Developmental evidence for foraging traditions in wild bottlenose dolphins

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Patterns of social learning in bottlenose dolphins (*Tursiops* spp.) may help explain behavioural variants and selection pressures favouring cultural evolution, but evidence for social transmission derived from field observations is controversial. The dolphins of Shark Bay, Australia are known for diverse, individually specific foraging behaviours, including tool use with marine sponges. We examined the relative contributions of habitat, maternal foraging and foraging behaviours of associates to the use of seven foraging tactics by bottlenose dolphin calves (*Tursiops* sp.). Three tactics were predicted by maternal foraging, one was predicted by water depth, one was weakly predicted by several factors, and two tactics were not predicted by any variable. Our findings provide support for the social learning of foraging behaviours in wild dolphins, illustrate the diverse pathways of foraging development, and offer insight into conditions that are likely to favour reliance on social information The evidence for vertical social learning (mother-to-offspring) indicates the dominance of a 'do what mother does' strategy, rather than copying the foraging behaviour of associates. However, since not all foraging behaviours were predicted by whether a calf's mother used them, dolphins may only use social information in some contexts, perhaps for more difficult tactics. This study provides unprecedented support for socially learned foraging tactics in wild dolphins by simultaneously addressing multiple factors during behavioural development, and thus illustrates the benefits of using multivariable techniques on ontogenetic data to identify social learning in wild animals.

Researchers have long sought to understand the origins of complex cognition and culture, and their implications for adaptation. Bottlenose dolphins demonstrate complex cognitive abilities in laboratory settings (Marino et al. 2007) and show behavioural variation both between and within populations, which may be socially learned or 'cultural' (e.g. Rendell & Whitehead 2001; Mann & Sargeant 2003; Krützen et al. 2005). Dolphins are also candidates for 'complex culture' because they may transmit multiple foraging behaviours via social learning (Whiten & van Schaik 2007). However, foraging variation may also be explained by habitat heterogeneity (Laland & Janik 2006; Sargeant et al. 2007), and no study to date has explicitly addressed multiple causal factors in dolphin foraging development. Thus, despite expectations derived from captive studies and ethnographic patterns, evidence for social learning and cultural patterns in wild dolphins has been controversial.

Social learning, or learning from observation of or interaction with others or their products (Heyes 1994), allows animals to match the demands of their environments quickly (Galef &

Giraldeau 2001; Laland 2004), and is considered to be a critical underpinning of complex cognition, behavioural flexibility and individual differences (e.g. Estes et al. 2003; Whiten & van Schaik 2007). Social learning is also considered the most basic requisite for 'culture' in animals (Laland & Hoppitt 2003). Despite demonstrations of social learning capabilities in diverse taxa (e.g. Palameta & Lefebvre 1985; Galef 1996; Laland & Williams 1997; Whiten et al. 2005) and theoretical expectations that it is highly adaptive under certain conditions (e.g. Laland 2004; Whitehead 2007), few field studies provide strong evidence for social learning in wild populations (Laland & Janik 2006). Most studies have failed to examine closely the ecological and genetic explanations for a behaviour before excluding them in favour of cultural ones, and attempting to identify a single causal factor fails to address behaviours with multiple and/or interacting causes, or intrapopulation variation (Fragaszy & Perry 2003; Laland & Janik 2006).

In our long-term study of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, over 13 different foraging tactics have been observed (Mann & Sargeant 2003; see Table 1 for tactics addressed in the current study). Social learning probably contributes to the development of some tactics that show similarity between mothers and calves (Mann & Sargeant 2003; Sargeant et al. 2005) and/or high matrilineal relatedness at the genetic level

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Table 1
Foraging tactics used by wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay Western Australia

Tactic	Relative use*		Min age (months)†	Mother–Calf similarity‡	Ecological component?	Other comments	Source
	M	C					
Bottom grubbing Dolphin orients towards and pokes rostrum into sea grass or the sea floor, with the body positioned vertically	40 18	22 30	4.1	Yes§	Occurrence ↓ with depth, ↑ with sea grass, ↑ in cold season		Mann & Sargeant 2003; Sargeant et al. 2007
Leap and porpoise foraging Dolphin shows multidirectional surfacings and high leap or porpoise rate	36 11	18 17	6.1	No	Large fish schools	Usually occurs in large groups of dolphins	Mann & Sargeant 2003
Mill foraging Dolphin surfaces irregularly and changes directions on each surface, often with rapid surfaces	43 18	31 18	3.4	Yes			Mann & Sargeant 2003
Rooster-tail foraging Dolphin swims rapidly near the surface so that a sheet of water trails off the dorsal fin	19 12	8 13	7.2	Yes§			Mann & Sargeant 2003
Snacking Dolphin chases fish belly-up and traps fish at the surface of the water	38 4	65 58	2.8	Yes	Occurrence unrelated to depth, sea grass, season	First tactic observed in calves; declines with age	Mann & Smuts 1999; Mann & Sargeant 2003; Sargeant et al. 2007
Sponge carrying Dolphin carries a sponge on its rostrum during stereotyped tail-out dive/peduncle dive foraging	23 97	7 80	20.2	Yes	Occurrence ↑ with depth and presence of marine sponges	Significantly biased towards females; increased matrilineal and overall relatedness	Smolker et al. 1997; Mann & Sargeant 2003; Krützen et al. 2005; Mann et al. 2008
Tail-out/peduncle dive foraging Dolphin surfaces in discrete bouts with tail-out and/or peduncle dives at a rate of 0.3/min, remaining submerged 1–3 min	74 53	54 43	6.8	No	Occurrence ↑ with depth		Mann & Sargeant 2003; Sargeant et al. 2007

* Upper number is the percentage of total focal dolphins (observed 1990–2004) that used the tactic; lower number is the mean percentage of foraging time that the tactic was used (averaged over dolphins that used the tactic); M = mothers, C = calves.
† Minimum age at which the behaviour was first observed in focal dolphins.
‡ Associations between mother and calf foraging using all data (Mann & Sargeant 2003).
§ Similarity remained when maternal foraging was determined using the first year of each calf's focal data and calf foraging was determined using subsequent years (see Mann & Sargeant 2003).

(Krützen et al. 2005). Additionally, bottlenose dolphins possess characteristics thought to promote social learning (Coussi-Korbel & Fragaszy 1995; van Schaik et al. 1999), including social tolerance (Scott et al. 2005), coordination in time and space (Mann et al. 2000a), complex cognition (Marino et al. 2007) and motor imitation (Herman 2002). Vertical social learning (mothers to calves) is particularly likely because calves are exposed to maternal foraging for 3–8 years before weaning (Mann et al. 2000a), but begin capturing fish at 3–4 months of age, and, like their mothers, show diverse and individually distinctive foraging tactics (Mann & Sargeant 2003). However, several additional factors, including age, sex and habitat use, are also correlated with the use of specific tactics (Mann & Sargeant 2003; Sargeant et al. 2005, 2007; Mann et al. 2008; see Table 1). For example, sponge carrying, in which dolphins carry sponges over their beaks while foraging, is heavily biased towards females, developed by calves later than most other tactics, and used by dolphins that spend more time in deep water habitats where marine sponges are common (Mann & Sargeant 2003; Sargeant et al. 2007; Mann et al. 2008). The strength of the evidence that sponge carrying is socially learned has been fiercely contested (Krützen et al. 2005, 2007; Laland & Janik 2006, 2007), but no study has systematically controlled for multiple factors. Based on 14 years of longitudinal data on dolphin mothers and their calves, we used multiple regression to determine the extent to which social information and habitat use contributed to variation in the development of specific foraging tactics by dolphin calves. Our analysis provides statistically rigorous evidence for social transmission in wild dolphins and identifies social learning strategies (sensu Laland 2004) possibly shaped by conditions under which the use of social information is adaptive.

METHODS

Shark Bay, Western Australia (25°47'S, 113°43'E) is a shallow sea grass ecosystem, featuring a mosaic of sea grass banks and sand flats (<4 m), embayment plains (4–13 m) and deeper channels (>6 m). The wild bottlenose dolphins of Shark Bay have been the focus of a longitudinal research project based at Monkey Mia since 1984 (Connor et al. 2000). Individual dolphins were identified by their natural dorsal fin shapes and markings using a photographic identification catalogue. Sexes were determined by the presence of a dependent calf, views of the genital area, and/or DNA analyses (Smolker et al. 1992; Krützen et al. 2003).

Dolphin mothers and calves were observed from 1990 to 2004 during a longitudinal mother–calf study, using a focal animal follow protocol and standard behavioural sampling techniques (Altmann 1974; Mann 1999). Observations were typically made from 4–5 m dinghies equipped with 6–45 hp motors, positioned within 50 m of focal dolphins. During follows from 1990 to1996, activities (including foraging tactics) were recorded using predominant activity sampling for diving intervals in deep water or for 2.5 min intervals in shallow water (Mann 1999). During 1997–2004, activity data were collected using 1 min point samples. Foraging tactics were identified either in the field, or post hoc based on detailed descriptions (as in Mann & Sargeant 2003; Sargeant et al. 2007). The foraging tactics examined in this study are defined in Table 1. Because predominant activity sampling and point sampling yield virtually identical time budgets (Tyler 1979; Mann 1999), and all tactics occur in bouts long enough to be recorded by both methods, tactics were unlikely to have been missed as a result of the type of sampling method used.

For each calf, we used the group compositions recorded during focal follows to identify the number of their associates known to use each tactic. Bottlenose dolphins have a fission–fusion social structure, in which group membership is temporally and spatially

variable (Smolker et al. 1992; Connor et al. 2000). We recorded group composition every 5 min during 1990–1996 and every 1 min after 1996. Group membership was defined using a 10 m chain rule (i.e. all dolphins within 10 m of another group member were considered part of the group; Smolker et al. 1992). For every associate that was also a focal individual, we used focal data to determine whether that associate had ever used particular tactics except for sponge carrying. For sponge carrying, we consulted long-term data records to determine use because sponge carriers can be identified from survey methods because of their high degree of specialization (Mann et al. 2008).

We broadly quantified habitat use for each calf by the average water depth, where depth was recorded every 5 min during focal follows. Although this is a rough measure of habitat use, the study area can be categorized broadly as shallow sea grass banks and deeper areas with little sea grass (Heithaus & Dill 2002), and depth was important in predicting the occurrence of several foraging tactics in previous analyses (Sargeant et al. 2007). Because a previous cross-sectional transect-based study found that sponge carrying was strongly correlated with the presence of marine sponges and particular channel habitats (Sargeant et al. 2007), we also calculated for each calf the percentage of their sightings (each GPS position recorded during focal follows) in areas (transect zones) where sponge carrying was common in the previous study. Use of this variable in place of average depth in the sponge-carrying model resulted in the same final model as that obtained with water depth. We used these measures as proxies for the habitat used while foraging since they correspond to the time during which foraging was observed and they should be correlated with recorded foraging behaviours if such behaviours are indeed predicted by habitat type.

Seven of the foraging tactics observed in Shark Bay were analysed using logistic regression (one regression model per tactic). Other known tactics were not observed with enough frequency to include in the analysis or involved provisioning by humans. Although 47 dolphin mothers and 83 calves were observed from 1990 to 2004, we included only one calf per mother in these analyses to reduce potential effects of pseudoreplication. For observations of mothers with more than one calf, we selected calves of known sex that had adequate ecological data and the greatest observation time. Thus, the data set included 31 calves (17 females, 14 males) born to separate mothers, each observed 1–113 h (mean ± SE: 35 ± 4.98 h). We always included observation time as a covariate in the models to control for differences in observation effort between mother–calf pairs. We used penalized maximum likelihood logistic regression to examine the contributions of the following six metrics to the probability that a calf used a particular foraging tactic (one regression model per tactic): (1) sex (1 = female, 0 = male); (2) maternal foraging (whether or not the mother used the tactic, 1 = yes, 0 = no); (3) associate foraging (number of associates known to use the tactic); (4) calf habitat use (average depth); (5) the interaction of maternal foraging and calf habitat use; (6) the interaction of associate foraging and calf habitat use. Thus, our models were designed to determine whether calves' use of foraging tactics could have resulted from exposure to their mothers or to their associates. Power to detect effects of calf sex was probably low in some cases because of low replication, but we included it in initial full models because several behaviours are biased towards females (Mann & Sargeant 2003; Sargeant et al. 2005; Mann et al. 2008). We were unable to explicitly examine age-related effects because of low samples for a repeated measures approach and because calves were assessed over several years making a single age term inappropriate. However, most calves (27 of 31) were older than 30 months when observed, which is beyond the minimum age at which all foraging tactics addressed in this

study have been documented. Therefore, it is unlikely that social or ecological effects were undetected because calves were too young to engage in foraging tactics. Correlations between explanatory values were weak enough to allow independent evaluation in the regression (all Spearman correlations $|r| < 0.75$ except for one case where $|r| = 0.76$) (Meyers et al. 2006).

We used penalized maximum likelihood (PML) logistic regression based on Heinze & Schemper's (2002) Firth-based method because (1) it allows parameter estimation and generation of confidence intervals under conditions of complete separation (where explanatory variable(s) completely separate the response into yes or no), which was common in our data sets; and (2) it is appropriate for very small data sets in which the number of parameters is large relative to the sample size (Heinze & Schemper 2002; Heinze 2006). PML logistic regression was performed using SAS (SAS 9.1, SAS Institute, Inc., Cary, NC, U.S.A.) and the %fl macro (version 2006.09) developed by Heinze & Schemper (2002) (available at www.meduniwien.ac.at/msi/biometrie/programme/fl). Model selection was conducted using backward stepwise elimination using $\alpha = 0.15$, since use of low alphas on small data sets can lead to poor model performance (Steyerberg et al. 2000). When interactions did not contribute to the model ($P > 0.15$), they were removed first because of their correlations with main effects. Tests of significance of the final global model were conducted with penalized likelihood ratio tests. Profile penalized likelihood ratio confidence intervals and penalized likelihood ratio tests are reported for all parameter estimates. The percentage of cases correctly classified was calculated based on the predicted probability of a positive response for each observation; calves with a predicted probability of >0.5 were classified as being predicted to use the tactic. Plots of model-predicted values were used to illustrate effect sizes.

RESULTS

Table 2 shows, for each tactic, explanatory variables retained in multiple regression models following backward elimination model selection. Tests of model fit (penalized likelihood ratio test) and the odds ratio estimates and corresponding penalized likelihood ratio tests for each explanatory variable are also provided. The odds ratio can be interpreted as a measure of effect size and represents the increase in odds of a particular outcome with each unit increase in the explanatory variable when controlling for effects of the other explanatory variables. For example, the lower bound odds ratio of 5.59 for the effect of maternal foraging on calf sponge-carrying (Table 2) indicates that the odds that calves whose mothers do use sponge carrying will use it is 5.59 times the corresponding odds of calves whose mothers do not use sponge carrying.

The degree to which maternal foraging (whether or not the mother used the tactic), associate foraging (number of associates known to use the tactic) and habitat use (average water depth) predicted whether a calf used a given tactic varied among tactics examined (Table 2). Calf use of two tactics (tail-out/peduncle dive foraging and snacking) was not significantly related to any explanatory variable included in the model. These behaviours were extremely common in the population and showed relatively little individual variation relative to other tactics. Maternal use predicted calf use for three tactics (sponge carrying, mill foraging and rooster-tail foraging) (Table 2, Fig. 1). The model predicted that, at an average level of observation effort, nearly 80% of calves born to sponge-carrying mothers would develop the sponge carrying tactic (Fig. 1). Over 60% of calves born to mill-foraging mothers were predicted to develop that tactic (Fig. 1), while about 30% of calves were predicted to develop rooster-tail foraging if their mothers did (Fig. 1). For sponge carrying and rooster tailing, no calf showing the behaviour had a mother that had failed to do so, while one calf used mill foraging although its mother did not. However, the reverse was not true; not all calves whose mothers used these tactics also used them. Seventy-one per cent of calves born to sponge carriers used sponge carrying, 44% of calves born to rooster-tailing mothers used rooster tailing, and 68% of calves born to mill-foraging mothers used mill foraging. For sponge carrying, there are no known cases in the population in which calves, juveniles or adults adopted this tactic when their mother did not (Mann et al. 2008). Calf use of one tactic (bottom grubbing) was inversely related to their average water depth (Table 2, Fig. 2). According to model-predicted data, calves spending most of their time in shallow waters (≤ 4 m) are most likely to develop bottom grubbing. Additionally, there was a sharp decline with depth such that fewer than 20% of calves that spend most of their time in deep water (≥ 6 m) should develop bottom grubbing (Fig. 2). A final tactic, leap and porpoise feeding, was not strongly predicted by any variable, but showed a tendency to increase with maternal foraging, water depth and associate foraging (variables where $0.05 < P < 0.10$; Table 2).

Table 2
Final penalized maximum likelihood logistic regression models for foraging tactics

Tactic	No. of calves*	Global test†	Correct classifications‡	Explanatory variables	Odds ratio estimates§	Odds ratio tests
Bottom grubbing	11	$\chi^2_2=22.14$ $P<0.0001$	90%	Hours observed Water depth	1.02 (0.98–1.08) 0.17 (0.02–0.52)	$P=0.3486$ $P<0.0001$
Leap and porpoise feeding	7	$\chi^2_5=11.08$ $P=0.0499$	90%	Hours observed Water depth Maternal foraging Associate foraging Sex	1.00 (0.95–1.04) 2.00 (0.94–9.50) 7.88 (0.73–609.15) 1.33 (0.97–2.33) 5.73 (0.60–125.92)	$P=0.8589$ $P=0.0756$ $P=0.0963$ $P=0.0842$ $P=0.1362$
Mill foraging	14	$\chi^2_2=12.64$ $P=0.0018$	81%	Hours observed Maternal foraging	1.02 (0.99–1.07) 10.82 (1.83–114.20)	$P=0.1569$ $P=0.0075$
Rooster-tail foraging	4	$\chi^2_2=12.73$ $P=0.0017$	97%	Hours observed Maternal foraging	1.05 (1.00–1.27) 29.81 (2.07–39761.51)	$P=0.0634$ $P=0.0094$
Snacking	22	$\chi^2_1=13.98$ $P=0.0002$	84%	Hours observed	1.12 (1.04–1.28)	$P=0.0002$
Sponge carrying	5	$\chi^2_2=15.26$ $P=0.0005$	94%	Hours observed Maternal foraging	1.02 (0.92–1.15) 143.97 (5.59–13908460.00)	$P=0.5699$ $P=0.0006$
Tail-out/peduncle dive foraging	25	$\chi^2_1=2.87$ $P=0.0905$	81%	Hours observed	1.04 (0.96–1.11)	$P=0.0905$

* Number of calves that used the tactic of $N = 31$ in the data set.
† Penalized likelihood ratio tests (see Methods).
‡ Percentage of cases correctly classified based on predicted probability.
§ 95% confidence intervals of odds ratios in parentheses.
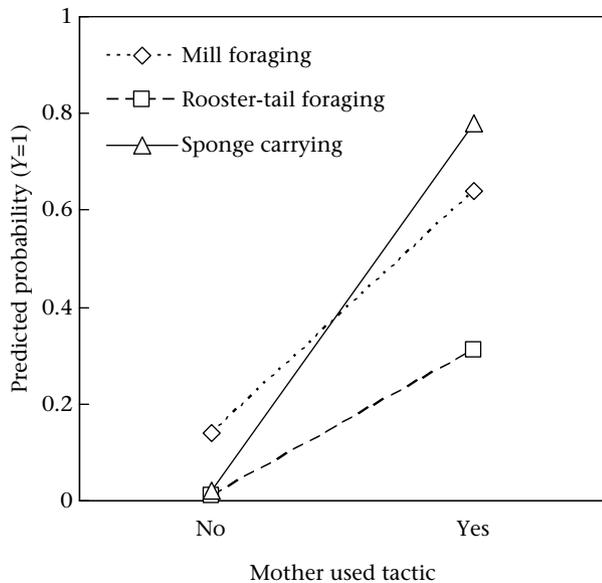
Figure 1. Model-predicted probability of a positive response (calf used a tactic, $Y = 1$) depending on whether or not their mother used the tactic, for sponge carrying, mill foraging and rooster-tail foraging, assuming an observation time of 34.8 h.

DISCUSSION

Although social learning is thought to contribute to foraging development in wild dolphins, this is the first study that provides evidence for social learning while statistically accounting for additional factors. Despite independent correlations between foraging, sex and habitat use evident in previous studies, we identified strong, robust patterns that remained even after incorporating multiple factors into a single model. Thus, our findings illustrate that invoking ecological or social explanations independently can be deeply flawed. Although this approach requires individual variation and may fail to identify instances of social learning for common behaviours, the use of multivariable models significantly advances the study of social learning in wild animals by providing a rigorous, conservative test. In addition, this study highlights the value of developmental data, which can provide critical evidence for social learning in wild populations (Lonsdorf et al. 2004; Thornton & McAuliffe 2006). Ethnographic methods and regression techniques applied to cross-sectional data may not detect relevant predictors if social or ecological conditions change following initial development. Finally, by identifying factors that
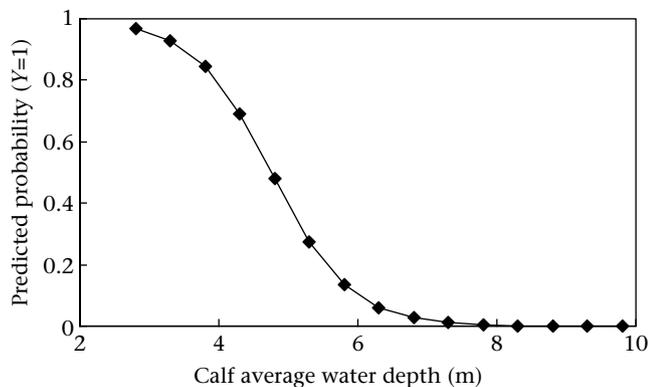
Figure 2. Model-predicted probability of a positive response (calf used bottom grubbing, $Y = 1$) depending on the calf's average water depth, assuming an observation time of 34.8 h.

explain variation in each of several tactics, we found novel support for the context-specific use of social information in dolphins.

For three tactics (sponge carrying, rooster-tail foraging and mill foraging), depth, associate foraging and sex did not explain variation in development by calves beyond what was explained by maternal foraging, strongly suggesting a role for social transmission. Foraging in this population involves a lengthy developmental period, including 'practise' foraging (Mann & Smuts 1999; Mann & Sargeant 2003), and all 11 adult females that we have observed for more than a decade have used the same tactics that they developed as calves. This suggests that patterns of similarity are long-lasting and not the result of opportunistic behaviours linked temporally and/or spatially, or social facilitation. Thus, these behaviours appear to meet the definition of 'traditions', 'enduring behaviour patterns shared among members of a group that depend to a measurable degree on social contributions to individual learning, resulting in shared practices among members of a group' (Fragaszy & Perry 2003).

Compared to vertical social learning (mother to offspring), horizontal (learning from conspecifics of all ages) and oblique (learning from older nonparents) social learning do not appear to contribute substantially to early development of the foraging tactics in this population that we examined in this study. Only one behaviour, leap and porpoise feeding, showed a possible (although statistically nonsignificant) relationship with associate foraging. Dolphins occasionally travel several kilometres to join these foraging groups, possibly as a result of local enhancement if dolphins receive long-distance visual or acoustic information from foraging conspecifics. Although we measured whether associates were known to use each tactic, and did not directly measure calves' opportunities to observe associates foraging, undetected effects of horizontal transmission were relatively unlikely because exposure to foraging by nonmothers is low (approximately 4% of calf time budgets, Mann et al. 2007).

Matrilineal transmission in this population appears to be a case of 'directed' social learning, in which social learning occurs differentially as a function of demonstrator identity (Coussi-Korbel & Fragaszy 1995). Directed social learning is likely to create within-group differences in behaviour (Coussi-Korbel & Fragaszy 1995), such as those observed in Shark Bay. Learning from mothers is more likely simply because of the substantial amount of time that mothers and dependent calves spend together, but it could also be most adaptive. Environmental similarity is thought to promote social learning (Laland & Kendal 2003; Whitehead 2007), and female offspring are incorporated into their mother's social network after weaning (e.g. Smolker et al. 1992) and appear to have similar patterns of habitat use. Low reliance on horizontal learning may explain why in some cases dolphins do not adopt foraging tactics shown by others nearby (e.g. sponge carriers are occasionally in groups with non-sponge-carriers, Mann et al. 2008). Selectively learning from kin or familiar conspecifics may be a successful strategy for acquiring information (Laland 2004), but this hypothesis has so far found mixed experimental support in other species (Swaney et al. 2001; Galef & Whiskin 2008; Schwab et al. 2008a, b). Vertical transmission patterns may be relatively common in cetaceans with matrilineal social groups showing distinctive patterns of habitat use and/or vocal dialects (e.g. Mann et al. 2000b; Whitehead & Rendell 2004; Hauser et al. 2007). However, insofar as context-dependent learning strategies generate intrapopulation differences, the extent to which individual dolphins socially learn multiple behaviours characteristic of 'complex cultures' (sensu Whiten & van Schaik 2007) remains unclear.

Several tactics did not show evidence of social transmission. Final models for snacking and tail-out/peduncle dive foraging did not include any of the predictor variables. These tactics are

extremely common in the population, and occur at other locations (e.g. Leatherwood 1975; Nowacek 2002), suggesting no obvious social learning requirement. Snacking is the first behaviour developed by calves and declines with age (Mann & Sargeant 2003), indicating that it may be an easy but relatively inefficient tactic. Alternatively, social learning may be involved in the development of these tactics but was undetected because of insufficient individual variation. Bottom grubbing occurs in shallow sea grass flats (Sargeant et al. 2007), and the current analysis shows that variation in habitat use helps explain variation in its development. Hence, ecological heterogeneity must be addressed before social learning can be invoked as the explanation for behavioural variation. Because some behaviours appear to involve social learning while others do not, our findings suggest that dolphin calves may be selective in their use of, or do not require, socially provided information for some behaviours. Theoretical models predict that costly skills should be most likely to be learned socially (Laland & Kendal 2003), and dolphin foraging behaviours for which social learning has been implicated may be more physically complex. For example, sponge carrying may be especially demanding given that dolphins must locate appropriate sponges, tear them loose, wear them while hunting, and remove them before catching prey. A tactic not addressed in this study, beach hunting, shows similar patterns (mother–calf similarity, lengthy development) and appears to involve sophisticated motor skills and the risk of becoming stranded on the beach (Sargeant et al. 2005).

We emphasize that while our analyses identify factors with strong net effects on calf foraging development, there were some limitations. Some effects may have been undetected because of low power, or low variation in tactic use. For example, even though maternal use is the overwhelming influence on the development of sponge carrying, a marked sex difference is clear when additional data are considered (Mann & Sargeant 2003; Mann et al. 2008). Sex was not significant in the current analysis because only one male calf born to a sponge carrier was included in this data set. In addition, these analyses aim to explain variation in foraging development, but additional factors may also be essential for development to occur. For example, availability of sponges and appropriate habitat are clearly required for sponge carrying, but variation in habitat use is apparently insufficient to explain why only some calves develop it. Finally, it has been suggested that genetic transmission may explain behavioural variation in the absence of social learning (Laland & Janik 2006). One strategy for addressing genetic contribution would be to add relatedness to our regression models. However, in our data set, where relatedness and association tightly covary, social learning would generate correlations between relatedness and behavioural similarity even in the absence of genetic determinism (see also Krützen et al. 2005). Although we cannot rule out genetic or physiological mechanisms underlying variation in foraging tactics, several lines of evidence point to social rather than exclusively genetic mechanisms. Because tactics such as sponge carrying do not develop in calves with non-sponge-carrying mothers, genetic variation alone is unlikely to cause variation in the behaviour since there is no evidence for assortative mating by tactic (Krützen et al. 2005; but see Laland & Janik 2006). Bottlenose dolphins are also well known for their plasticity and cognitive ability in laboratory settings (e.g. Herman 2002), which should enable them to learn a wide range of behaviours in the wild.

Few studies have explicitly quantified ecological and social contributions to behavioural diversity, and context-specific patterns under which socially provided information is learned have only recently been explored. Using long-term observations of calf foraging development, we found support for multigenerational foraging traditions in wild dolphins. Our findings also suggest that calves may learn easy foraging tactics without social input (e.g. snacking) and rely on social learning from mothers when individually learning a foraging tactic is difficult (e.g. sponge carrying). Together, these patterns of foraging development may reflect 'when' and 'who' strategies of social learning (Laland 2004), explaining the mixture of individually and socially learned foraging tactics used by individuals and providing the framework for the functional benefits of social learning. Since the origins of behavioural diversity in natural populations have implications for conservation, community ecology and evolution of brain size, cognitive abilities and interspecific differences (Reader & Laland 2002; Bolnick et al. 2003; Whitehead et al. 2004), greater appreciation of the roles and contexts of social learning in shaping behavioural diversity is needed. Multivariable analyses of developmental data offer a path forward in accounting for multiple drivers of behavioural diversity and identifying social learning patterns in wild animals.

Acknowledgments

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267, doi:10.1163/156853974X00534.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, **161**, 1–28, doi:10.1086/343878.

Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 91–126. Chicago: University of Chicago Press.

Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**, 1441–1453, doi:10.1016/0003-3472(95)80001-8.

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T. & Lyon, B. E. 2003. Individual variation in prey selection by sea otters: patterns, causes, and implications. *Journal of Animal Ecology*, **72**, 144–155, doi:10.1046/j.1365-2656.2003.00690.x.

Fragaszy, D. M. & Perry, S. 2003. Towards a biology of traditions. In: *The Biology of Traditions: Models and Evidence* (Ed. by D. M. Fragaszy & S. Perry), pp. 1–32. Cambridge: Cambridge University Press.

Galef Jr, B. G. 1996. Social enhancement of food preferences in Norway rats: a review. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B.G. Galef Jr), pp. 49–64. San Diego: Academic Press.

Galef Jr, B. G. & Giraldeau, L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3–15, doi:10.1006/anbe.2000.1557.

Galef, B. G. & Whiskin, E. E. 2008. Effectiveness of familiar kin and unfamiliar nonkin demonstrator rats in altering food choices of their observers. *Animal Behaviour*, **76**, 1381–1388, doi:10.1016/j.anbehav.2008.07.004.

Hauser, D. D. W., Logsdon, M. G., Holmes, E. E., VanBlaricom, G. R. & Osborne, R. W. 2007. Summer distribution patterns of southern resident killer

whales *Orcinus orca*: core areas and spatial segregation of social groups. *Marine Ecology Progress Series*, **351**, 301–310, doi:10.3354/meps07117.

Heinze, G. 2006. A comparative investigation of methods for logistic regression with separated or nearly separated data. *Statistics in Medicine*, **25**, 4216–4226, doi:10.1002/sim.2687.

Heinze, G. & Schemper, M. 2002. A solution to the problem of separation in logistic regression. *Statistics in Medicine*, **21**, 2409–2419, doi:10.1002/sim.1047.

Heithaus, M. R. & Dill, L. M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**, 480–491, doi:10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2.

Herman, L. M. 2002. Vocal, social, and self-imitation by bottlenose dolphins. In: *Imitation in Animals and Artifacts* (Ed. by K. Dautenhahn & C. L. Nehaniv), pp. 63–108. Cambridge: Massachusetts Institute of Technology.

Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–231, doi:10.1111/j.1469-185X.1994.tb01506.x.

Krützen, M., Sherwin, W. B., Connor, R. C., Barre, L. M., Van de Casteele, T., Mann, J. & Brooks, R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proceedings of the Royal Society B*, **270**, 497–502, doi:10.1098/rspb.2002.2229.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 8939–8943, doi:10.1073/pnas.0500232102.

Krützen, M., van Schaik, C. & Whiten, A. 2007. The animal cultures debate: response to Laland and Janik. *Trends in Ecology & Evolution*, **22**, 6, doi:10.1016/j.tree.2006.10.011.

Laland, K. N. 2004. Social learning strategies. *Learning & Behavior*, **32**, 4–14.

Laland, K. N. & Hoppitt, W. 2003. Do animals have culture? *Evolutionary Anthropology*, **12**, 150–159, doi:10.1002/evan.10111.

Laland, K. N. & Janik, V. M. 2006. The animal cultures debate. *Trends in Ecology & Evolution*, **21**, 542–547, doi:10.1016/j.tree.2006.06.005.

Laland, K. N. & Janik, V. M. 2007. Response to Krützen et al.: further problems with the 'method of exclusion'. *Trends in Ecology & Evolution*, **22**, 7, doi:10.1016/j.tree.2006.10.010.

Laland, K. N. & Kendal, J. R. 2003. What the models say about social learning. In: *The Biology of Traditions: Models and Evidence* (Ed. by D. M. Fragaszy & S. Perry), pp. 33–55. Cambridge: Cambridge University Press.

Laland, K. N. & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, **53**, 1161–1169, doi:10.1006/anbe.1996.0318.

Leatherwood, S. 1975. Some observations of feeding behavior of bottlenose dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. *Marine Fisheries Review*, **37**, 10–16.

Lonsdorf, E. V., Eberly, L. E. & Pusey, A. E. 2004. Sex differences in learning in chimpanzees. *Nature*, **428**, 715–716, doi:10.1038/428715a.

Mann, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science*, **15**, 102–122, doi:10.1111/j.1748-7692.1999.tb00784.x.

Mann, J. & Sargeant, B. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In: *The Biology of Traditions: Models and Evidence* (Ed. by D. M. Fragaszy & S. Perry), pp. 236–266. Cambridge: Cambridge University Press.

Mann, J. & Smuts, B. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, **136**, 529–566, doi:10.1163/156853999501469.

Mann, J., Connor, R. C., Barre, L. M. & Heithaus, M. R. 2000a. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, **11**, 210–219.

Mann, J., Connor, R. C., Tyack, P. L. & Whitehead, H. (Eds). 2000b. *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press.

Mann, J., Sargeant, B. L. & Minor, M. 2007. Calf inspections of fish catches in bottlenose dolphins (*Tursiops* sp.): evidence for oblique social learning? *Marine Mammal Science*, **23**, 197–202, doi:10.1111/j.1748-7692.2006.00087.x.

Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C. & Patterson, E. 2008. Why do dolphins carry sponges? *PLoS One*, **3**, e3868, doi:10.1371/journal.pone.0003868.

Marino, L., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., Lusseau, D., McCowan, B., Nimchinsky, E. A., Pack, A. A., Rendell, L., Reidenberg, J. S., Reiss, D., Uhen, M. D., Van der Gucht, E. & Whitehead, H. 2007. Cetaceans have complex brains for complex cognition. *PLoS Biology*, **5**, 966–972, doi:10.1371/journal.pbio.0050139.

Meyers, L. S., Gamst, G. & Guarino, A. J. 2006. *Applied Multivariate Research: Design and Interpretation*. Thousand Oaks, California: Sage.

Nowacek, D. P. 2002. Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, FL. *Behaviour*, **139**, 1125–1145, doi:10.1163/15685390260437290.

Palameta, B. & Lefebvre, L. 1985. The social transmission of a food-finding technique in pigeons: what is learned? *Animal Behaviour*, **33**, 892–896, doi:10.1016/S0003-3472(85)80023-3.

Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 4436–4441, doi:10.1073/pnas.062041299.

Rendell, L. & Whitehead, H. 2001. Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**, 309–382, doi:10.1017/S0140525X0100396X.

Sargeant, B. L., Mann, J., Berggren, P. & Krützen, M. 2005. Specialization and development of beach hunting, a rare foraging behavior, by wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, **83**, 1400–1410, doi:10.1139/z05-136.

Sargeant, B. L., Wirsing, A. J., Heithaus, M. R. & Mann, J. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behavioral Ecology and Sociobiology*, **61**, 679–688, doi:10.1007/s00265-006-0296-8.

van Schaik, C. P., Deaner, R. O. & Merrill, M. Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, **36**, 719–741, doi:10.1006/jhev.1999.0304.

Schwab, C., Bugnyar, T. & Kotrschal, K. 2008a. Preferential learning from non-affiliated individuals in jackdaws (*Corvus monedula*). *Behavioural Processes*, **79**, 148–155, doi:10.1016/j.beproc.2008.07.002.

Schwab, C., Bugnyar, T., Schloegl, C. & Kotrschal, K. 2008b. Enhanced social learning between siblings in common ravens, *Corvus corax*. *Animal Behaviour*, **75**, 501–508, doi:10.1016/j.anbehav.2007.06.006.

Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L. & Connor, R. C. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male–male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, **142**, 21–44, doi:10.1163/1568539053627712.

Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123**, 38–69, doi:10.1163/156853992X00101.

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.

Steyerberg, E. W., Eijkemans, M. J. C., Harrell Jr, F. E. & Habbema, J. D. F. 2000. Prognostic modelling with logistic regression analysis: a comparison of selection and estimation methods in small data sets. *Statistics in Medicine*, **19**, 1059–1079.

Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, **62**, 591–598, doi:10.1006/anbe.2001.1788.

Thornton, A. & McAuliffe, K. 2006. Teaching in wild meerkats. *Science*, **313**, 227–229, doi:10.1126/science.1128727.

Tyler, S. 1979. Time sampling: a matter of convention. *Animal Behaviour*, **27**, 801–810.

Whitehead, H. 2007. Learning, climate and the evolution of cultural capacity. *Journal of Theoretical Biology*, **245**, 341–350, doi:10.1016/j.jtbi.2006.10.001.

Whitehead, H. & Rendell, L. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, **73**, 190–196, doi:10.1111/j.1365-2656.2004.00798.x.

Whitehead, H., Rendell, L., Osborne, R. W. & Würsig, B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation*, **120**, 427–437, doi:10.1016/j.biocon.2004.03.017.

Whiten, A. & van Schaik, C. P. 2007. The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B*, **362**, 603–620, doi:10.1098/rstb.2006.1998.

Whiten, A., Horner, V. & de Waal, F. B. M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*, **437**, 737–740, doi:10.1038/nature04047.