

Investigating the impact of observation errors on the statistical performance of network-based diffusion analysis

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Experiments in captivity have provided evidence for social learning, but it remains challenging to demonstrate social learning in the wild. Recently, we developed network-based diffusion analysis (NBDA; 2009) as a new approach to inferring social learning from observational data. NBDA fits alternative models of asocial and social learning to the diffusion of a behavior through time, where the potential for social learning is related to a social network. Here, we investigate the performance of NBDA in relation to variation in group size, network heterogeneity, observer sampling errors, and duration of trait diffusion. We find that observation errors, when severe enough, can lead to increased Type I error rates in detecting social learning. However, elevated Type I error rates can be prevented by coding the observed times of trait acquisition into larger time units. Collectively, our results provide further guidance to applying NBDA and demonstrate that the method is more robust to sampling error than initially expected. Supplemental materials for this article may be downloaded from <http://lb.psychonomic-journals.org/content/supplemental>.

In many animal species, individuals learn socially by observing the behavior of other individuals. Sophisticated experiments on captive animals have identified different learning mechanisms in animals (Galef & Giraldeau, 2001; Hoppitt & Laland, 2008), but inferring the existence of social learning in wild animals remains an important and challenging task. Abandonment of the highly controlled experimental settings of captive studies is necessary for investigating how social and ecological conditions in wild animals affect social learning dynamics and the emergence of traditions and, more generally, for understanding the evolution of social learning and culture. However, the lack of experimental control also introduces new methodological problems. Important methods of inferring social learning in wild animals, such as the *ethnographic method* (Perry & Manson, 2003; Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999) and diffusion curve analysis (Reader, 2004), can have low statistical power to detect social learning and can produce a high rate of false positives (Franz & Nunn, 2009; Galef, 2004; Laland & Galef, 2009; Laland & Hoppitt, 2003; Laland & Janik, 2006; Laland & Kendal, 2003; Reader, 2004). Thus, new methods are needed for investigating social learning.

Recently, we developed network-based diffusion analysis (NBDA; Franz & Nunn, 2009) to overcome the limita-

tions of previous approaches. NBDA makes the reasonable assumption that social learning is more likely to take place among conspecifics that are relatively more closely linked in a social network (Coussi-Korbel & Frigaszy, 1995). In the case of a food processing technique that is transmitted socially, for example, we can expect food-related behaviors to spread most quickly among individuals that often feed together and, thus, have strong connections in a co-feeding network (for an example, see Figure 1). In the case of social learning—but *not* in asocial learning—we expect the structure of a social network (i.e., the strength of connections among individuals) to influence how a novel behavior spreads through a group of animals. NBDA aims to identify whether such an influence occurs in the observed diffusion of a novel behavior. For this purpose, alternative agent-based models (ABMs) of social and asocial learning are fitted to the observed diffusion of a novel behavior. These models provide a way to estimate the probabilities with which each individual learns through social or asocial learning during the different stages of a diffusion. By comparing these probabilities to the actual learning events, one can assess which learning mechanism was most likely to have caused the observed diffusion.

The statistical analysis of NBDA is based on maximum likelihood model fitting. The original NBDA version de-

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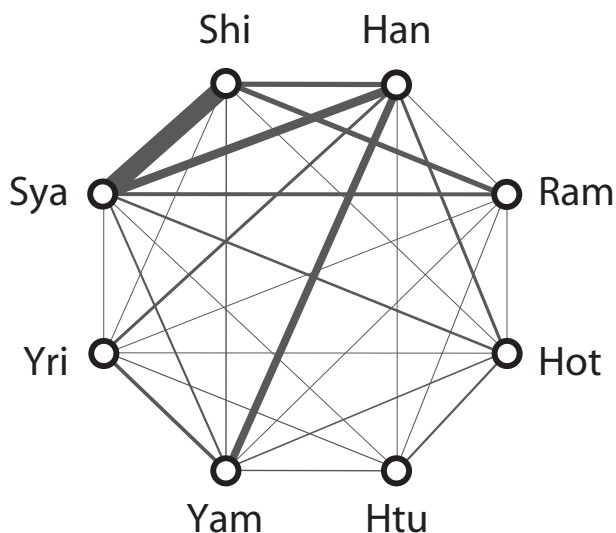


Figure 1. Schematic representation of a cofeeding network of 8 Japanese macaques (see Ventura, Majolo, Koyama, Hardie, & Schino, 2006). Circles represent individuals, and lines indicate social connections between individuals. Line widths are proportional to time spent feeding together in close proximity.

veloped by Franz and Nunn (2009) is based on two alternative models: (1) *pure asocial learning*, in which each individual acquires the new behavior independently of others, and (2) *pure social learning*, in which each individual (except the “inventor”) acquires the new behavior by social learning. In the asocial learning model, learning is assumed to occur with a constant probability in each time step. In the social learning model, the probability of learning from other group members is assumed to be determined by the strength of the connections to others in the social network. Thus, the likelihood that an individual follows another in the diffusion of the novel behavior is dependent on the strength of its relationship to the knowledgeable individual. The identification of the best fitting model is based on the Akaike information criterion (Burnham & Anderson, 2002).

NBDA thus uses a flexible statistical framework that compares the fit of different a priori models (Bolker, 2008; Burnham & Anderson, 2002). This flexibility is important because it provides a powerful platform for investigating more complex learning processes than those included in the simple NBDA version of Franz and Nunn (2009). Thus, different versions have been developed that include mixed learning models with both social and asocial learning (Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010; Hoppitt, Kandler, Kendal, & Laland, 2010)—models in which individual specific variables, such as dominance rank or neophobia, can influence asocial learning dynamics (Hoppitt, Boogert, & Laland, 2010)—and models that include task structure, such as learned behaviors that consist of multiple steps (Hoppitt, Kandler, et al., 2010).

In addition, Hoppitt, Boogert, and Laland (2010) developed a variation of NBDA in which model fitting only focuses on the order, rather than the actual timing, in which

individuals acquired the new behavior. They referred to this method as *order-of-acquisition diffusion analysis* (OADA), and to methods that use explicit information on the timing of events as *time-of-acquisition diffusion analysis* (TADA). Included under TADA is the original method of Franz and Nunn (2009) and extended versions developed by Hoppitt, Boogert, and Laland. Focusing on the order of diffusion and ignoring the exact timing of learning events is a fundamental difference from the NBDA method developed by Franz and Nunn. However, OADA is also a network-based method that analyses diffusion dynamics by fitting alternative models of social and asocial learning (in which social learning depends on network structure). Therefore, Hoppitt, Boogert, and Laland proposed using *NBDA* as an umbrella term for network-based analyses of trait diffusion. In the following, we adopt this classification of NBDA methods and, therefore, also refer to the methods developed by Franz and Nunn as *TADA*.

Basic analysis of NBDA performance has revealed that the power to detect social learning increases with increasing group size (Franz & Nunn, 2009; Hoppitt, Kandler, et al., 2010) and length of diffusion (Hoppitt, Boogert, & Laland, 2010). Heterogeneity in weights of network edges seems to have a stronger impact on the performance of OADA than on that of TADA (Hoppitt, Boogert, & Laland, 2010). Furthermore, Hoppitt, Boogert, and Laland showed that violating assumptions of specific NBDA implementations, such as ignoring effects of individual-level variables (e.g., dominance rank) on asocial learning, can lead to decreased power to detect social learning and increased Type I error rates.

These analyses give a first impression of the factors that impact the probability of correctly or erroneously inferring social learning using NBDA. To effectively apply NBDA methods, however, we need a richer understanding of how basic factors, such as group size and network features, influence statistical performance, including interactions among the factors. Furthermore, we have very limited knowledge about the effects of observation errors on the statistical performance of NBDA. Observation errors can potentially increase Type I error rates and decrease power, resulting in Type II errors. Trait diffusion in wild animals is rarely (if ever) known with absolute certainty, especially when the trait is performed rarely and when observations do not cover the entire activity period of the group. Investigating the effects of observation errors is, thus, of particular importance for applying NBDA methods to wild animals, for which unfettered observations of each individual across a given time period are typically impossible.

In the present study, we addressed these problems by significantly extending our previous analyses of the TADA method, which Franz and Nunn (2009) referred to as *extended NBDA*. This method fits a pure asocial learning model and a mixed learning model with both social and asocial learning. Specifically, we investigated the effects of group size, network heterogeneity, duration of trait diffusion, and sampling errors on times of trait acquisition

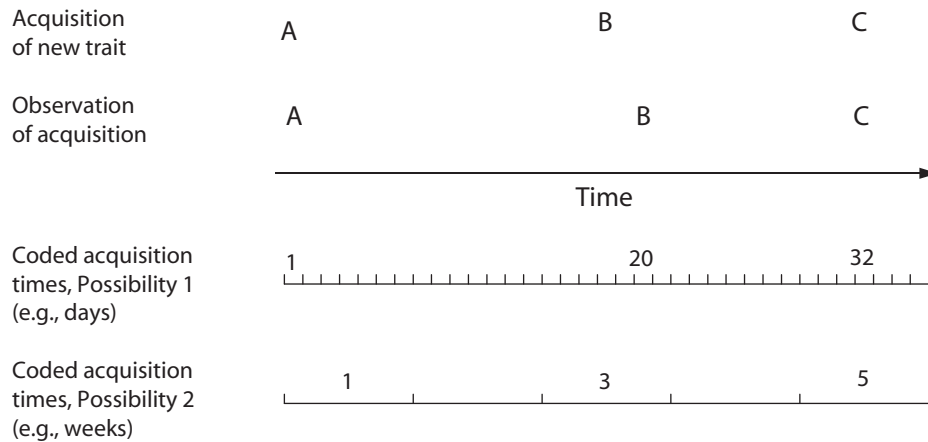


Figure 2. Example that illustrates observation errors and coding of diffusion times. The positions of A, B, and C mark times when 3 different individuals acquired a new trait and when an observer first recorded the new trait in each of these individuals. In addition, two possible ways of coding these data into discrete time steps of different lengths are shown. To illustrate how *length of coded time step* and *diffusion duration* are calculated in our analysis, we can assume that the depicted learning dynamics were simulated with a model in which one time step represents 1 day. The length of coded time steps in Possibility 1 would then be 1, and in Possibility 2 it would be 7. The diffusion duration using Possibility 1 would be 32, and using Possibility 2 it would be 5.

for each individual. We also investigated whether recoding these observations into discrete time steps (Figure 2) could offset negative effects of sampling errors. To systematically investigate these effects, we simulated artificial diffusion data and the observation and coding of these data using extensions of the ABMs described by Franz and Nunn. To simulate errors in observing trait diffusion and the analysis of diffusion data (including different coding schemes for diffusion times), we implemented a virtual observer and a virtual analyst.

METHOD

One part of our analysis focuses on assessing Type I error rates—that is, the probability of erroneously inferring social learning when only asocial learning causes the spread of a novel behavior. For this purpose, we simulated learning dynamics with pure asocial learning and then applied the extended NBDA method to the diffusion data generated by these simulations. The other part of our analysis focused on assessing the statistical power to detect social learning when it actually occurred. Although we expect that, in real animals, social learning usually co-occurs with asocial learning, we performed simulations with pure social learning. Because we focused on this extreme case, our results revealed the upper limit of the power to detect social learning.

We used the extended NBDA method because we aimed to assess the performance of a method that can be applied to wild animals for which we expect a new trait to spread through a mixture of individual and social learning, instead of through pure social learning. The extended NBDA method is more suited to this case because it fits two models: one involving pure asocial learning and another in which both social and asocial learning take place.

To generate artificial diffusion data, we used the social and asocial learning ABMs described by Franz and Nunn (2009). These models assume that, initially, one individual (the inventor) is already skilled (i.e., has already learned the new behavior). All other individuals are assumed to be naive (i.e., have not yet learned the new behavior). In the asocial learning model, each naive individual can acquire the new trait with a fixed probability in every time step, independent

of others in the simulated population. In the social learning model, naive individuals learn from skilled individuals with whom they have social contact. Specifically, learning probabilities depend on the strength of social network connections to skilled group members and a parameter τ , which determines how connection strengths are translated into social learning probabilities. Increasing the value of τ generally results in higher probabilities of social learning among connected individuals and, thus, shorter diffusion durations (see Franz & Nunn, 2009). Therefore, by varying this parameter, we were able to investigate the effects of diffusion duration on the statistical performance of NBDA.

We extended these models by explicitly simulating an observer and an analyst. The observer records the first performance of the new trait for each individual. By using an observer, we were able to simulate observation and sampling errors by varying the probability that the observer would identify when an individual first performed the new trait. For this purpose, we assumed that, in each time step, the observer has a fixed probability of detecting a performed behavior. Thus, the observer can detect the behavior when it first occurs or some time thereafter (e.g., Figure 2). The analyst takes the data from the observer and codes the recorded times of acquisition into time units that might be larger than the time units that were used by the observer (i.e., the simulated time steps) (see Figure 2). These coded data were then used as input to TADA.

NBDA methods require as input a social network that is assumed to reflect social learning opportunities for the observed trait. We assumed that the analyst had a perfect knowledge about the social network. Therefore, the social network used to simulate social learning dynamics was also used as input to TADA.

We used Latin hypercube sampling to investigate how multiple parameters influenced the performance of TADA (Rushton, Lurz, Gurnell, & Fuller, 2000; Seaholm, Ackerman, & Wu, 1988). Latin hypercube sampling is a type of stratified Monte Carlo sampling that has been used in epidemiological modeling and explores parameter space more efficiently than random sampling procedures can. We varied (1) group size, (2) network heterogeneity, (3) learning speed, (4) probability that the observer would record a performed behavior, and (5) the length of time units that the analyst used to code the observed data (Figure 2). Table 1 gives the ranges in which these parameters were varied. We used Latin hypercube sampling to generate 1,000,000 parameter sets separately for social and asocial learning

Table 1
Ranges in Which Varied Parameters Were Sampled

Parameter	Range
Group size	5–50
Network heterogeneity (<i>h</i>)	0–10
Observation probability	.02–1
Length of coded time unit	1–50
Asocial learning rate (only in the asocial learning model)	.01–.1
τ (determines social learning rates in the social learning model)	.05–.5

simulations. For each of these parameter sets, we simulated a single diffusion, in which a randomly chosen individual was initially set to be the skilled inventor.

To generate social networks with different degrees of heterogeneity, we draw all edge weights (or connection strengths between individuals) from differently skewed distributions. The weight *w* for an edge between two individuals *i* and *j* was calculated on the basis of a random number *r* from the interval between 0 and 1 and a heterogeneity coefficient *h*:

$$w_{i,j} = \frac{r^h}{\frac{1}{N} \sum_{\text{all } i,j} w_{i,j}}, \tag{1}$$

where *N* is the number of individuals in a group. Setting *h* to 0 results in a homogeneous network. A value of 1 results in uniformly distributed edge weights. Values larger than 1 result in more skewed distributions with many weak and few strong edges. Dividing by the mean sum of edge weights from 1 individual to all others ensures that diffusion duration is largely independent of group size and network heterogeneity. In real animals, group size and network heterogeneity might have an effect on the duration of diffusion, which, for instance, could lead to an indirect influence of group size on performance of TADA. In our analysis, we tried to eliminate such indirect effects because we wanted to infer the direct effects of group size, network heterogeneity, and diffusion duration on TADA performance.

To analyze the performance of TADA, we coded results in which the method inferred social learning as a 1 and, otherwise, as 0. We then used these codes as the dependent variable in the statistical analysis, focusing in particular on the probability of detecting social learning when data were generated under social learning (a correct inference) or under asocial learning (an incorrect inference). In addition, we calculated the duration of the observed diffusion after the analyst coded the observed data into new time units.

To identify the important predictor variables and possible interactions among them, we performed classification tree analysis

(De’ath & Fabricius, 2000) using the “tree” package in the statistical software R (R Development Core Team, 2007). Classification tree analysis hierarchically splits the data set into subcategories in a way that minimizes the variance of the response variable in the emerging subsets. Graphical output based on this analysis can reveal and help to visualize complex interactions among predictor variables. In our analysis, we used five predictor variables: group size, degree of network heterogeneity (*h*), diffusion duration (measured in the number of coded time units; see also Figure 2), length of coded time unit (measured in simulated time steps; see also Figure 2), and observation probability per coded time unit (which reflects the probability that the observer will record the behavior performed by an individual in one time unit that was coded by the analyst). In the electronic supplemental materials associated with this article, we provide an R script with the performed simulations and analyses.

RESULTS

We first examined the results involving pure asocial learning. We found that the probability to incorrectly infer social learning depended mainly on two factors: observation probability and diffusion duration. Note that observation probability and diffusion duration are measured in the coded time units used by the analyst (rather than in simulated time steps). Group size, network heterogeneity, and length of coded time unit had no major influence on the probability of erroneously detecting social learning.

The classification tree is shown in Figure 3. At the base of this tree is the observation probability, which illustrates the importance of observation errors. In general, higher observation probabilities resulted in lower Type I error rates. Whereas observation probabilities lower than .37

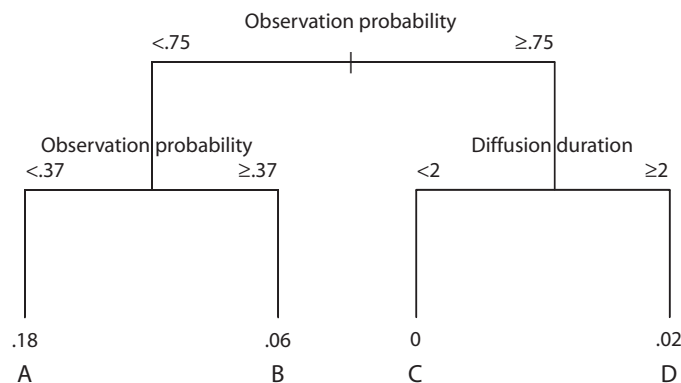


Figure 3. Classification tree of results from simulations of pure asocial learning. Numerical values of the leaves (A–D) indicate proportions of data sets in which social learning was erroneously inferred (representing Type I errors). The leaves are labeled to facilitate discussion of the results depicted in the tree.

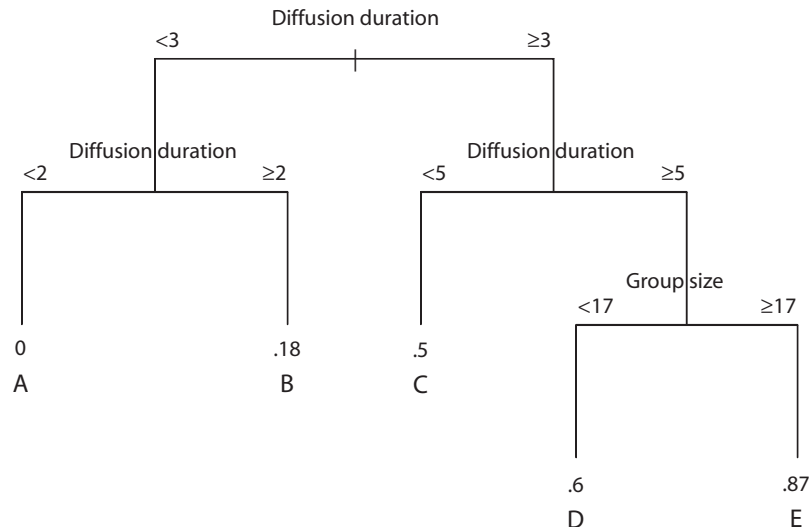


Figure 4. Classification tree of results from simulations of pure social learning. Numerical values of the leaves (A–E) indicate proportions of data sets in which social learning was correctly inferred. The leaves are labeled to facilitate discussion of the results depicted in the tree.

resulted in an 18% probability of incorrectly inferring social learning (Leaf A), observation probabilities between .37 and .75 led to an incorrect inference of social learning in only 6% of the simulations (Leaf B). When observation probabilities were at least .75, incorrect inferences of social learning were predicted to occur in no more than 2% of the simulated data sets (Leaves C and D). Under these conditions, very short diffusion durations additionally decreased Type I error rates (Leaf C).

In order to assess statistical power, we then examined data generated under pure social learning. The classification tree analysis revealed that the probability of correctly inferring social learning also depended mainly on two factors: diffusion duration and group size. Observation probability, network heterogeneity, and the length of coded time units had no major influence on the probability of correctly detecting social learning.

Figure 4 shows the classification tree from the analysis of traits spread through social learning. The probability of correctly inferring social learning was very low when the diffusion duration was shorter than three time units (Leaves A and B). In these cases, TADA could not infer social learning because information from the spread of the new behavior was insufficient to allow a better fit of the combined asocial and social learning model, relative to that of the pure asocial learning model. Higher probabilities of inferring social learning emerged when the diffusion duration was equal to or longer than three coded time units (Leaves C, D, and E), but it was limited to 50% when the diffusion duration did not exceed four (Leaf C). Note that, for Leaves A, B, and C, the statistical power was completely determined by diffusion duration and not strongly affected by any other predictor variable.

When the duration of coded diffusion was equal to or larger than 5, group size had a strong effect on the power to detect social learning. In groups with at least 17 indi-

viduals, social learning was correctly inferred in 87% of the cases (Leaf E). For smaller group sizes (the simulated minimum was 5), social learning was inferred in 60% of the simulations (Leaf D).

DISCUSSION

We investigated how group size, network heterogeneity, diffusion duration, observation probability, and length of coded time units influence the statistical performance of NBDA. In our analysis, we focused on Franz and Nunn’s (2009) extended NBDA, which involves the comparison of a mixed model of social and asocial learning with a model of pure asocial learning. Our most significant finding was that observation errors, when severe enough, can lead to increased Type I error rates. Elevated Type I error rates can be prevented by coding the observed diffusion times into larger units before applying TADA.

Observation errors might occur because animals cannot be observed continuously—for example, when focal sampling is used (Altmann, 1974). In our simulations, observation errors resulted in delayed recording of the acquisition times of the diffusing behavior (Figure 2). It is important to note that observation errors of this type can also result in errors in the order of trait diffusion. Indeed, we found that, in 89% of our simulated data sets, observation errors created sequence differences between the simulated and observed diffusion (i.e., changes in order of acquisition). Observation errors will generally become more pronounced when sampling effort per individual decreases and when the new behavior is performed less frequently.

To assess the power to detect social learning and Type I error rates, we used simulated diffusion dynamics created by pure social and asocial learning as inputs to TADA. The statistical analysis of TADA results was performed using classification trees. This method hierarchically splits the

data set into subcategories in a way that minimizes the variance of the response variable in the emerging subsets. Graphical output from the classification tree analysis can reveal and help to visualize complex interactions among predictor variables. However, resulting numbers indicating sharp differences on the tree should not be viewed as thresholds that involve sudden jumps in power or Type I errors. They may, in fact, represent thresholds, but they may also reflect an underlying gradual effect of one or more predictors.

We found that observation errors can lead to elevated Type I error rates (Figure 3). To our surprise, however, TADA was more robust to observation errors than we anticipated. Previously, we suggested that the length of the coded time units should be long enough to ensure that each acquisition of the new behavior will occur with high certainty in the coded time step (Franz & Nunn, 2009). In the example displayed in Figure 2, this would require us to choose Coding Possibility 2. The results of the present study led us to modify this requirement. We now offer a rule of thumb that at least a 50% probability that the acquisition of the behavior will occur in the coded time step is sufficient for preventing elevated Type I error rates (i.e., a bit more conservative than the $>37\%$ shown on Figure 3, since the predicted Type I error rate at 37% is .06). In Figure 2, this would allow us to choose Coding Possibility 1 because, in this case, 2 out of 3 individuals acquired the new trait in the same coded time step in which they were first observed performing this trait. In cases with a lower observation probability, appropriate coding of time steps can be used to keep the probability of Type I errors low.

Previously, we advised users to keep coded time steps short enough to avoid the possibility of 2 individuals learning in the same coded time step, because we expected that this would reduce the power to detect social learning. Our present results suggest that this advice, too, can be relaxed. Increasing the length of coded time steps only became a problem in our analyses when the resulting duration of the diffusion dropped below 5. Therefore, we advise users of TADA who are uncertain about the extent of observation errors on diffusion times to code diffusion times in rather long time units if this does not lead to a very short duration of the coded diffusion. Our analysis indicates that such a procedure minimizes Type I errors while not strongly affecting the power to detect social learning.

In contrast to our method, the TADA methods developed by Hoppitt, Boogert, and Laland (2010) and Hoppitt, Kandler, et al. (2010) are time continuous. In other words, they allow users to include observation times directly rather than having to code observed data into discrete time steps. Nevertheless, it can be expected that time-continuous TADA methods are as susceptible to observation errors as the time-discrete TADA method we used in the present study. Thus, if observation errors are strong enough, coding of time steps would also be needed when using these other methods.

The OADA method proposed by Hoppitt, Boogert, and Laland (2010) may, however, be more robust than TADA

to observation errors in the times of behavior acquisition. OADA does not use information about the time of behavior acquisition; it uses information about the corresponding order instead. As long as observation errors do not change the order of the diffusion, the performance of OADA should not be affected. However, it is difficult to predict how strongly the performance of OADA is affected in cases in which observation errors lead to changes in the order of the observed diffusion.

Our finding—that group size can strongly increase the power to detect social learning and that network heterogeneity has little effect—is in agreement with previous studies of the performance of TADA by Franz and Nunn (2009) and Hoppitt, Boogert, and Laland (2010). Note that this result does not imply that including the network into the analysis of diffusion dynamics is not necessary. Franz and Nunn showed that diffusion curve analysis (Reader, 2004), which ignores social network structure, can strongly reduce the power to detect social learning and increase the probability of erroneously inferring social learning. The results of our present analyses do not contradict these findings. Nevertheless, one might intuitively expect the power to detect social learning to increase with increasing network heterogeneity because the more heterogeneous a social network is, the stronger the likelihood that it determines the pathway that a diffusion can take through a group of individuals. This argument makes sense and also explains why the power of OADA to detect social learning increases with increasing network-heterogeneity dynamics (Hoppitt, Boogert, & Laland, 2010).

However, to distinguish between alternative learning models, TADA takes into account both order of the diffusion and information about the timing of individual learning events (or at least the first observed production of the behavior). This information becomes increasingly important for distinguishing among alternative learning models in more homogeneous social networks. In completely homogeneous networks, TADA exclusively uses data on the timing of learning events and is, therefore, equivalent to diffusion curve analysis (Reader, 2004). The timing of learning events can be used to distinguish between social and asocial learning because social learning, but not asocial learning, can be expected to result in a positive feedback of the number of skilled individuals and learning rate (but see Hoppitt, Kandler, et al., 2010). The greater the number of individuals that have acquired a novel behavior, the more opportunities exist for others to observe and learn this behavior. The influence of this feedback mechanism is weak in heterogeneous social networks because learning dynamics are strongly determined by the structure of the network. However, with increasing network homogeneity, the influence of the feedback mechanism on diffusion dynamics increases. Thus, in more homogeneous social networks, TADA makes greater use of information on the timing of learning events to distinguish between alternative learning models. This explains why decreasing network heterogeneity does not lead to a decrease in the power to detect social learning.

In this context, we additionally emphasize that we explored only the effect of network heterogeneity that was based on the distribution of connection strengths in randomly created networks. Thus, we did not explicitly explore possible effects of other network characteristics, such as community modularity, which can vary substantially in real-world networks (Kasper & Voelkl, 2009; R. L. Kendal et al., 2010). Furthermore, in our analysis, we did not consider from which individual in the network the diffusion starts. As indicated by the results of Franz and Nunn (2009), this can also affect Type I error rates and power.

Other factors that can strongly affect the statistical performance of TADA, but that we did not consider in our analysis, include (1) that a new trait spreads through combined effects of social and asocial learning, which would reduce the power to detect social learning (Hoppitt, Boogert, & Laland, 2010); (2) that observations might begin long before the innovation and spread of the new behavior, which would increase the power to detect social learning; (3) observation errors in the structure of the social network; and (4) errors associated with incorrect identification of individuals in the group, so that behaviors are assigned to individuals who may not have learned how to perform the behavior. Results from Franz and Nunn (2009) indicate that TADA is robust to small disturbances in network structure. To investigate observation errors in network structure in more detail, it might be suitable to follow the approach we have taken in this study and explicitly simulate observations that are used to construct social networks.

In summary, our results confirm that TADA can be a statistically powerful tool for inferring social learning in wild animals. Although the method seems to be robust to a moderate degree of observation errors on recorded times of behavior acquisition, the coding of diffusion time steps allows it to cope with strong observation errors. Our results suggest that the power to detect social learning will not be strongly affected by observation errors. In cases in which observation errors cannot be precisely estimated, we therefore recommend relying on a conservative approach by using long time units for coding diffusion times.

Using NBDA to study social learning in wild animals might enable us to gain important new insights about culture in animals and the evolution of cultural capacities in humans. Whereas many social learning studies have focused on identifying the existence of social learning mechanisms in different species (Galef & Giraldeau, 2001; Hoppitt & Laland, 2008), NBDA methods provide a way to study and compare dynamics that are created by and influence social learning. Understanding which learning biases or social learning strategies (Laland, 2004) drive social learning dynamics in groups of animals and humans has received increasing attention in empirical and theoretical studies (e.g., Boyd & Richerson, 1985; Enquist, Eriksson, & Ghirlanda, 2007; Henrich & Boyd, 1998; J. R. Kendal, Giraldeau, & Laland, 2009; J. R. Kendal, Rendell, Pike, & Laland, 2009; R. L. Kendal, Coolen, & Laland, 2004; Laland, 2004; McElreath et al., 2008; McElreath et al., 2005; Mesoudi & Lycett, 2009). How-

ever, most empirical studies that investigated related questions (for reviews, see R. L. Kendal, Coolen, & Laland, 2009; R. L. Kendal, Coolen, van Bergen, & Laland, 2005) were performed with captive animals. Extensions of current NBDA approaches offer a way to approach these questions in the wild.

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REFERENCES

- ALTMANN, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, **49**, 227-266.
- BOLKER, B. M. (2008). *Ecological models and data in R*. Princeton, NJ: Princeton University Press.
- BOYD, R., & RICHERSON, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- BURNHAM, K. P., & ANDERSON, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.
- 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
- DE'ATH, G., & FABRICIUS, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, **81**, 3178-3192.
- ENQUIST, M., ERIKSSON, K., & GHIRLANDA, S. (2007). Critical social learning: A solution to Rogers's paradox of nonadaptive culture. *American Anthropologist*, **109**, 727-734. doi:10.1525/AA.2007.109.4.727
- FRANZ, M., & NUNN, C. L. (2009). Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society B*, **276**, 1829-1836. doi:10.1098/rspb.2008.1824
- GALEF, B. G., JR. (2004). Approaches to the study of traditional behaviors of free-living animals. *Learning & Behavior*, **32**, 53-61.
- GALEF, B. G., JR., & GIRALDEAU, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3-15. doi:10.1006/aneb.2000.1557
- HENRICH, J., & BOYD, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution & Human Behavior*, **19**, 215-241. doi:10.1016/S1090-5138(98)00018-X
- HOPPITT, W., BOOGERT, N. J., & LALAND, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, **263**, 544-555.
- HOPPITT, W., KANDLER, A., KENDAL, J. R., & LALAND, K. N. (2010). The effect of task structure on diffusion dynamics: Implications for diffusion curve and network-based analyses. *Learning & Behavior*, **38**, 243-251.
- HOPPITT, W., & LALAND, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior*, **38**, 105-165. doi:10.1016/S0065-3454(08)00003-X
- KASPER, C., & VOELKL, B. (2009). A social network analysis of primate groups. *Primates*, **50**, 343-356. doi:10.1007/s10329-009-0153-2
- KENDAL, J. [R.], GIRALDEAU, L.-A., & LALAND, K. [N.] (2009). The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical Biology*, **260**, 210-219.
- KENDAL, J. R., RENDELL, L., PIKE, T. W., & LALAND, K. N. (2009). Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behavioral Ecology*, **20**, 238-244. doi:10.1093/beheco/arp016
- KENDAL, R. L., COOLEN, I., & LALAND, K. N. (2004). The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, **15**, 269-277. doi:10.1093/beheco/arl008
- KENDAL, R. L., COOLEN, I., & LALAND, K. N. (2009). Adaptive trade-offs in the use of social and personal information. In R. Dukas & J. M. Ratcliffe (Eds.), *Cognitive ecology II* (pp. 249-271). Chicago: University of Chicago Press.
- KENDAL, R. L., COOLEN, I., VAN BERGEN, Y., & LALAND, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Ad-*

- vances in the *Study of Behavior*, **35**, 333-379. doi:10.1016/S0065-3454(05)35008-X
- KENDAL, R. L., CUSTANCE, D. M., KENDAL, J. R., VALE, G., STOINSKI, T. S., RAKOTOMALALA, N. L., & RASAMIMANANA, H. (2010). Evidence for social learning in wild lemurs (*Lemur catta*). *Learning & Behavior*, **38**, 220-234.
- LALAND, K. N. (2004). Social learning strategies. *Learning & Behavior*, **32**, 4-14.
- LALAND, K. N., & GALEF, B. G., JR. (Eds.) (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.
- 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., & KENDAL, J. R. (2003). What the models say about social learning. In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 33-55). Cambridge: Cambridge University Press.
- MCÉLREATH, R., BELL, A. V., EFFERSON, C., LUBELL, M., RICHERSON, P. J., & WARING, T. [M.] (2008). Beyond existence and aiming outside the laboratory: Estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B*, **363**, 3515-3528. doi:10.1098/rstb.2008.0131
- MCÉLREATH, R., LUBELL, M., RICHERSON, P. J., WARING, T. M., BAUM, W., EDSTEN, E., ET AL. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution & Human Behavior*, **26**, 483-508. doi:10.1016/j.evolhumbehav.2005.04.003
- MESOUDI, A., & LYCETT, S. J. (2009). Random copying, frequency-dependent copying and culture change. *Evolution & Human Behavior*, **30**, 41-48. doi:10.1016/j.evolhumbehav.2008.07.005
- PERRY, S., & MANSON, J. H. (2003). Traditions in monkeys. *Evolutionary Anthropology*, **12**, 71-81. doi:10.1002/evan.10105
- R DEVELOPMENT CORE TEAM (2007). R: A language and environment for statistical computing [Software environment]. Vienna, Austria: R Foundation for Statistical Computing.
- READER, S. M. (2004). Distinguishing social and asocial learning using diffusion dynamics. *Learning & Behavior*, **32**, 90-104.
- RENDELL, L., & WHITEHEAD, H. (2001). Culture in whales and dolphins. *Behavioral & Brain Sciences*, **24**, 309-382. doi:10.1017/S0140525X0100396X
- RUSHTON, S. P., LURZ, P. W. W., GURNELL, J., & FULLER, R. (2000). Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: A possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology*, **37**, 997-1012. doi:10.1046/j.1365-2664.2000.00553.x
- SEAHOLM, S. K., ACKERMAN, E., & WU, S.-C. (1988). Latin hypercube sampling and the sensitivity analysis of a Monte Carlo epidemic model. *International Journal of Bio-Medical Computing*, **23**, 97-112. doi:10.1016/0020-7101(88)90067-0
- VAN SCHAİK, C. P., ANCRENAZ, M., BORGES, G., GALDIKAS, B., KNOTT, C. D., SINGLETON, I., ET AL. (2003). Orangutan cultures and the evolution of material culture. *Science*, **299**, 102-105. doi:10.1126/science.1078004
- VENTURA, R., MAJOLO, B., KOYAMA, N. F., HARDIE, S., & SCHINO, G. (2006). Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138-1149. doi:10.1002/ajp.20314
- WHITEN, A., GOODALL, J., MCGREW, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., ET AL. (1999). Cultures in chimpanzees. *Nature*, **399**, 682-685. doi:10.1038/21415

SUPPLEMENTAL MATERIALS

An R script to simulate social and asocial learning dynamics, the observation of these dynamics, and their analysis via network-based diffusion may be downloaded from <http://lb.psychonomic-journals.org/content/supplemental>.

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