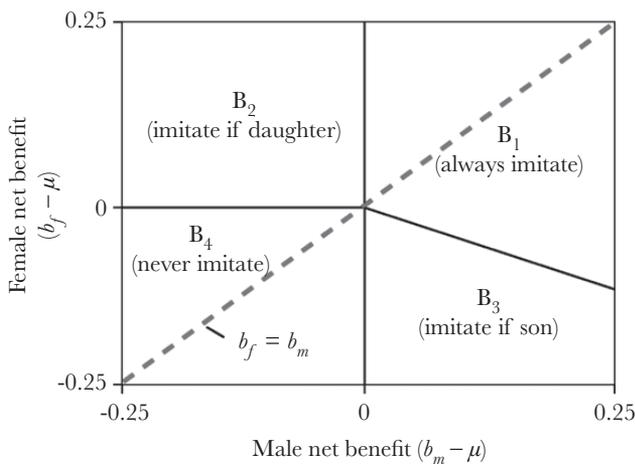
Disparate benefits model results

The disparate benefits model does not result in the pattern of sex-biased cultural transmission in bottlenose dolphins. When a cultural trait gives females a greater reproductive benefit than males (above the dotted line in Figure 3a–c), there are 3 possible results. First, when $b_f > b_m > \mu$, the allele for imitation by both sexes goes to fixation in the population along with the cultural trait. When $b_f > \mu > b_m$, the allele for imitating by daughters increases to fixation, but the allele for imitating by sons disappears. Consequently, all females learn the cultural trait, but males never learn it. When $\mu > b_f > b_m$, alleles for imitation disappear from the population and the cultural trait is not transmitted to offspring of either sex. Figure 4 shows the conditions where each genetic allele goes to fixation.

No combination of parameters reflects the pattern of cultural transmission observed in the Shark Bay dolphin population. Cultural transmission is an all-or-nothing affair for each sex. Either all females learn the trait or, if the benefits of the trait are too low, none learn it. Either all males learn the trait or, if the benefits of the trait are too low, none of them learn it.
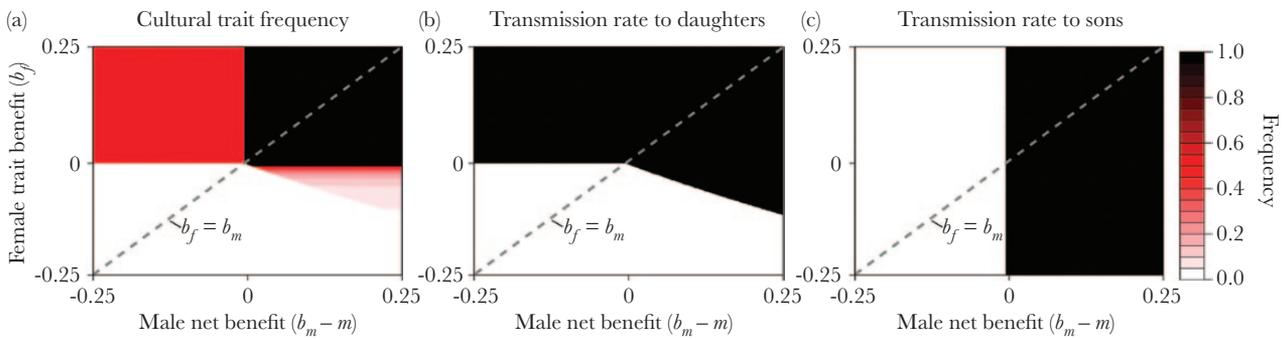
Figure 3
In the disparate benefits model, neither the distribution of alleles nor the cultural transmission patterns are similar to observed distributions in bottlenose dolphins. (a) The frequency of the cultural trait in the population for various combinations of $b_f - \mu$ and $b_m - \mu$. Where $b_f > b_m > \mu$, the trait goes to fixation in both males and females. When $b_f > \mu > b_m$, the trait goes to fixation in females and is lost in males. When $c > b_f > b_m$, the trait is lost in both males and females. (b) The rate of transmission from encultured mothers to daughters that is either zero or one when $b_f > b_m$. (c) The rate of transmission from encultured mothers to sons that is also either zero or one when $b_f > b_m$. Along the line where $b_f = b_m$, when $b_f = b_m > \mu$, mothers teach all offspring and the cultural trait goes to fixation. When $b_f = b_m < \mu$, mothers teach no offspring and the cultural trait is lost.

Figure 4
One of the 4 genetic alleles always goes to fixation in the disparate benefits model. The fixation conditions shown here for each allele depend on the relationship between b_f, b_m and μ. For the disparate benefits condition ($b_f > b_m$), B_1 goes to fixation when $b_f > \mu$ and $b_m > \mu$, B_2 goes to fixation when $b_f > \mu$ and $b_m < \mu$, and B_3 goes to fixation when $b_f < \mu$ and $b_m > \mu$.

The results of stability analysis of this model's monomorphic equilibria analysis show a close correspondence with the results of the numeric simulation and are presented in Supplementary Appendix B. The results of the disparate benefits model with transmission errors, as presented in Supplementary Appendix C, had a similar pattern of cultural transmission frequency (though lower overall trait frequency) and also does not reproduce the empirical transmission patterns.

In general, the differences in the results between the uniparental teaching and the disparate benefits models should be robust to many formulations. Because uniparental teaching necessarily causes reproductive conflict between parents and offspring, it causes balancing selection on maternal teaching strategies. Because purely observational learning does not cause reproductive conflict between parents and offspring, it does not have an obvious mechanism for balancing selection on learning strategies. A viable alternative to the uniparental teaching hypothesis would need such a mechanism.

DISCUSSION

The results of the uniparental teaching model replicate otherwise unexplained empirical patterns in the Shark Bay dolphin population: The cultural trait is maintained at a low frequency in the population, the trait is transmitted to daughters at a high rate, and the trait is transmitted to sons at a much lower rate. The disparate benefits model did not replicate these patterns, suggesting that even if daughters receive greater reproductive benefit from culturally transmitted behaviors than sons, these benefits are neither necessary nor sufficient to explain sex-biased cultural transmission.

Potential application to other species

Are these findings applicable to other species with uniparental transmission? Without additional population-level data on transmission patterns or direct observation of mothers preferentially teaching daughters, it is hard to be sure. However, good test cases for future empirical analysis of this sort may be chimpanzee "nut-cracking" and "termite fishing" behaviors. These examples are particularly useful because they demonstrate that the type of active teaching common in humans, is likely to be rare in nonhuman animals. Researchers looking for evidence of teaching in other species would want to examine the evidence of teaching by, for example, stimulus enhancement and social tolerance.

Like sponging in dolphins, the cultural transmission of nut-cracking and termite fishing in chimpanzees is sex-biased and uniparentally transmitted. In one chimpanzee community, 2 complicated nut-cracking techniques, cracking Coula nuts while in a tree and cracking Prada nuts on the ground with precise strikes of a properly sized stone, have a strong sex bias (Boesch C and Boesch H 1981, 1984). In field observations about 80% of incidences of both behaviors were performed by females and about 20% were performed by males. Females also cracked nuts with a greater efficiency than males (Boesch C and Boesch H 1984). However, a simpler behavior, cracking of Coula nuts on the ground, does not have a similar sex bias (Boesch C and Boesch H 1981, 1984).

Unlike sponging in dolphins, the teaching of chimpanzee nut-cracking is readily observed in the field. Most of this is "teaching by stimulus enhancement" Kline (2015), where a mother gives her offspring a hammer, uncracked nuts and access to an anvil. Sometimes a mother leaves her offspring alone with an uncracked nut she left

in the anvil. These behaviors decrease a mother's foraging efficiency because she will spend some time searching for a new hammer or more uncracked nuts after providing them to her offspring. Female chimpanzees without infants have never been observed to search for more nuts while uncracked nuts still remained in or near the anvil (Boesch 1991; Matsuzawa et al. 2001). Infants are also not very good at cracking nuts and it would often be more efficient for mothers to simply crack nuts themselves before providing them to their offspring.

In addition to stimulus enhancement, Boesch twice observed direct active teaching where a mother, seeing her offspring struggling with cracking a nut, demonstrated proper nut-cracking technique, increasing her offspring's proficiency (Boesch 1991). However, these are the only 2 recorded episodes of direct active teaching recorded over many years of field studies, so it is likely to be an extremely rare form of teaching in chimpanzees, at best (Lonsdorf 2006; Kline 2015).

Social transmission of chimpanzee "termite fishing," where chimpanzees fashion sticks to extract termites from termite mounds, is also sex-biased. Daughters learn the behavior faster and at a higher proficiency than sons and, unlike sons, use similar fishing techniques as their mothers (Lonsdorf et al. 2004; Lonsdorf 2005). Field observations suggest that termite fishing appears to be transmitted primarily through "teaching by social tolerance" Kline (2015), where mothers are highly tolerant of interference to their own termite fishing by their offspring (Lonsdorf 2006).

Evidence that cultural transmission in chimpanzees is both sex-biased and uniparentally taught strongly suggests that the uniparental teaching hypothesis is at play. However, further empirical evidence is needed to determine if the uniparental teaching hypothesis actually explains the sex bias. While observations of costly teaching behavior certainly supports the uniparental teaching hypothesis, Lonsdorf (2006) failed to find evidence that mothers spend more effort teaching daughters than sons. Additionally, an investigation of population-level patters of transmission would provide evidence for or against the uniparental teaching hypothesis. The female bias in nut-cracking, for example, was reported as a frequency of observations of the behavior, while analysis of the percentage of individuals who have learned the behavior (as reported for the Shark Bay bottlenose dolphins) would be more useful for examining the uniparental teaching hypothesis. For example, if the patterns of transmission were similar to sponging in bottlenose dolphins, it would provide evidence for the uniparental teaching hypothesis.

However, even if empirical evidence suggests that female and male chimpanzees learn cultural behaviors with similar frequency, but females learn them with greater proficiency, this might still be consistent with the uniparental teaching hypothesis. If offspring of both sexes can learn a behavior by observational learning (of their mother or other conspecifics) alone, but mothers augmented this learning by teaching for daughters, females may become more proficient with the behavior even if males and females learn it with the same frequency. For example, if both male and female chimpanzees learn termite fishing by observational learning (Matsuzawa et al. 2001), but mothers also preferentially teach daughters, daughters may develop greater termite fishing proficiency than sons. This hypothesis is consistent with the observation that female's termite fishing techniques closely resemble their mothers' techniques, while male's techniques do not (Lonsdorf 2006). It is also consistent with the observation that both males and females employ simple nut-cracking behaviors with similar frequency. However females more

frequently master complicated nut cracking techniques than males, perhaps because mothers more frequently teach these techniques to daughters than sons. More research into both the individual-level mechanisms and population-level patterns of cultural transmission of these behaviors may resolve the question of whether mixed observational learning and teaching in a uniparental species can account for the sex bias in the proficiency of tool use in chimpanzees.

A more detailed analysis of chimpanzee tool use is perhaps the most promising avenue for investigating the uniparental teaching hypothesis. However the hypothesis may also apply to other organisms. For example, tool use in sea otters has also been reported to have a sex bias (Perry 2012; Mann and Patterson 2013), though there are conflicting reports (Fujii et al. 2014) and it is unclear whether tool use in otters is transmitted uniparentally (Fujii et al. 2014). Teaching has been increasingly described in nonhuman animals (Hoppitt et al. 2008), but whether taught behaviors are transmitted with a sex bias has not been investigated for most of them.

Coevolution of teaching and life history

The uniparental teaching hypothesis suggests that uniparental care, sex-biased cultural transmission and animal life history coevolve. This coevolution implies a different direction of evolutionary causation than is commonly hypothesized. For example, female dolphins take longer to wean than males (Gibson and Mann 2008). It has been proposed that daughters learn more than sons because of these longer weaning times. This explanation, however, begs the question of why dolphin life history evolved so that sons have shorter weaning times than daughters. The uniparental teaching hypothesis suggests that longer weaning may be at least partly the result of a mother's greater willingness to invest in her daughters' learning. In fact, it suggests that longer weaning times may be an important component of the higher teaching costs mothers pay for daughters than for sons.

In another example, female bottlenose dolphins tend to be more geographically constrained than males after weaning. One version of the disparate benefits hypothesis suggests that this difference in dispersal patterns is a cause of sex-biased transmission: Females preferentially learn niche-specific traits because they are more geographically constrained than males. However, the uniparental teaching hypothesis suggests that females are able to use smaller ranges because their mother teaches them niche-specific foraging techniques. Similarly, in another variation of the disparate benefits hypothesis, it is sometimes suggested the female chimpanzees put more effort into learning to crack nuts because they do not obtain as much protein through hunting as males. However, the uniparental teaching hypothesis suggests that hunting by male chimpanzees may have started as an adaptive response to not receiving adequate instruction in the art of cracking nuts, termite fishing, or other locally relevant foraging techniques.

The uniparental teaching hypothesis is presented above with a fairly simple stylized model. Its simplicity demonstrates that merely adding a teaching cost to uniparental cultural transmission can cause sex-biased transmission to evolve without more complicated assumptions about variations in local ecology or developmental complexity. More complex models incorporating these factors, as well as any trade-offs between multiple behaviors in both sexes, might help explain even more of the life history of a particular organism.

Evidence for teaching from population data

The existence of teaching, especially in nonhuman animals, is often controversial. Although some controversy is driven by semantic disagreement over what constitutes "teaching" (Kline 2015), even when there is semantic agreement, the standard criteria for identifying teaching relies on controlled experiments (Thornton and Raihani 2010) and many researchers do not accept its existence without such experiments (Galef 1992; Maestripieri and Whitham 2001).

The analysis in this article suggests that population-level patterns of cultural transmission may provide evidence for teaching, even when experiments and observation of the behavior are difficult or impossible. For example, population-level patterns of sponging behavior provide evidence for teaching in dolphins even though the individual instances of teaching might occur unobserved, deep in the inky shadows of Shark Bay. Individual cultural transmission is also difficult to observe in other species, but we still may be able to identify evidence for teaching if care is uniparental, if a cultural trait is rare in the population, and if the trait is more frequently or accurately transmitted from caregiving parent to offspring of the same sex. These population-level empirical patterns may give researchers interested in teaching behaviors an indication of where to focus individual-level empirical efforts.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

REFERENCES

Bacher K, Allen S, Lindholm AK, Bejder L, Krützen M. 2010. Genes or culture: are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.)? Behav Genet. 40:706–714.

Bender CE, Herzing DL, Bjorklund DF. 2009. Evidence of teaching in Atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. Anim Cogn. 12:43–53.

Boesch C. 1991. Teaching among wild chimpanzees. Anim Behav. 41:530–532.

Boesch C, Boesch H. 1981. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. J Hum Evol. 10:585–593.

Boesch C, Boesch H. 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. J Hum Evol. 13:415–440.

Boyd R, Richerson PJ. 1985. Culture and the evolutionary process. Chicago (IL): University of Chicago Press.

Byrne RW, Rapaport LG. 2011. What are we learning from teaching? Anim Behav. 82:1207–1211.

Caro TM, Hauser MD. 1992. Is there teaching in nonhuman animals? Q Rev Biol. 67:151–174.

Cavalli-Sforza LL, Feldman MW. 1983. Paradox of the evolution of communication and of social interactivity. Proc Natl Acad Sci USA. 80:2017–2021.

Enquist M, Strimling P, Eriksson K, Laland K, Sjostrand J. 2010. One cultural parent makes no culture. Anim Behav. 79:1353–1362.

Fogarty L, Strimling P, Laland KN. 2011. The evolution of teaching. Evolution. 65:2760–2770.

Fujii JA, Ralls K, Tinker MT. 2014. Ecological drivers of variation in tool-use frequency across sea otter populations. Behav Ecol. 26:519–526.

Galef BG. 1992. The question of animal culture. Hum Nat. 3:157–178.

Galef BG. 2001. Where's the beef? Evidence of culture, imitation, and teaching, in cetaceans? Behav Brain Sci. 24:335–335.

Gibson QA, Mann J. 2008. Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. Anim Behav. 76:375–387.

Guinet C. 1991. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). Can J Zool. 69:2712–2716.

Guinet C, Bouvier J. 1995. Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. Can J Zool. 73:27–33.

Haldane JBS. 1962. Conditions for stable polymorphism at an autosomal locus. Nature. 193:1108.

Herman LM, Pack AA. 2001. Laboratory evidence for cultural transmission mechanisms. Behav Brain Sci. 24:335–337.

Hoppitt WJ, Brown GR, Kendal R, Rendell L, Thornton A, Webster MM, Laland KN. 2008. Lessons from animal teaching. Trends Ecol Evol. 23:486–493.

Kline MA. 2015. How to learn about teaching: an evolutionary framework for the study of teaching behavior in humans and other animals. Behav Brain Sci. 38:e31.

Kopps AM, Sherwin WB. 2012. Modelling the emergence and stability of a vertically transmitted cultural trait in bottlenose dolphins. Anim Behav. 84:1347–1362.

Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB. 2005. Cultural transmission of tool use in bottlenose dolphins. Proc Natl Acad Sci USA. 102:8939–8943.

Kuczaj S. 2001. Cetacean culture: slippery when wet. Behav Brain Sci. 24:340–341.

Lonsdorf EV. 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Anim Cogn. 9:36–46.

Lonsdorf EV. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. Anim Behav. 70:673–683.

Lonsdorf EV, Eberly LE, Pusey AE. 2004. Sex differences in learning in chimpanzees. Nature. 428:715–716.

Maestripieri D, Whitham J. 2001. Teaching in marine mammals? Anecdotes versus science. Behav Brain Sci. 24:342–343.

Mann J. 2001. Cetacean culture: definitions and evidence. Behav Brain Sci. 24:343–343.

Mann J, Patterson EM. 2013. Tool use by aquatic animals. Philos Trans R Soc Lond B Biol Sci. 368:20120424.

Mann J, Sargeant BL. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In: Fragaszy DM, Perry S, editors. The biology of traditions: models and evidence. Cambridge (UK): Cambridge University Press. p. 236–266.

Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, Patterson E. 2008. Why do dolphins carry sponges? PLoS One. 3:e3868.

Mann J, Stanton MA, Patterson EM, Bienenstock EJ, Singh LO. 2012. Social networks reveal cultural behaviour in tool-using dolphins. Nat Commun. 3:980.

Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G. 2001. Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T, editor. Primate origins of human cognition and behavior. 1st ed. Hong Kong: Springer. p. 557–574.

Mitchell RW. 2001. On not drawing the line about culture: inconsistencies in interpretation of nonhuman cultures. Behav Brain Sci. 24:348–349.

Patterson EM, Krzyszczyk E, Mann J. 2015. Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. Behav Ecol. doi: 10.1093/beheco/arv164.

Patterson EM, Mann J. 2011. The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (*Tursiops* sp.). PLoS One. 6:e22243.

Perry JA. 2012. Variation in the frequency of tool use across and within sea otter (*Enhydra lutris*) populations [dissertation]. [Santa Cruz (CA)]: University of California.

Premack D, Hauser MD. 2001. A whale of a tale: calling it culture doesn't help. Behav Brain Sci. 24:350–351.

Rapaport LG, Byrne RW. 2012. Reply to Thornton & McAuliffe 2012. Anim Behav. 84:e1–e3.

Rendell L, Whitehead H. 2001. Culture in whales and dolphins. Behav Brain Sci. 24:309–324; discussion 324.

Richerson PJ, Boyd R. 2005. Not by genes alone. Chicago (IL): University of Chicago Press.

Smolker R, Richards A, Connor R, Mann J, Berggren P. 1997. Sponge carrying by dolphins (*Delphinidae, Tursiops* sp.): a foraging specialization involving tool use? Ethology. 103:454–465.

Thornton A, McAuliffe K. 2012. Teaching can teach us a lot. Anim Behav. 83:e6–e9.

Thornton A, Raihani NJ. 2008. The evolution of teaching. Anim Behav. 75:1823–1836.

Thornton A, Raihani NJ. 2010. Identifying teaching in wild animals. Learn Behav. 38:297–309.